A Study of the Arteries of the Brain of the Spiny Anteater (Echidna aculeata), to Illustrate the Principles of Arterial Distribution

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PHILOSOPHICAL TRANSACTIONS.

I. *A Study of the Arteries of the Brain of the Spiny Anteater* (Echidna aculeata), *to Illustrate the Principles of Arterial Distribution.*

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(PLATES 1–6.)

Introduction.

Previous investigations into the arterial supply of the brain may be divided into two classes depending in great part on the nature of the material and on the methods employed. Firstly, there are investigations which have been primarily concerned with the determination of the exact limits of supply of individual arteries to particular regions and structures of the brain; and secondly, there are investigations whose purpose has been to enquire into the morphology of the vessels without particular regard to the exact area of supply of the vessels, which is either inferred or neglected. The two classes of investigations find their parallel in the series of researches which led to the development of the theory of nerve components.

The writings of CHARCOT (1883), DURET (1874), BEEVOR (1909), STOPFORD (1915) and others, are the best examples of the first class. Whilst these writers have not altogether neglected the topographical features and variations of the arteries outside of the brain, they have attacked the problem of arterial distribution with the avowed intention of determining its clinical significance. Their attention has therefore been concentrated on discovering the field of arterial supply within the brain, the relative automony of these fields and the amount of variation present. Naturally the material which has been used by them has been almost exclusively human.

The second class, typified in the writings of DE VRIES (1905), HOFMANN (1900) and many others, deals with the morphology and evolution of the cerebral arteries. In this class we look for information on the variety of pattern of the major arteries, on the difference in distribution in different animals and on the series of evolutionary changes which account for the difference in pattern. The material used has been derived from lower forms, and so has not been altogether suitable for a discriminating analysis of the terminal supply of individual arteries.

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A critical examination of the literature of both classes leaves the impression that there is so much variation in arterial distribution as to discountenance the hypothesis set forth in this paper, that the distribution of the arteries is precise, and that the final areas of arterial supply coincide with structural areas of functional value.

One of the causes why the underlying principles of distribution have been obscured, is to be found in the use of wrong nomenclature. Most of the names given to the arteries of the brain have been derived from the study of human anatomy and in applying those names to arteries in the brain of lower forms homology has been inferred without sufficient warrant. The criteria for homology in nerve investigation are sought for at the source of origin of the nerve, in its intermediate distribution and its terminal relations. The variability of the intermediate distribution obscured the phylogenetic and ontogenetic precision of supply of a peripheral nerve, until STRONG (1890), HERRICK (1899) and others propounded the theory of nerve components, by an insistence on the correct use of criteria for homology.

Now the test of homology should conform to the principles laid down by JOHN HUNTER in identifying nerves. It is therefore desirable to digress for a moment and consider these principles.

> JOHN HUNTER says: "the nerves being in themselves perhaps the most difficult parts of the animal body to dissect, becomes a reason why we are still unacquainted with many of their minuter ramifications; yet if a knowledge of these, together with that of their origin, union, and reunion, is all connected with their physiology, the more accurately they are investigated the more perfectly will the functions of the nerves be understood."
>
> "I have no doubt, if their physiology was sufficiently known, that we should find the distribution and complication of nerves so immediately connected with their particular uses as readily to explain many of those peculiarities for which it is now so difficult to account. What naturally leads to this opinion is, the origins and number of nerves being constantly the same, and particular nerves being invariably destined for particular parts, of which the fourth and sixth pair of nerves are remarkable instances. We may therefore reasonably conclude, that to every part is allotted its particular branch, and that however complicated the distribution may be, the complication is always regular" (1837).

Here JOHN HUNTER clearly postulates the theory of nerve components, which found its confirmation in the work of STRONG (1890) on the cranial nerves of the Amphibia, and of HERRICK (1899) on the cranial nerves of *Menidia*.

The writer's conception of the distribution of the arteries can be adequately expressed by substituting the word "arteries" for "nerves" in HUNTER's statement. The investigation of the arteries of the body should proceed along the same lines as that taken in investigating the nerves. It is felt that as more and more information comes to hand it will be found that the arteries are remarkably constant in their final fields of supply and that variability affects mainly their intermediate course. HERRICK (1899), almost repeating JOHN HUNTER'S words, says of the distribution of the nerves :—

> "I would reiterate the position taken by most of the recent students of nerves, that the morphological value of a given nerve is to be determined primarily by its terminal relations, *i.e.*, its central nucleus and its peripheral end-organ. These appear to be very constant, while its intermediate course may be modified by so many cenogenetic factors as to be of relatively small value in determining the homologies."

Another cause of misconception in the literature is that the intermediate course of the arteries has been used in determining homologies, with the result that confusion has arisen and the underlying principles of arterial distribution have not been discerned.

From the writings of the two classes of investigators referred to above, two great truths relating to blood supply—precision and variation—are clearly enunciated. These are apparently contradictory characteristics; it will be seen however that a study of the morphology of the vessels eliminates the element of incompatibility. CHARCOT (1883), before the time when accurate observations had been made on the distinctive areas of the cerebral cortex, suggested that different arteries had autonomous areas of supply and stated "that the explanation of the commonest anatomical localisation in the encephalon is to be sought in the mode of distribution of the vessels." BEEVOR (1909) found that the anterior nucleus of the thalamus stood out as an island after injection of the posterior cerebral artery. It is from STOPFORD'S work, however, that we have the most striking examples of precision in arterial supply (1915). He found that "invariably the trigonum hypoglossi was accurately defined by the stain of the injection" from the anterior spinal artery; that, after injection of the vertebral artery, "the injection always demarcated the trigonum vagi"; and that, after injection of the posterior spinal artery, the "descending ramus supplied the funiculi gracilis and cuneatus with their nuclei, and in all cases where the branch was present this distribution was found to be absolutely constant."

In quoting these writers in support of precision, it is only right to say that they appear to stress the variation rather than the precision. For example, BEEVOR says :

> "The fact that so small a body as the corpus subthalamicum can receive its blood supply from two different arteries is against the theory that the arrangement of the blood supply can have functional significance, as it appears to be purely anatomical and not distributed according to the physiological action of the part."

This is in marked contrast with JOHN HILTON'S conception (1880) :—

> "There is a disposition on the part of anatomists to think and to teach that nerves are distributed with designed accuracy, but that there is little design in the distribution of the arteries. . . . Look at the arterial distribution of blood to the soft palate, derived from several different sources. The soft palate is

> functionally connected with respiration, deglutition, and mastication, so we ought to discover that its arteries are derived from the trunks of those arteries which supply the face and lips, those which supply the masticatory apparatus, and the walls of the pharynx. Curiously enough, this soft palate receives six arteries, three on each side: one from the facial, the ascending palatine, which seems to take a wandering, devious course up to the soft palate; one from the ascending pharyngeal artery; and one from the internal maxillary, the true 'masticatory artery.' Here, then, is a simple piece of anatomy, which shows the precision and purpose of the distribution of arteries which seem to be associated with three different important functions."

I have deemed it necessary, considering the purpose of this paper, to quote extensively from these authors, in order to show the sources from which my own conception took origin, and in order faithfully to express my appreciation of the accuracy of the observations made by them. In my own observations on the arterial supply of the brain I have confirmed in detail the greater part of their findings and have concluded that the arterial supply of the brain is as precise as they have recorded. Furthermore, I have determined that the arteries of the cerebrum are in many places intimately related to defined areas of the cortex (1927 *a*), (1927 *c*).

No clearer expression of the constancy of arterial supply is found, however, than is given in the beautiful figures which illustrate AITKEN'S report on the circulation of the lobar ganglia (1909). Only one who has worked on the distribution of the vessels in this region can appreciate the accuracy which underlies the artistry of his pictures. His fig. 10, which shows the distribution of HEUBNER'S artery, is described thus:—"Showing that HEUBNER'S artery with its branches, after it has entered the brain, remains unchanged as a system, notwithstanding variations of source" (1909). HEUBNER'S artery is the artery which I named, in 1920, the recurrent branch of the anterior cerebral artery (1920). This artery exists in all the mammalian forms which I have examined. It will be discussed later.

In the writings of the second class the best examples of variation are found; for here the intermediate distribution of the arteries is considered without particular regard to supply. The reader is referred to p. 585 in KEIBEL and MALL'S text-book of human embryology, where the characteristics of precision and variation are discussed (1912).

So far the course of the nerves has been compared with that of the arteries; let us now consider the structure supplied. If the structure supplied is to be the final criterion for the institution of homology, then it follows that the structure supplied must be as precise as the nerve supplying it; in other words, the nerve and the organ supplied are a constant unit. Precision of nerve distribution implies a precision of nerve-organ distribution. There is clear evidence that this unit mechanism has in many instances a common origin in ontogeny. Thus the olfactory nerves arise from the olfactory placode in common with the olfactory sense organ; the eighth nerve arises from the otic vesicle in common with the peripheral end organ; the nerves of taste arise peripherally from the placodes which give rise to the taste buds; and finally, the optic neurones arise in common with the rods and cones. We have here evidences of nerve-organ continuity from the beginning. In the case of other nerve-organ units there is a difference of opinion as to how the nerve comes into contact with its end organ, although there seems little doubt that the nerve never fails to get to its right place in development. In cases of repair, however, the nerve may actually grow out to its wrong end organ. It may be said that, despite the appearances seen in tadpoles undergoing repair, there are no general and universally accepted views on the development of peripheral nervous system (see HARRISON (1924), p. 127).

This has a very important bearing on the distribution of the arteries for, assuming a constancy of nerve-organ mechanism, the constancy of a nerve must be an index of the constancy of the organ supplied. Again, the variation in the position of an organ should be the index of the variation in the intermediate distribution of the nerve; from which it follows, since the arteries are supplied by the sympathetic nerves, that the variations in arteries should be explainable by variation in the intermediate distribution of the sympathetic nervous system. But whilst it may be admitted that the relationship of the nerves to their organs of supply is a precise one, it does not follow that the inter-relationship between the organs themselves is also precise. The nerve-organ unit is a minor unit in a greater functioning mechanism, and the aim of neurological study is to show how the minor units are linked together in these greater functioning mechanisms. In the same way I conceive that the aim of the study of the arteries is to show how they are related to functioning mechanisms. The methods to be employed in such a study are: (1) The determination of the exact area of supply of end arteries. (2) The determination of the topographical relationships of the arteries outside of their final area of supply. (3) The determination of the position of anastomoses and, if possible, their meaning. (4) The determination of variation and the effect of such variation on final supply. (5) The determination of the anatomical and physiological relationship of the sympathetic nervous system to the arteries. In the present communication the first method could not be fully employed on account of the nature of the material, although inferences are made from the findings of STOPFORD and others. The fifth method was not used.

My object, however, in examining the arterial supply of the brain of Echidna was not only to examine the distribution of the arteries, but also to ascertain whether the examination of the blood supply might throw light on general problems of brain morphology and brain development. For it is conceivable that the vessel-organ unit is constant in phylogeny.

The examination of the arteries of the brain of the Orang utan revealed a definite precision in their distribution. In Man and in the Orang certain of the circumscribed areas of the cerebral cortex have autonomous vascular supplies (1927); and, further, it has been shown that the visual, or striate, cortex is an autonomous vascular area in the anthropoids generally. The study of the arteries thus resolves itself into their analysis in terms of their final components. The analysis made in this paper is dependent on a classification of arteries into two types—firstly "arteries of supply," and secondly "arteries of intermediate distribution."

The significance of this classification will be more fully discussed after the arteries have been described; suffice it to say for the moment that such arteries as the aorta, basilar, vertebral, longitudinal anterior spinal, etc., are regarded as arteries of distribution, whereas the branches of the longitudinal anterior spinal artery which enter the brain stem and other arteries of the same order are regarded as arteries of supply.

My observations have so far led me to the opinion that the method of distribution of the arteries of supply is constant, which naturally implies that there is a vessel-organ unit. If such be the case, we have in the study of the evolution of the arteries a useful auxiliary to other methods of examining the structure and evolutionary changes of the brain. Now Echidna is a very interesting form on which to test such a method, for, as Prof. ELLIOT SMITH has said :—

> "The most obtrusive feature of this brain is the relatively enormous development of the cerebral hemispheres, which are much larger, both actually and relatively, than those of the Platypus. In addition the extent of the cortex is very considerably increased by numerous deep sulci. The meaning of this large neopallium is quite incomprehensible. The factors which the study of other mammalian brains has shown to be the determinants of the extent of the cortex, fail completely to explain how it is that a small animal of the lowliest status in the mammalian series comes to possess this large cortical apparatus" (1902).

It is suggestive in the light of ELLIOT SMITH's opinion that the arterial supply to the cortex of this animal differs from that of all the other mammalian forms which I have had the opportunity of examining. The middle cerebral artery is almost confined in its supply to the pyriform area, whereas in other mammalian forms examined this artery supplies a large extent of the neopallium. In Echidna the greater part of the cerebral mantle is supplied by the same artery which supplies the fascia dentata and the hippocampal formation, which might suggest that factors determining the extent of the cortex differ in this animal from those of other forms.

GENERAL DESCRIPTION.

The Arteries of the Fore-brain.

Brief accounts of the different regions of the brain of Echidna are given to facilitate the description of the arteries. The *olfactory bulbs* are large pedal-shaped bodies which are pivoted on the under surface of the frontal poles of the hemispheres (Plate I, fig. 1). There was no specimen which showed the olfactory nerves, but, from the roughened appearance of the inferior surface of the bulbs, they appear to be received into the whole of the surface. The bulb measures in length 1·8 cms., in breadth 1 cm., and in height about 0·5 cm. Comparing the size of the olfactory bulbs with the extent of the cerebral cortex in this animal and in a macrosmatic animal, such as *Myrmecophaga jubata* (fig. 2) (the giant anteater), it is obvious, as ELLIOT SMITH has shown (1902), that the extent of the cortex in Echidna cannot be wholly accounted for by reference to the extent of the olfactory areas. There is, however, the possibility that the method of operation of the olfactory sense in this animal differs from that of any other.

Seen from above (fig. 3) the olfactory bulbs project for a quarter of their length in front of the anterior pole of the hemisphere. It is also to be noticed that the anterior end of the pyriform lobe, covered by the lateral olfactory tract, is visible from above as it passes to the dorsal and lateral region of the olfactory bulb. The fissura rhinalis, continued forward from the lateral surface of the hemisphere (fig. 4), becomes merged into the deep fissure which separates the frontal pole from the bulb. If the overhanging cortex is turned back (fig. 4) the pyriform cortex is seen to bury itself into the exposed dorsal surface of the bulb. Medial to this insertion the fibres of the medial portion of the olfactory peduncle, pass inwards and backwards to the tuberculum olfactorium and the area precommissuralis.

The *pyriform lobe* (fig. 1) presents the peculiar twisted and rolled appearance which has been noted by ELLIOT SMITH :—

> "The latter (the pyriform lobe) is a peculiar, sinuously curved band of cortex which extends along the whole length of the base of the hemispheres. The extraordinary twisted form of the pyriform lobe is quite distinctive of this brain."

In order to get a correct appreciation of the form of the anterior end of the pyriform lobe it is necessary to examine it in section. Viewed in this way the lobe is seen to form a shelf lying under cover of the overhanging neopallium. The rhinal fissure is extraordinary deep and so there is a large area of both pyriform and general cortex lying under cover of it (fig. 5). This shelf extends forwards and, narrowing, telescopes itself as it were, into the dorsal aspect of the olfactory bulb. The anterior end of the pyriform lobe has thus a large dorsal buried surface, a lateral narrow exposed surface and an inferior surface. The inferior surface is bounded internally by the tuberculum olfactorium and externally by the rhinal fissure. It is divided into an inner and an outer region by a shallow, but well-marked, sulcus. The outer region is continuous with the cortex of the posterior region ot the pyriform lobe ; the inner strip narrows rapidly and ends in a rounded swelling immediately on the lateral side of the posterior angle of the tuberculum olfactorium. This rounded swelling constitutes the nucleus of the lateral olfactory tract (fig. 7). The anterior region of the pyriform lobe ends at the level of the pseudo-Sylvian sulcus and at this level the pyriform lobe sweeps inwards to form a curved, rounded gyrus which overlaps the nucleus of the lateral olfactory tract, and then, directed backwards at the leval of the optic chiasma, forms with its fellow of the opposite side a deep recess in which lies the tuber cinereum and the locus perforatus posticus.

This recess is further accentuated by the prominence of the anterior border of the pons Varolii.

The *tuberculum olfactorium* is a roughly triangular elevation lying immediately posterior to the olfactory peduncle and partly covered anteriorly by the olfactory bulb. On the medial surface of the hemisphere the tuberculum olfactorium is well defined and indents the area precommissuralis. Posteriorly it forms a blunt angle related to the locus perforatus anticus and to the nucleus of the lateral olfactory tract. Laterally the tuberculum is separated by a definite fissure from the inner region of the inferior surface of the pyriform lobe.

The Internal Carotid Artery.

The severed end of the internal carotid artery lies midway between the optic chiasma and the upper border of the pons. It is shown in fig. 19 in which the thalamic region has been removed. In size it is very much smaller than the longitudinal trunk which extends from the so-called posterior cerebral artery to the point of bifurcation into anterior and middle cerebral arteries ; nevertheless, in order to conform with the usual description, it can be said to divide into a cranial and a caudal branch although the branches are much larger than the parent artery. The relative size of the various arteries affects not so much their morphological value as their distributing value ; thus in Echidna, as we shall see, the main flow of blood to the cerebrum is from the vertebral and anterior spinal arteries. Here THOMAS' law becomes operative on vessels already laid down—" an acceleration of the current leads to an enlargement of the lumen of the vessel."

The cranial branch passes forwards between the hemisphere and the tuber cinereum to end at the locus perforatus anticus by dividing into anterior and middle cerebral arteries. The caudal branch passes backwards to join the so-called posterior cerebral artery. It is convenient to call this artery the posterior communicating artery although it must be emphasised that these names do not necessarily imply homology with the arteries bearing the same name in man.

The circle of WILLIS is completed anteriorly by the fusion of the two anterior cerebral arteries. It is interesting to compare this condition seen in Echidna with that found in *Myrmecophaga jubata.* In Echidna the posterior communicating artery is hidden under the medial border of the pyriform lobe, whereas in Myrmecophaga (fig. 2) the topography of the arteries stands out on account of the wider separation of the hemispheres. In Myrmecophaga the stem of the posterior cerebral artery (so-called) and the posterior communicating artery appear to form one channel connecting the basilar artery with the internal carotid artery. For the moment we may say that this channel appears to be analogous with the vertebral artery posteriorly. We know that the vertebral artery is in great part a longitudinal anastomotic channel connecting the stems of the segmental arteries. I suggest from the appearance in Echidna and in Myrmecophaga and in many other specimens which I have examined that the channel formed by the stem of the so-called posterior cerebral artery and by the posterior communicating artery is in like manner a longitudinal anastomotic channel connecting metameric arteries of the hind-, mid-, and fore-brain. This will be discussed more fully later.

The Branches of the Internal Carotid Artery.

1. The anterior choroidal artery arises from the cranial branch of the internal carotid artery close to the point of division of the main artery. It passes backwards and outwards, crossing the tuberculum hippocampi, and enters the inferior end of the choroidal fissure (fig. 19). Its further distribution could not be determined.

2. Fine branches arise from the cranial branch which pass to the optic chiasma and to the locus perforatus anticus. Their internal distribution could not be ascertained; although in a series of sagittal sections at University College, London, it was possible to trace a large branch which extended from the region of the locus perforatus anticus as far as that portion of the lamina terminalis which lies between the fornix commissure and the anterior commissure. This artery is well shown in fig. 6. No definite information could be obtained regarding the distribution of the arteries to the optic chiasma in Echidna, but it is of interest to consider the condition found in Macropus and in the Crocodile. In both these animals an arterial ring is formed around the tuber cinereum from which branches pass to the optic tracts. There is, as it were, an inner circle within the circle of WILLIS (figs. 9 and 12).

The Anterior Cerebral Artery.

3. The anterior cerebral artery is formed at the posterior angle of the locus perforatus anticus by the division of the cranial branch of the internal carotid artery into the anterior and middle cerebral arteries. The middle cerebral artery is slightly larger than the anterior. From its point of origin the anterior cerebral artery passes inwards and forwards, dorsal to the optic nerve, to fuse with its fellow in the middle line at the level of the posterior boundary of the tuberculum olfactorium. In three of the nine specimens examined, there is a marked inequality in size between the two anterior cerebral arteries. In fig. 1 the two arteries are equal in size. The distribution in all the specimens is substantially the same; and the following description is taken from the specimen figured.

There is strictly speaking no anterior communicating artery; for the fusion of the two vessels forms an unpaired median artery. This unpaired anterior cerebral artery lies in the median cleft between the two tubercula olfactoria, and extends forwards to the medial surface of the olfactory bulb. At this point it breaks up into a leash of vessels which supply the medial surface of the bulb and the neopallium in the immediate vicinity of the frontal pole.

From the first part of the anterior cerebral artery branches pass to the locus perforatus anticus and to the postero-medial region of the tuberculum olfactorium. From the second, or unpaired, part branches proceed to the medial region of the tuberculum and to the area precommissuralis; and finally, before breaking up into its terminal leash of arteries, the unpaired artery gives rise to a large branch which passes directly outwards under cover of the projecting posterior border of the bulb (fig. 7). This branch ends by inosculating with a branch of the middle cerebral artery and there is formed a complete arterial ring round the tuberculum olfactorium. This branch supplies the inferomedial region of the olfactory bulb, the antero-medial region of the olfactory tubercle and the ventral aspect of the olfactory peduncle. This artery agrees in every respect with the artery I referred to as the recurrent branch of the anterior cerebral artery in man (1920) and in the Orang utan (1927), which AITKEN named Heubner's artery (1909). After giving off the recurrent branch, the unpaired artery proceeds forwards for a short distance, gives fine branches to the medial surface of the bulb and ends by breaking up into branches on both sides which can be traced to the upper surface of the bulb and to the cortical region of the frontal pole which is numbered 7 in figs. 15 and 22 showing the cortical distribution of the individual branches of the anterior, middle and posterior cerebral arteries.

