THE MORPHOLOGY OF THE FORE-BRAIN ARTERIES, WITH ESPECIAL REFERENCE TO THE EVOLUTION OF THE BASAL GANGLIA

By A. A. ABBIE, M.B., B.S., B.Sc. (SYDNEY)[1]

Institute of Anatomy, University College, London

THE morphology of the cerebral arteries has been investigated in particular by Hofmann (1) and de Vriese (2), who regarded the vessels merely as an isolated morphological unit and failed to correlate changes in vascular pattern with any evolutionary progress in the brain itself. Shellshear, in many papers (3, 4, 5, 6, 7, 8), has claimed that the arteries together with the brain constitute a single functional unit, a neurovascular mechanism of which neither component is independent of the other. He has shown that the arteries are constant in their terminal supply; consequently the evolution of the vessels is dependent upon, and proceeds hand in hand with, the evolution of their field of distribution.

A survey of the literature relating to cerebral blood supply reveals a great amount of variation and apparent contradiction of the principle of vascular constancy. Much of this apparent incompatibility is due to the failure to appreciate the significance of the principles of economy of distribution and convenience of source. These have been discussed briefly in previous papers (9, 10); here they will be exemplified more fully. We may say that the brain and its blood supply are not independent variables, the arteries of the brain are as much a part of the neurovascular mechanism as is the brain itself; any change in brain structure is reflected in an equivalent alteration in its blood supply. Thus the two components of this mechanism evolve in harmonious co-operation. As the brain expands to meet new situations, its arteries extend to satisfy the increased functional demand. Cerebral evolution would not be possible were it not accompanied by a corresponding evolution in the vascular pattern.

The following work was undertaken to determine the blood supply of the brain in as complete a phylogenetic series as was available. It is considered that the results form a complete vindication of the principle of vascular constancy, that principle first dimly visualised by Guyot in 1825 (11), stated as an explicit law by Duret in 1874 (12), and since reaffirmed by Shellshear.

MATERIAL AND METHODS

The brains studied were of every vertebrate phylum from Fish to Man, but excluding Birds. The Fish was a single brain of *Squalus acanthias* which had been preserved in formalin for some time. For Amphibia, four brains of *Rana temporaria* were used, and of Reptiles one *Sphenodon* and two crocodile brains were studied. The mammalian series included two Marsupials (*Macropus*

thetidis and *M. eugenii*); one Rodent (*Castor canadensis*); one Carnivore (*Cynaelurus jubatus*); several Ungulates including four sheep (*Ovis aries*), one reindeer (*Rangifer tarandus*), one kudu (*Strepsiceros strepsiceros*) and one tapir (*Tapirus terrestris*); one lemur (*L. variegatus*); six apes including species of *Lagothrix, Papio, Cercopithecus* and *Macacus*; and forty human brains. The frog brains were injected with Indian ink, the *Sphenodon* with carmine gelatine, and in those mammalian brains available for dissection the anterior choroidal artery was generally injected with Indian ink.

The arteries of the various brains were first studied in their surface distribution and subsequently dissected in the frog, crocodile, Marsupial, sheep, reindeer, lemur, ape and Man. Both hemispheres were used, and some of the hemispheres of each type were cut horizontally and others coronally in sections to ensure accuracy of localisation. In the dissections the arterial branches were followed individually to their destinations with the aid of a binocular microscope.

The vessels of the brain of the dogfish, frog, tuatara, sheep and Man will be described in detail. Those of the other types will be discussed only in so far as they conform to, or appear to contradict, the theory of constancy in the vascular pattern of the fore-brain.

DOGFISH (*SQUALUS ACANTHIAS*)

Hofmann[1] and Kappers[13] have both studied the cerebral vessels of Fishes and describe a medial and a lateral olfactory artery passing forwards to the fore-brain from the cranial division of the internal carotid artery. In fig. 1 these vessels can be seen running along the medial and lateral borders of the hemisphere to the anterior aspect; they are related more to the ventral than the dorsal half of the hemisphere and, by small anastomotic channels, form a closed vascular ring just ventral to the horizontal equator. The main vessels also communicate with each other dorsally and ventrally to form a closed network which holds the hemisphere within its meshes. Thus the medial and lateral olfactory arteries are not, indeed, separate arteries, they are merely channels in a closed primitive vascular net which have enlarged in response to a specific functional demand.

Many writers—Elliot Smith[14, 15], Dart[16] and others—have shown that the ventral part of the Fish brain is more primitive than the dorsal. Dart calls it the palaeo-olfactorium, and has shown[17] that from its cortical cells have developed the tuberculum olfactorium, the islets of Calleja, the nucleus of the diagonal band of Broca, the anterior olfactory nucleus of Johnston[18] and the palaeo-striatum. The dorsal part forms the neo-olfactorium comprising the primordia of the pyriform cortex, hippocampus and hypopallium.

The medial and lateral olfactory arteries form a vascular ring around the palaeo-olfactorium and lie in medial and lateral grooves which separate it from the neo-olfactorium. The vascular channels over the palaeo-olfactorium are larger than those over the neo-olfactorium, as would be expected in view of

the greater functional activity of the former in this primitive brain. A simple schematic section through the anterior part of the hemisphere of such a brain (fig. 2) shows the medial and lateral olfactory arteries related to their respective
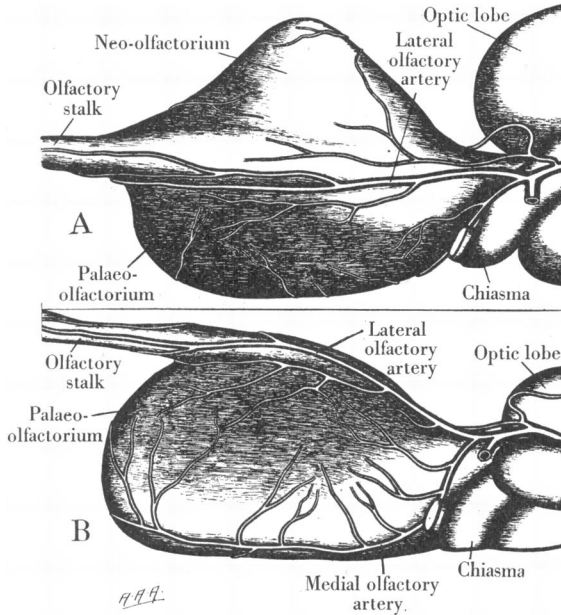

Fig. 1. The arteries of the brain of the dogfish (*Squalus acanthias*). A, left lateral aspect; B, ventral aspect of left hemisphere.
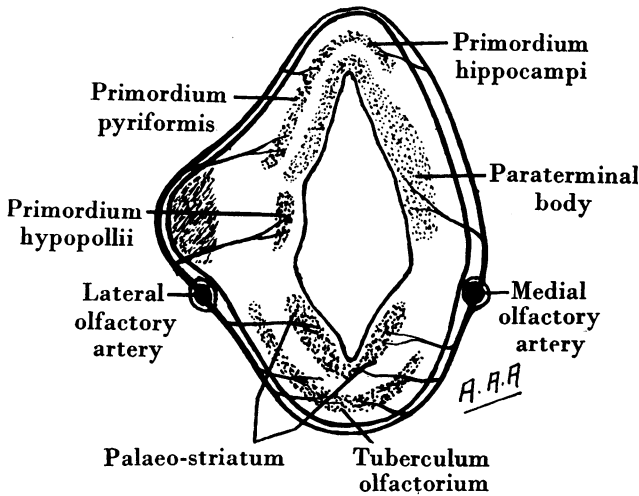

Fig. 2. Schematic section through the anterior part of the right hemisphere of the dogfish brain showing the relation of the lateral and medial olfactory arteries to the neo- and palaeo-olfactoria.

grooves and connected dorsally and ventrally by small channels. In the ventral part lie the cortex of the palaeo-olfactorium and the palaeo-striatum; in the dorsal the primordia of the pyriform lobe, hippocampus and hypopallium. The palaeo-olfactorium is supplied medially from the medial, and laterally from the lateral olfactory channel; in the neo-olfactorium the lateral olfactory channel supplies the primordia of the hypopallium and pyriform area and most of that of the hippocampus, the medial channel the most medial part of the primordium hippocampi and the paraterminal body. It will be observed that those channels which have been called the medial and lateral olfactory arteries are almost symmetrically disposed and present the simplest and most economical method of distributing blood to all parts of the brain through their subsidiary branches.

Summary

1. In the Fish there is a simple cerebral hemisphere composed chiefly of palaeo- and neo-olfactoria. These are separated medially and laterally by slight grooves which lie just ventral to the horizontal equator.

2. The arterial supply is maintained through a closed primitive vascular network which holds the brain within its meshes.

3. From this network certain channels have enlarged to support the chief burden of blood carriage. These are the medial and lateral olfactory arteries related to the medial and lateral grooves described above.

4. The medial and lateral olfactory arteries are symmetrically placed so that all parts of the brain are within easy reach of either. This forms the most economical method of blood distribution.

5. The lateral olfactory artery supplies the structures which are nearest: the lateral part of the palaeo-olfactorium and the primordia of the hypopallium, pyriform lobe and most of that of the hippocampus. The medial olfactory artery reaches the medial part of the palaeo-olfactorium, the paraterminal region and the medial part of the primordium hippocampi. The blood supply to the palaeo-olfactorium is richer than that to the neo-olfactorium.

AMPHIBIA

In the frog, as in the dogfish, the internal carotid artery divides into cranial and caudal divisions at the side of the hypophysis. The cranial division (fig. 3) passes forwards over the optic tract at whose anterior border it divides into medial and lateral olfactory branches. It is evident that these are not quite the same as the medial and lateral olfactory arteries of the dogfish. In the Fish the lateral olfactory artery arises from the cranial division at the lateral border of the hemisphere; in the frog it takes origin from one of the arteries to the diencephalon. The hemisphere has grown posteriorly over the diencephalon and the artery has simultaneously shifted its site of origin. No new artery has appeared, this anastomotic channel between the telencephalic and diencephalic arteries was present in the dogfish. The channel has merely

enlarged to provide a closer source of blood for the lateral olfactory artery. This vessel passes forwards over the dorso-lateral aspect of the hemisphere and ends on the lateral border of the olfactory stalk by anastomosing with branches of the medial olfactory artery.

In its passage anteriorly the lateral olfactory artery gives off many fairly large branches which reach structurally differentiated portions of the hemisphere. Some pass to the dorso-medial aspect of the telencephalic wall to supply most of the primordium hippocampi. These also reach the posterior part of the paraterminal body and anastomose anteriorly with branches of the medial
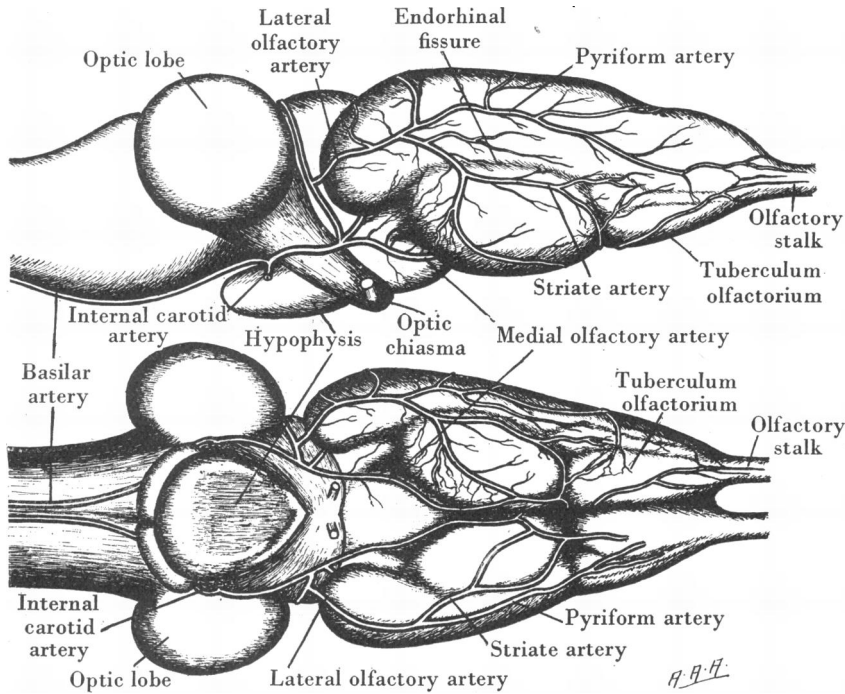

Fig. 3. The arteries of the brain of the frog (*Rana temporaria*). Note that the lateral olfactory artery arises from a diencephalic stem.

olfactory artery. They may be called hippocampal arteries. The main channel of the lateral olfactory artery runs forwards over the primordium pyriformis to anastomose with the medial olfactory branches to the olfactory stalk. This is the pyriform artery. The next large branch passes ventrally and then anteriorly in the groove between the primordium pyriformis and the ventro-lateral wall of the hemisphere to anastomose anteriorly with branches of the medial and lateral olfactory arteries over and around the tuberculum olfactorium. This is the striatal artery. Finally, a large arterial channel runs from the striatal artery across the ventral part of the hemisphere to join the medial olfactory artery.