The Middle Cerebral Artery

The middle cerebral artery takes origin from the cranial branch of the internal carotid artery at the posterior angle of the locus perforatus anticus. It passes obliquely outwards and forwards to reach the posterior extremity of the sulcus which limits the tuberculum olfactorium on the lateral side; in this it continues its course as far forward as the level of the anterior border of the tuberculum olfactorium (fig. 7). At this level it leaves the fissure, turns outwards and forwards across the lateral olfactory tract and ends by dividing into terminal branches to the infero-lateral region of the bulb and an artery of supply to the anterior region of the pyriform lobe—a vessel which I propose to name the anterior pyriform artery.

Branches of the Middle Cerebral Artery.

The branches of this artery are basal and cortical. In the first part of its course, between its origin and the posterior end of the sulcus separating the tuberculum from the lateral olfactory tract, the middle cerebral artery supplies basal branches to the locus perforatus anticus, to the nucleus of the lateral olfactory tract and to the posterior angle of the tuberculum olfactorium. In the second part of its course, where it lies in the arcuate fissure, large branches are given to the corpus striatum. These branches pass directly upwards and so cannot be shown in the figures; I have been able to follow them in section however (fig. 8). As the artery is leaving the fissure to enter on the third part of its course, it gives off a branch which continues the direction of the parent trunk. This branch gives off basal branches which pass into the fissure at its anterior end, and then divides into two terminal branches, a lateral one which supplies the infero-lateral region of the olfactory bulb and medial one which passes inwards to inosculate with the recurrent branch of the anterior cerebral artery. This branch supplies the antero-lateral angle of the tuberculum olfactorium and the olfactory peduncle. The third part of the middle cerebral artery, lying on the lateral olfactory tract, gives fine branches to the under surface of the pyriform lobe and then divides into anterior and posterior terminal branches. The anterior branch supplies the lateral surface of the olfactory bulb ; the posterior supplies the anterior region of the pyriform lobe.

The Homologies of the Non-cortical Branches of the Anterior and Middle Cerebral Arteries.

It is convenient to discuss at the present juncture the condition found in Echidna with that in other forms. Before accurate homology can be instituted clear definition must be given to the structures under consideration. In human anatomy the basal or ganglionic branches are said to enter the substance of the brain through the anterior perforated substance (see GRAY'S "Anatomy," 1926, p. 642 (1926). This region is thus made to include the tuberculum olfactorium and the olfactory peduncle. Furthermore, the openings for the vessels are depicted as being distributed over the entire area without any particular order, whereas in reality they are arranged in a very uniform pattern which is constant throughout the mammalia. The locus perforatus anticus is here defined as that region which lies between the posterior border of the tuberculum and the optic tract. Another term which requires definition is the endorhinal fissure, since it forms such an important phylogenetic landmark. ELLIOT SMITH (1902) defines it as follows :—

> "To the medial side of the anterior half of the pyriform lobe there is a deep endorhinal fissure separating it from an elliptical projection of peculiar cortex, commonly known as the tuberculum olfactorium."

In Echidna there is a deep cleft on the lateral side of the tuberculum olfactorium separating it from the structure which I have suggested to be the nucleus of the lateral olfactory tract from the resemblance to the condition found in *Orycteropus* as described by WOOLLARD (1925). If such is the case the endorhinal fissure must be more laterally placed. For the purpose of this description the endorhinal fissure will be taken to be the sulcus lying more laterally (see fig. 8) ; the sulcus, in which the middle cerebral artery is lying, will be identified as the arcuate sulcus. The reader is referred to WOOLLARD'S paper on *Orycteropus*, p. 1187, for further particulars (1925). The necessity of correct definition is imperative on account of the great diminution in the area occupied by these important structures in man ; for if the branches above described are to be homologised in man, their representatives must be included within that greatly diminished area.

In 1920, Prof. ELLIOT SMITH suggested to me the determination of the blood supply of the claustrum as a useful piece of research work. It was this work which led me to the opinion that the study of the development of the body was a study of the development of operative mechanisms in the body, and that all the parts of the mechanism are developed together. It seemed to me that methods of investigation in which one worker confined himself to the nerves, one to the muscles and one to the arteries could not lead to fruitful results since the exclusive study of one system tended to divorce that system from its place in a completed mechanism. On looking back over the influence which formulated the views expressed in this paper, two stand out most clearly. The first which impressed itself most strongly was the following paragraph from ELLIOT SMITH'S paper on the "morphology of the corpus striatum and the origin of the neopallium" (1919):—

> "One of the most remarkable items of evidence in corroboration of the reality of the homologies expressed in these diagrams is the constancy of the position and relations of the lateral striate artery. . . . In any mammalian or reptilian brain this arrangement will be found. It is shown by RETZIUS in the human brain, and I have found it in members of almost every mammalian order."

The second influence was the diagrammatic representation of the nuclei of the medulla after injection of the arteries in STOPFORD'S work.

The distribution of the anterior and middle cerebral arteries in Echidna, as far as the material permitted its elucidation, appears to correspond exactly with that in the reptilia, the edentata, the anthropoids and man.

In fig. 9 the distribution of the arteries to the primitive forebrain structures in the crocodile is shown. The internal carotid artery divided into a cranial and a caudal branch. The cranial branch is seen to pass forward round the tuber cinereum and to divide into anterior and middle cerebral arteries. The middle cerebral artery is seen to supply perforating branches which pass to the corpus striatum lateral to the tuberculum olfactorium and medial to the region which corresponds to the pyriform lobe in higher forms; its terminal branches continue on to supply the pyriform region and end by anastomosing with the artery which supplies the hippocampal region. This anastomotic area corresponds in position with the primordium neopallii. A reference to the figures of Miss CROSBY'S work on the forebrain of the Alligator will make these relations clear (1917). The anterior cerebral artery supplies the inner region of the tuberculum as well as the area precommissuralis. It is to be remarked, that, when a new area—the neopallium—is interpolated between two primitive areas, these areas retain their original blood supply and the new area lies in the anastomotic area between them. The question whether light might thus be shed on the origin of a structure from its blood supply will be discussed later.

Turning now to the blood supply of the primitive forebrain structure in the anthropoids, let us consider the condition in the Orang utan. Fig. 13 shows the region of the inferior surface of the frontal lobe and, as this figure was inadvertently omitted from my communication on the arteries of the brain of the Orang, I shall describe it in some detail.

The internal carotid artery divides in the region of the anterior perforated space into its anterior and middle cerebral branches. The anterior cerebral artery takes the usual course described in human anatomy. It gives off perforating branches to the anterior perforated space, supplies the inner area of the tuberculum and the area precommissuralis. Immediately prior to its junction with the anterior communicating artery it reveals a large foramen. From the outer loop of the foramen a branch is given off which turns outwards and ends at the antero-lateral angle of the tuberculum olfactorium by inosculating with a branch of the middle cerebral artery. This branch supplies the olfactory tract, but whether it also supplies the olfactory bulb could not be determined. The perforating branches of the middle cerebral artery are seen at the outer border of the tuberculum olfactorium piercing the site of the erased endorhinal fissure. The arrangement of the vessels to the primitive forebrain structures is constant. A reference to my earlier paper on the arterial supply of the claustrum suffices to show that there is no essential difference between the condition found in man and that found in the forms above described (1920). And, furthermore, a reference to AITKEN'S paper (1921), whose figure is here reproduced as fig. 14, shows that not only did he like HEUBNER describe this arrangement, but also that he had apparently recognised the separate character of the arteries to the claustrum as shown in his fig. 23.

The criteria for homologising the arteries are almost fully satisfied. The relations to neighbouring structures, the method of distribution, the points of origin of the branches agree in every detail. The final areas of supply appear to be the same, but, unfortunately, these cannot be determined in small animals with the precision with which they can in man. Assuming then that the supply to individual structures is accurately portrayed in the above description, as would appear to be the case, there is a very definite arrangement of the vessels in relation to brain structures constituting vessel-organ units. These organs have, as we know from the work of ELLIOT SMITH and others, peculiar significance in being the primitive parts from which the more highly developed cerebral structures arose ; and we shall see in the next section that the vessels, supplying the primitive organs, have provided by their branches the arterial supply of the more highly developed structures. Before passing to the description of the arteries to the cerebral cortex I should mention a paper by DART entitled "The Law of Infiltration in Forebrain Evolution," and emphasise the close parallel that exists between the arterial distribution of the anterior and middle cerebral arteries and the extent of those regions which he names palæo-olfactory and neo-olfactory. One might almost be tempted to suggest that the anterior cerebral artery is the palæo-olfactory artery and the middle cerebral artery is in part the neo-olfactory artery. In the present state of my investigations on the morphology of the arteries to the hippocampus, however, it is not yet possible to give a complete account of the phylogenetic meaning of the individual branches of the cerebral arteries. For this reason I would here recant a statement made in the paper on the arteries of the brain of the Orang utan that

> "The anterior cerebral artery is the great artery of the olfactory sense, including the hippocampus. The middle and posterior cerebral arteries are the arteries of the pyriform and neopallial areas."

The Cortical Branches of the Middle Cerebral Artery.

The cortical branches are three in number and it is convenient to name them the anterior, middle and posterior pyriform arteries. The *posterior pyriform artery* arises at the posterior end of the arcuate fissure on the left side, and somewhat more anteriorly on the right side of the specimen depicted in fig. 1. It takes a curved course over the pyriform lobe and reaches the posterior rhinal fissure a short distance from the pseudo-sylvian sulcus. Here it divides into anterior and posterior branches. The anterior branch passes to the region of the pseudo-sylvian sulcus where it supplies the pyriform lobe and a small strip of adjoining general cortex. The posterior branch of the posterior pyriform artery at once divides into two terminal branches. One of these—the lateral branch—is exclusively neopallial in its supply, the other exclusively pyriform. The neopallial branch is of peculiar interest because it is the only cortical branch of either the anterior or middle cerebral arteries which extends beyond the immediate confines of the rhinal fissure to supply the neopallium. It supplies the neopallial area which is numbered 3 in fig. 15 of this paper. This area is wedge-shaped with the apex, directed superiorly, and having its anterior border resting on sulcus "α" (fig. 20). (The sulci are named in accordance with ELLIOT SMITH's description in the catalogue of the Royal College of Surgeons.) The only observations which have been made in the cortical lamination in Echidna are those of SCHUSTER and two of his figures are here reproduced as fig. 16. It will be seen that the extent of the area supplied by this neopallial artery closely coincides with an area of distinctive cortex; furthermore, fig. 15 was drawn before I had access to SCHUSTER's paper (1909). This branch is present in all the brains examined. It anastomoses with a branch of the posterior cerebral artery supplying area 11. The second terminal branch of the posterior division of the posterior pyriform artery follows the posterior rhinal fissure and is confined in its distribution to the posterior region of the pyriform cortex. Posteriorly it anastomoses with branches of the posterior cerebral artery which encroach on this area from behind.

The *middle pyriform artery* arises from the middle cerebral artery near the middle of the arcuate fissure. It crosses the lateral olfactory tract and enters the fissura rhinalis a short distance anterior to the pseudo-sylvian sulcus. It supplies the pyriform cortex in the region of this sulcus and a small area of neopallium numbered 2 (fig. 15). It anastomoses with the branch of the posterior cerebral artery which supplies area 4.

The *anterior pyriform artery* is one of the two terminal branches of the middle cerebral artery. It crosses the anterior end of the lateral olfactory tract, gives perforating branches to it and then passes to the anterior end of the rhinal fissure. It supplies the anterior region of the pyriform lobe and a narrow strip of adjoining cortex numbered 8. It anastomoses with the cortical branch of the posterior cerebral artery to area 5.

The cortical distribution in Echidna from the middle cerebral artery (fig. 20) thus includes the whole of the pyriform lobe, a narrow strip of neopallium adjoining the rhinal fissure, anteriorly supplied by the anterior and middle pyriform arteries, and finally posteriorly a somewhat more extensive area involving the protuberant lobe of general cortex which hides the pyriform lobe from view laterally.

The Posterior Cerebral Artery.

The posterior cerebral artery follows a distribution in the human brain which has been determined by complex phylogenetic factors. The very complexity of these factors makes its interpretation one of the most difficult problems in arterial homology; nevertheless the problem should be capable of solution by starting from lower forms to explain the human condition, in place of the reverse method which has been adopted hitherto. Since the anterior and middle cerebral arteries follow so closely their relations to the primitive fore-brain structures and do not lose their identity in supplying the cerebral cortex beyond the boundaries of these structures, one might reasonably expect to find a primitive artery of supply to the posterior elements of the fore-brain vesicle around which the profound modifications have taken place in the formation of the human condition.

Let us therefore enquire firstly into the factors which have modified the primitive fore-brain structures and secondly into the arterial supply in such an animal as the crocodile. A perusal of the writings of Miss CROSBY and ELLIOT SMITH (1919) reveal these factors quite clearly and they can best be summed up in ELLIOT SMITH's own words :—

> "A noteworthy increase in the number of the tactile and optic fibres proceeding from the thalamus to the lateral border of the pallial formation, and probably the addition of the new thalamo-cortical tract conveying acoustic impulses, was responsible for the origin of the reptiles from a primitive Amphibian (Stegocephalian) stock. The immediate effect of the admission of this fuller representation of touch, vision and hearing into the domain of cerebral functions was manifested in an expansion of the cerebral cortex."

If we now turn to figs. 9, 10 and 11, showing the arteries of the brain of the crocodile we find that the anterior and middle cerebral arteries have the arrangement which has been described above and that the homologies of these arteries can be traced from this stage right through the vertebrate series. The condition of affairs is very different in the posterior region of the cerebral vesicle. Under the third nerve, that is dorsal to it, are two large arteries and several smaller ones (not figured in detail). The anterior large artery is to all appearances the continuation of the internal carotid artery; the internal carotid artery before it gives off this branch is connected by a longitudinal channel with the terminal branch of the basilar artery. The arrangement of this longitudinal channel conforms to the description of the internal carotid artery dividing into a cranial and a caudal branch; the caudal branch is a longitudinal channel and should be the posterior communicating artery both from its position and connections; but in that case the posterior large artery from its relations with the third nerve, its origin from the basilar artery and its connection with the internal carotid corresponds with the posterior cerebral artery of human anatomy. They agree with the first part of the description in CUNNINGHAM'S "Text Book of Anatomy" (1913): "The posterior cerebral arteries are the two terminal branches of the basilar. They run backwards and upwards . . . and parallel to the superior cerebellar arteries, from which they are separated by the oculo-motor and trochlear nerves"; but entirely disagree with the second part of the description, for whereas in man they are described as giving "branches to the inferior surface of the cerebrum, etc.," in the crocodile the two terminal branches of the basilar artery (fig. 11) turn backwards and caudally to supply the dorsal surface of the mid-brain and the cerebellum. At the risk of being tedious it is necessary for a thorough understanding of the principles set forth in this paper to account for the great difference in supply of an artery which has the same origin in such different forms as man and the crocodile. A reference to fig. 2 showing the same region in Myrmecophaga throws light on the question. The terminal branches of the basilar artery are longitudinal channels which connect a number of transverse channels. The basilar artery, the stem of the so-called posterior cerebral artery and the posterior communicating have every right, in virtue of the constancy of their form and relations in all animals, to be regarded as distinct morphological entities, and it is the constancy of this channel of connection between the basilar artery and the internal carotid artery, together with the constancy of the anterior cerebral artery, in keeping with the fixity of the relations of the structures it supplies, which accounts for the circle of WILLIS being such a constant landmark in a region where the lateral branches appear to be variable. This is merely an appearance, however, for the lateral and apparently metameric arteries bear a uniform pattern in phylogeny.

Fig. 17 shows the Circle of Willis, as drawn for WILLIS himself by Sir CHRISTOPHER WREN in 1682. Although not accurate in all details, this figure clearly portrays the more primitive condition in which the posterior communicating artery is directly continuous with the stem of the posterior cerebral artery.

In the crocodile the posterior large branch of the internal carotid artery—the large anterior artery dorsal to the third nerve—forms the exclusive supply of the hippocampal and parahippocampal regions (fig. 11). The primitive fore-brain structures forming the hilum, as it were, of the more highly evolved cerebrum are all supplied by the internal carotid artery. The area which Miss CROSBY (1917) recognises as the primordial general cortex is nourished by the anastomoses at the meeting place of the areas of supply of the anterior and middle cerebral with this primitive artery to the hippocampus. It was at this stage in evolution that other senses than smell came to dominate the cerebral cortex. In the mammalia the distribution of blood to the newly formed and relatively enormous neopallium uses only two avenues of approach—an internal carotid approach and a basilar approach. These two routes remain constant. In the spinal cord there are approaches by way of the vertebral, the anterior spinal and both divisions of the posterior spinal arteries. In other words, longitudinal channels form themselves at certain levels of the metameric arteries. Now in the crocodile the caudal continuation of the so-called posterior cerebral artery is on the level of the posterior spinal longitudinal anastomosis.

In the mammalia the invasion of the cerebral hemisphere by visual, tactile and auditory tracts from the mid-brain and thalamus would seem to have had the effect of grouping together the metameric branches to the corpora quadrigemina, the geniculate bodies and the thalamus. The great increase in blood flow through the terminal branches of the basilar arteries enlarges the proximal portion of the longitudinal channel connecting the basilar and internal carotid arteries in such a way that the stem of the posterior cerebral artery appears to have a different value from the posterior communicating artery. Furthermore, the metameric branches to the mid- and fore-brain making use of this posterior line of vascular approach appear to be merely subsidiary branches of the posterior cerebral artery. It is in Myrmecophaga that the transition between the reptilian and the human stages is most clearly seen ; for on the left side of this brain (fig. 2) the metameric nature of the branches is clearly shown, whereas on the right side these branches have fused together so that the branches to the mid-brain, geniculate bodies and thalamus are now branches from a common stem, being as it were an expression of the grouping of those impulses which have led to the evolution of the neopallium. This grouping together seems to have caused the primitive supply to the hippocampal and parahippocampal regions to be included with the supply to the thalamus and mid-brain. I have to admit however that I am not yet able to determine the homologies of that artery which supplies the hippocampus in the crocodile. We are now in a position to describe the posterior cerebral artery in Echidna.

The *posterior cerebral artery* in Echidna is shown in figs. 18 and 19. For the purposes of description it can be divided into three parts. The first part is formed by the division of the basilar artery at the cranial border of the pons. It passes slightly forwards and outwards, hooks round the third nerve and then comes to lie hidden in the groove between the subthalamic region and the overhanging medial portion of the cerebrum. The first part ends by dividing into two branches the posterior communicating artery and the second part of the posterior cerebral. The branches of the first part of the posterior cerebral artery were difficult to follow to their termination on account of the facts that the arteries were not injected, that the deep cleft between the cerebellum and the overhanging cerebrum made their observation with the binocular microscope difficult, and that only one of the nine brains examined was open for dissection. I was able to ascertain however that branches, arranged in parallel series, were distributed to the two corpora quadrigemina, and to the sides of the mid-brain. On removing the thalamic region of the brain to see the deep course of the posterior cerebral artery these vessels were severed and their severed ends are clearly shown in fig. 19. These observations were made in Hong Kong and the conclusion was arrived at that these branches had definite metameric value. This opinion was amply confirmed when I was able to investigate a large series of brains at University College, of which the brain of Myrmecophaga is a type; and, further, through the kindness of Prof. ELLIOT SMITH, I had access to literature which is not available in Hong Kong. It therefore strengthens my opinion that the posterior cerebral artery of human anatomy is made up of various components, to find that HOFMANN (1900) in dealing with the comparative anatomy of these vessels, had already recognised this composite nature of the posterior cerebral artery.

> "Von den Aesten des Ramus caudalis der Arteria carotis cerebral is ist bemerkenswerth, dass das Gebiet einer Arteria cerebri posterior hominis von vier vollkommen verschiedenen Arterien übernommen werden kann, von denen jede allein, oder zwei, oder mehrere gemeinsam sich an der Grosshirnversorgung betheiligen können. Die vier Arterien, die schon im descriptiven Theile als Arteria cerebri posterior, α, β, γ, und δ bezeichnet wurden, sind, &c., &c."

The first part of the posterior cerebral artery is then a longitudinal distributing channel connecting metameric arteries of supply.

The second part of the posterior cerebral artery extends from the posterior communicating artery to the point where it is seen to emerge on the medial surface of the cortex in figs. 18 and 19. It follows the curve of the fimbria and lies very deeply between the hippocampal region and the thalamus. It gives off numerous branches to the thalamus anteriorly and to the hippocampal region posteriorly. These posterior branches supply the posterior region of the fascia dentata, the hippocampus and cortical branches to the occipital pole. I was unable to determine whether it gave any branches to the choroidal plexus.

The third part of the posterior cerebral artery passes vertically up the medial wall of the hemisphere and then turning over the dorsal border of the hemisphere has a very extensive cortical distribution. The description of the branches of the third part of the posterior cerebral artery will be facilitated by a brief description of the cerebral cortex in this animal.

Fig. 18 shows the essential features on the medial aspect of the hemisphere. The posterior cerebral artery is seen at the point where it emerges between the thalamus and the cerebrum. The *fascia dentata* comes to the medial surface from under the overhanging cortex at the point where the posterior cerebral artery becomes superficial. It now extends forwards, still hidden by the thalamus, to become clearly visible above and behind the fornix commissure. It arches over this commissure and extends forwards and downwards as a well-marked rounded gyrus which forms the antero-superior boundary of the area precommissuralis. Above it is separated from the neopallium by a clearly defined hippocampal fissure. In front the fascia dentata appears to become continuous with the medial olfactory peduncle.

In the line which is taken by the posterior cerebral artery to the dorsal surface, there is a shallow sulcus in which the artery lies. This is the furrow which is identified by ELLIOT SMITH (1902) as *sulcus* "ψ." He described it as a deep sulcus extending to the dorsal surface, and in many cases joining the sulcus "β." In the specimen under consideration this is not the case, and, moreover, the other sulci which he describes on the medial surface are mere depressions. In eight other specimens, however, the sulci are deeper and correspond with his description.

On the dorsal and lateral aspects of the hemisphere the arrangement of the sulci agrees very closely with this description and so only brief mention will be necessary. The *sulcus* " α " arises posterior and slightly inferior to the pseudo-sylvian sulcus. This point of origin was found in all the nine brains examined. It passes in an upward and backward direction towards the caudomesial border of the hemisphere. Its mode of termination is variable; in some cases it extends to the medial surface, whilst in others it falls short of the medial border. In its lower part it forms the anterior boundary of the area 3 supplied by the middle cerebral artery; in the remainder of its course it is related to areas supplied by the posterior cerebral artery. SCHUSTER depicts it as a sulcus bounding distinctive structural areas. Lying anterior and parallel to sulcus " α " is the constant sulcus " β." It arises in a bifurcated extremity dorsal to the pseudo-sylvian and anterior rhinal fissures. It may end by joining sulcus " ψ " on the mesial surface or it may end before reaching the dorsal border of the hemisphere. Whilst it is more common to find it as a continuous sulcus, it is not unusual to find it broken into two or three segments. The sulci which lie anterior to sulcus " β " correspond with the sulcus " λ," " δ," and " ε " of ELLIOT SMITH (1902). In all the specimens examined these sulci, together with those which lie posterior to sulcus " α " are so similar to this description that no further mention of them is here necessary.

The distribution of the posterior cerebral artery to the cerebral cortex shows a close similarity in every specimen. On the medial surface several branches are given off. Anteriorly a constant branch, which I shall name the anterior hippocampal artery, passes forwards in the hippocampal fissure and gives branches to the fascia dentata, the hippocampal cortex, and the general cortex bordering these structures anteriorly and superiorly. Posteriorly a large cortical branch arises, which supplies area 12 on the medial and dorsal surfaces. The other branches are insignificant.

At or close to the dorsal border the posterior cerebral artery divides into two main branches which immediately associate themselves with the sulci " α " and " β." The posterior or " sulcus ' α ' branch," follows sulcus " α " to its lower extremity where it ends by anastomosing with the branch of the posterior pyriform artery supplying area 3. Posteriorly it gives off two branches supplying areas 10 and 11 (fig. 15). The main branch supplies the cortex in the vicinity of sulcus " β " and is numbered 9.

The anterior branch of the posterior cerebral artery follows sulcus " β " throughout its whole length, it is therefore convenient to name it the " sulcus ' β ' branch." It anastomoses with the terminal branches of the middle pyriform artery in the region of the anterior rhinal and pseudo-sylvian fissures. It supplies the areas numbered 4, 5 and 6 in the figures. Area 4 is supplied by the main artery which passes down the sulcus. Areas 5 and 6 are supplied by branches which are given off anteriorly. The artery to area 6 is associated with sulcus " λ " and it anastomoses with the terminal branches of the anterior cerebral artery which supply the area 7. The artery to area 5 is associated with sulcus " ε " and anastomoses with the terminal branches of the anterior pyriform artery which supplies the neopallium bordering the anterior end of the anterior rhinal fissure.

In the various brains which I have studied there is a certain amount of variability; for example, the main artery on reaching the dorsal surface of the hemisphere may be associated with either sulcus " α " or " β." It may divide into its anterior and posterior branches on the medial surface of the hemisphere, in which case the anterior branch is always associated with sulcus " β " and the posterior branch with sulcus " α." Generally speaking, however, the distribution is the same. There is present in all the specimens the wedge-shaped area lying posterior to the inferior extremity of sulcus " α," which is supplied by the posterior pyriform artery. The line of junction of the posterior cerebral system with the anterior and middle cerebral systems, related to areas 7, 8, 2 and 3, is distinguishable in every case. Areas 4, 5 and 6 of the posterior cerebral artery were ascertained before I had access to the paper by SCHUSTER. His description would indicate that these areas are of uniform structure, which would suggest that there is no need to subdivide the individual areas of the anterior branch of the posterior cerebral artery.

The most arresting feature in the distribution of the posterior cerebral artery is probably the supply of the fascia dentata anteriorly. From its terminal relations this artery to the fascia dentata is homologous with the artery which supplies the same structure in the crocodile (fig. 12). In the present state of our knowledge of the changes which have taken place in the transformation of the posterior cerebral group of arteries, it is perhaps better to defer any discussion on the invasion of the posterior region of the cerebral vesicle by its blood vessels. Fig. 19, however, suggests that the second and third parts of the posterior cerebral artery in Echidna are the continuation of the caudal branch of the internal carotid artery.

The Arteries of the Hind-brain.

Fig. 1 shows the general arrangement of the arteries on the ventral aspect of the hind-brain in Echidna. The figure likewise gives a good idea of the general form and the relations of the various structures. Emerging from the cleft between the posterior expanded region of the pyriform lobe and the upper border of the pons Varolii, the broad ribbon-like trigeminal nerves form a prominent landmark. They have the appearance of being inserted wholly in front of the pons. The pons Varolii bulges forwards in the middle line so as to overhang and deepen the locus perforatus posticus. The anterior border of the pons is thus bow-shaped. The posterior border is defined by the exits of the sixth and eighth nerves. Placed between the rootlets of the hypoglossal and first cervical nerves on the medial side and the rootlets of the vagus and glossopharyngeal nerves on the lateral side, the prominent tuberculum quinti extends from the lower border of the pons into the cervical region of the cord. In its upper part the tuberculum quinti is crossed superficially by fascicles of the corpus trapezoides.

The vascular pattern throws a great deal of light on the distribution and supply of the arteries in higher forms. The arteries are clearly arranged in two systems ; firstly, arising from the basilar and vertebral arteries are transverse vessels crossing the pons and medulla. These are metameric in disposition and are regarded by me as arteries of supply. Secondly, besides the obvious basilar and vertebral longitudinal channels, there are connections between the metameric arteries arranged in definite positions which are regarded as distributory in nature. Their interpretation will be attempted after the individual vessels have been described. Another important feature which has an important bearing on the interchangeability of origin of the internal auditory, anterior inferior cerebellar and posterior inferior cerebellar arteries in higher forms is the relationship of these metameric arteries to the nerves of the pons and medulla.

The Vertebral Artery.

In all the specimens this vessel has been severed at the lower end of the medulla oblongata. Here it lies ventral to the accessory nerve ; it passes thence forwards and inwards between the rootlets of the first cervical and hypoglossal nerves, to end in the middle line, a short distance below the pons, by joining with its fellow to form the basilar artery. This junction takes place at the level of the uppermost rootlet of the hypoglossal nerve. In all the specimens the two arteries were equal in size and symmetrically arranged. In the specimen figured the stem branches, forming by their union the longitudinal anterior spinal artery, are equal in size with the vertebral artery. In all the other specimens, whilst the anterior spinal stems were of considerable size, they were somewhat smaller than the vertebral artery. The mode of union of the two vertebral arteries is indicated by the presence of foramina in the proximal part of the basilar artery.

The Basilar Artery.

The basilar artery is formed by the union of the two vertebral arteries at the level of the uppermost rootlet of the hypoglossal nerve, and ends by dipping into the locus perforatus posticus and dividing into the two so-called posterior cerebral arteries. The basilar artery lies in a distinct groove on the ventral surface of the pons. The peculiar rounded bulging of the anterior border of the pons, so as to overhang the locus perforatus posticus, produces an almost right-angled bend in the artery, so that an appreciable portion of the artery is hidden from view when looked at from the ventral aspect. From this hidden portion of the vessel a number of pontine and cerebellar branches arise ; and since these vessels lie above the fifth nerve there is a region of the pons hidden from view above the point of entrance of the fifth nerve It is not therefore strictly true to say that the trigeminal nerves are situated wholly in front of the pons in this animal, although the impression is given that such is the case. As mentioned above there are two foramina in the basilar artery, indicating its origin by fusion of a bilaterally arranged network.

The Branches of the Vertebral and Basilar Arteries.

The *anterior spinal artery* arises on either side from the vertebral artery at the level of the second last hypoglossal rootlet, immediately cranial to the site of origin of the posterior inferior cerebellar artery, which passes between the last two rootlets of this nerve. In Echidna the stems of origin of the anterior spinal artery are remarkable for their large size; being in fact as large as the vertebral artery itself. This question of size has an important bearing on the distribution of blood to the higher centres of the brain. In man, from the experiments of MOXON "there is good reason to conclude that the anterior spinal fills from above downwards" (1881); whereas here in Echidna one is justified in assuming that the longitudinal channel fills from the opposite direction. This difference in direction of blood flow indicates how a channel, originally designed to enhance the distribution within one functional area, may be called upon to assist in supplying the demands of a more distant area—in the case of Echidna the posterior cerebral area—without in any way losing its identity and original function. The stems of origin of the anterior spinal artery arise at approximately the same level in all the specimens examined. In the specimens, other than that figured, the anterior spinal stems were somewhat smaller than the vertebral artery, nevertheless they were of considerable size. The two stems pass inwards and caudally to join with one another at an angle of 70 degrees thus forming the median unpaired longitudinal anterior spinal artery. The meeting of the two vertebral arteries above and of the stems of origin of the anterior spinal artery below, produces a diamond-shaped area on the ventral aspect of the medulla. This area is a constant feature throughout the vertebrates. HOFMANN (1900) refers to it in *Acanthias* as follows:—

> "Am Uebergange der Arterie basilaris in den Tractus spinalis ventralis findet sich bei allen injicirten Gehirnen eine schmale Insel eingeschaltet, deren beide Schenkel nahezu parallel nebeneinander liegen. Sie soll als Circulus arteriosus spinalis primus bezeichnet werden."

The longitudinal anterior spinal artery is formed at the level of the uppermost rootlet of the first cervical nerve. Only a short segment of the vessel is seen in the specimens before the level is reached at which the brain was sectioned. The branches of the anterior spinal artery are small vessels which are distributed within the area bounded by the median and antero-lateral sulci. In man, STOPFORD has found that these branches are distributed to the medial region of the cord and bulb; in fact, in man he has found that the trigonum hypoglossi is invariably delineated in injected specimens (1916). This I have confirmed (1927).

In the left side of the specimen depicted in fig. 1 there is, however, a branch which arises from the left stem of origin and which proceeds laterally to inosculate with the posterior spinal artery. This branch is not present in the other specimens, and in a large series of other mammalian brains I have not encountered it. Its presence is therefore emphasised, since it has an important bearing on the hypothesis put forward by me in this and other papers. There is a foramen at the commencement of the longitudinal anterior spinal artery of similar appearance to those seen in the basilar artery and probably produced by the same factors.

The branches of the anterior spinal and basilar arteries which are distributed to the medial regions of the pons and medulla are in all probability serially homologous and of different value from those to be described as the lateral branches.

The Lateral Branches of the Vertebral and Basilar Arteries.

These branches are described under one heading as they are regarded as being serially arranged and homologous. They are typical transverse arteries of supply and bear a constant relation to the nerves of the hind-brain. The clinical importance of this relationship has been emphasised in the writings of CUSHING (1910) and STOPFORD (1916–17) in the case of the internal auditory and anterior inferior cerebellar arteries with reference to sixth-nerve paralysis. From the morphological point of view, however, the relationship of the remaining lateral branches to the nerves is just as important. The lateral arteries pass outwards between the individual rootlets of the hypoglossal nerve and through the intervals between the hypoglossal and abducens nerves and between the abducens and oculomotor nerves. More laterally these arteries similarly bear a constant relationship with the fifth, seventh, eighth, ninth and tenth nerves. There are clear indications that these arteries are arranged segmentally and that originally there exists an artery to each segment; many factors, however, analogous to those which influence the distribution of the posterior cerebral artery, play a part in obscuring this primitive arrangement. The development of the descending root of the trigeminal from segments other than those derived from the neuromeres from which it took origin, play their part in so modifying the pattern of the blood vessels that the distribution of blood to them is enhanced. As in other parts of the body this enhancement is brought about by the development of longitudinal channels between the primitive vessels and the subsequent atrophy of some of the stems feeding these longitudinal channels. From this it is apparent that such arteries as the posterior and anterior inferior cerebellar arteries cannot be regarded as pure segmental arteries but as composite arteries, having the same type of variation as is found elsewhere in the body. In order to emphasise this conception it is advisable in the next section to compare the posterior cerebellar artery in Echidna with that of Man.

The Posterior Inferior Cerebellar Artery.

In Echidna this artery arises from the vertebral artery at a level corresponding to the interval between the last two rootlets of the hypoglossal nerve. This is the site of origin which is regarded as the normal one in man; and further, if one examines a human brain in which the artery arises at an unusually high level, there will be found a small vessel of segmental value arising at the normal site of origin. In all the specimens of Echidna which I have examined the arrangement of the posterior inferior cerebellar artery conforms to a fairly uniform pattern; so that with the aid of fig. 1 one description will suffice for them all.

The vessel passes between the last two rootlets of the hypoglossal nerve and then connects with a lateral anastomotic field which can be traced in many cases as far as the upper border of the pons. In some of the specimens a longitudinal channel is formed. This channel is joined by the higher metameric lateral medullary and pontine vessels. On the left side the posterior inferior cerebellar artery continues beyond the longitudinal anastomosis to reach the dorsal region of the medulla. It divides in this part of its course into two branches. The anterior and larger branch continues the direction of the main stem. It gives branches to the lateral region of the bulb and continuing its course supplies the rhombic area and thence is distributed to the choroidal plexus of the fourth ventricle and the cerebellum. The posterior and smaller branch passes dorsally and inferiorly between the medulla and the accessory nerve. It is lost at the point where the brain is sectioned. This branch I take to be the posterior spinal artery. It will be seen from the figure that this branch likewise sends branches to the rhombic area; these branches anastomose with rhombic branches of the anterior branch. There is in fact a continuous plexus on the restiform body which is reinforced by the transverse branches of the vertebral and basilar artery which arise at a higher level.

There are therefore two longitudinal plexuses in relation to the posterior inferior cerebellar artery—one lateral to the hypoglossal rootlets and one on the restiform body. A reference to fig. 10 showing the distribution in the crocodile reveals the same restiform or rhombic plexus. An interesting condition is seen on the right side in fig. 1; for here the posterior inferior cerebellar artery divides so as to pass on either side of the last rootlet of the hypoglossal nerve; and then immediately lateral to this rootlet the two branches are joined by the longitudinal channel in such a way as to enclose the last rootlet in an arterial ring. The posterior of the two branches in this case divides, after passing between the medulla and the accessory nerve, into an anterior branch which supplies the choroidal plexus and the cerebellum and a posterior branch which is the posterior spinal artery.

It might here very reasonably be contended that the selection of the artery above described as the posterior inferior cerebellar artery is an arbitrary one; for transverse branches of the vertebral artery which arise above this level supply corresponding areas in the higher segments. The reply to the contention is important for it gives not only the clue to the meaning of the distribution of the artery bearing the same name in man, but also reveals the methods by which the distribution of the blood to outlying areas is improved in order to cope with structural and functional increases within those areas. We have seen how this has been carried out in the posterior cerebral area. Let us consider therefore in the same way the distribution of the posterior inferior cerebellar artery in man, in order to see how far, if at all, this artery can be compared with lower forms. For this purpose the description given by STOPFORD (1916) is used as a basis for comparison. In 70 per cent. of cases the artery arises at the level of the lower border of the olive. In the remaining cases it would accord with STOPFORD's description to say that it may arise at any of the levels indicated by the position of the lateral branches in Echidna. It is to be noted that this equally applies to the anterior inferior cerebellar and the internal auditory arteries.

The stem of origin in man may therefore be regarded as the stem of one of these metameric arteries, the commonest site of origin being that which corresponds with the metameric branch in Echidna, which has been described above as the posterior inferior cerebellar artery. In man these lateral branches are grouped as intermediate branches of the vertebral artery by STOPFORD, who says of them—

> "They are very variable in size and number, and are frequently absent. As I have previously pointed out this variability is largely dependent upon the course and distribution to the bulb of the posterior inferior cerebellar artery."

The normal course, taken by the posterior inferior cerebellar artery, is between the lower rootlets of the hypoglossal nerve; it then ascends on the surface of the medulla for a short distance before forming its characteristic loops. The condition in Echidna seems to leave little room for doubt that this ascending portion in man corresponds with the longitudinal plexus which lies immediately lateral to the hypoglossal rootlets. This part of the artery differs in nature from its stem of origin; it is of the nature of a distributing trunk which encroaches on the cranially situated metameric areas. The higher stems connecting the vertebral artery with this distributing trunk are no longer required, and so are dispensed with, in exactly the same manner as the stems of the limb arteries are dispensed with when the seventh stem takes over the distribution to the limb. If the posterior inferior cerebellar artery fails to take over this longitudinal channel the lateral arteries arise from the vertebral artery. The morphological supply of the bulb is not thereby altered, but the method of distributing the blood to the supplying vessels is variable. STOPFORD's statement just quoted therefore requires modification by substituting for "they" "the stems of the lateral branches." This then explains the dependence of the variability of the stems of origin upon the course and distribution to the bulb of the posterior inferior cerebellar artery. By thus clearly separating the distributing elements of an artery from its supplying elements the characteristics of precision and variation, so ably discussed by EVANS in KEIBEL and MALL's "Embryology," are reconciled as being the characteristic of two different types of vessels.

The precise relations of the bulbar supply of these vessels has been so fully investigated by STOPFORD from the point of view, both of anatomical bearing and clinical interpretation, that no further mention is here necessary.

In the next part of its course the posterior inferior cerebellar artery passes through the rootlets of the vague to join the restiform or rhombic longitudinal plexus, from which the blood is distributed to the cerebellum. The particular element of the posterior inferior cerebellar artery which passes through these rootlets is an element of metameric value, corresponding with the lateral branch belonging to that metamere. In other words, the same process of suppression of the stems of the more distally situated region of the lateral arteries permits of an enhanced flow to the cerebellum, which develops, as it were, at the periphery of the vascularised regions of the hind-brain. When a cranially situated stem is selected, the loop of the posterior inferior cerebellar artery may extend as high as the lower border of the pons, or actually higher in those cases where the cerebellar distribution is taken over by the anterior inferior cerebellar artery. If, however, the selected stem belongs to the same segment as the stem of origin the course of this artery accords with the following description by STOPFORD :—

> " In the final group the artery curved backwards and caudally to the spinal cord or directly outwards on to the cerebellum ; in either case it usually failed to provide any bulbar branches ; this configuration was found in 31 per cent. on the right and 29 per cent. on the left ; and is curiously the one most in accordance with the standard description."

This description corresponds very closely with the condition in Echidna, and is sufficient warrant for naming that artery in Echidna the posterior inferior cerebellar artery.

The *lateral branches* of the vertebral and basilar arteries have been sufficiently described in the last section to indicate that they can be divided into three parts for the purpose of description. The first part extends from their point of origin to the longitudinal bulbar plexus, the second part from this plexus to the longitudinal restiform plexus, and the third part extends from this plexus to the cerebellum. The second part supplies the bulbar branches to the tuberculum quinti and other structures; and it is the distribution of these branches which produces the characteristic bulbar symptoms of posterior inferior cerebellar occlusion. The third part supplies the choroidal plexus and the cerebellum. The second parts are related to the rootlets of the fifth, seventh, eighth, ninth and tenth nerves, proximal to the longitudinal plexus on the restiform body, or, more correctly, the region of the rhombic lip. In human anatomy there is an impression that only three of these arteries supply the cerebellum, and on account of the fact that this appearance is warranted, if only the sites of origin of the arteries are used for nomenclature, it is desirable to retain the description for practical purposes. The condition in Echidna, however, makes it clear that these arteries in virtue of their relations to the nerves have as much right to a special name as the internal auditory artery. This was recognised by HOFMANN in his important paper, where he describes a series of cerebellar branches and the relations of the arteries to the nerves in various animals. The relationship of arteries to the trigeminal nerve was so striking that he named the upper two transverse arteries of the pons the "arteriae nervi trigemini superior et inferior." In writing of the arrangement in Anser domesticus he says:—

> "Die Arteria basilaris entsendet:
>
> "1. Eine Reihe metamerer Rami ad Medullam oblongatam. Unter diesen sind ein bis zwei Gefässchen, die als Arteriae nervi trigemini superior und inferior bezeichnet werden können, stark ausgebildet und versorgen die Wurzel des Nervus trigeminus;
>
> "2. Eine Arteria cerebelli B. Dieser stärkste Ast der Arteria basilaris entspringt gegenüber dem der anderen Seite oder, etwas cranial- oder caudalwärts verschoben, beiläufig aus der Mitte der Länge der Arteria basilaris, und verläuft cranial von der Wurzel des Nervus abducens, lateral- und caudalwärts, wobei kleine Aestchen zur Unterseite der Medulla oblongata abgegeben werden. Der Hauptstamm der Arterie aber gibt, an der Seite des verlängerten Markes angelangt, ein Aestchen zu den Corpora restiformia und den Plexus ventriculi IV, biegt cranialwärts zu um, umgreift in scharfen Bogen den Flocculus und gelangt an die Seite des mächtig entwickelten Oberwurms."