The lateral olfactory artery has progressed beyond the condition of the similarly named vessel of the dogfish. The only representative of this is the striatal artery running forwards in the groove between the primordium pyriformis and the ventro-lateral wall of the hemisphere. The primordium pyriformis is part of the neo-olfactorium, the ventro-lateral wall part of the palaeo-olfactorium and the groove between is the endorhinal fissure of Elliot Smith or the sulcus palaeo-olfactorius lateralis of Dart. Thus, the striatal artery of the frog is the representative of the lateral olfactory artery of the dogfish. It maintains its old connection with the cranial division through the rich anastomosis at the posterior end of the endorhinal fissure. The neo-olfactorium has so increased its functional development that it claims the major part of the lateral olfactory artery. The old anastomotic channels over the dorsal part of the hemisphere have enlarged to carry the increased flow of blood which is more conveniently supplied directly from the diencephalic vessels. Thus the lateral olfactory artery has become more exclusively devoted to the growing neo-olfactorium and is evolving definite pyriform, hippocampal and striatal branches in accordance with the differentiation of this part of the hemisphere. It will be seen that it still retains some of its palaeo-olfactory branches.

The medial olfactory artery is the anterior continuation of the cranial division. It runs anteriorly along the ventro-medial border of the hemisphere to anastomose with lateral olfactory branches on the olfactory stalk. This vessel is related more closely to the palaeo-olfactorium and retains its old disposition almost unchanged. The greater relative growth of the neo-olfactorium has displaced the artery somewhat ventrally so that it comes to lie at the ventro-medial border instead of at the medial equatorial groove. On the medial wall of the hemisphere the medial olfactory artery still supplies most of the paraterminal body and the anterior end of the hippocampus where it anastomoses with hippocampal branches of the lateral olfactory artery. The primitive arterial network remains intact, but more of its channels have enlarged to carry the increased volume of blood demanded of them.

The brain of existing Amphibia, as shown by Elliot Smith(20), closely resembles that of a lowly dipnoan. Kappers(21) and Herrick(22) in particular have described the amphibian brain and Hines(23) has shown how closely it resembles a developmental stage of higher brain forms. It is possible to distinguish the neo- and palaeo-olfactory areas of Dart; to these Johnston(19) has added a primitive general cortex. The palaeo-olfactorium contains the paraterminal body, tuberculum olfactorium and nucleus of the diagonal band, and the palaeo-striatum. The neo-olfactorium comprises the primordia of the pyriform lobe, hippocampus and hypopallium, but Kappers calls the last epistriatum(25) after the nomenclature of Edinger(26).

In fig. 4 are shown schematic sections through the anterior and posterior parts of the hemisphere of the brain of the frog indicating the relation of the arteries to the principal cell masses. It will be seen that the medial olfactory

artery still supplies the medial part of the palaeo-olfactorium containing the medial portions of the tuberculum olfactorium, nucleus of the diagonal band and palaeo-striatum. In consequence of the ventro-lateral shift of the main bulk of the medial olfactory artery, some of the channels to the lateral part of the palaeo-olfactorium come to receive their blood from the medial rather than from the lateral olfactory artery, so that most of the lateral aspect of the palaeo-olfactorium is also supplied from the medial olfactory artery. Thus the ventro-lateral part of the tuberculum olfactorium and the ventral aspects of the palaeo-striatum and the primitive amygdala are supplied from the medial olfactory artery, but the lateral olfactory artery retains its distribution
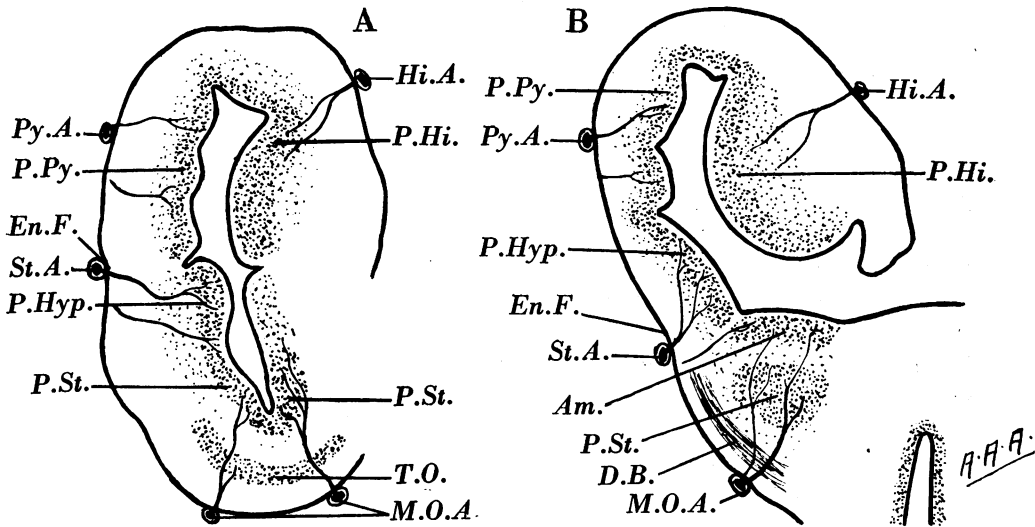

Fig. 4. Schematic sections through A the anterior and B the posterior parts of the right hemisphere of the frog, showing the relation of the arteries.

Am. amygdala; *D.B.* diagonal band; *En.F.* endorhinal fissure; *Hi.A.* hippocampal artery; *M.O.A.* medial olfactory artery; *P.Hi.* primordium hippocampi; *P.Hyp.* primordium hypopallii; *P.Py.* primordium pyriformis; *P.St.* palaeo-striatum; *Py.A.* pyriform artery; *St.A.* striate artery; *T.O.* tuberculum olfactorium.

to the dorsal parts of these structures. In one case the branches from the medial olfactory artery to the primitive amygdala and posterior part of the palaeo-striatum were represented by a single large trunk instead of a series of small vessels. The paraterminal body still obtains most of its blood from the medial olfactory artery which thus retains this portion of its palaeo-olfactory field.

The neo-olfactorium receives most of its blood through the hippocampal, pyriform and striatal branches of the lateral olfactory artery. The hippocampal artery supplies most of the primordium hippocampi and anastomoses anteriorly with the hippocampal and paraterminal branches of the medial olfactory artery. The pyriform artery supplies all the primordium pyriformis and the

striatal artery all the primordium hypopallii as well as the dorso-lateral derivatives of the palaeo-olfactorium.

Thus the arteries of the amphibian brain are strictly comparable with those of the Fish; the various changes observed can be attributed to the increased cerebral development of the amphibian.

Summary

1. In the frog the primitive arterial network is maintained.

2. In this network it is possible to discern the original enlarged channels which, in the dogfish, were known as the medial and lateral olfactory arteries. Other channels have enlarged to meet the increased demands of the structures they supply. These extra demands come almost entirely from the neo-olfactorium and are satisfied by enlargement of the dorsal anastomotic channels which receive most of their blood from the lateral olfactory artery.

3. The lateral olfactory artery comprises a striatal branch which represents the lateral olfactory artery of Fishes, and hippocampal and pyriform branches. A nearer source of supply has been provided by the opening up of one of the diencephalic anastomotic channels, while the old stem is represented in the anastomoses at the posterior end of the endorhinal fissure. The lateral olfactory artery supplies most of the primordium of the hippocampus and all the primordia of the pyriform lobe and hypopallium as well as the dorsal parts of the primitive amygdala and the lateral parts of the striatum, tuberculum olfactorium and diagonal band.

4. The medial olfactory artery supplies most of the palaeo-olfactorium including most of the tuberculum olfactorium and diagonal band and its nucleus, the medial and the ventral parts of the palaeo-striatum and the ventral part of the primitive amygdala. In addition, it supplies most of the paraterminal body and the anterior end of the hippocampus.

REPTILIA

The following account is based upon the examination of a single *Sphenodon* brain, the arteries having been injected with carmine gelatine. The arteries of the brains of two crocodiles were studied to supplement the information thus obtained. In addition, there was a series of coronal sections through the whole head of a young *Sphenodon* which were 250 μ thick, stained with eosin and haematoxylin. In these it was possible to trace the terminal arteries to the various cell masses.

The cerebral arteries of *Sphenodon* have been well described by Dendy[27], those of various Reptiles by Hofmann[1] and Kappers[13], and of the crocodile by Shellshear[7]. In this account special attention will be paid to the functional differentiation of the vessels.

In fig. 5 A the arteries of *Sphenodon* are seen from the ventral aspect. The internal carotid artery divides at the side of the hypophysis into cranial and caudal divisions. Near its origin the cranial division gives off the posterior

cerebral artery and, near the posterior end of the endorhinal fissure, the inferior cerebral artery of Dendy. Slightly anterior to this the middle cerebral arises, while the anterior continuation of the cranial division constitutes the anterior cerebral artery.

The posterior cerebral artery runs dorsally between the posterior pole of the hemisphere and the optic lobe to the dorso-medial border of the hemisphere and proceeds along this to the anterior pole. In its course it supplies
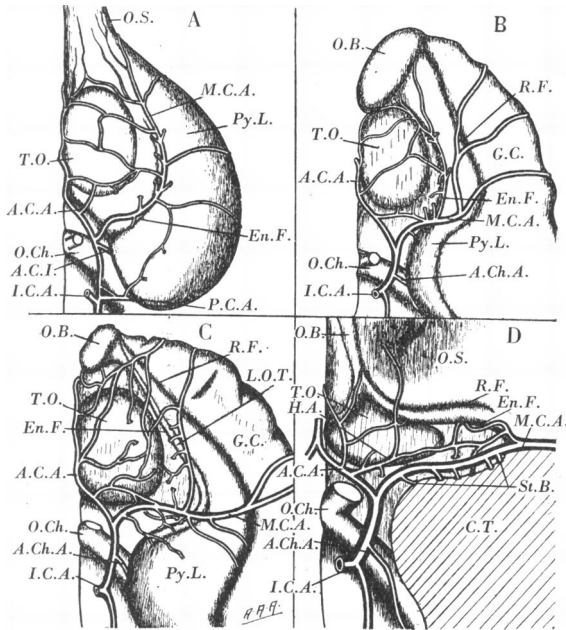

Fig. 5. The arteries of the base of the brain of: A, *Sphenodon*; B, a marsupial (*M. thetidis*); C, an ungulate (*S. strepsiceros*); D, a Primate (*C. sabaeus*); showing the relation of the anterior and middle cerebral arteries to the palaeo-striatum, and the formation of Heubner's artery.