In Echidna I have been able to confirm the presence of these arteries passing superior and inferior to the trigeminal nerve. There can be no doubt then that the pattern of the vessels to the hind-brain can be explained in all animals by recognising the primitive metameric arrangement. Such variations as occur are all readily explainable in the different methods of distribution to the morphological units. This is perhaps best seen in the relations of the internal auditory and anterior inferior cerebellar arteries. In Echidna these arteries are at once recognised by their relations to the sixth nerve. The internal auditory artery lies cranial and dorsal to the nerve, the anterior inferior cerebellar artery lies caudal and ventral. It was these relationships to which attention was called by CUSHING and STOPFORD in man on account of their clinical significance.

From what I have written on the distribution of the posterior inferior cerebellar artery there is little need to discuss the morphological meaning of STOPFORD's findings in the cases of these two arteries. It will be sufficient to point out the anastomotic connections between these two arteries in the brain of Echidna shown in fig. 1 and to quote the passages which are explained:—

> "II. *The Anterior Inferior Cerebellar Artery.*"
>
> "*Relation to the Abducent Nerve.*—At the present time this neuro-vascular relation is clinically of very considerable interest; yet our anatomical knowledge of the subject is, unfortunately, incomplete and far from satisfactory."
>
> "The present investigation has shown the artery ventral on both sides in 74 per cent. and dorsal in 8 per cent., and there is a difference in this neuro-vascular relationship on the two sides in 18 per cent."

"III. *The Internal Auditory Artery.*"

> "*Origin.*—The conclusion drawn from this examination is that it arises more frequently from the anterior inferior cerebellar than the basilar, as in 62 per cent. on the right and 62 per cent. on the left it was given off by the former artery. It is usually seen to arise at the point where the anterior inferior cerebellar leaves the brachium pontis and extends on to the cerebellum, a point where the artery is in close relationship with the auditory and facial nerves."

No more striking testimony to the accuracy of STOPFORD's observations could be given than fig. 1 of this paper, which shows the union of the two arteries in close relationship to the auditory and facial nerves, at the same time it reveals the constancy of arterial distribution. I would finally suggest that, whilst no good purpose would be served in changing the nomenclature, the above statement would be more in accord with morphological facts if it were made to read that the internal auditory and anterior inferior cerebellar arteries frequently arise by a common stem from the basilar artery; this stem is the stem of the so-called anterior inferior cerebellar if it lies ventral to the abducent nerve, and internal auditory if it lies dorsal to it. It must not be forgotten, however, that stems even higher or lower may be employed for cerebellar distribution; in fact, a stem so low as that of the posterior inferior cerebellar artery may take over the distribution of blood to the supplying arteries of the higher segments.

This description of the vessels of the hind-brain, whilst indicating a uniform underlying pattern, shows the difficulty of the interpretation of symptoms following lesions of them. One cannot expect to find a definite syndrome for any particular artery because of its complex and variable nature, nevertheless STOPFORD's work on trigeminal lesions in the hind-brain suggests that the metameric branches are distributed to areas of functional value.

GENERAL DISCUSSION.

In 1920 the examination of the basal arteries of the fore-brain led to the enunciation of two principles:—

1. That arteries are laid down with a definite relation to function.
2. That the distribution of arteries obeys some definite ontogenetic and phylogenetic law.

Following up this investigation with fuller researches into the arterial supply of the brain, I put forward the following hypotheses to explain the constancy of the supply of arteries (1926).

1. That the segmental arteries of the body are developed *in situ* in relationship with the organ which they are to supply; that these arteries are phylogenetically and ontogenetically stable; that having been developed to supply an organ, they supply that organ throughout life; and, finally, that when a primitive functional area develops greater function, the vessels supplying the greater functioning area are derived from those supplying the primitive area.

2. That the distribution of the blood to the supplying arteries is determined by longitudinal or intersegmental anastomosis between the segmental arteries at certain definite levels.

The interpretation of the final pattern of the arteries to organs which are admittedly segmental in origin, such as to the forelimb or to the intercostal spaces, is comparatively easy ; but in the case of the brain, where the segmental value of the structures is obscured, if indeed the fore-brain is even of segmental origin, the interpretation of the arterial distribution in terms of a primitive segmental pattern is rendered difficult. Bearing this in mind, it nevertheless should help the solution of the vexed question of the segmentation of the vertebrate head to examine the arterial supply in relation with such structures as the nerves and neuromeric derivatives. The terms " serial," " metameric," and " segmental " as used in this paper must not therefore be too rigidly interpreted as indicating a segmental value, although such an interpretation is not altogether unwarranted.

Bearing these difficulties in mind, however, the conception that the portion of the internal carotid artery, herein described, is a component of the segmental artery to the first or olfactory segment, is here put forward as a working hypothesis. The distribution in the crocodile supports this view. The internal carotid divides into a cranial and a caudal branch. The cranial branch divides into the anterior and middle cerebral arteries, The distribution of these arteries is directly comparable in the crocodile, Echidna and all other animals which I have examined. Proximally the anterior cerebral artery is distributed to areas on the medial wall, which are known from the works of ELLIOT SMITH, HERRICK, ARIENS KAPPERS, DE LANGE, CROSBY, HINES, CAIRNEY and many others, to be important morphological entities. The pattern of the distribution, the relations to neighbouring structures, and, as far as can be ascertained at present, the supply is the same in all forms. The middle cerebral artery likewise, in its supply to the tuberculum olfactorium, the corpus striatum and the pyriform cortex, reveals a phylogenetic constancy in its distribution and supply. In the crocodile the primitive fore-brain elements, constituting the hippocampal formation, are supplied by the caudal branch of the internal carotid artery.

The only formation whose supply has not yet been determined is the amygdaloid complex. If one ignores the size of the vessels in this region in the brain of Echidna (for actual size cannot be regarded as a criterion for homology, but rather of the direction of distribution) the second and third parts of the posterior cerebral artery appear to be homologous with the caudal branch in the crocodile. The supply to the cerebral vesicle is thus from the internal carotid artery, and from this artery individual and constant branches supply morphological elements of the vesicle. In Echidna the enormous development of the neopallium has called for a more efficient distribution of blood beyond the primitive regions ; and this demand has been responded to by the increase in size of the vertebral and anterior spinal approach.

BERTHA DE VRIES fully appreciated these changes which had taken place—" Ce sont les artères carotides internes qui seules fournissent le sang du cerveau," but failed to distinguish the morphological entity of the vessels in suggesting that the same branch may in one case arise from one artery and in another case from another artery—" L'ontogénie prouve, comme la phylogénie, que les artères cérébrales postérieures sont des branches collatérales, primitivement du domaine carotidien caudal et reprises secondairement par le systême encéphalique vertébral." She failed to appreciate that changes in the direction of blood flow and in the size of arteries affect not their supplying value but their distributing value.

This constancy of blood supply to the primitive structures, together with the results so far published by me on the arteries to the cerebral cortex in man (1927), lead one to turn to the evolution of the arteries of the cerebral cortex as a means of determining the series of changes which the neopallium has passed through in reaching its highest development in man. In the crocodile, as we have seen, the area which Miss CROSBY (1917) terms the general cortex in the alligator, and which CAIRNEY (1926) likewise describes in Sphenodon, is generally accepted as being the precursor of the neopallium. She says :—

> " The great significance of this general cortex in the alligator is the appearance of a somatic centre having a high cortical type of integration. Nevertheless, since the general cortex is under tolerably direct olfactory influence from the adjacent hippocampal and pyriform (and possibly from other sources), it cannot be regarded as fully differentiated neopallium, though it is undoubtedly the immediate precursor of that type of cortex."

In the crocodile the blood is supplied to this new area at the junctional anastomosis between the arteries which supply the pyriform and hippocampal areas, and it is reasonable to assume that on its further differentiation and enlargement it will be supplied by arteries which are secondary branches of those which supply the pyriform and hippocampal areas. The invasion of this newly-formed cortex by sensory tracts from lower segments of the brain causes the longitudinal anastomoses between those segments to increase in size and so lead to a greater blood flow from the caudal approaches. Furthermore, this result is improved by a grouping together of those arteries which supply the lower centres in the thalamus and mesencephalon from which these sensory impulses are derived. In this way the primitive metameric arrangement of the vessels to these lower centres is obscured. The cells of the primordial general cortex are interpolated between the pyriform and hippocampal areas and at the same time are influenced by those areas; for the olfactory sense is also playing its part in that differentiation.

In fig. 21, showing the distribution to the lateral surface of the brain of Macropus, the three pyriform branches of the middle cerebral artery are seen overflowing the pyriform area to be distributed over the major part of this surface as far as the medial border of the hemisphere ; in *Myrmecophaga* the middle cerebral distribution extends as far as the conjoint corono-lateral sulcus (ELLIOT SMITH, 1902): in the Carnivora, of which I have examined many injected specimens, the middle cerebral distribution is limited superiorly almost constantly by the endo-lateral sulcus; and, finally, in the anthropoids and in man the middle cerebral distribution extends far beyond the contracted area of the pyriform lobe to an almost constant distribution. It seems reasonable to infer that this great middle cerebral distribution is in response to a differentiation of the general pallium on the pyriform side. In the same way the differentiation on the hippocampal side should be indicated by a development of the terminal branches to the hippocampal region. If such be the case then the general pallium among macrosmatic animals may receive in some cases its greatest olfactory contributions from the pyriform cortex and in others from the hippocampal region. In the comparison which ELLIOT SMITH makes (1902) between the macrosmatic Echidna and the other macrosmatic animals, he says:—

> "The factors which the study of other mammalian brains has shown to be the determinants of the extent of the cortex, fail completely to explain how it is that a small animal of the lowliest status in the mammalian series comes to possess this large cortical apparatus. In other small, terrestrial, insect-eating mammals such as the Pangolins and the Anteaters, and in the fossorial Bandicoots, Hedgehogs, and Armadillos, we find highly macrosmatic brains with small neopallia; and yet in Tachyglossus, whose mode of life is not dissimilar to many of these mammals, we find alongside the large olfactory bulb and great pyriform lobe of the highly macrosmatic brain a huge complicated neopallium."

Is it possible that the arterial supply gives the clue to this problem? The study of the arteries in other places seems to confirm the hypothesis that "when a primitive functional area develops greater function, the vessels supplying the greater functioning area are derived from those supplying the primitive area." The greater extent of the neopallium in the Echidna is supplied by the posterior cerebral artery and it is therefore tempting to suggest that the neopallium in the Echidna has received the greater part of its olfactory impressions from the hippocampal region; in other words that this cortex differs from that of other mammals in being to a great extent parahippocampal in origin. The accession of non-olfactory impressions in the fore-brain of the reptile would then have caused a divergence of type in three directions. One type develops into the avian brain, in which the hypopallial formation is hypertrophied; the second into the prototherian type of brain, such as that of Echidna, in which growth involves mainly the parahippocampal cortex; and the third into the Metatherian and Eutherian types in both of which the true neopallium (*i.e.* the parapyriform cortex) undergoes the greatest expansion. Furthermore, ELLIOT SMITH (1902) has shown that

> "The ventral commissure has a much wider distribution than the anterior commissure of most Eutheria, for it connects the whole of the two cerebral hemispheres excepting the hippocampal formations only. Now in the Eutheria part of the

> neopallium is connected to the other hemisphere by means of the corpus callosum, so that the ventral commissure of the Spiny Anteater represents not only the anterior commissure, but also the corpus callosum of the Eutheria."

It might be contended, however, that the fact of one animal receiving its cortical supply from the middle cerebral artery, and of another from the posterior cerebral, is not sufficient to allow it to be postulated that the cortices of the two are different in character. This investigation, however, is concerned with the attempt to correlate the vascular pattern with what is known of the morphology of the structure supplied; and the writer fully appreciates the need for caution in interpretation in a field which has not previously been explored. The determination of the cortical fields of supply was made by following the individual branches until they anastomosed with other arteries. If one examines the junctional field between areas 5 and 8 in figs. 15 and 22 one sees that the exact line of demarcation cannot be accurately found, for here the vessels inosculate with one another; and since size by itself cannot be used for homology, it is evident that the middle cerebral distribution may be more extensive than that indicated in the figures. Nevertheless it seems unlikely that this is the case; for the arterial distribution in Echidna used solely as an auxiliary to other methods of morphological enquiry, appears to confirm the findings of ELLIOT SMITH (1902) and SCHUSTER (1909).

It must be admitted that the work of SCHUSTER is complete, but the comparison of his figures with my own reveals a remarkable similarity. GRAY (1924), apparently hoping to compare his results on the cortical pattern of the opossum with those of SCHUSTER, found that in an examination of SCHUSTER's paper, "the topographical extent over the hemisphere of cortically distinct areas is quite bizarre. No similarity with the cortical charts of other mammals is apparent." The hypothesis that the distribution of the blood vessels affords a clue to the homologies of the cortical territory would interpret this quality of bizarreness by the claim that the major part of the cortex of Echidna, being parahippocampal, is not identical with that of other mammals, which is neopallial.

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DESCRIPTION OF FIGURES. (PLATES 1–6.)

Abbreviations.

A.C., anterior commissure.
Ar.A.Ce., anterior cerebral artery.
Ar.A.I.Crb., anterior inferior cerebellar artery.
Ar.A.Py., anterior pyriform artery.
Ar.A.Sp., anterior spinal artery.
Ar.Ba., basilar artery.
Ar.Int.Ca., internal carotid artery.
Art.Int.Au., internal auditory artery.
Ar.M.Ce., middle cerebral artery.
Ar.M.Py., middle pyriform artery.
Art.P.Ce., posterior cerebral artery.
Ar.P.Co., posterior communicating artery.
Ar.P.I.Crb., posterior inferior cerebellar artery.
Ar.P.Py., posterior pyriform artery.
Ar.P.Sp., posterior spinal artery.
Ar.Prf., prefrontal artery.
Art.R.A.Ce., recurrent anterior cerebral artery.
Art.St. striate artery.
A.S.CRB., superior cerebellar artery.
Ar.V., vertebral artery.
Br.Op.Ch., branch to optic chiasma.
B.O., olfactory bulb.
Crb., cerebellum.
C.B., commissure bed.
Co.Ma., corpora mammillaria.
D.C., dorsal commissure.
D.Crb.Ar., dorsal cerebral artery.
Fa.De., fascia dentata.
Fi.Arc., arcuate fissure.
Fi.En., endorhinal fissure.
Fi.P.Sy., pseudosylvian fissure.
Fi.Rh., rhinal fissure.
Fo.Mo., foramen of Monro.
Hi., hippocampal formation.
Lo.OP., optic lobe.
Lo.Py., pyriform lobe.
L.P.A., locus perforatus anticus.
N.L.O.T., nucleus lateral olfactory tract.
O.P., olfactory peduncle
Pl.R., restiform plexus.
Pri.G.C., primordium general cortex.
Sc., Sulci α, β, ε, and δ.
S.p-Sy., pseudo-sylvian sulcus.
T.O., tuberculum olfactorium.

Plate 1.

Fig. 1.—The brain of Echidna seen from the ventral aspect showing the distribution of the arteries and the general anatomical features.

Fig. 3.—The dorsal surface of the brain of Echidna.

Fig. 4.—The mode of attachment of the pyriform lobe to the dorsal surface of the olfactory bulb is shown. The frontal pole of the hemisphere has been retracted.

Fig. 5.—A transverse section through the anterior end of the hemisphere of Echidna. It shows the shelf-like appearance of the anterior end of the pyriform lobe, the depth of the rhinal fissure and the mode of attachment of the pyriform lobe into the olfactory bulb.

Plate 2.

Fig. 2.—The arteries of the brain of Myrmecophaga jubata seen from the ventral aspect.

Fig. 6.—A sagittal section through the brain of Echidna taken about 2 mm. from the middle line. It shows the course of the perforating branch of the cranial division of the internal carotid artery which supplies the commissure bed.

Plate 3.

Fig. 7.—An enlarged view of the region of the tuberculum olfactorium to show the anterior recurrent branch of the anterior cerebral artery in Echidna.

Fig. 8.—A transverse section of the brain of Echidna at the level of the commissures, showing a large branch of the middle cerebral artery entering the arcuate fissure and being distributed to the corpus striatum. Note the endorhinal fissure lateral to the arcuate fissure.

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Fig. 20.—The lateral view of the brain of Echidna showing the distribution of the arteries. Compare with fig. 15.