    A.C.A. anterior cerebral artery; *A.C.I.* inferior cerebral artery; *A.Ch.A.* anterior choroidal artery; *C.T.* cut surface of temporal lobe; *G.C.* general cortex; *En.F.* endorhinal fissure; *H.A.* Heubner's artery; *I.C.A.* internal carotid artery; *L.O.T.* lateral olfactory tract; *M.C.A.* middle cerebral artery; *O.B.* olfactory bulb; *O.Ch.* optic chiasma; *O.S.* olfactory stalk; *P.C.A.* posterior cerebral artery; *Py.L.* pyriform lobe; *R.F.* rhinal fissure; *St.B.* striate branches; *T.O.* tuberculum olfactorium.

branches to the anterior part of the optic lobe and to the posterior part of the pyriform lobe, there to anastomose with branches of the middle cerebral artery. It also supplies the choroid plexus of the third and lateral ventricles. As the artery passes along the dorso-medial border it supplies the upper part of the pyriform lobe anastomosing with branches of the middle cerebral artery, but its main supply is to the hippocampal formation. A few branches reach the posterior part of the paraterminal body. At the anterior end of the hippocampus the posterior cerebral artery anastomoses with hippocampal and paraterminal branches of the anterior cerebral artery, and over the primordium

neopallii—the newly formed "general cortex" of Crosby (28)—it enters into anastomosis with branches of the anterior and middle cerebral arteries, as Shellshear showed for the crocodile.

The inferior cerebral artery passes dorsally between the hemisphere and optic tract to reach the posterior part of the corpus striatum.

The middle cerebral artery runs laterally to the endorhinal fissure to which it is closely applied in its anterior course. At the anterior pole of the hemisphere this vessel passes on to the dorso-lateral aspect of the olfactory stalk. In its passage it supplies many branches to the pyriform lobe, these anastomose with posterior cerebral branches; in particular, there is one very large anastomotic union between pyriform branches of the middle and posterior cerebral arteries over the posterior end of the pyriform lobe. The main channel of the middle cerebral artery passes along the endorhinal fissure and supplies perforating branches to the pyriform lobe, endorhinal fissure and lateral part of the palaeo-olfactorium. Over and around the palaeo-olfactorium is a rich series of anastomotic vessels between the middle and anterior cerebral arteries. The middle cerebral artery ends by anastomosing over the dorso-lateral aspect of the olfactory stalk with branches of the anterior cerebral artery, and over the general cortex in the common anastomosis between the three major arteries.

The anterior cerebral artery runs anteriorly along the ventro-medial border of the hemisphere to about the level of the tuberculum olfactorium where it bends dorsally and passes to the medial wall of the hemisphere. On its way it supplies branches to the medial part of the palaeo-olfactorium and some which pass laterally to join middle cerebral branches. The general anterior direction of the artery is maintained by small branches which run forwards along the medial border of the palaeo-olfactorium and on to the medial aspect of the olfactory stalk to anastomose with branches of the middle cerebral artery. From these small branches, too, twigs are given to the medial part of the palaeo-olfactorium and also anastomotic branches to the middle cerebral artery. The main trunk of the anterior cerebral artery passes to the medial wall of the hemisphere to supply the anterior part of the hippocampus and most of the paraterminal body (anastomosing with the posterior cerebral artery) and ends in the common anastomosis over the primordium neopallii.

The first significant work on the cell masses of *Sphenodon* was published in 1902 (20) and in 1919 (29) by Elliot Smith when he described the hypopallium in its relationship to the pyriform cortex and lateral striate arteries. Subsequently, Cairney (30) and Durward (31) gave more complete accounts of the structure of the *Sphenodon* brain. The fore-brain can be divided into palaeo-olfactorium and neo-olfactorium. The palaeo-olfactorium contains the tuberculum olfactorium, paraterminal body, the diagonal band and its nucleus and the palaeo-striatum. The neo-olfactorium includes the well-developed hippocampus, pyriform lobe and hypopallium; the hypopallium has been subdivided by Dart, Johnston and others into hypopallium anterius related to the

"general cortex" and hypopallium posterius related to the pyriform cortex and amygdala (the archistriatum of Kappers). In addition, the primordium neopallii lies anteriorly on the dorso-lateral aspect of the hemisphere, interposed between hippocampus and pyriform lobe.

In fig. 6 is shown a series of sections through a *Sphenodon* brain. In these the relationship of the terminal arteries to the cell masses is clearly depicted. In the first section the inferior cerebral artery arises from the cranial division of the internal carotid artery and, entering the brain substance, passes dorsally
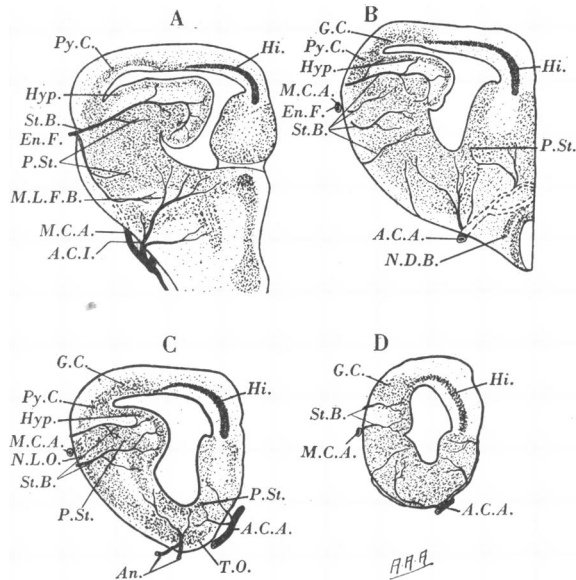

Fig. 6. A series of sections of the brain of a young *Sphenodon* from behind forwards, cut at 250 μ and stained with eosin and haematoxylin. The sections are cut obliquely so that the upper part is well anterior to the lower.

A.C.A. anterior cerebral artery; A.C.I. inferior cerebral artery; An. anastomosis over the tuberculum olfactorium; En.F. endorhinal fissure; G.C. general cortex; Hi. hippocampus; Hyp. hypopallium; M.C.A. middle cerebral artery; M.L.F.B. medial and lateral fore-brain bundles; N.D.B. nucleus of diagonal band; N.L.O. nucleus of lateral olfactory tract; P.St. palaeo-striatum; Py.C. pyriform cortex; St.B. striate branches; T.O. tuberculum olfactorium.

through the fore-brain bundles to the ventro-medial part of the primitive amygdala and the associated part of the palaeo-striatum; more dorsally branches of the middle cerebral artery enter the palaeo-olfactorium to supply the dorso-lateral parts of these structures. These middle cerebral branches also supply the whole of the hypopallium—in this case hypopallium posterius. The next section, anterior to the last, shows the anterior cerebral artery, passing medially. On its way it gives branches to the ventral and medial parts of the primitive amygdala and the palaeo-striatum, the nucleus of the diagonal band and the paraterminal body. The middle cerebral artery lies in

relation to the endorhinal fissure and its branches enter the brain through the pyriform cortex, through the fissure itself and through the dorsal part of the palaeo-olfactorium. In general it may be said that the striate branches of the middle cerebral artery fall into three groups. Those which pierce the pyriform cortex pass just dorsal to the nucleus of the lateral olfactory tract to reach the dorsal fold of the hypopallium; those which pass through the endorhinal fissure (these are most numerous and constitute the lateral striate arteries of Elliot Smith) to supply the dorsal part of the palaeo-striatum and primitive amygdala and the most medial fold of the hypopallium; the branches which enter the palaeo-olfactorium ventral to the endorhinal fissure supply the dorso-lateral parts of the primitive amygdala and palaeo-striatum.

The third section lies anterior to the amygdala and passes through the tuberculum olfactorium. Here the main stem of the anterior cerebral artery lies close to the paraterminal body which it supplies, and sends branches to the palaeo-striatum. Over the tuberculum olfactorium there is an anastomotic union between branches of the anterior and middle cerebral arteries. From this vessels pass to the tuberculum and to the ventral part of the palaeo-striatum. The middle cerebral artery lies close to the endorhinal fissure and its branches pass to the hypopallium and the dorsal part of the palaeo-striatum. The fourth section lies still more anteriorly. It shows a branch of the anterior cerebral artery supplying nearly all the palaeo-olfactorium in this region and also the most ventral part of the anterior hippocampus. Branches of the middle cerebral artery reach the "general cortex" and the hypopallium anterius. In these sections the posterior cerebral artery is not drawn, as its simple relation to the hippocampus requires no further elaboration.

In relation to the manner in which the striate branches enter the brain to reach the hypopallium, Johnston (18) states (p. 355) that the vessels which supply the caudate nucleus frequently pierce the pyriform cortex, although he agrees that the majority of these arteries actually enter the endorhinal fissure. As shown above (fig. 6), several of the middle cerebral branches certainly pass through the pyriform cortex—mostly dorsal to the nucleus of the lateral olfactory tract—and these are devoted mainly to the more dorsal fold of the hypopallium. They will be considered further in relation to the mammalian striatum. It may be mentioned that branches of the middle cerebral artery could be traced into the most anterior part of the hypopallium although Durward states that he was unable to find such arteries.

The posterior cerebral artery is related to the dorsal part of the pyriform lobe and most of the hippocampus and represents the hippocampal artery of the frog. Its origin has, however, been shifted posteriorly with the backward expansion of the hemisphere and a still more posterior diencephalic artery has been employed as the most convenient stem. In addition, the posterior cerebral artery uses the same parent stem to supply blood to the choroid plexus and the anterior part of the optic lobe. It has "taken over" the blood supply of these regions. The origin of the lateral olfactory artery of the frog

persists in the large anastomotic channel between the posterior and middle cerebral arteries over the posterior part of the pyriform lobe—a connection which is never lost. Hofmann regarded the lateral olfactory artery of the frog as a posterior cerebral artery and called it the *arteria cerebralis posterior α*, but this homology cannot be entirely correct because the posterior cerebral artery of *Sphenodon* represents only the hippocampal branch of the lateral olfactory artery of the frog.

The inferior cerebral artery supplies the posterior parts of the palaeo-striatum and primitive amygdala. In the crocodile(9) there is no separate inferior cerebral artery. It is represented by a series of minute anastomotic channels arising from the stem of the carotid artery and running posteriorly along the optic tract to join the posterior cerebral artery. In the specimen of *Sphenodon* which I examined such a connection probably existed but was uninjected and so the inferior cerebral artery appeared to be a discrete vessel. I suggest that this is the true arrangement in all Reptiles and consider that my previous description was only partly correct(9). In *Sphenodon* there is no separate inferior cerebral artery, the vessel which was so named by Dendy is the anterior part of this anastomotic chain which has become enlarged in response to the greater functional demands made upon it by the palaeo-striatum. I had previously homologised this anastomotic chain of Reptiles with the anterior choroidal artery of Mammalia and this I still believe to be correct. The inferior cerebral artery is the enlarged anterior part of the anasto-mosis between the cranial division of the internal carotid artery and the posterior cerebral artery and its predecessor is to be found in the series of similar anastomoses in this region in the frog (fig. 3). Thus the primitive vascular network is still intact and no new arteries have been introduced.

The middle cerebral artery is closely related to the endorhinal fissure and supplies the pyriform lobe and the lateral part of the palaeo-olfactorium as well as the whole of the hypopallium and the dorsal part of the palaeo-striatum. Clearly, its main trunk represents the striatal branch of the lateral olfactory artery of the frog and all of the lateral olfactory artery of the dogfish. In addition, it includes pyriform branches of the frog which were not de-veloped to any degree in the dogfish. Kappers(13) has noted this similarity and homologises the lateral olfactory artery of Fishes with the middle cerebral artery of Reptiles. There is considerable justification for this homology, but to make it complete it is necessary to add to the lateral olfactory artery of Fishes the pyriform artery of Amphibia. The two vessels together represent the middle cerebral artery of higher animals.

The brain of existing Amphibia is known to be specialised and regressive. It remains to be decided whether the brain is the survivor of an aberrant form off the main line of evolution which passed from Fish to Reptile, or whether it is the living representative of a ?Stegocephalian ancestor intermediate be-tween Fish and Reptile and now extinct. The arteries give some clue to the interpretation of the status of the brain of the frog. The posterior cerebral

artery is obviously developed from the hippocampal artery of a lower form, but the origin of the middle cerebral artery presents a difficulty. It has evolved from the lateral olfactory artery of Fishes, retaining the origin and course of this vessel but has acquired pyriform branches. Such pyriform branches are found in the frog, but there they arise from the more dorsal development of the lateral olfactory artery—the stem and hippocampal branches of which represent the posterior cerebral artery of Reptiles. In the frog the striatal artery—the first representative of the middle cerebral—also takes origin from this potential posterior cerebral artery, its old direct connection with the cranial division of the internal carotid artery surviving as a few anastomotic channels at the posterior end of the endorhinal fissure. The differentiation of the cerebral arteries of the frog suggests a corresponding evolution of the parts they supply, and these arteries present all the cardinal channels necessary for the formation of the cerebral arteries of higher animals. It would appear that the frog is the degenerated descendant of an ancestor which possessed the potentialities for laying down the cerebral vascular pattern of higher animals. Such an ancestor had representatives of separate anterior, middle and posterior cerebral arteries. From this intermediate condition the vascular pattern of modern Reptiles has evolved, but the brain of existing Amphibia has so degenerated that the precursor of the middle cerebral artery has lost its need for a rich blood supply to the striatal region and its direct connection with the cranial division has dwindled to the remaining anastomotic channels. Evolution thus appears to have passed from Fish to Reptiles through a now extinct intermediate ancestor, from this common ancestor the frog has degenerated to its present regressive condition.

In the crocodile, as shown by Shellshear, the middle cerebral artery is not a single large vessel but is represented by a series of smaller anastomotic channels. This fact is not noted in the Reptiles described by Hofmann and Kappers, nor does it appear to hold in Birds. It may reflect a still unsettled condition of the striatal region in crocodiles.

The anterior cerebral artery presents a simpler problem. This vessel is the descendant of the medial olfactory artery of Fishes and Amphibia. One great change in volume of distribution, however, demands attention. In lower animals the main trunk of the medial olfactory artery passes to the olfactory stalk, but in Reptiles the greater part of the blood is diverted to the medial wall of the hemisphere—to the paraterminal body, the anterior part of the hippocampus and the new "general cortex." This suggests a greater functional demand from these regions. The old channel is indicated by the small branches which run anteriorly along the medial border of the palaeo-olfactorium to the olfactory stalk and which suffice for the requirements of these parts. Thus the palaeo-olfactorium retains the old vascular ring which, existing in fishes as the two major arteries—the medial and lateral olfactory arteries—is represented in Reptiles by the middle cerebral artery and small branches of the anterior cerebral artery.

Summary

1. The reptilian brain is still enveloped by a closed primitive vascular network. From this network three major channels—the anterior, middle and posterior cerebral arteries—have become enlarged to carry the bulk of blood in relation to the structures they supply. In addition, an inferior cerebral artery has been described for *Sphenodon* by Dendy.

2. The anterior cerebral artery represents the medial olfactory artery of lower forms. It supplies the medial aspect of the palaeo-olfactorium including the paraterminal body. In addition it reaches the anterior part of the hippo-campus and ends in the general anastomosis over the primordium neopallii. The original course of the artery is indicated by a few small branches running forwards along the medial border of the palaeo-olfactorium. The main stream of blood has been deflected to the medial wall of the hemisphere, probably in response to the increased demands made by the expanding paraterminal body and the developing "general cortex."

3. The middle cerebral artery appears as an entity for the first time in Reptiles and has probably developed from the lateral olfactory artery of Fishes through an intermediate ancestral form which has since disappeared. Its representative in Amphibia is the striatal branch of the lateral olfactory artery together with the pyriform branches. The middle cerebral artery supplies the lateral part of the palaeo-olfactorium, the hypopallium and most of the pyriform lobe, and ends in the general anastomosis over the primordium neopallii.

4. The arteries to the basal ganglia comprise three groups. One enters the pyriform cortex to reach the dorsal fold of the hypopallium, the second enters the rhinal fissure to supply the medial part of the hypopallium and the dorsal parts of the palaeo-striatum and primitive amygdala and the third enters the lateral part of the palaeo-olfactorium to supply the lateral parts of the palaeo-striatum and primitive amygdala.

5. The inferior cerebral artery was described by Dendy as a separate entity in the brain of *Sphenodon*, but does not exist as such in the crocodile. In this animal it is represented by an anastomotic chain between the cranial division of the internal carotid artery and the posterior cerebral artery. The condition found in crocodiles probably represents the reptilian pattern. In *Sphenodon* the inferior cerebral artery is the enlarged anterior part of this anastomotic chain which, nevertheless, is still intact, although its posterior part has remained so small that it is not seen in the injected specimen. The inferior cerebral artery supplies the ventro-medial aspect of the posterior part of the striatum and the ventral part of the primitive amygdala. It also gives a few branches to the posterior part of the pyriform cortex and reaches the posterior part of the medial and lateral fore-brain bundles.

6. The posterior cerebral artery[1] is mainly the hippocampal artery which has acquired a nearer source of origin for its blood by means of a more posterior anastomosis with the cranial division of the internal carotid artery. It supplies nearly all of the hippocampal formation and the posterior part of the paraterminal body. In addition, it supplies the posterior part of the pyriform lobe and primitive amygdala, and joins the common anastomosis over the "general cortex."

7. Finally, each cerebral artery anastomoses at the periphery of its superficial distribution with branches of its fellows and so the primitive vascular net remains intact. The only area over which all three major arteries meet is the newly formed "general cortex."

MAMMALIA

The description of the mammalian cerebral arteries falls into two groups, sub-Primates and Primates. The account of the former group will be based upon the condition found in the sheep, supplemented by reference to other animals where necessary; the condition in Primates will be illustrated by the human pattern as the similarity of the cerebral arteries of apes renders a separate description unnecessary.

SUB-PRIMATES

The great gap between Reptile and Mammal is reflected in the enormous overgrowth of the neopallium which forms a continually enlarging cerebrum in an ascending phylogenetic series. This expansion has caused a secondary deformation of the cerebral hemispheres, so that eventually they appear to have become folded on themselves between the amygdaloid nucleus and foramen of Monro. The palaeo-olfactorium has maintained its original position and the neo-olfactorium has developed around and above it. The primordium neopallii has appeared between the hippocampus and pyriform lobe and by its rapid expansion has pushed these ventrally and then medially so that they come to be relegated to a comparatively insignificant position at the hilum of the brain. Associated with these changes are the appearance of the corpus callosum, the breaking through of the internal capsule and the consolidation of the basal ganglia. Equivalent and comparable alterations have occurred in vascular distribution, but the arteries are the same as in lower forms and, while retaining their old connections and fields of supply, they have contrived to deal adequately with the greatly increased demands made upon them.

When we examine the base of the brain of a primitive Mammal (fig. 5 B and C) we notice that in consequence of the dorso-posterior expansion of the

---

[1] In a previous paper(9) I have described the posterior cerebral artery of Reptiles as part of the caudal division of the internal carotid artery. This is incorrect because the posterior cerebral artery of Reptiles has no direct relation to the caudal division. It is not until the mammalian stage of evolution is reached that the posterior cerebral artery acquires its connection with the caudal division.

hemisphere, the pyriform lobe becomes bent. This is accompanied by a bending of the rhinal and endorhinal fissures. As we ascend the phylogenetic scale this lateral bend becomes progressively more acute until in Primates the anterior and posterior parts of the endorhinal fissure lie almost parallel. It will simplify the subsequent description if we refer to these parts as the anterior and posterior endorhinal fissures respectively.

In fig. 5 C is shown the base of the brain of a kudu (*S. strepsiceros*) which is sufficiently like that of a sheep to serve for illustration. The internal carotid artery divides alongside the hypophysis into cranial and caudal branches: the cranial division passes anteriorly over the optic tract while the caudal division runs posteriorly to join the basilar artery as before. It will be noticed that the posterior cerebral artery no longer arises from the cranial division. Hofmann has shown how the posterior cerebral artery appears to arise more and more posteriorly as we ascend the phylogenetic scale, these successively posterior positions he has called α, β, γ, and δ. In sub-Mammalia the posterior cerebral artery arises from the cranial division of the internal carotid artery, in Mammalia it receives the bulk of its blood from the basilar artery. At present we can note without comment that the posterior cerebral artery in Mammals appears to arise from the basilar artery.

The posterior cerebral artery runs to the medial surface of the hemisphere where it supplies the general cortex of the posterior parts of the medial, lateral and inferior surfaces, and the posterior pole. Some of the branches to the inferior surface pass forwards to supply the posterior part of the pyriform cortex and anastomose there with the pyriform branches of the middle cerebral and anterior choroidal arteries. As in Reptiles, the posterior cerebral artery supplies most of the hippocampal formation. In true Mammals the growth of the corpus callosum has stretched the antero-superior part of this structure which remains as an attenuated remnant—the supracallosal hippocampus. This survivor represents the part supplied by the anterior cerebral artery in sub-Mammals and so the hippocampal branches of the posterior cerebral artery extend only to the posterior end of the corpus callosum where they anastomose with hippocampal branches of the anterior cerebral artery. In Marsupials where there is no corpus callosum to stretch the paraterminal body and antero-superior part of the hippocampus, the condition approaches that in Reptiles but the hippocampal branches of the posterior cerebral artery do not extend as far anteriorly on the medial wall of the hemisphere as in sub-mammalia. At the antero-inferior part of the hippocampal formation the posterior cerebral branches anastomose with anterior choroidal branches which supply a portion of this formation. The posterior cerebral artery supplies the choroid plexus of the third ventricle and most of that of the lateral ventricle. The posterior cerebral artery usually supplies a small part of the tail of the caudate nucleus. By its stem of origin this vessel also supplies the anterior and superior parts of the mid-brain.

The next artery of importance is the anterior choroidal which takes origin

from the cranial division of the internal carotid artery, now the stem of the internal carotid artery. The artery runs posteriorly along the optic tract and ends by joining the posterior cerebral artery over the lateral geniculate body (9). In its posterior passage (fig. 7) it supplies a small part of the pyriform cortex, the postero-medial aspect of the underlying amygdaloid nucleus and most of the tail of the caudate nucleus. It sends branches to the optic tract, the dorsal nucleus of the lateral geniculate body, the middle third of the crus cerebri and the antero-inferior parts of the hippocampal formation and choroid plexus. Other branches pierce the optic tract to supply the posterior part of the posterior limb of the internal capsule and most of the medial two-thirds of the globus pallidus. A few twigs reach the ventro-lateral nucleus of the thalamus. The anterior choroidal artery anastomoses with the middle and posterior cerebral arteries over the pyriform cortex, with the posterior cerebral artery over the lateral geniculate body and crus cerebri and in the choroid plexus of the lateral ventricle, and with the anterior and middle cerebral and posterior communicating arteries over the anterior part of the optic tract and chiasma (see figs. 7, 10 and 11).

The middle cerebral artery in Mammalia has so enlarged that it appears to be the main trunk of the cranial division (it is often so described in standard text-books) while the anterior cerebral artery—the true anterior continuation—is relatively much smaller. The middle cerebral artery passes laterally in the posterior endorhinal fissure to which it is closely attached as far as the lateral bend; at this spot the main trunk of the vessel passes across the pyriform cortex and rhinal fissure to reach the general cortex laterally and dorsally (fig. 5 C). A small branch, however, runs forwards in the anterior endorhinal fissure to reach the lateral aspect of the olfactory stalk as a reminder of the original course of the artery. The middle cerebral artery supplies most of the pyriform lobe, the antero-lateral aspect of the amygdaloid nucleus, parts of the striatum and most of the lateral aspect of the general cortex.