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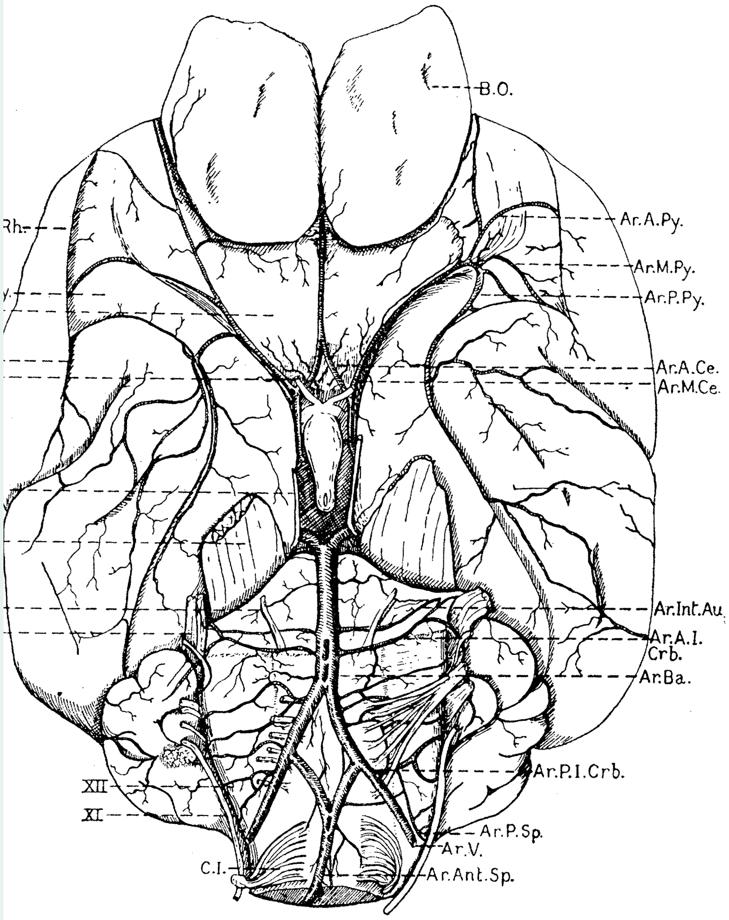
Fig. 22.—The vascular areas seen from the dorsal aspect in Echidna. Compare with fig. 3.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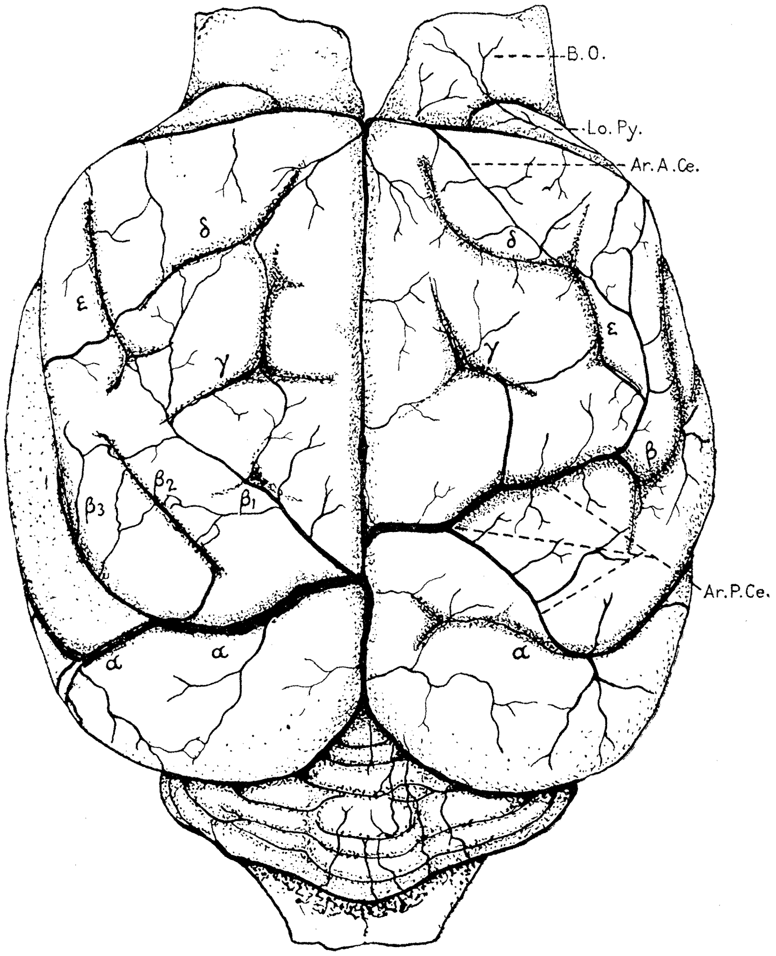
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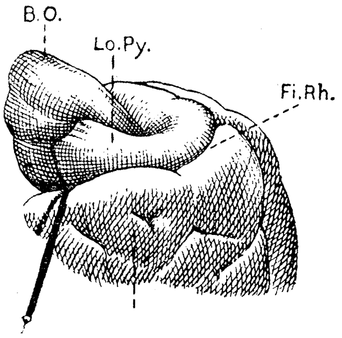
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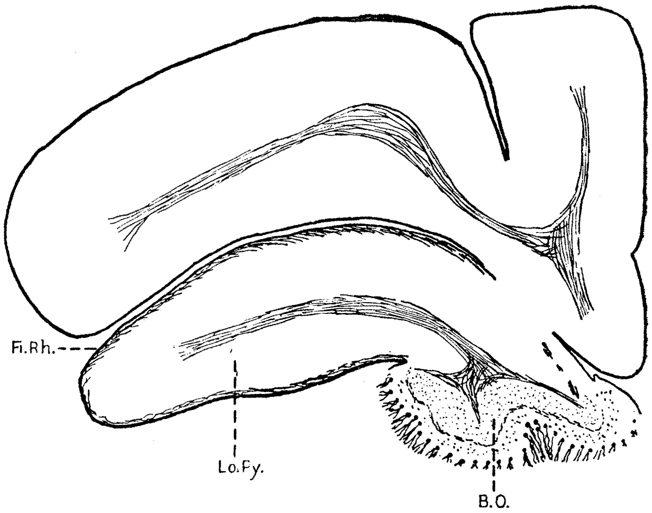
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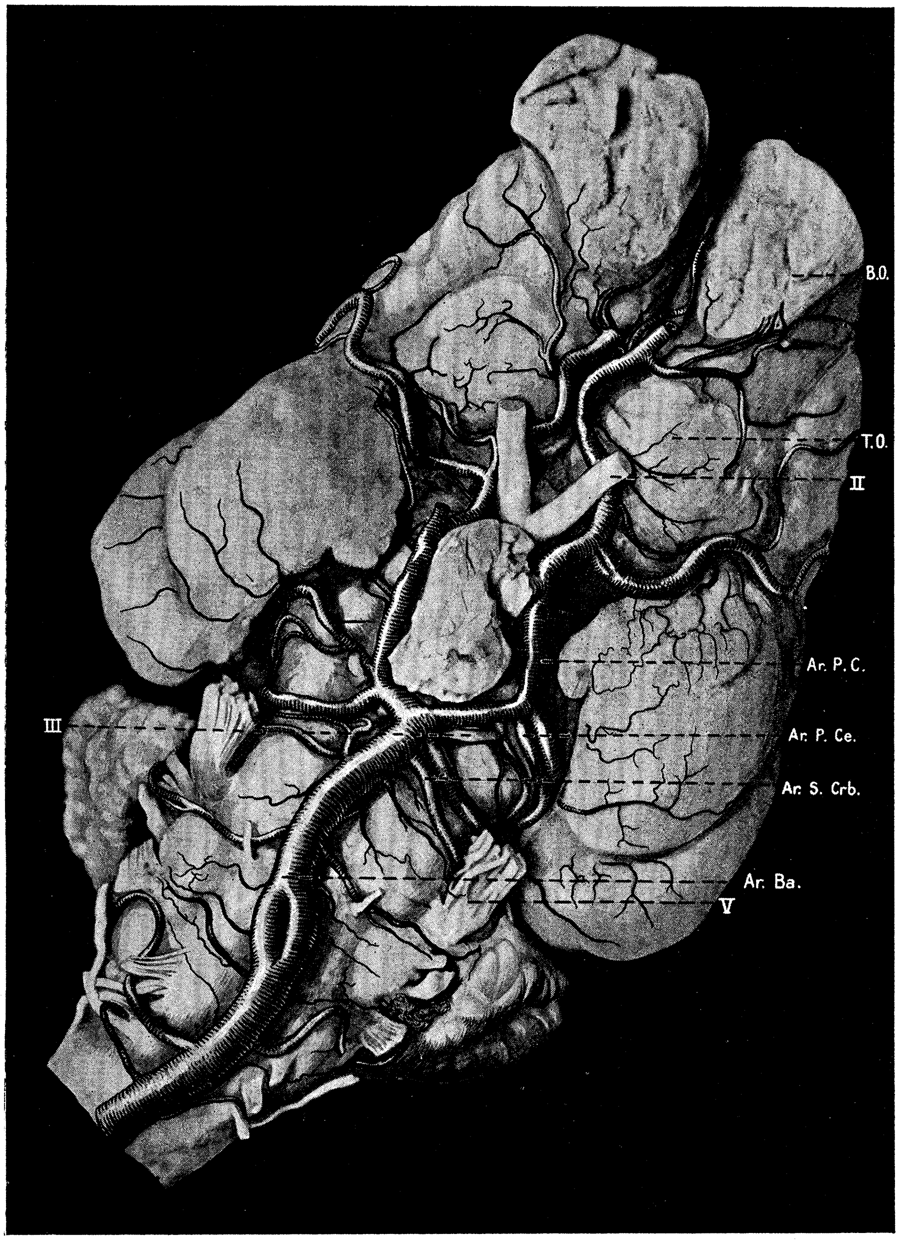

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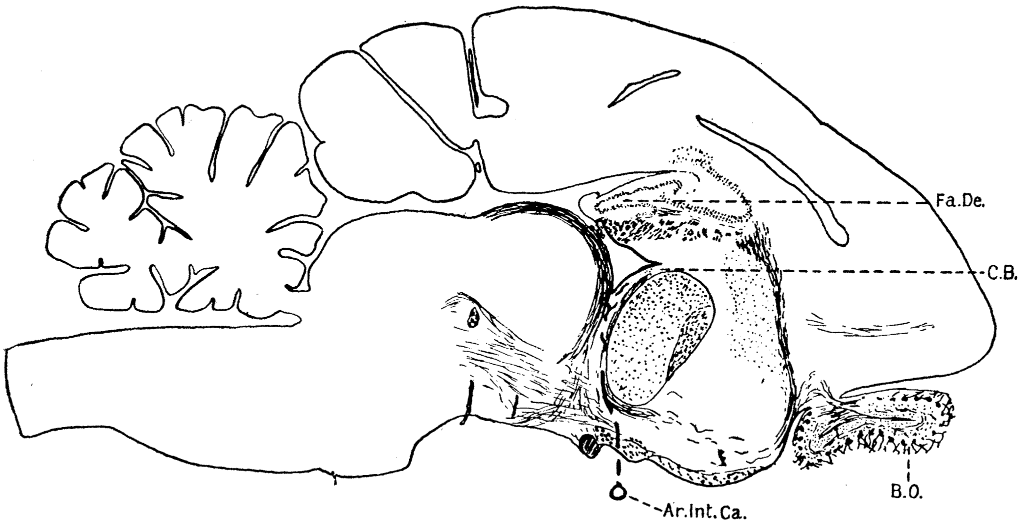

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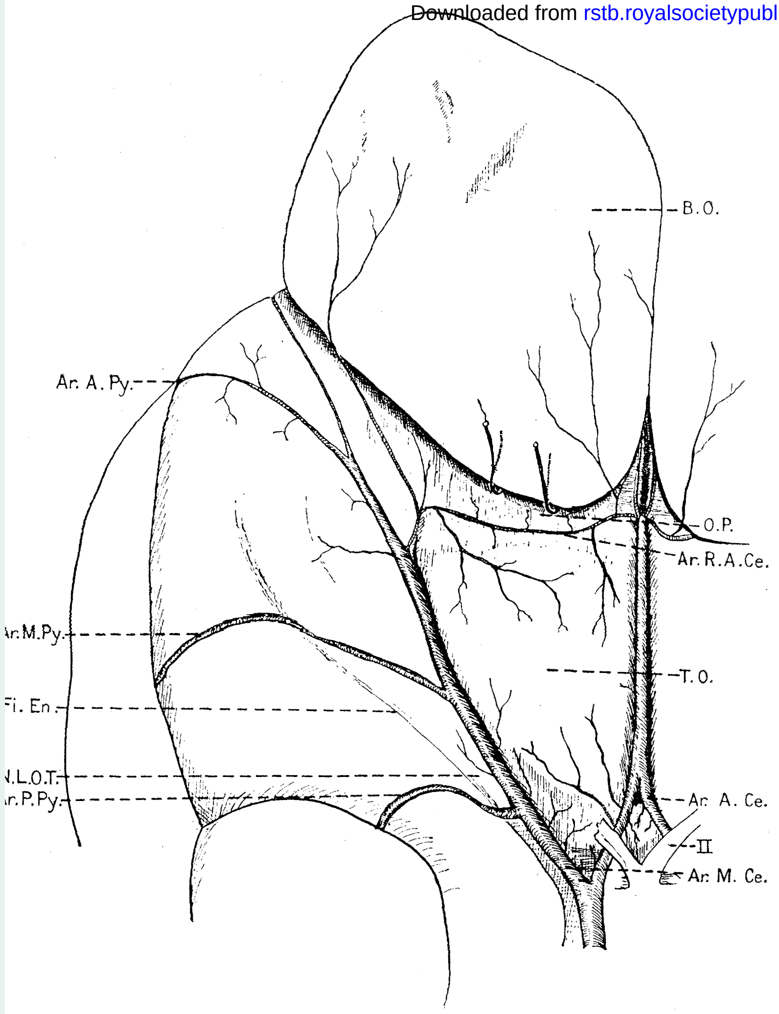
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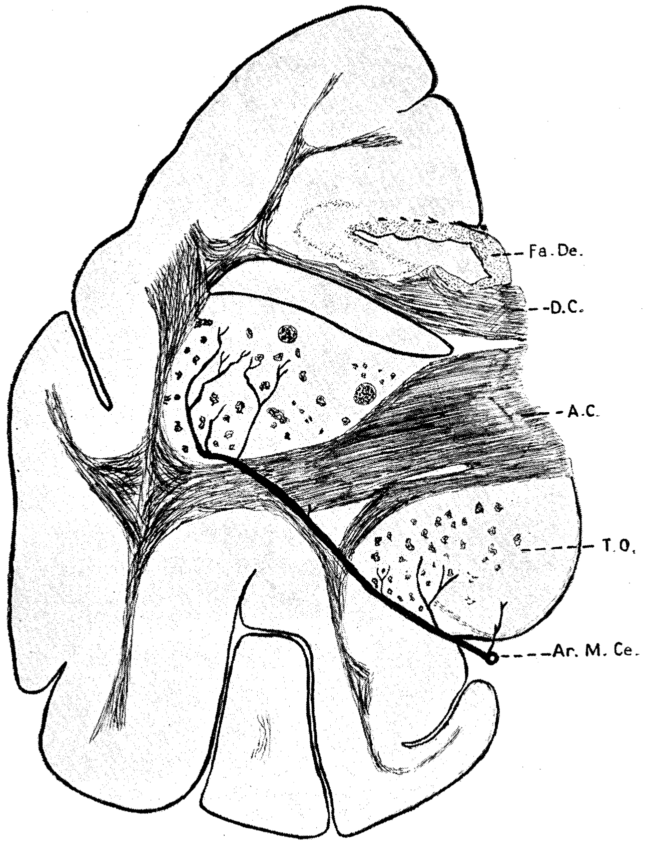
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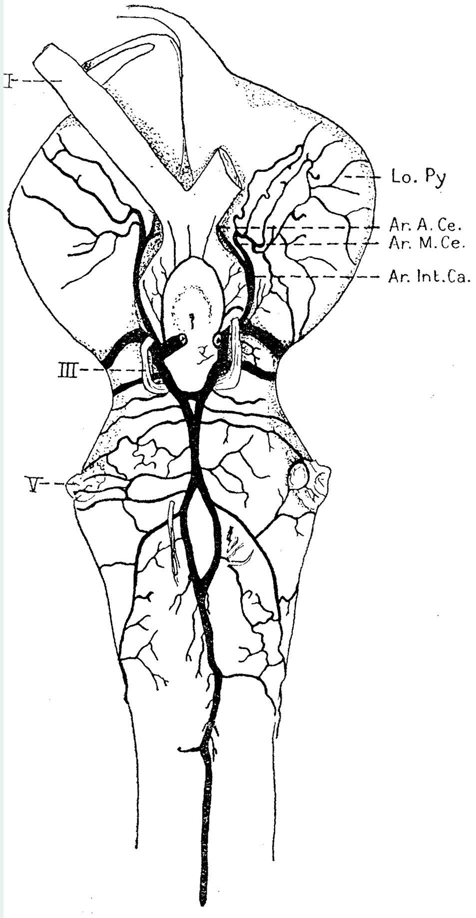
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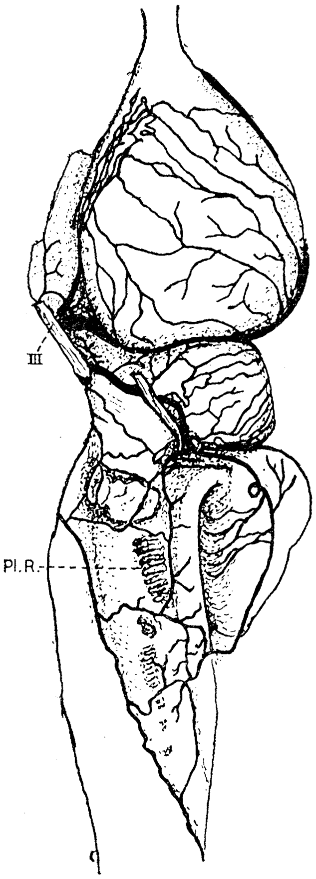
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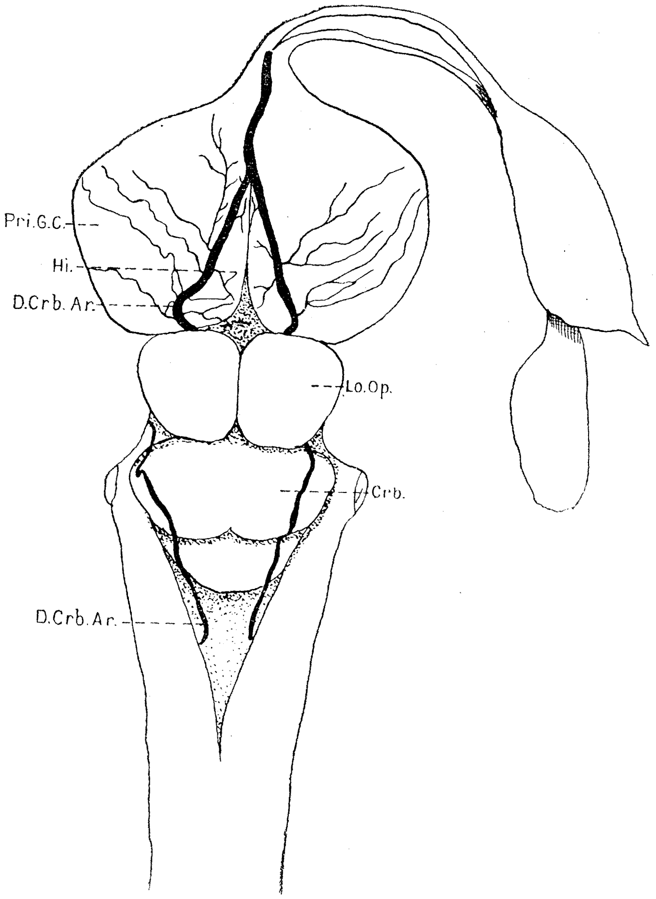
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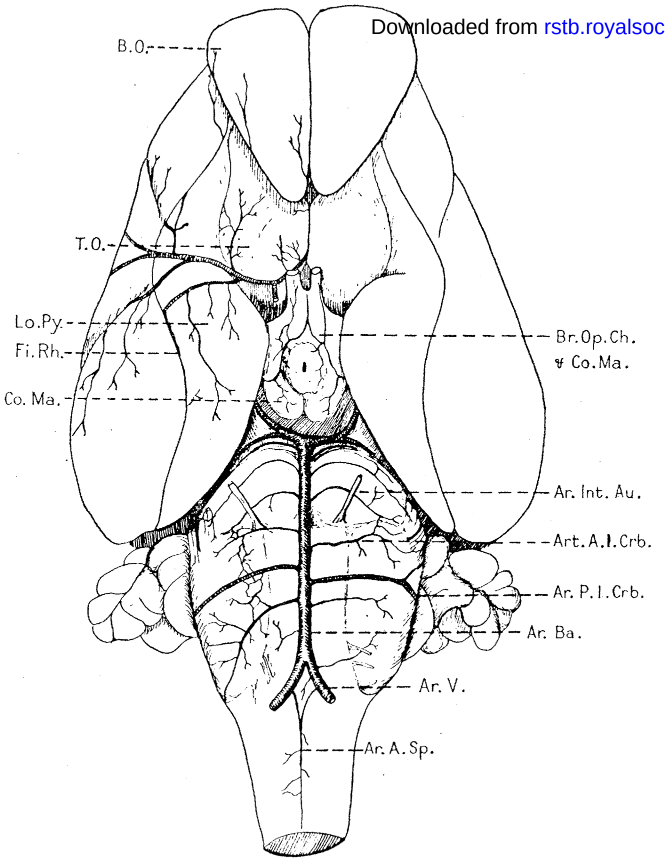
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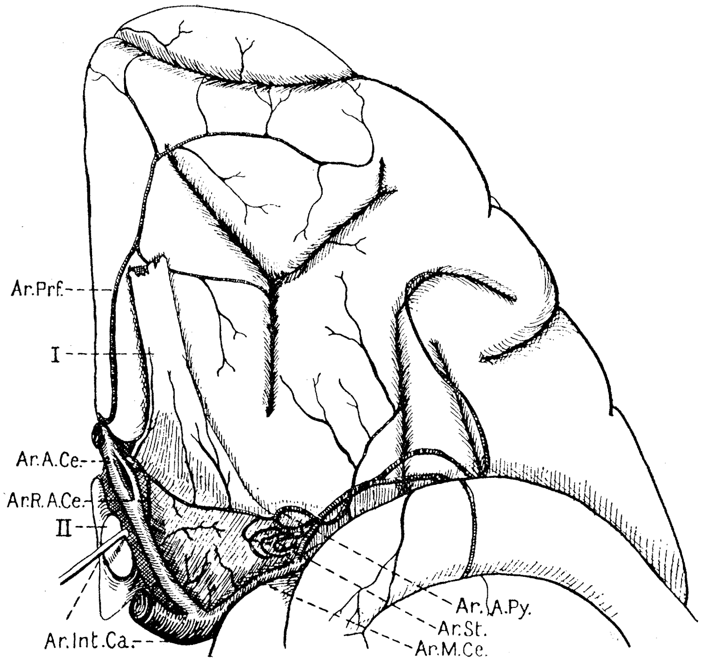
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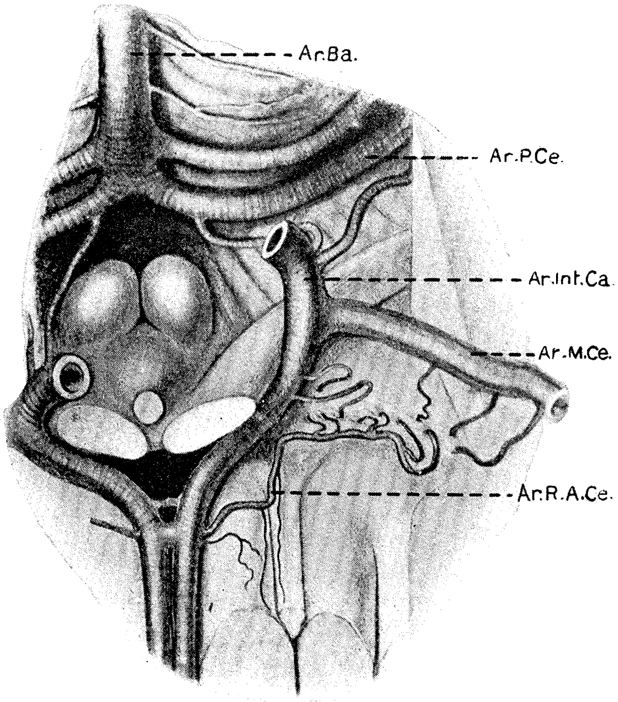
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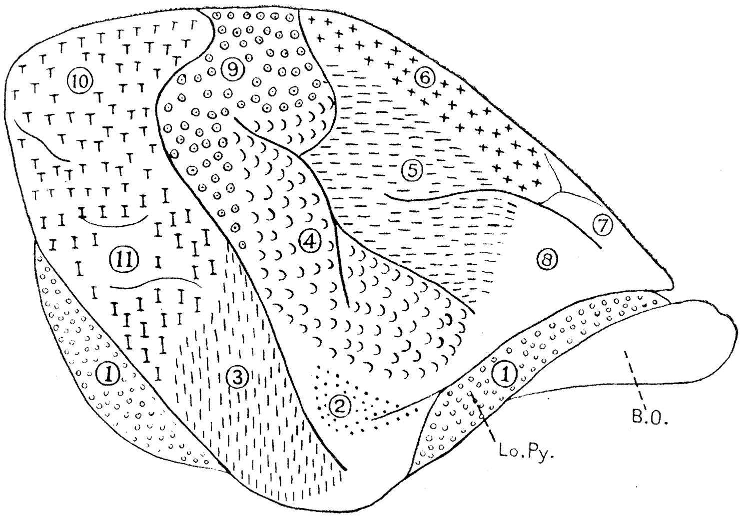
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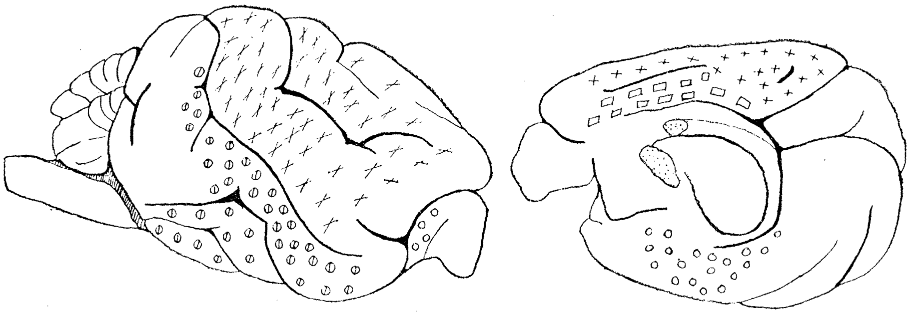

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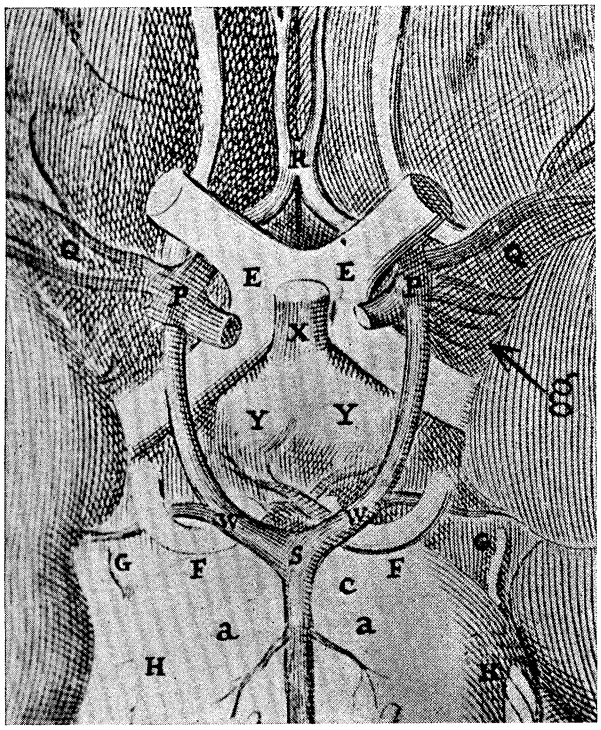
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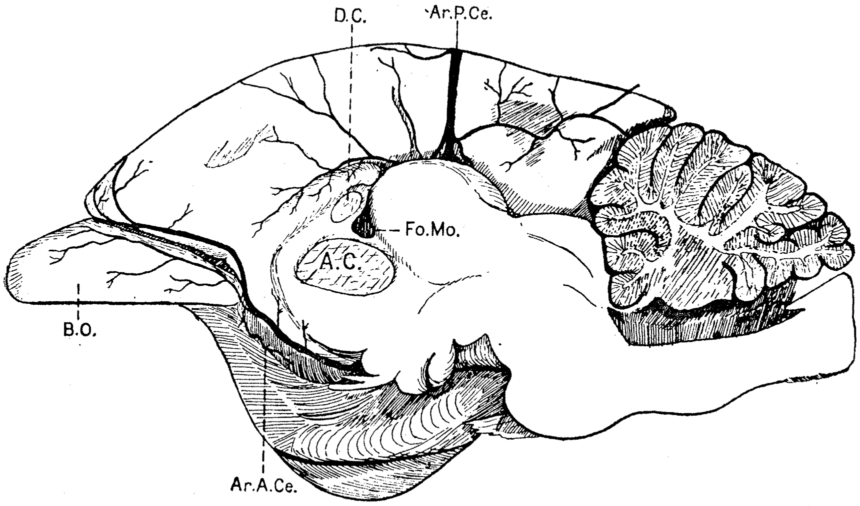
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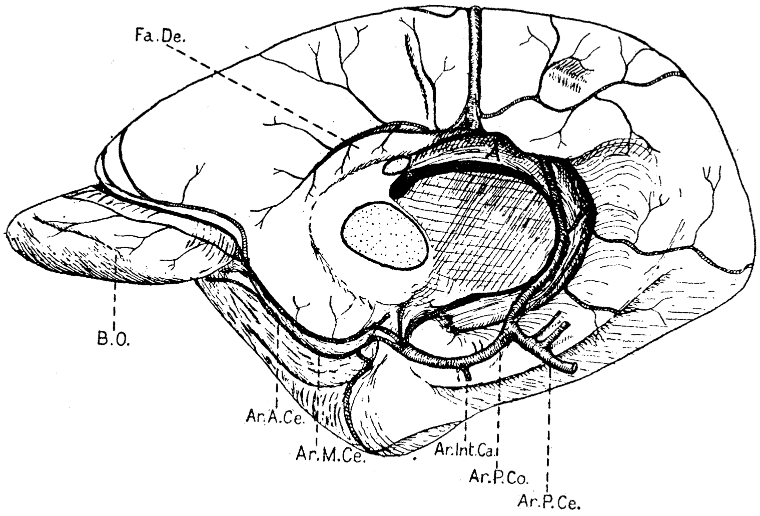
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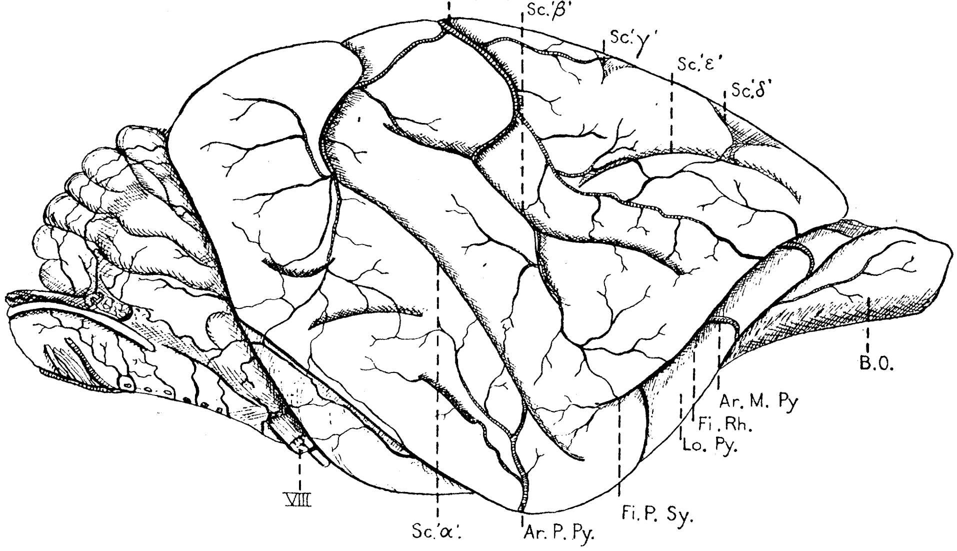
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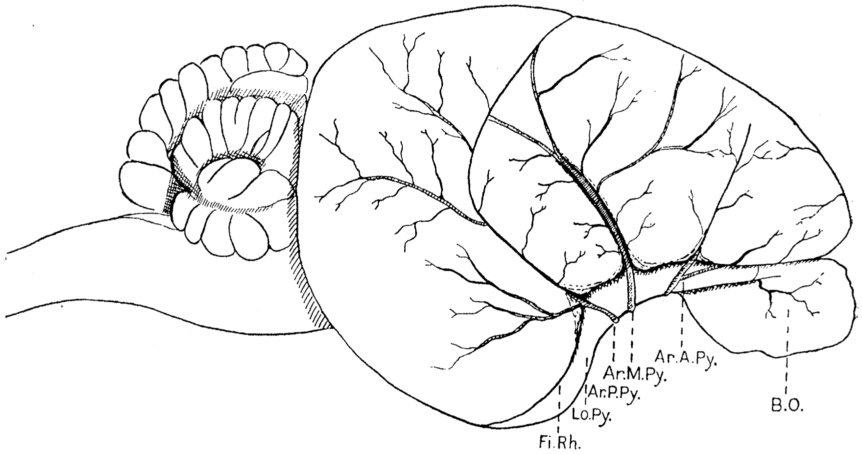
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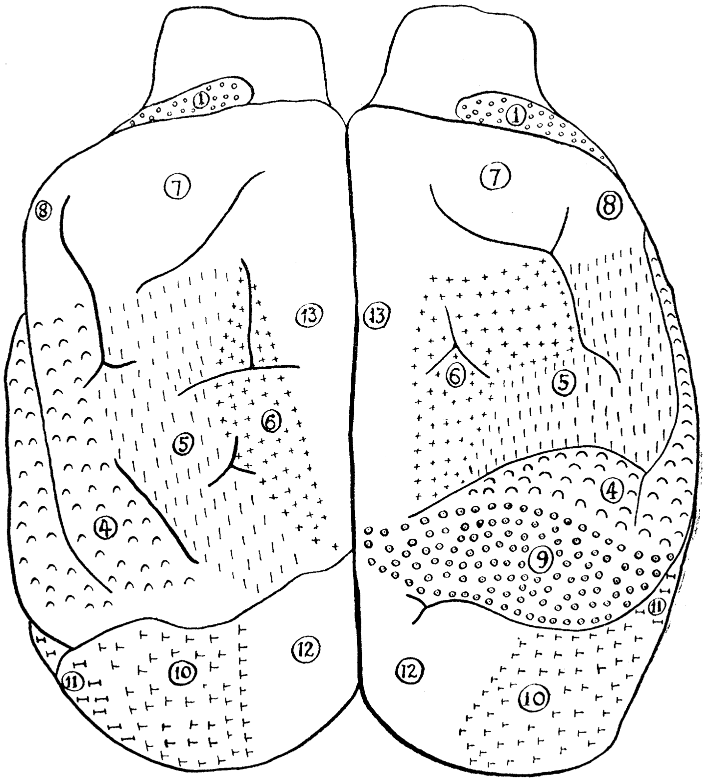
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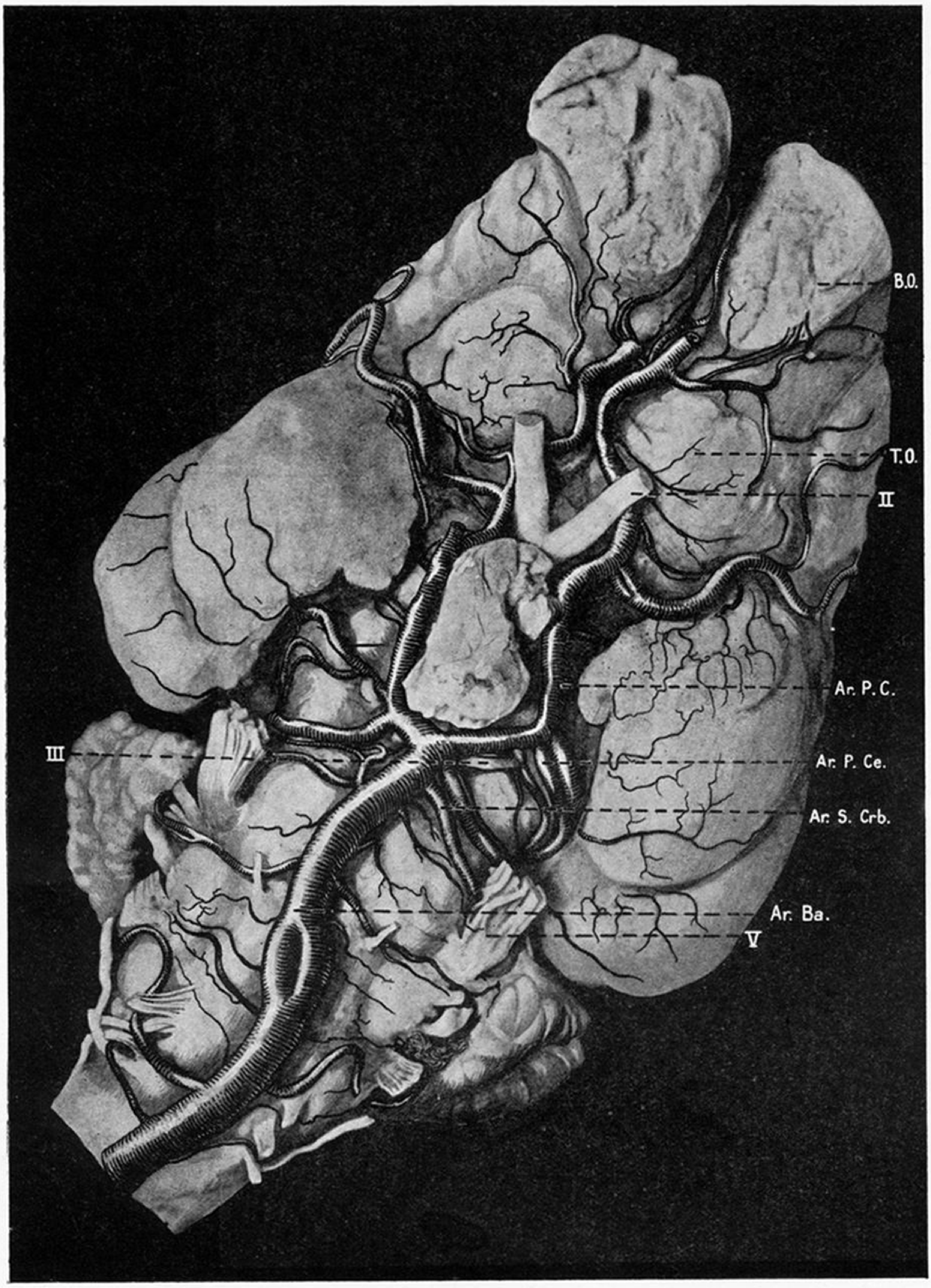

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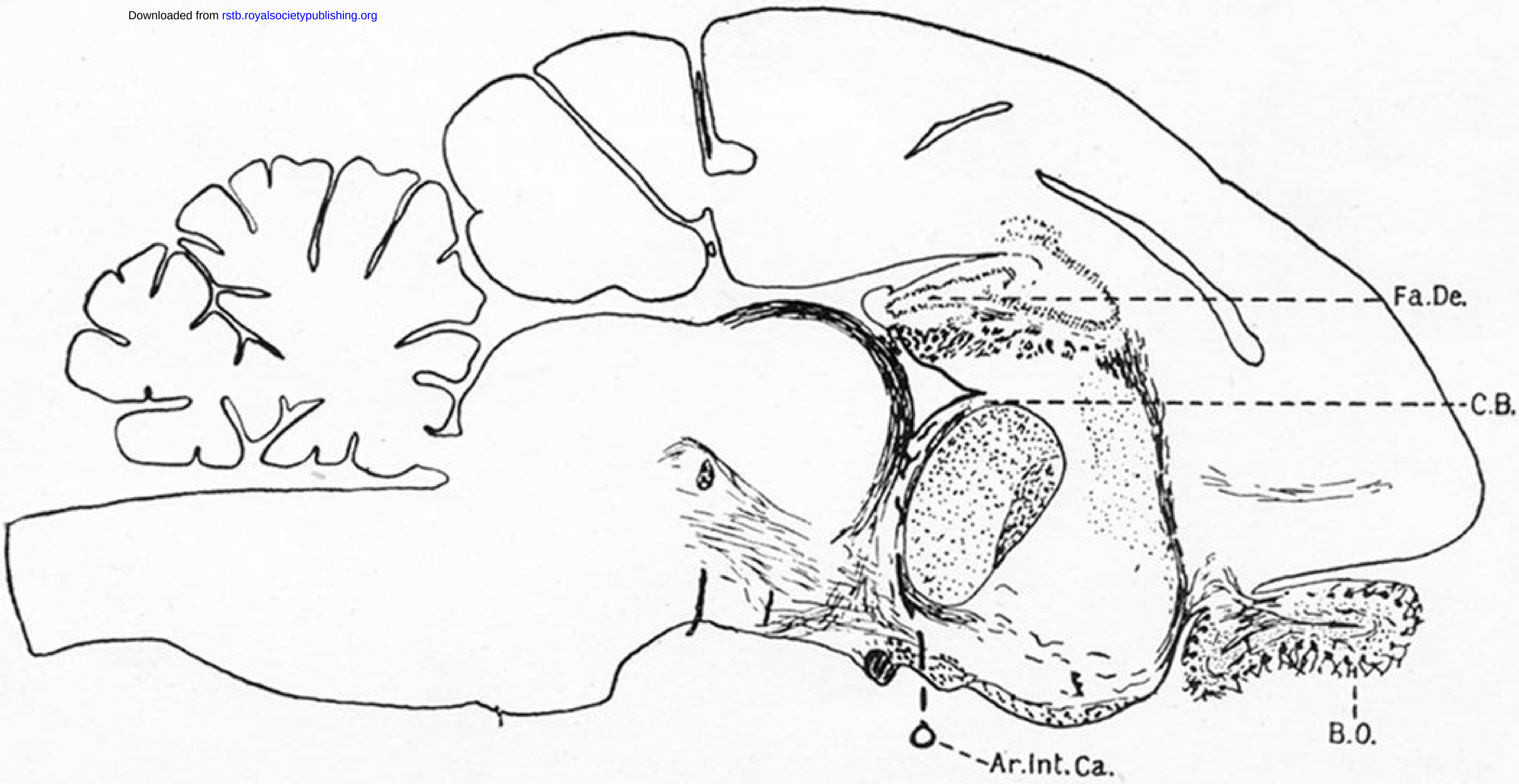

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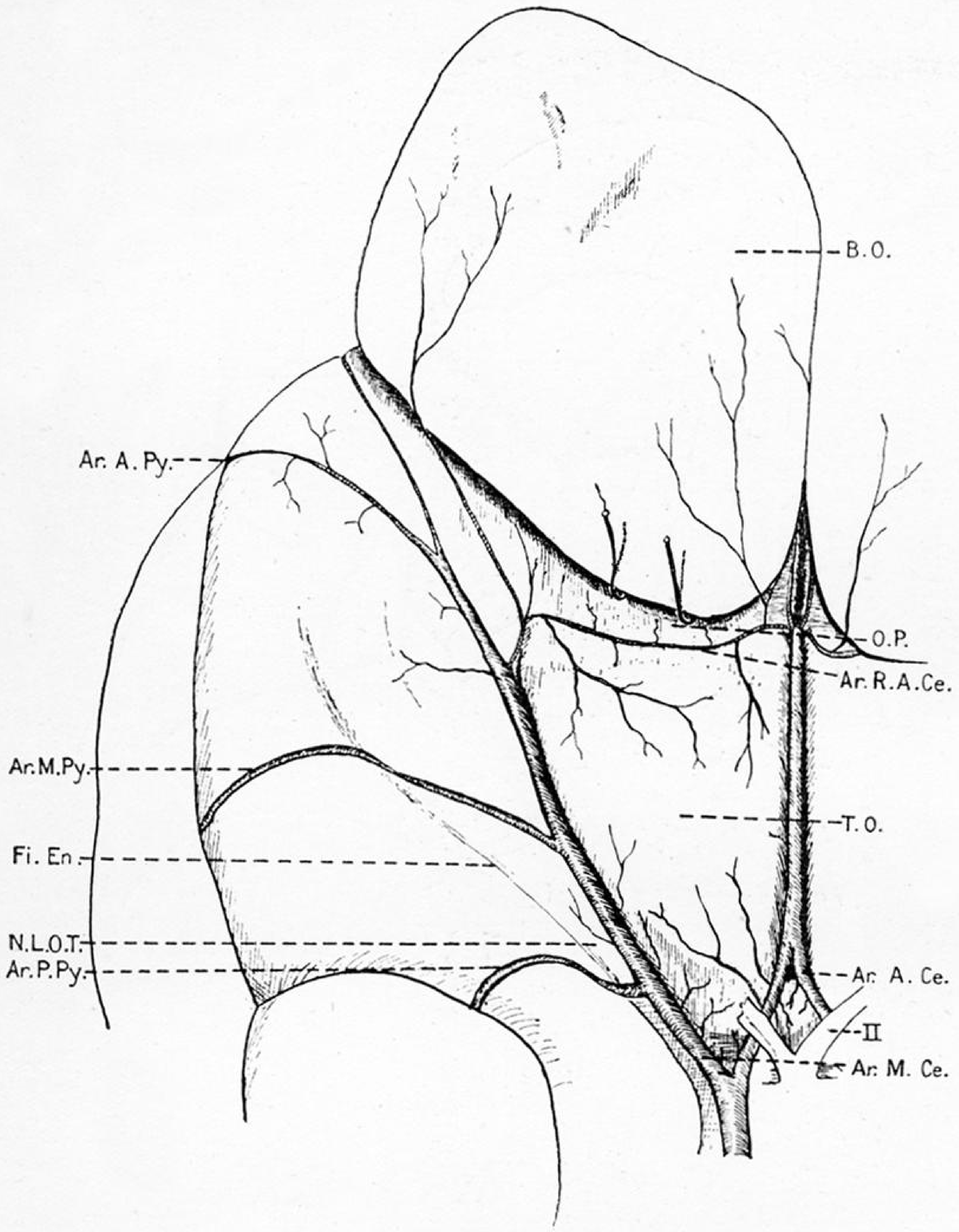
PLATE 2.

G. 2.—The arteries of the brain of Myrmecophaga jubata seen from the ventral aspect.

G. 6.—A sagittal section through the brain of Echidna taken about 2 mm. from the middle line. It shows the course of the perforating branch of the cranial division of the internal carotid artery which supplies the commissure bed.