The striatal branches fall again into three groups: through the pyriform cortex, the endorhinal fissure and the lateral part of the palaeo-olfactorium (fig. 10). Those which pierce the pyriform cortex run into the external capsule and reach the claustrum, and it will be noticed (fig. 5 C) that the majority pass into the groove just lateral to the lateral olfactory tract and its nucleus. They were described for *Echidna* by Shellshear (7), who follows the description of Sonntag and Woollard for *Orycteropus* (32) and calls the endorhinal fissure the arcuate fissure and the fissure lateral to the nucleus of the lateral olfactory tract the endorhinal fissure. (This information I obtained in a personal communication from Prof. Shellshear who agrees with my interpretation of this region.) The lateral striate arteries proper enter the endorhinal fissure and pass to the external capsule between the claustrum and putamen. They then enter the putamen and, passing dorsally through it, cross the superior part of the internal capsule to end in the caudate nucleus (fig. 7). Anteriorly, these arteries supply the dorso-lateral part of the head of the caudate-putamen

mass and the upper part of the anterior limb of the internal capsule; more posteriorly they pass through the putamen and across the upper part of the posterior limb of the internal capsule to reach the body of the caudate nucleus. The striatal branches through the palaeo-olfactorium supply the lateral part of the globus pallidus and amygdaloid nucleus. The majority of the branches to the amygdaloid nucleus pass through the pyriform cortex and endorhinal fissure.

The small continuation of the middle cerebral artery in the anterior endorhinal fissure supplies striatal branches, branches to the pyriform cortex and
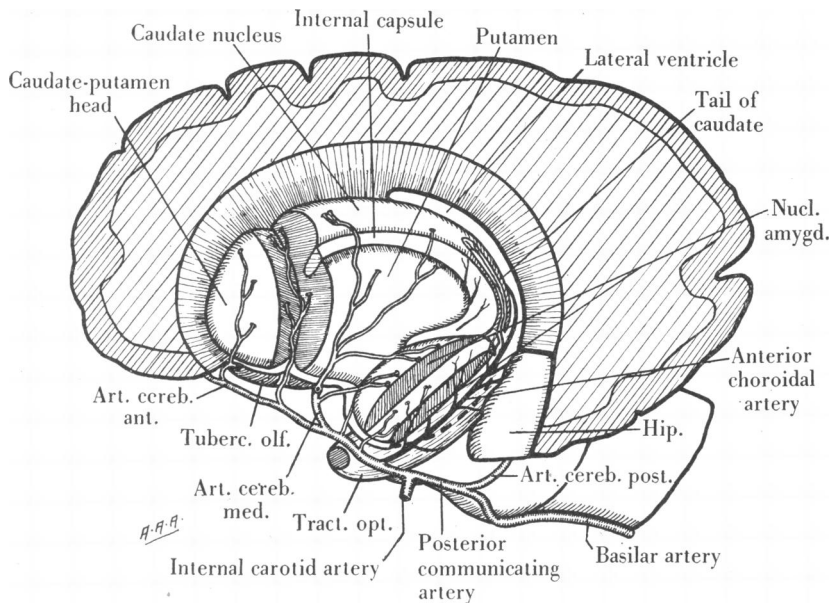

Fig. 7. Brain of sheep, dissection of the basal ganglia and their arteries from the lateral aspect. The amygdaloid nucleus has been cut in steps to show its double blood supply, and a section has been cut from the caudate-putamen head to show the distribution of an anterior cerebral branch. Anterior choroidal artery in black. Note branch of anterior choroidal artery in tail of caudate nucleus, and in posterior limb of internal capsule.

palaeo-olfactorium, and anastomotic branches to the anterior cerebral artery over the palaeo-olfactorium, and finally passes on to the lateral aspect of the olfactory bulb where it ends by joining more anterior cerebral branches. Thus the stem of middle cerebral artery in the posterior endorhinal fissure, and the small branch in the anterior endorhinal fissure together represent nearly all of the middle cerebral artery of Reptiles and preserve its distribution and relations exactly. The rest of the artery in Mammals has developed from the common anastomosis in relation to the growing neopallium.

The anterior cerebral artery is the forward continuation of the cranial division of the internal carotid artery. From its point of origin (fig. 5 C) it

passes forwards and then medially to the medial border of the palaeo-olfac-
torium where it usually joins its fellow of the opposite side. Thence the
combined vessel ascends over the front of the corpus callosum where it divides
again into its components which run posteriorly over the dorsum to anasto-
mose finally with hippocampal branches of the posterior cerebral artery. This
is merely an extension of the course of the homologous vessel of the Reptile
due to the stretching of the anterior part of the hippocampal formation by
the growing corpus callosum. As in the Reptile, the primitive course of the
anterior cerebral artery along the medial border of the palaeo-olfactorium is
maintained by some small branches which reach the medial aspect of the
olfactory bulb and anastomose with branches representing the primitive
course of the middle cerebral artery. From the main stem of the anterior
cerebral artery, and from its forward continuing branches twigs are given to
the medial part of the palaeo-olfactorium—tuberculum olfactorium and dia-
gonal band. Many of these branches enter the base of the brain and supply
the infero-medial part of the head of the caudate-putamen mass and the
inferior part of the anterior limb or the internal capsule, others—more pos-
teriorly—reach the anterior part of the globus pallidus (fig. 10 B).

The main trunk of the anterior cerebral artery supplies the paraterminal
body and the structures which have developed with it—most of the anterior
commissure, nearly all of the corpus callosum, the septum pellucidum and
most of the hippocampal commissure (Elliot Smith (33)). The posterior part of
the paraterminal region is supplied from the posterior cerebral artery and
the survivors of the primitive anastomoses between the hippocampal and
medial olfactory arteries in this region in the frog. The anterior cerebral artery
supplies the supracallosal hippocampus which is the morphological anterior
part of the hippocampal formation (Elliot Smith (34)). Finally, branches of
the anterior cerebral artery supply the neopallium anterior to and above the
corpus callosum and anastomose laterally and posteriorly at the periphery
of their field of distribution with branches of the middle and posterior cerebral
arteries respectively.

The homologies of these arteries are clear, but the posterior cerebral artery
merits closer attention. This vessel arises from the basilar artery in Mammals
and supplies much of the anterior part of the mid-brain. From the posterior
cerebral artery a number of small branches pass to the anterior part of the
temporal region (which is morphologically the posterior pole of the pyriform
lobe) and join pyriform branches of the cranial division—from the stem of
the carotid artery and the middle cerebral artery—some of which represent
the stem of the reptilian posterior cerebral artery. Frequently these twigs
receive their blood from the anterior choroidal artery and constitute the
pyriform branches of this vessel, their true nature is thus often obscured but
such vessels are always present and show the way by which the posterior
cerebral artery has passed.

The posterior communicating artery runs from the internal carotid artery

to the basilar and is clearly the caudal division of the internal carotid. Branches of this vessel join the anterior choroidal in a rich anastomosis over the optic tract and thus may supply indirectly some of the anterior choroidal field. These communications are usually slight, and the amount of blood they convey negligible, but cases have been described by Kolisko(35) and others, and I have seen one such, where the anterior choroidal is minute or even represented by a series of tiny twigs. Under these circumstances the posterior communicating artery enlarges and takes over nearly the whole of the field of the anterior choroidal artery. On the other hand the posterior communicating artery may be very small; in this case the anterior choroidal artery shows a compensatory enlargement. Sometimes, when the communication with the basilar artery is small and the posterior communicating artery diminished, the posterior cerebral artery receives most of its blood from the anterior choroidal channel which thus forms its stem.

Hofmann calls the lateral olfactory artery of Amphibia the *arteria cerebralis posterior* α; this has been discussed. He also calls the anterior choroidal artery of Mammals the *arteria cerebralis posterior* α and is justified in so far as the anterior choroidal artery arises from the cranial division of the internal carotid artery and occasionally forms the stem of the posterior cerebral artery. But, as I have shown elsewhere(9), the anterior choroidal artery is the homologue of the inferior cerebral artery of *Sphenodon* plus its anastomotic connection with the posterior cerebral artery and its more recently acquired choroidal branches. When it acts as the stem of the posterior cerebral artery of Mammals it does so not because it is reassuming an old function, but because other factors have come into play. The true primitive stem of the posterior cerebral artery exists among the small anastomotic channels over the posterior part of the pyriform lobe. That these often receive their blood through the anterior choroidal artery is to be regarded as another example of the principle of economy of distribution.

In Mammalia the posterior cerebral artery is said to arise from the basilar artery. What is really implied is that it receives its main contribution of blood through the basilar artery. The main trunk of the posterior cerebral artery supplies the anterior part of the mid-brain. Frequently some of its mid-brain distribution is undertaken by smaller vessels which may remain discrete at their origin from the basilar artery or may arise from a common stem with the posterior cerebral artery to separate later. In an ascending phylogenetic scale these separate mid-brain vessels become progressively less frequent, they are commonly found in lower Mammals, less often in higher. As the cerebral hemispheres become pushed backwards over the mid-brain the distribution of the posterior cerebral artery becomes separated more and more from its source of supply. Consequently it appears to shift its stem of origin posteriorly as successively posterior anastomotic channels enlarge to carry the main stream of blood from a nearer source. Thus the posterior cerebral artery grows so far away from its primitive parent—the internal

carotid artery—that even the caudal division will not suffice for its require-
ments. It takes more and more of its blood from the nearest large vessel—
the basilar artery—and this it does through anastomotic channels with mid-
brain vessels, while the basilar artery itself enlarges to meet the increased
demands. Sometimes the internal carotid artery exerts its old influence and
supplies the posterior cerebral artery through the posterior communicating or
anterior choroidal channels, but such cases are rare and but repetitions of
primitive patterns. When the posterior cerebral, or any other artery, employs
as its medium of supply a vessel which has its own definite field of distribution
the common trunk serves to provide both areas and the larger vessel appears
to absorb the smaller. The posterior cerebral artery of higher Mammals uses
the anterior mid-brain arteries as its nearest source of blood and gives the
impression that the posterior cerebral artery is an artery of the anterior part
of the mid-brain.

Hofmann's classification of the posterior cerebral artery in terms of its
points of origin is justified, but it must be emphasised that these are not
new vessels. The channels have always existed in the primitive network which
envelopes the brain. As the posterior cerebral artery has grown away from
its old source the next posterior channel has enlarged to carry the main flow
of blood; when this is discarded to give place to a yet more posterior source
it does not disappear but reverts to its original state as a small anastomotic
channel in the primitive network, and should circumstances demand, it will
again enlarge to carry out its old function.

The stem of the middle cerebral artery is the same in origin and course
as its predecessor in the Reptile, and the first part of its trunk which is so
closely related to the posterior endorhinal fissure has only altered in size.
Thereafter the character of the vessel changes completely. In reptiles the
main course of the artery is along the endorhinal fissure to the olfactory stalk,
while the pyriform branches are of subsidiary importance; in Mammals the
main trunk of the artery leaves the endorhinal fissure at its lateral angle and
traverses the pyriform lobe to reach the neopallium. The old main vessel is
represented by a small branch which runs in the anterior endorhinal fissure to
reach the olfactory bulb (fig. 5 C). This small vessel, however, suffices for the
needs of all the structures supplied by this part of the original middle cerebral
artery. The call for extra blood has come from the growing neopallium and
has been met by an enlargement of the pyriform branches which now cross
the pyriform cortex and rhinal fissure to supply the general cortex. The new
main flow of blood is through the stem and pyriform branches of the middle
cerebral artery but the old channel in the anterior endorhinal fissure, having
little or no extra demand to meet, persists comparatively unchanged.

The anterior cerebral artery, although much larger, pursues the same course
as in Reptiles. Its greatest flow of blood is to the medial wall of the hemi-
sphere to supply the expanding paraterminal body and general cortex. The
original course and distribution are served through the small branches which

run forwards along the medial border of the palaeo-olfactorium to the olfactory bulb.

Thus, in Mammals the enormous growth of the neopallium has made use of the old stem arteries for its supply of blood, but the cortical arteries have developed from the common anastomosis of the three major vessels over the primordium neopallii of Reptiles. No new arteries have been formed, the demand has been satisfied by the enlargement of existing arterial channels. The palaeo-olfactorium of the dogfish was so important that it formed a very large part of the hemisphere and the blood supply of this primitive brain encircled, and was evolved almost entirely for that structure. In Mammalia the palaeo-olfactorium is small and hidden at the base of the brain; it has changed little from its primitive condition and retains the arterial circle in its original state. Although the vessels of this circle are as large as, or even larger than, those of the original circle, they are diminutive in comparison with the other cerebral arteries. The demands of the neopallium have been more urgent and imperative.

The question of the evolution of the basal ganglia is difficult and controversial, but it is hoped that the study of the arterial supply may contribute towards its solution. If arteries are constant in their terminal supply it should be possible to trace homologous structures from sub-Mammals to Mammals.

The anterior cerebral artery supplies the medial and anterior part of the palaeo-striatum in *Sphenodon* (fig. 6); the homologous vessel in mammals supplies the infero-medial part of the head of the caudate-putamen mass and the anterior part of the medial two-thirds of the globus pallidus (fig. 10). It appears that inferior part of the caudate-putamen mass and this part of the globus pallidus have evolved from the antero-medial part of the palaeo-striatum.

The middle cerebral artery supplies the whole of the hypopallium and the dorso-lateral parts of the palaeo-striatum and primitive amygdala of sub-Mammals; in Mammals it reaches the supero-lateral part of the head of the caudate-putamen mass, the claustrum, the putamen and the body of the caudate nucleus, the antero-lateral aspect of the amygdaloid nucleus and the lateral one-third of the globus pallidus (fig. 10). Further, it was observed that the striatal branches formed three groups; through the pyriform cortex to the dorsal fold of the hypopallium, through the endorhinal fissure to the medial fold of the hypopallium and the dorsal part of the palaeo-striatum and primitive amygdala and through the lateral part of the palaeo-olfactorium to the lateral part of the palaeo-striatum. These groups are as distinct in the mammalian brain. The vessels through the pyriform cortex supply the claustrum, those through the endorhinal fissure the putamen and the body of the caudate nucleus as well as the dorso-lateral part of the head of the caudate-putamen mass and the lateral part of the globus pallidus and amygdaloid nucleus, those through the palaeo-olfactorium the intermediate parts of the globus pallidus and amygdaloid nucleus.

The anterior choroidal artery is represented in *Sphenodon* by the inferior cerebral artery and its anastomotic union with the posterior cerebral artery. In Mammals it acquires choroidal branches from the posterior cerebral artery. The inferior cerebral artery supplies the ventro-medial part of the primitive amygdala and of the posterior part of the palaeo-striatum (that is, all of this which is not supplied by the anterior and middle cerebral arteries). In Mammals the anterior choroidal artery supplies the postero-medial part of the amygdaloid nucleus and the posterior portion of the medial two-thirds of the globus pallidus as well as most of the tail of the caudate nucleus (see fig. 7). The rest of the tail is supplied by the posterior cerebral artery.

In fig. 11 I have tried to show diagrammatically the evolution of the basal mass and its arteries. In *Sphenodon* there is a conglomerate mass formed by the accretion of the separate primordia of the frog. With the expansion of the neopallium the dorsal hypopallium is pushed laterally and ventrally and comes to lie dorsal and lateral to the palaeo-striatum. At the same time the internal capsule has broken through the basal mass along the broken heavy line indicated in the *Sphenodon*. This it does without regard to individual cell masses as Johnston showed (18). Thus it separates the hypopallial fold in its dorsal and ventral parts giving rise to the body of the caudate nucleus which is almost completely cut off from the more ventral claustrum and putamen. Johnston has emphasised (p. 358) that the separation by the internal capsular fibres is incomplete, and that the caudate nucleus and putamen are connected in the upper part of the internal capsule by strands of cells which are continuous with both structures and indistinguishable from the cells of either. Anteriorly the separation is even less complete, the head of the caudate-putamen mass is broken through by the fibres of the anterior limb of the internal capsule but the strands of cells which persist between the bundles of fibres are so thick that they impart the striated appearance to which the body owes its name. Anteriorly, too, the medial and lateral masses of cells are continuous below the anterior limb of the internal capsule (fig. 10). Posteriorly, the break is again incomplete. It extends down into the primitive amygdala and splits off incompletely the posterior part of this body in such a way that this split-off part retains its connection below the posterior limb of the internal capsule with the parent cell mass. Superiorly it is continuous with the posterior end of the body of the caudate nucleus. This split-off portion of the primitive amygdala constitutes the tail of the caudate nucleus and retains the blood supply of the parent mass from the anterior choroidal and posterior cerebral arteries. In *Notoryctes typhlops* the cells of the amygdaloid nucleus are continuous with, and indistinguishable from, those of the tail of the caudate nucleus, nor can one tell where one gives place to the other. (Miss Fielding of this department kindly drew my attention to this circumstance.)

After the separation of the anterior, dorsal and posterior elements of the basal ganglia there remains undisturbed the larger part of the mass. This is composed of many cell groups. Anteriorly and lateral to the anterior limb is

the outer part of the head of the caudate-putamen mass comprising palaeo-striatum ventrally and some of the hypopallium dorsally. These are continued posteriorly into the main part of the lenticular nucleus which has globus pallidus (palaeo-striatum) medially and putamen (hypopallium) laterally. The putamen is continuous with the hypopallial part of the amygdaloid nucleus ventrally and the globus pallidus with the primitive amygdala (fig. 10).

Thus, it appears that the hypopallium has formed the claustrum from its dorsal fold and the body and part of the head of the caudate nucleus and the putamen from its most medial part. The posterior part of the hypopallium has formed the antero-lateral part of the amygdaloid nucleus. The primitive amygdala has evolved into the postero-medial part of the amygdaloid nucleus and the tail of the caudate nucleus, the palaeo-striatum into the globus pallidus and the infero-medial part of the head of the caudate-putamen mass. The arteries have maintained their field of supply constantly from sub-Mammal to Mammal.

In *Sphenodon* the inferior cerebral artery supplies the lower part of the lateral fore-brain bundle posteriorly and the anterior cerebral artery the anterior part. The middle cerebral artery supplies the upper part of the whole bundle. The blood supply of the internal capsule of Mammals corresponds. The anterior choroidal artery supplies the posterior part of the internal capsule to the upper level of the globus pallidus and the anterior cerebral artery the ventral part of the anterior limb; the middle cerebral artery supplies the dorsal parts of both limbs. There is little or no infralenticular development of the internal capsule in sub-Mammalia (fig. 7).

Summary

1. The brain of the sub-Primates retains the primitive arterial network intact. Within this the various arteries have enlarged to meet the demands of the growing neopallium.

2. The cerebral arteries have retained their old stems of origin and are named as in Reptiles the anterior, middle and posterior cerebral arteries. The enlargement has been provided from the common anastomosis over the primordium neopallii.

3. The anterior cerebral artery is very little changed in origin and course, it passes to the medial wall of the hemisphere to supply the paraterminal body and antero-superior part of the hippocampus (now supracallosal hippocampus) and its share of the neopallium. Its primitive course is followed by small branches which run along the medial border of the palaeo-olfactorium to the olfactory stalk and supply the medial parts of both.

4. The middle cerebral artery arises from the stem of the internal carotid artery and runs in the posterior endorhinal fissure as usual. At the lateral angle of the fissure the main channel crosses the pyriform lobe to reach the lateral aspect of the neopallium most of which it supplies. Small branches in

the anterior endorhinal fissure follow the old course to the olfactory bulb and supply the lateral parts of the palaeo-olfactorium and bulb. The palaeo-olfactorium thus retains its arterial circle, but this is relatively much diminished in size.

5. The striate branches of the middle cerebral artery again fall into three groups. One through the pyriform cortex to the claustrum, one through the endorhinal fissure to the putamen, the body of the caudate nucleus, the lateral part of the globus pallidus and the lateral part of the amygdaloid nucleus and one through the lateral part of the palaeo-olfactorium to the intermediate parts of the globus pallidus and amygdaloid nucleus. It is considered that these are homologous with the similar arteries of Reptiles.

6. The anterior choroidal artery has developed from the inferior cerebral artery of *Sphenodon* and its anastomosis with the posterior cerebral artery. In Mammals this vessel acquires some choroidal branches from the posterior cerebral artery to the antero-inferior part of the choroid plexus. Of the basal ganglia it supplies the postero-medial part of the amygdaloid nucleus, most of the tail of the caudate nucleus and most of the globus pallidus. It is considered that the tail of the caudate nucleus is the split-off posterior part of the primitive amygdala.

7. The posterior cerebral artery has had its field of supply moved posteriorly with the dorso-posterior expansion of the hemisphere. As a consequence, the vessel has shifted its stem posteriorly to maintain its blood supply from the nearest source. This it has done by employing successively posterior stems of origin. Eventually the posterior cerebral artery has come to receive its blood from anterior mid-brain channels which enlarge to carry the increased volume of blood. At the same time the basilar artery has enlarged to supply this greater volume of blood and the posterior cerebral artery appears to arise directly from the basilar. The successive stems of origin used are existing anastomotic channels from the primitive network, they revert to their former state when no longer required.

8. The posterior cerebral artery supplies most of the hippocampus, the posterior parts of the inferior, medial and lateral surfaces of the hemisphere, a small portion of the tail of the caudate nucleus and the anterior part of the mid-brain. The supply to the tail of the caudate nucleus corresponds with the supply from the homologous vessel to the posterior part of the primitive amygdala of Reptiles.

9. The cerebral arteries all anastomose at the periphery of their superficial fields of supply and maintain the primitive vascular network.

10. The evidence of the blood supply supports the view that the hypopallium has given rise to the claustrum, putamen, body and some of the head of the caudate nucleus and the antero-lateral part of the amygdaloid nucleus. The palaeo-striatum has formed the ventro-medial part of the head of the caudate-putamen mass and the globus pallidus; the primitive amygdala the

postero-medial part of the amygdaloid nucleus and the tail of the caudate nucleus.

PRIMATES

The cerebral arteries were examined in lemurs, apes and Man. Except in the case of the lemur whose vessels were somewhat anomalous, the arteries were so similar that the description of one will suffice. Change in the brain in the passage from sub-Primates to Man is of degree only. In the acquisition of the neopallium and corpus callosum the Mammals had accomplished their most difficult task and further alteration is expressed in the growing dominance of these structures. The arteries show little difference. Their pattern, course, and distribution habits have become fixed and, but for the increased supply to the enlarged neopallium, they are the same. The cerebral hemispheres in Man have carried the dorso-posterior expansion to an extreme degree. The mid-brain is entirely hidden and the bending of the pyriform lobe is so acute that its angle is buried with the insula. The corpus callosum has stretched the supracallosal hippocampus to an attenuated remnant, the cavum septi is closed in front, the internal capsular fibres have increased enormously and the tail of the caudate nucleus is drawn out to a thin band. The palaeo- and neo-olfactoria have been thrust away to the basal and medial surfaces of the hemisphere. These structures are still present, however, and despite the dominance of the neopallium, they demand and receive the same blood supply as they have always enjoyed.

The forebrain arteries of Man have been studied extensively by many workers—Duret(12), Heubner(36), Kolisko(35), Beevor(37), Aitken(38), and Shellshear(6). The majority have been content to describe what they found together with variations from what they considered to be the normal. Shellshear, alone, has tried to correlate evolutionary changes in the brains of apes and Man with the morphology of the arteries. He has dealt thoroughly with the cortical distribution of the arteries and his correlation can be extended with advantage to non-cortical areas.

The posterior cerebral artery has reached its ultimate posterior stem of origin, its field of supply lies almost directly over the mid-brain and it employs exclusively mid-brain vessels for its source of blood. Even in Man, however, some of the arteries to the anterior part of the mid-brain may arise separately from the basilar artery. More frequently they come from the posterior cerebral stem close to its origin. In Man, too, cases have been reported where the posterior cerebral artery obtained most of its blood from the internal carotid artery through the posterior communicating or anterior choroidal arteries. Such examples indicate the route by which the origin of the posterior cerebral artery has travelled backwards. The distribution of this vessel is in all ways comparable with that of lower Mammals: the posterior part of the general cortex and pyriform lobe, most of the hippocampal formation and choroid plexus of the third and lateral ventricles and a small part of the tail of the caudate nucleus. It anastomoses with the anterior cerebral artery over

the posterior part of the supracallosal hippocampus and general cortex of the dorso-medial wall of the hemisphere, with the middle cerebral artery over the posterior part of the pyriform cortex and the temporal and occipital lobes and with the anterior choroidal artery over the pyriform cortex, the lateral geniculate body and antero-inferior parts of the hippocampal formation and in the choroid plexus of the lateral ventricle.