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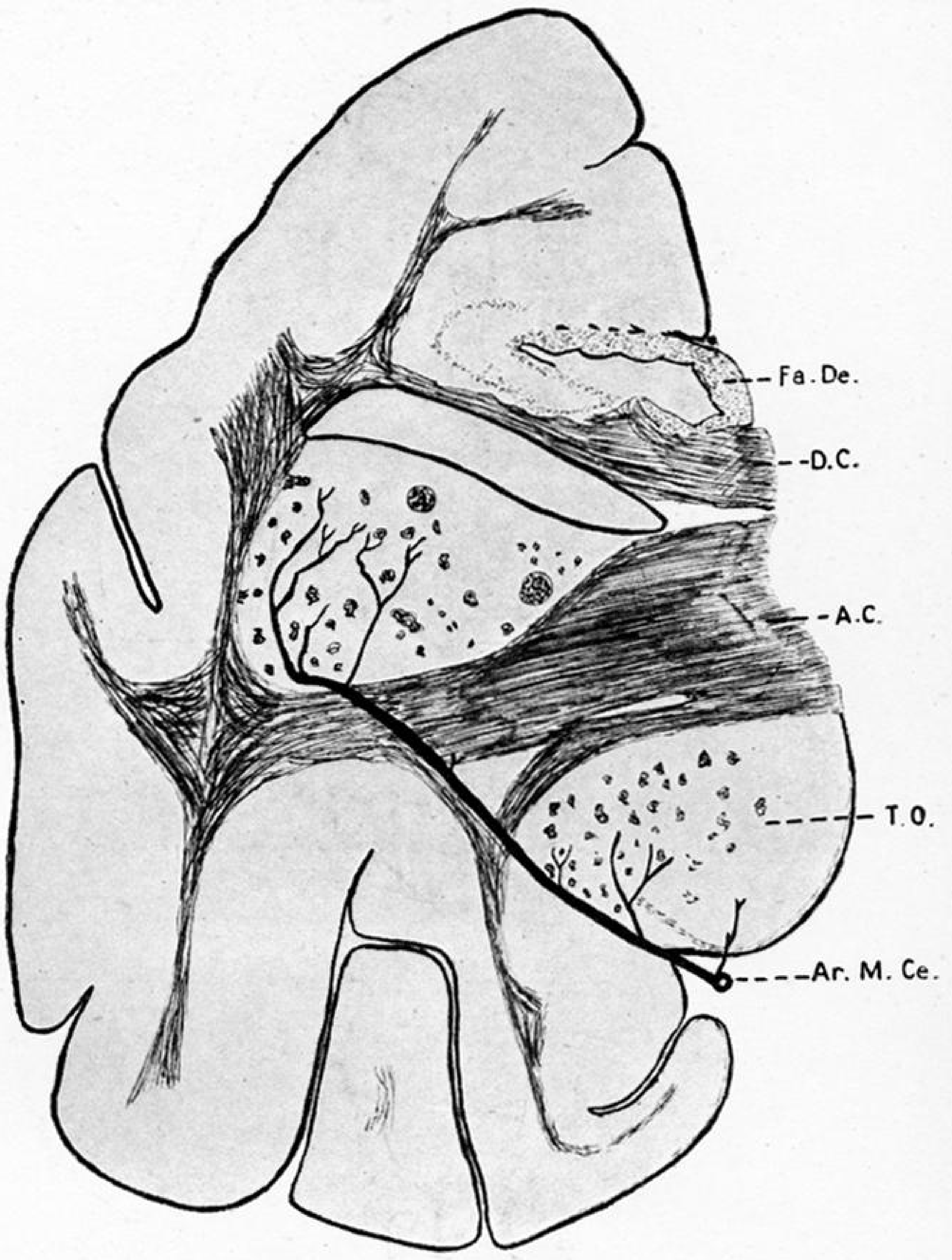

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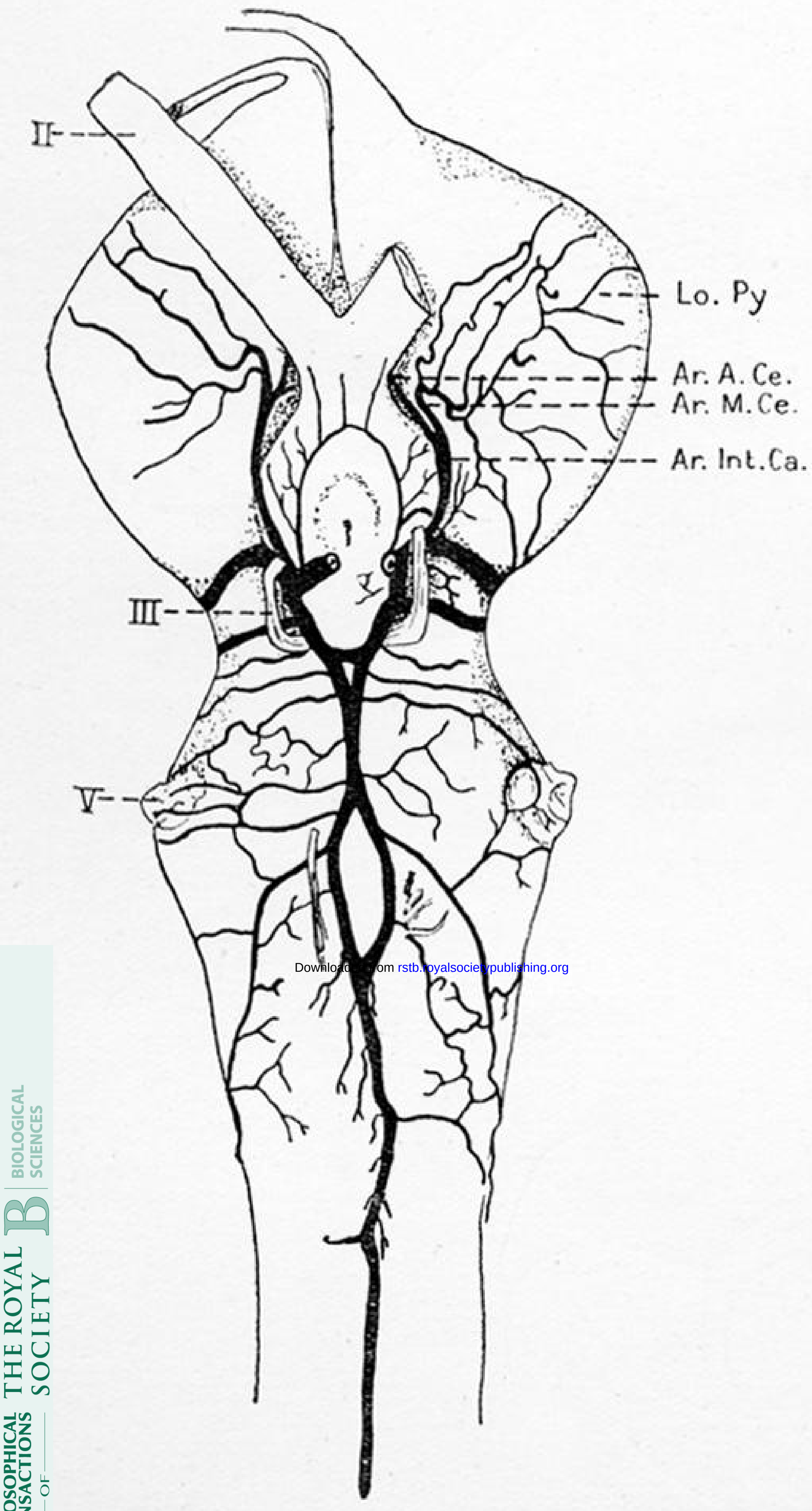

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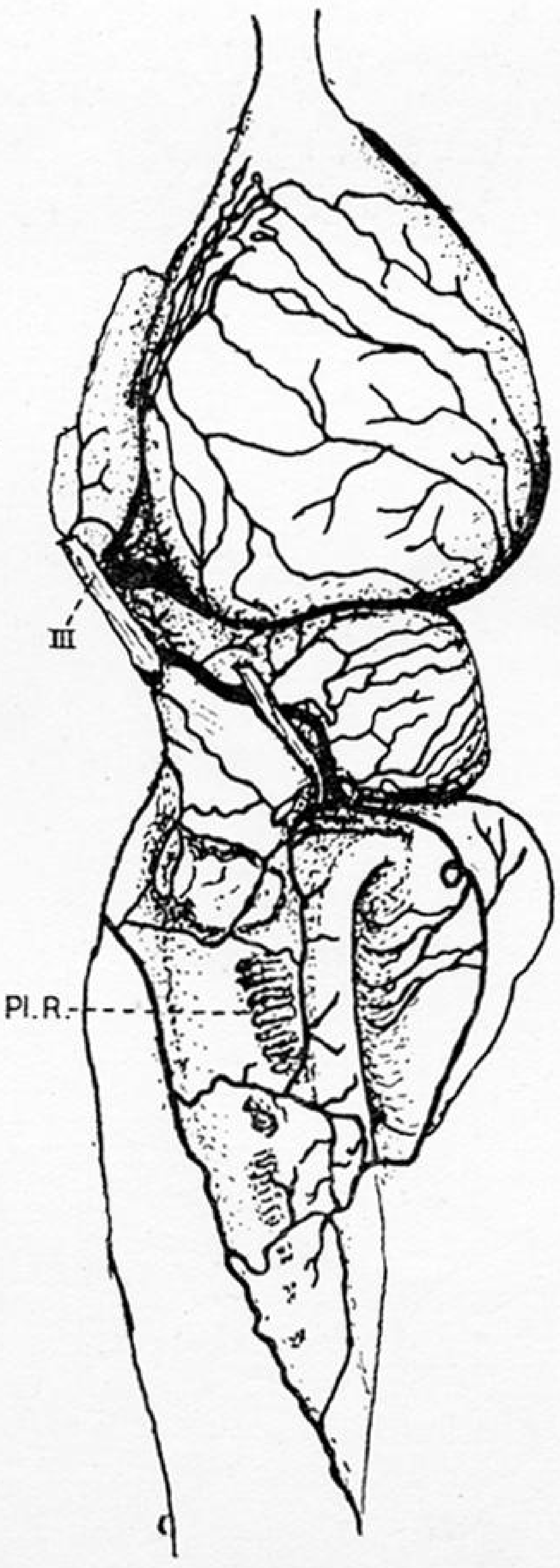

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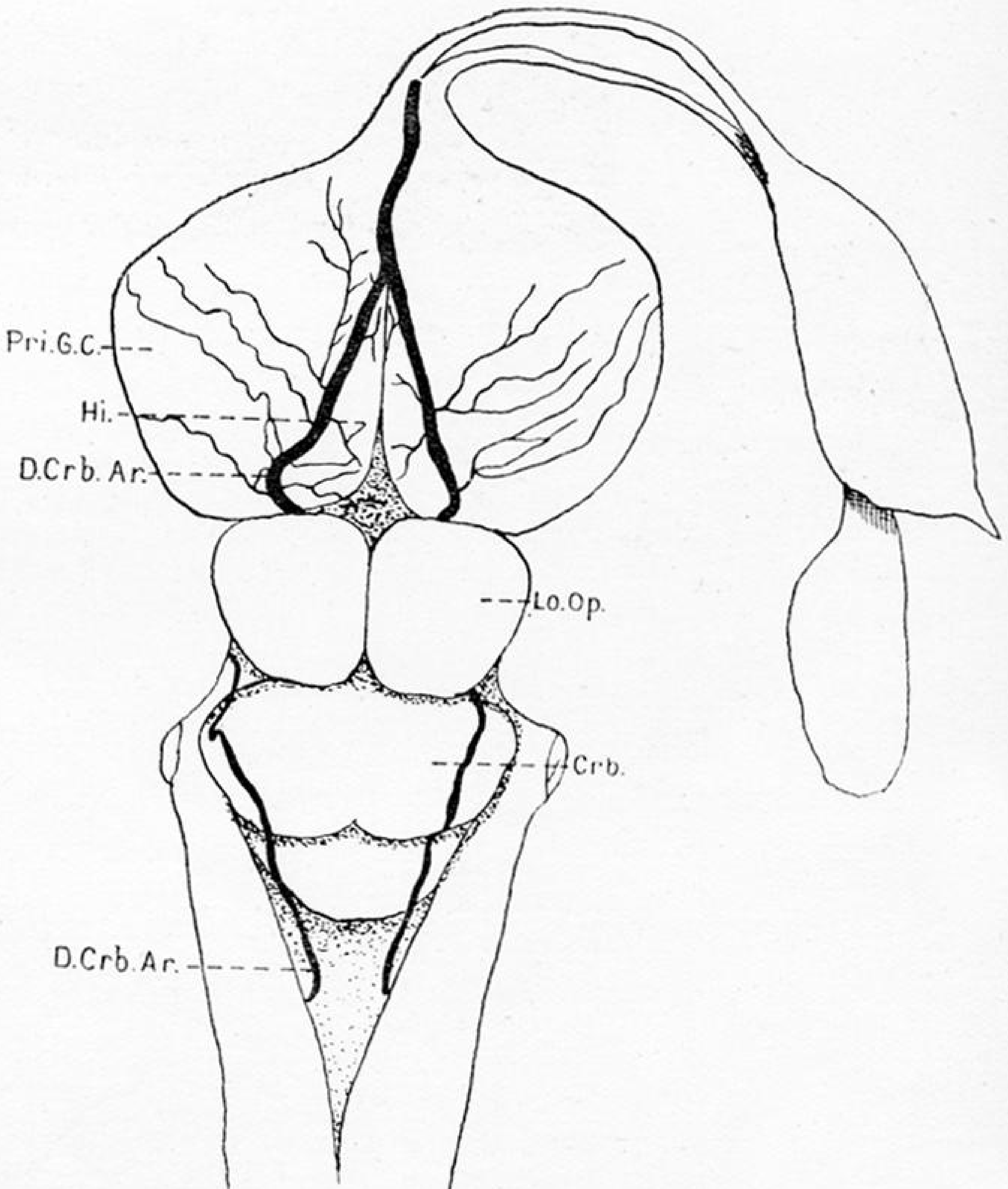

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FIG. 7.—An enlarged view of the region of the tuberculum olfactorium to show the anterior recurrent branch of the anterior cerebral artery in Echidna.

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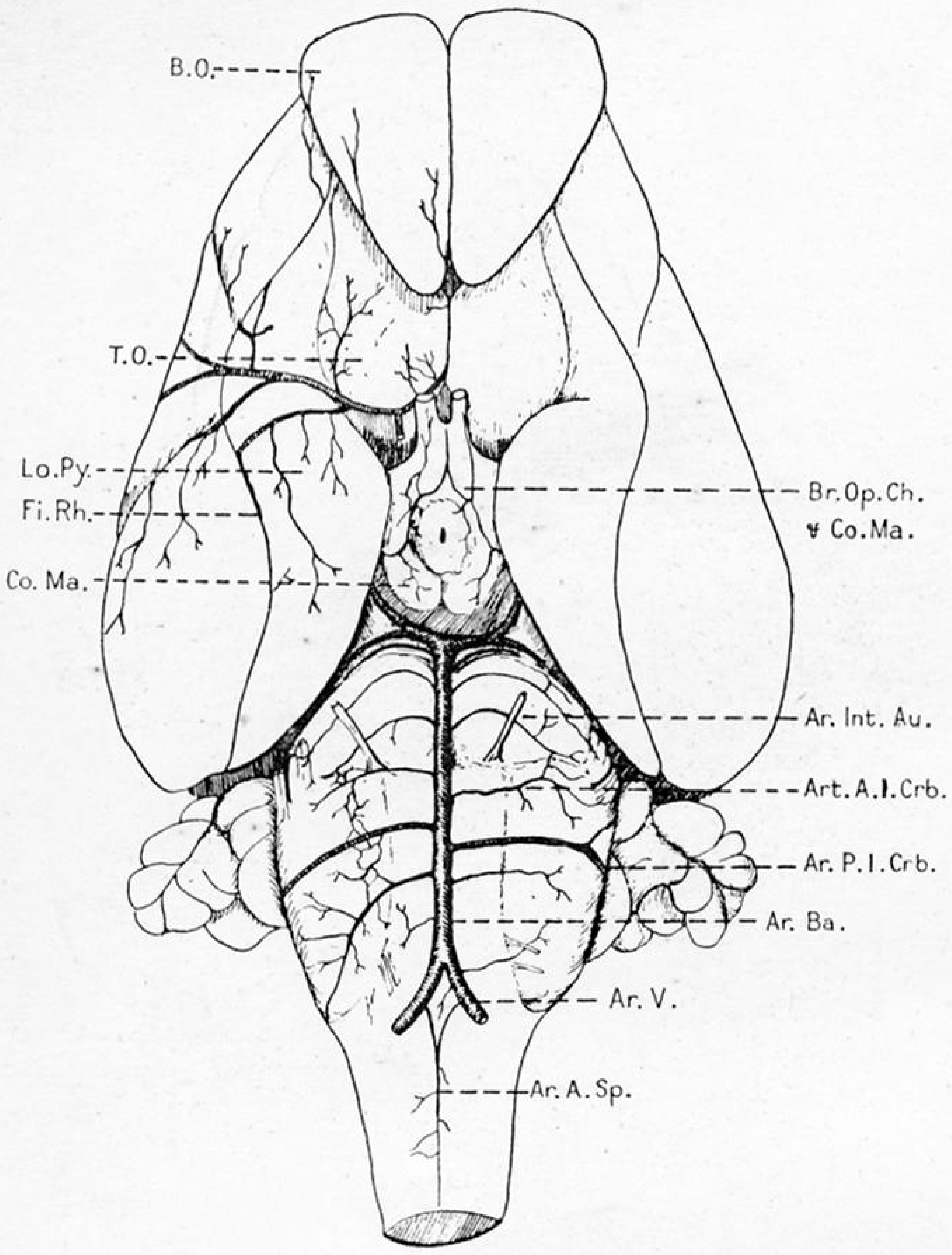

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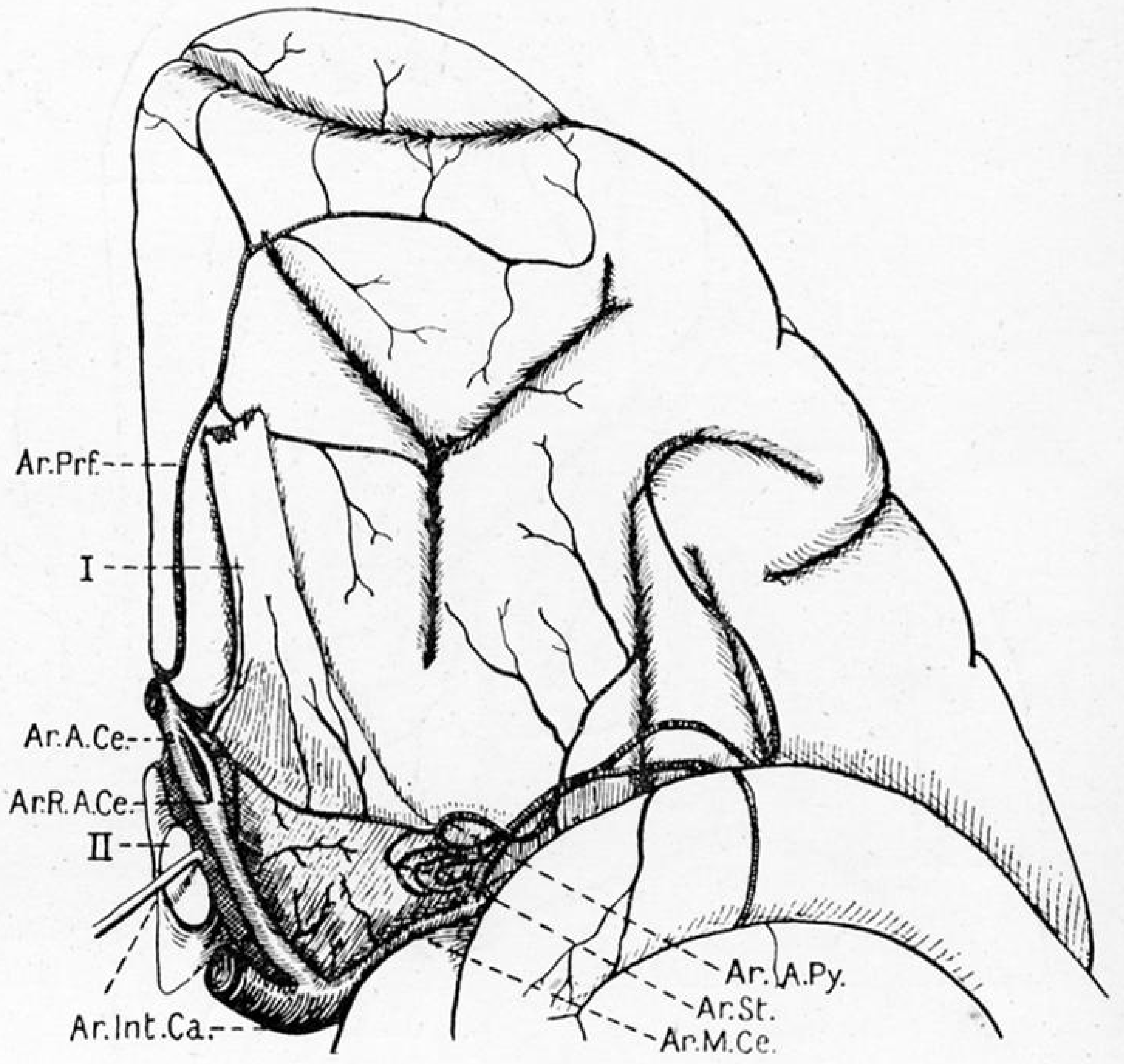