The anterior choroidal artery, with the elongation of the choroidal fissure, has acquired more choroidal branches but is otherwise little changed. It supplies some of the pyriform cortex, the postero-medial part of the amygda-
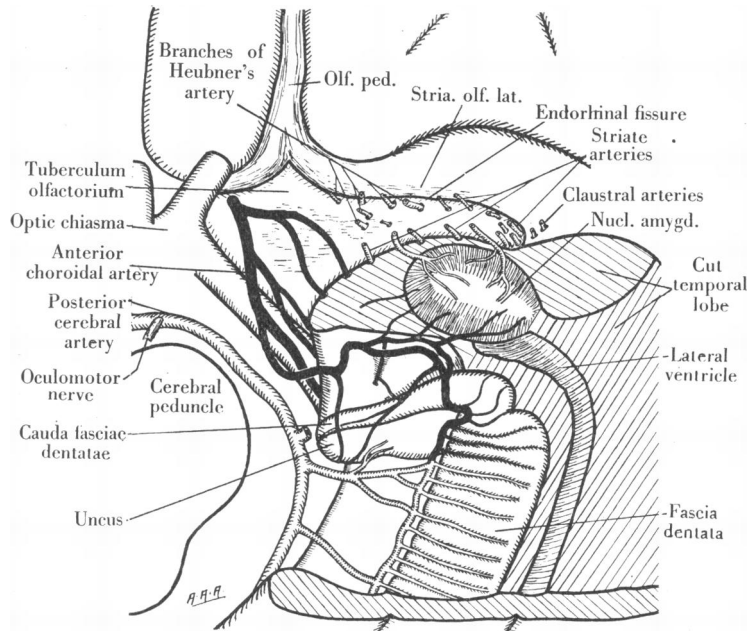

Fig. 8. Human brain dissected from the base to show the distribution of the striatal branches through the anterior perforated space and endorhinal fissure. This shows also the double blood supply to the amygdaloid nucleus and the distribution of the arteries to the uncus and fascia dentata. Anterior choroidal artery black.

loid nucleus, the uncus and the antero-inferior part of the hippocampal formation. It sends branches to the posterior two-thirds of the optic tract and the lateral part of the lateral geniculate body, the middle third of the crus, most of the tail of the caudate nucleus and the antero-inferior part of the choroid plexus of the lateral ventricle. Perforating vessels pass to the upper parts of the red nucleus and substantia nigra, frequently to the ventro-lateral nucleus of the thalamus and to the corpus subthalamicum. Others reach the beginning of the optic radiation, most of the medial part of the globus pallidus and the posterior two-thirds of the posterior limb of the internal capsule to the upper level of the globus pallidus (figs. 8, 9 and 10).

The middle cerebral artery supplies most of the area involved in the recent development of the cortex and shows some important changes. The bending of the endorhinal fissure has caused the anterior and posterior endorhinal fissures to lie almost parallel (fig. 5 D). The main trunk of the middle cerebral artery arises from the stem of the internal carotid artery and runs in the posterior endorhinal fissure. Over the limen insulae the artery leaves the fissure and crosses the pyriform lobe to reach the general cortex as in sub-Primates. The small branches in the anterior endorhinal fissure show the greatest changes. These branches dwindle as they pass medially away from their source of blood and as they approach the anterior cerebral artery the anastomoses with this vessel enlarge to supply the added field. Thus the anterior cerebral artery comes to supply regions which rightfully belong to the middle cerebral. This usurpation occurs chiefly in the most medial (morphologically anterior) part of the endorhinal fissure and the striate vessels in this region receive their blood from the anterior cerebral artery. The anterior cerebral artery also takes over the supply of some of the originally lateral part of the palaeo-olfactorium.

Other changes are apparent in this region. With the approximation of the anterior and posterior endorhinal fissures the anastomoses over and around the palaeo-olfactorium become crowded and there are too many for their requirements. One large channel will suffice and only one anastomosis is retained at the original standard. The remainder dwindle, but persist as tiny anastomotic channels which are never described. The single large vessel obtains nearly all of its blood from the anterior cerebral artery and the connection with the middle cerebral is reduced to a rudiment. The artery is usually referred to as the artery of Heubner, but Shellshear[4] has called it the anterior recurrent cerebral artery. Shellshear, too, has described its connection with the middle cerebral artery (see fig. 5 A–D).

Heubner's artery is the survivor of a series of anastomotic channels over and around the palaeo-olfactorium—the most primitive cerebral vascular system—and varies greatly in origin and course. Variations in origin depend upon which anastomotic channel—anterior, middle or posterior—is used as the stem of origin, and the vessel may arise early or late from the anterior cerebral artery. Variations in course depend upon which particular channel is picked out from the network over the palaeo-olfactorium, and the artery may cross this anteriorly or posteriorly or in an intermediate position, or through a trunk which has been derived from parts of all. Whatever its origin and course, the artery of Heubner always supplies the anterior cerebral field, and variations of its total area of distribution depend upon how much of the middle cerebral field it has taken over and how much has been left for the middle cerebral itself to supply.

The middle cerebral artery has been pulled away from its primitive anterior field of supply, and this field included the lateral part of the olfactory bulb. Again the anterior cerebral artery performs its vicarious function and takes

over this area and in Primates it supplies not only both sides of the olfactory bulb but also spreads out laterally to reach the medial part of the orbital surface of the frontal lobe (fig. 5 D). Thus the anterior recurrent cerebral artery affords one of the best examples of the principles of economy of distribution and convenience of source. Since there were too many arteries in this
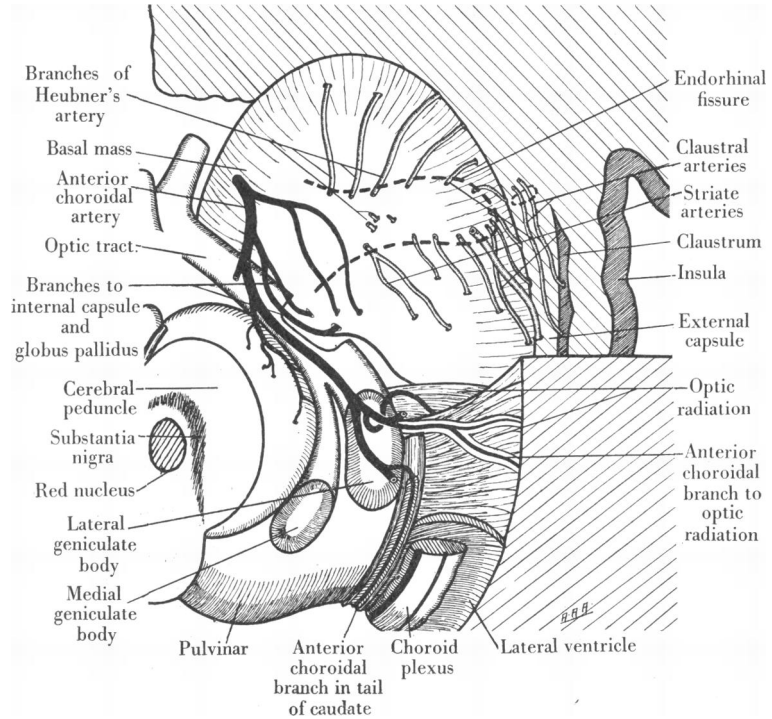

Fig. 9. Human brain, dissection from the base leaving the striatum and its arteries intact. The amygdaloid nucleus has been removed and the position of the endorhinal fissure is indicated by the broken heavy line. A segment has been removed from the optic tract to show how branches of the anterior choroidal artery reach the posterior limb of the internal capsule and the globus pallidus; a branch of the same artery has been dissected in the tail of the caudate nucleus, and the roof of the inferior horn of the lateral ventricle has been partly removed to show how branches of the anterior choroidal artery supply the first part of the optic radiation. Note that the claustral arteries do not pierce the endorhinal fissure but pass through the pyriform cortex to reach the external capsule. Anterior choroidal artery black.

region one was kept to act for all; because the field of supply was pushed away from the middle cerebral artery towards the anterior cerebral this vessel has taken over the supply. No new vessels have appeared and none has been lost. Some channels have enlarged and others dwindled but they are the anastomotic vessels that have always been present. The terminal arterioles are the same whether they receive their blood from the anterior or from the middle cerebral artery.
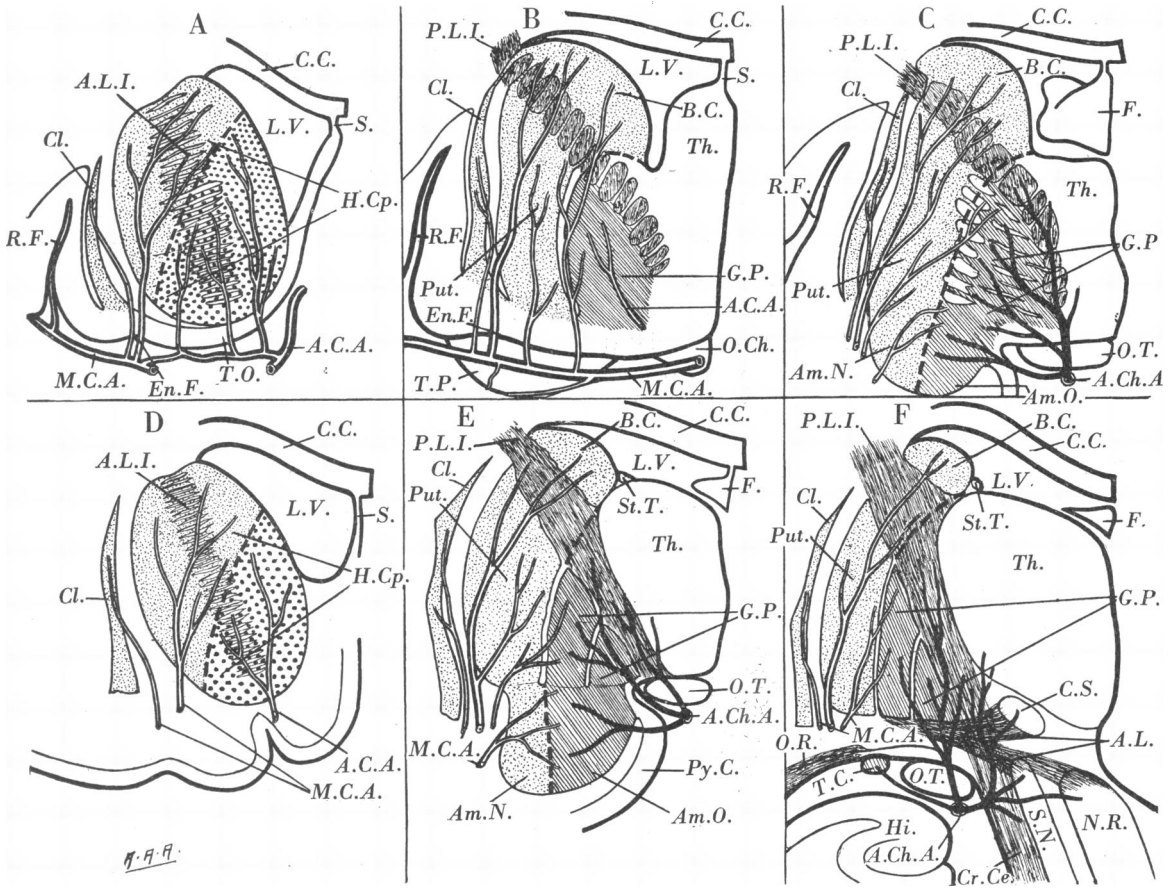
Fig. 10. A series of sections through the basal ganglia of an ungulate (*R. tarandus*, A. B, C) and of a human brain (D, E, F) showing the relation of the arteries. Hypopallium—stippled; palaeo-striatal part of head of caudate-putamen mass—large dots; old amygdala and globus pallidus—oblique lines. Note the three groups of striate branches from the middle cerebral artery and how the most medial of these reach the lateral part of the palaeo-striatum, a branch of the anterior cerebral artery to the globus pallidus (B) and the continuity of the putamen with the new amygdala and the globus pallidus with the old amygdala. The break through of the internal capsule is less complete in the reindeer than in Man. Anterior choroidal artery depicted in black. (Semi-schematic, but based on a large number of sections and dissections of both brains.)