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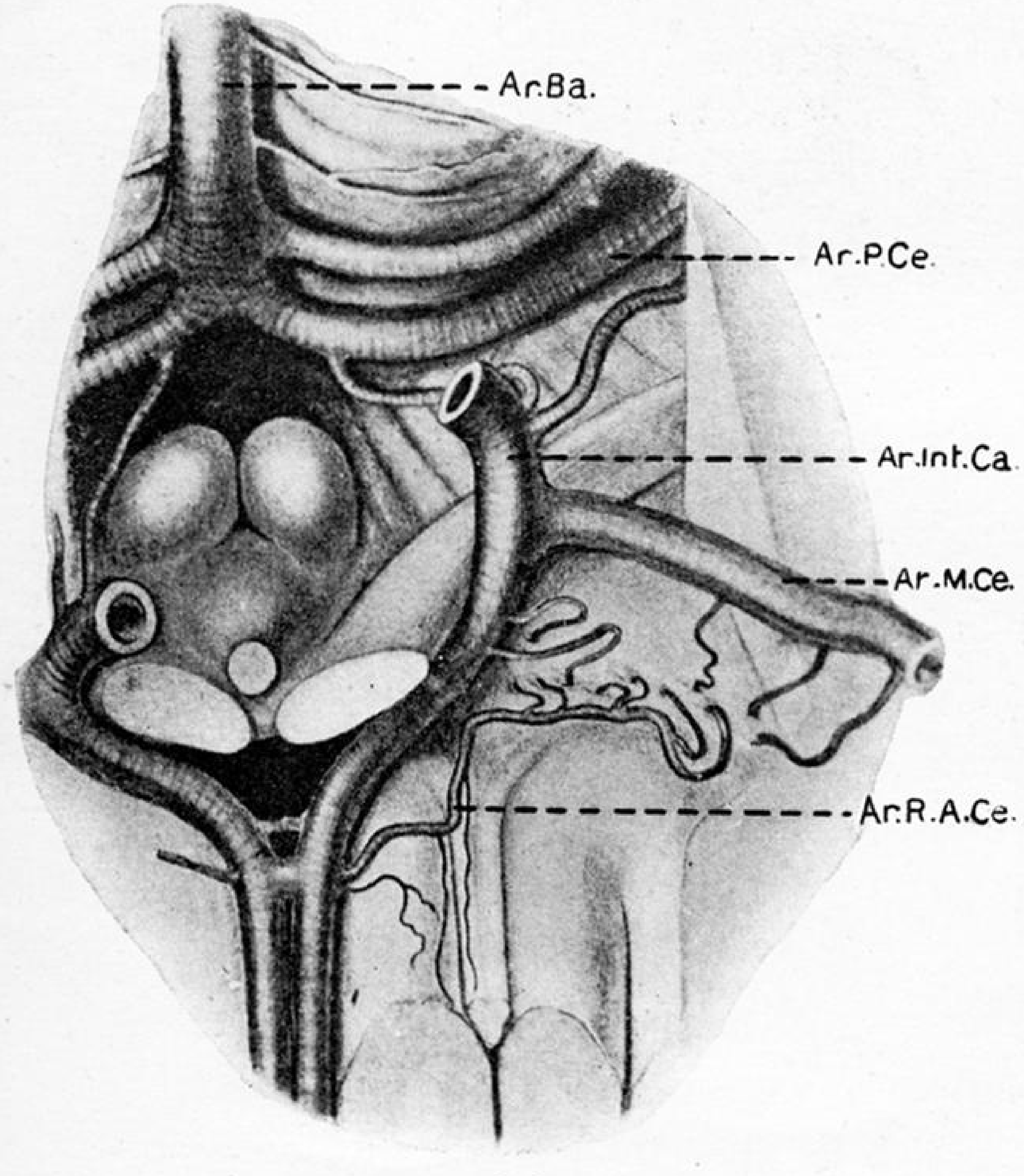

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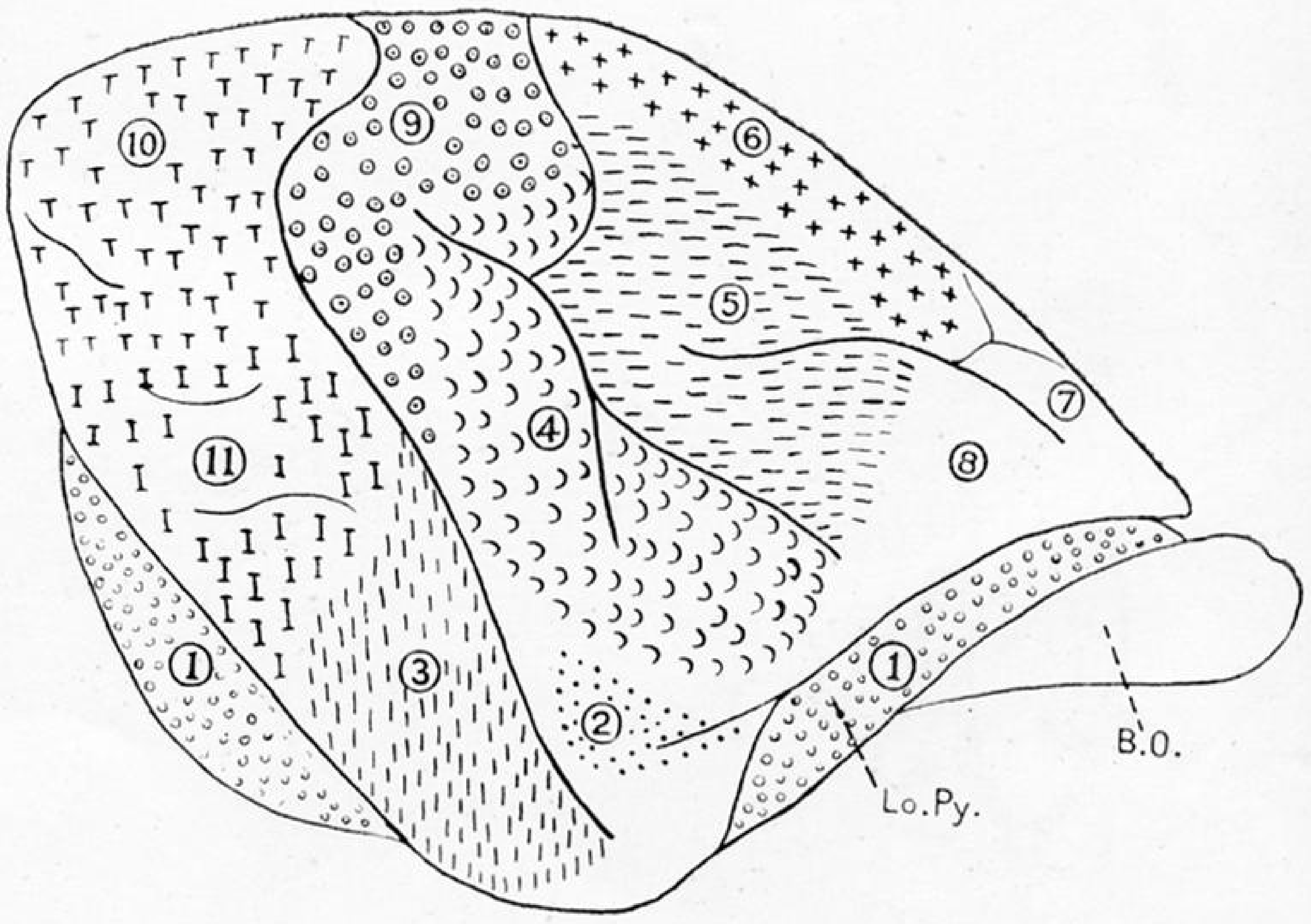

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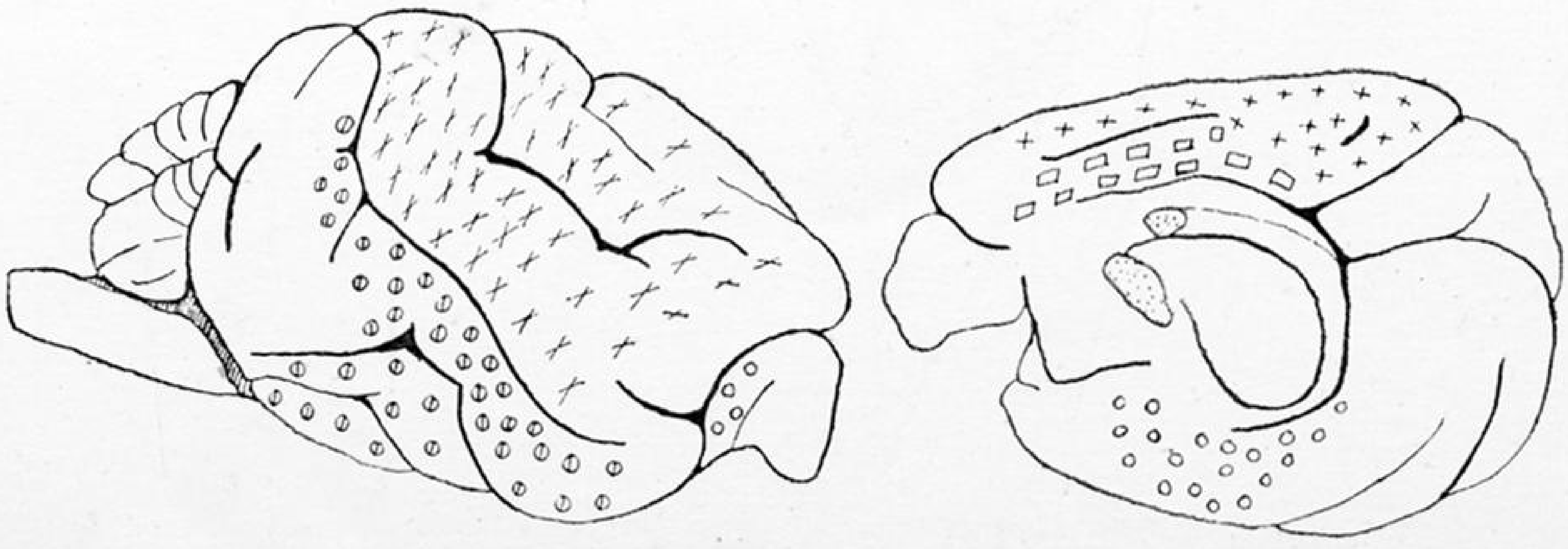

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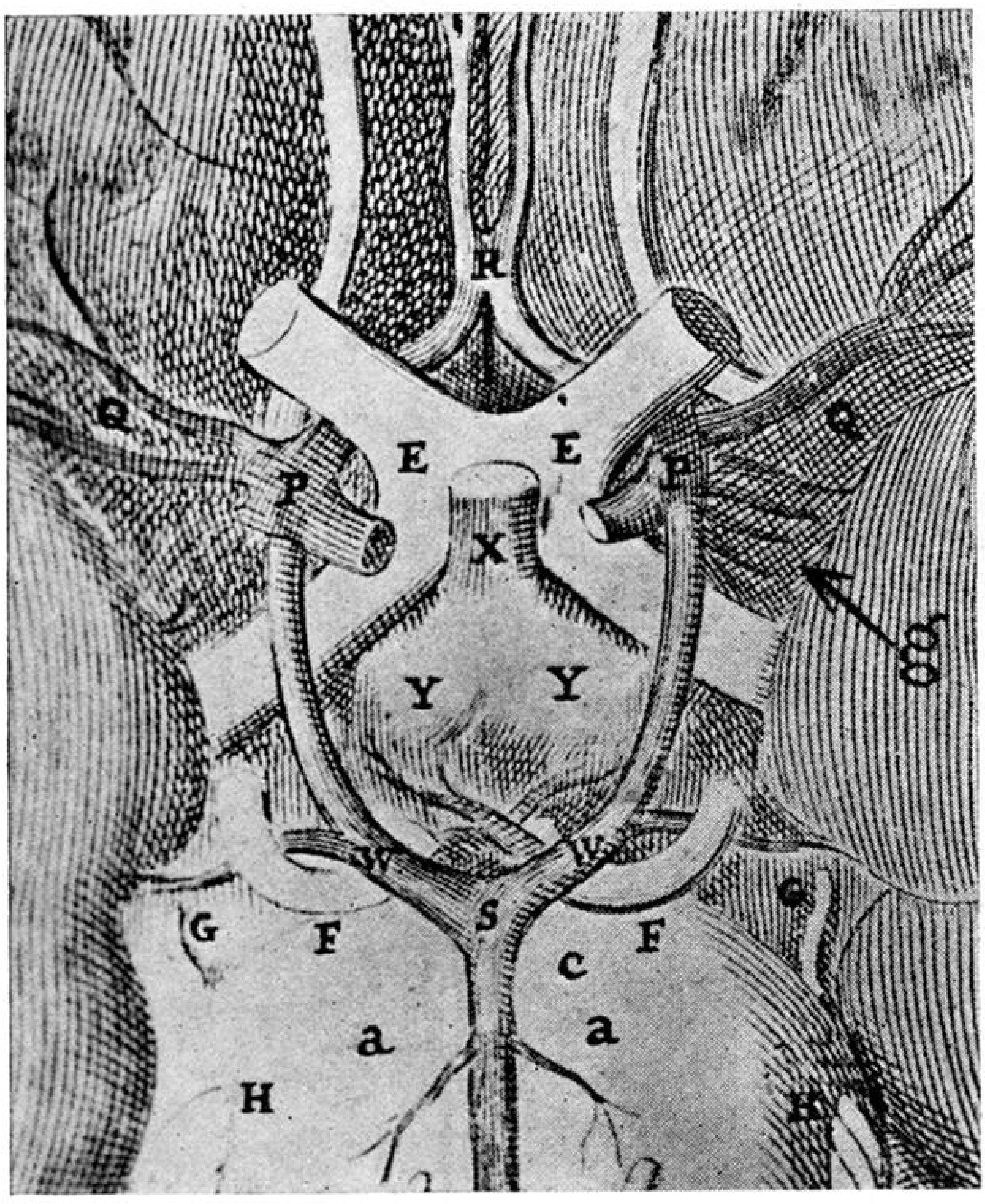

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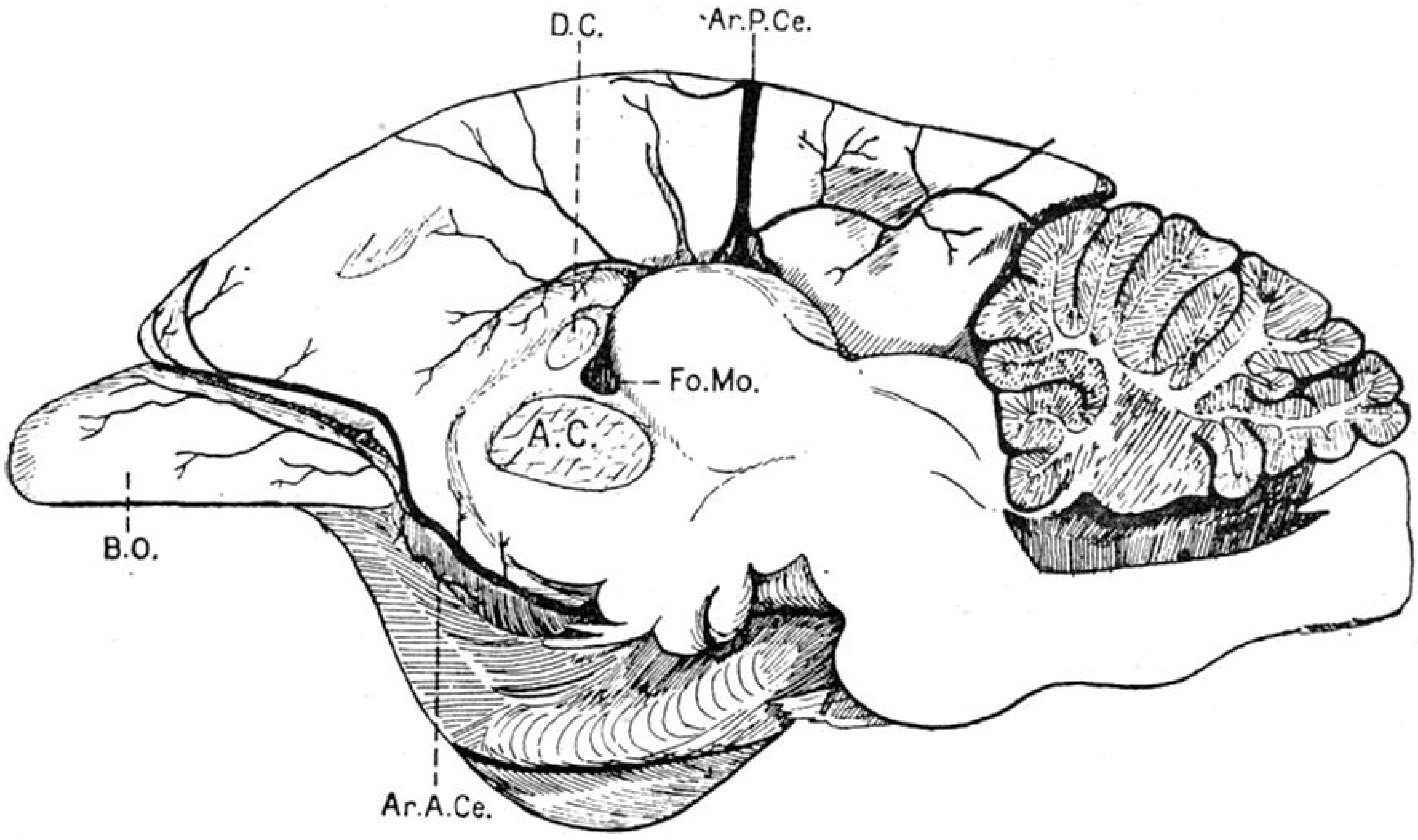

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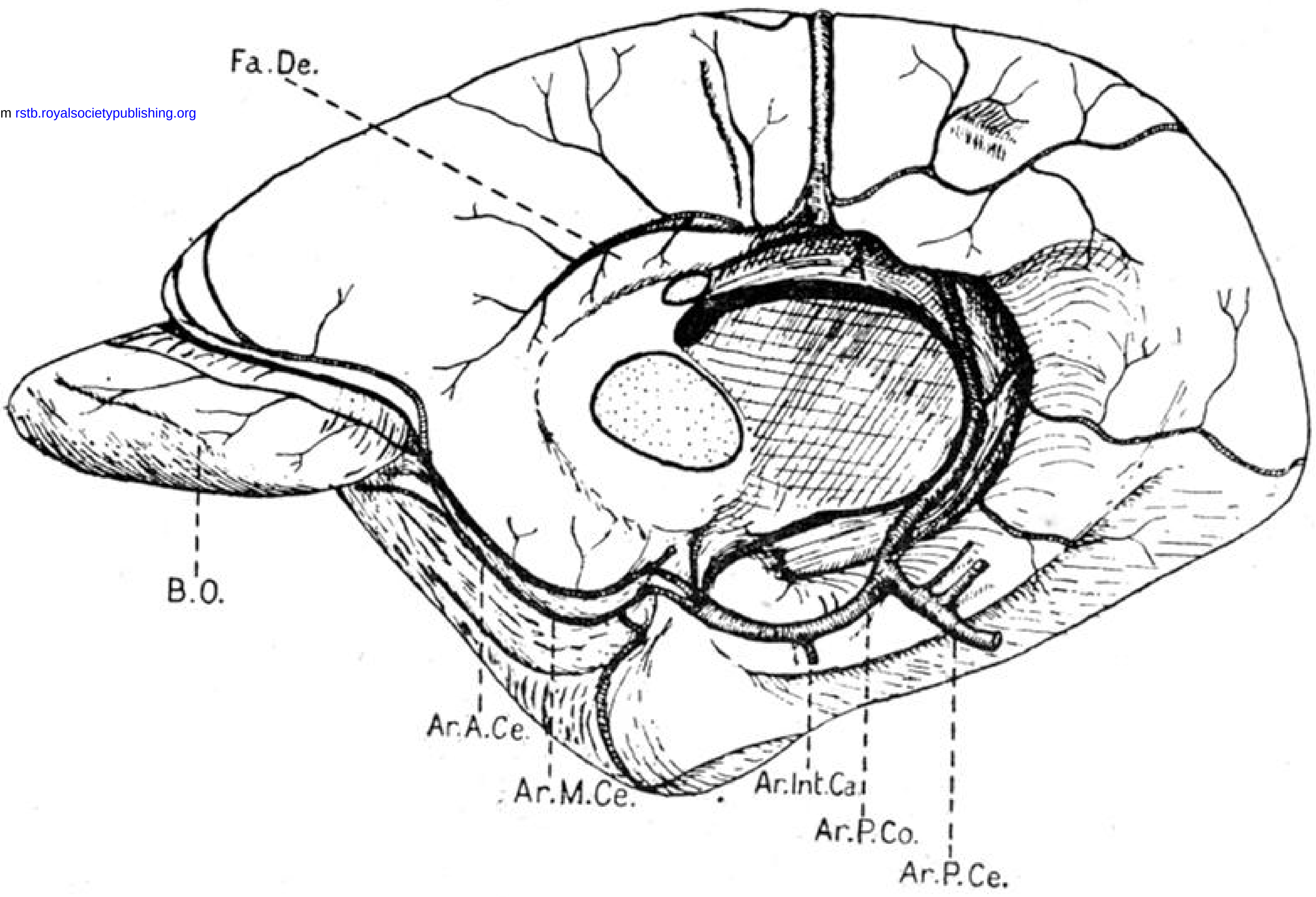

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