A.C.A. anterior cerebral artery; *A.Ch.A.* anterior choroidal artery; *A.L.* ansa lenti-cularis; *A.L.I.* anterior limb of internal capsule; *Am.N.* new amygdala; *Am.O.* old amygdala; *B.C.* body of caudate; *C.C.* corpus callosum; *C.S.* corpus subthalamicum; *Cl.* claustrum; *Cr.Ce.* crus cerebri; *En.F.* endorhinal fissure; *F.* fornix; *G.P.* globus pallidus; *H.Cp.* caudate-putamen head; *Hi.* hippocampus; *L.V.* lateral ventricle; *M.C.A.* middle cerebral artery; *N.R.* red nucleus; *O.Ch.* optic chiasma; *O.R.* optic radiation; *O.T.* optic tract; *P.L.I.* pos-terior limb of internal capsule; *Put.* putamen; *Py.C.* pyriform cortex; *R.F.* rhinal fissure; *S.* Septum; *S.N.* substantia nigra; *St.T.* stria terminalis; *T.C.* tail of caudate; *Th.* thalamus; *T.O.* tuberculum olfactorium; *T.P.* temporal pole.

The middle cerebral artery supplies most of the pyriform lobe and the antero-lateral part of the amygdaloid nucleus, the supero-lateral part of the head of the caudate-putamen mass and the body of the caudate nucleus, the lateral part of the globus pallidus, the upper parts of both limbs of the internal capsule and most of the lateral part of the general cortex. The striatal branches are arranged in the same three groups as in Reptiles: through the pyriform cortex to the claustrum (as was also shown by Shellshear(3)), through the endorhinal fissure to the lateral parts of the globus pallidus and amygdaloid nucleus, to the putamen and the body of the caudate nucleus and through the palaeo-olfactorium to the intermediate parts of the globus pallidus and amygdaloid nucleus. The only change is that the anterior cerebral artery has come to supply the most medial (morphologically anterior) striate arteries.

With the bending of the endorhinal fissure the most anterior and posterior extremities have become pulled away from the base of the external capsule which they must eventually reach; thus, as the fissure becomes more and more flexed, the striate branches at the angle enlarge and those at the medial ends dwindle (fig. 5 A–D). In an ascending phylogenetic scale there is an accumulation of large arteries at the lateral angle of the fissure and a progressively dwindling series passing medially (fig. 8). This has been shown by Aitken, Elliot Smith and Shellshear(3), Duret called the largest of these vessels the lenticulo-striate artery and Charcot showed(39) that it was the artery most frequently involved in cerebral haemorrhage. The concentration of a great number of arteries at the base of the external capsule (fig. 9)—a greater number than in any other part of the brain—explains why Charcot called this the site of election for cerebral haemorrhage. The chances of arterial rupture here are at least twice as great as anywhere else.

The anterior cerebral artery presents little change apart from the reduction in palaeo-olfactory anastomoses to form Heubner's artery, and the usurpation

---

Legend to Fig. 11

Fig. 11. Schema to illustrate the formation of the human striatum. A, amphibian, with the palaeo-striatum well differentiated and the primordium hypopallii (*P. Hyp.*) loosely applied, the arteries as in fig. 3. B, *Sphenodon*, the basal mass well compacted and the arteries differentiated, the broken thick line indicates the region of break through of the internal capsule. C, lower Mammal, the arrows indicate the direction of the capsular fibres, note that the tail of the caudate nucleus is the split-off posterior part of the old amygdala and retains its original blood supply, also the continuity of the new amygdala with the putamen and how the striatal branches pass between the claustrum and putamen to reach the body of the caudate. D, Primate, the dorso-posterior expansion of the hemisphere has drawn the tail of the caudate nucleus in the same direction, and the increase in capsular fibres has accentuated the separation of the caudate from the rest of the basal mass. In particular note the formation of an infralenticular portion of the internal capsule.

Hypopallium—stippled finely; palaeo-striatum and old amygdala—oblique lines; palaeo-striatal part of head of caudate-putamen mass—large dots; *Am.* amygdaloid nucleus; *An.* anastomosis over the pyriform lobe between the middle and posterior cerebral arteries; *C.P.A.* posterior communicating artery; *I.C.* internal capsule; *L.O.A.* lateral olfactory artery. Remaining letters as in previous diagrams.
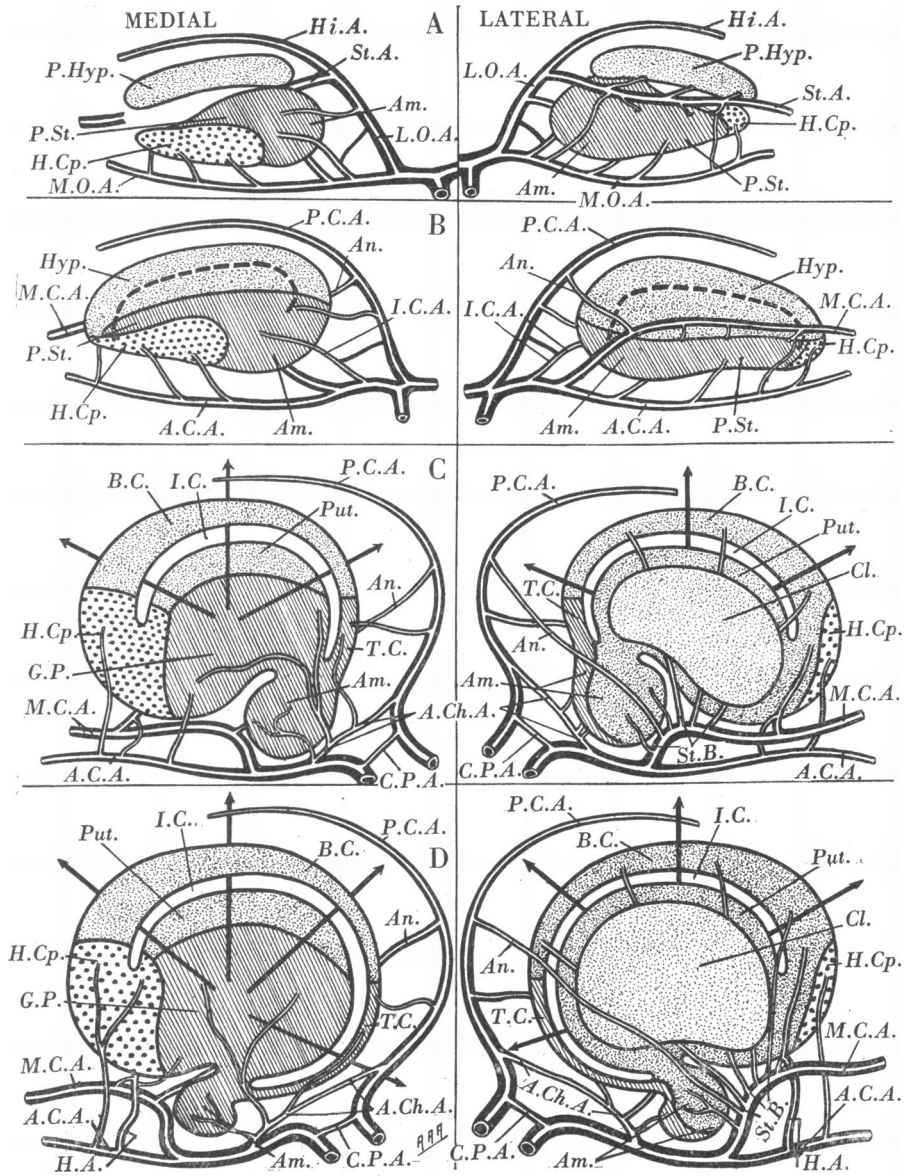
Fig. 11.

of part of the territory of the middle cerebral artery. The vessel forms the anterior continuation of the cranial division of the internal carotid artery as in lower Mammals and is distributed in a comparable manner. The main trunk passes to the medial wall of the hemisphere where it supplies the para-terminal region containing the three great commissures and the septum pellucidum, the supracallosal hippocampal vestiges, the general cortex of the anterior two-thirds of the medial wall of the hemisphere and of the upper part of the lateral wall to about the same extent. (For a detailed account of the cortical distribution of the various cerebral arteries see Shellshear's papers on the orang, chimpanzee and Man.) The primitive course of the anterior cerebral artery is again represented by small branches which run anteriorly along the medial border of the palaeo-olfactorium. These supply the anterior part of the globus pallidus and the infero-medial part of the head of the caudate-putamen mass as well as the inferior half or so of the anterior limb of the internal capsule (fig. 10). The branches also supply the medial parts of the tuberculum olfactorium and olfactory bulb and the medial orbital border and (in consequence of the adoption of some of the middle cerebral field) the lateral part of the olfactory bulb, some of the orbital surface of the frontal lobe lateral to the bulb and a varying amount of the anterior part of the striatum.

Shellshear has shown that the three major arteries always anastomose at the periphery of their cortical fields of supply. His lines of vascular demarcation are too well known to require further discussion. To this may be added that there is no such thing as a non-anastomotic artery on the surface of the brain although the anastomoses are not always sufficiently large to compensate for occlusion of some of them. Every vessel joins another and the primitive network whence they have all arisen remains intact. No cerebral artery becomes an end-artery until it has entered the brain substance, but once within the brain no artery appears ever to join another. When it enters the brain its distribution is fixed and it proceeds alone to the destination which has been its own ever since that part of the brain first appeared. There is no evidence to support Kolisko's statement that the middle cerebral, anterior choroidal and posterior communicating arteries anastomose in the upper part of the genu of the internal capsule. I have never found any evidence of this, or any other anastomosis within the brain substance. Beevor and Aitken have both denied the existence of the lenticulo-optic artery of Duret and Charcot. In this enquiry no trace of this vessel could be found.

Summary

1. In apes and Man the cerebral arteries form the same closed network as in lower animals. The major channels picked out—the anterior, middle and posterior cerebral arteries—are the same.

2. The anterior cerebral artery follows the same course as in sub-Primates, but has taken over some of the field of the middle cerebral artery because of

the bending of the endorhinal fissure. Thus, in addition to its own field of supply, the anterior cerebral artery comes to supply some of the most anterior part of the hypopallial derivatives, the lateral part of the olfactory bulb and some of the orbital surface of the frontal lobe. The expansion of the general cortex has increased the area of neopallial distribution of this vessel.

3. The middle cerebral artery has surrendered some of its striatal and palaeo-olfactorial distribution to the anterior cerebral artery. Otherwise its field of supply has only altered in so far as the growing neopallium demanded.

4. The anterior choroidal artery has acquired additional hippocampal and choroidal branches. Otherwise its field of supply is little changed. This vessel supplies most of the globus pallidus, usually the corpus subthalamicum and ventro-lateral nucleus of the thalamus, and the upper parts of the substantia nigra and red nucleus as well as the ansa lenticularis. Kinnier Wilson (40) has shown that the globus pallidus is connected with these other cell masses through the ansa, and it would appear that this part of the anterior choroidal artery is the channel chosen to supply the components of this single functional unit (see fig. 10).

5. The posterior cerebral artery has consolidated its most posterior stem of origin in the anterior mid-brain channels, but variations are not infrequent. The cortical field of supply shows an increase to meet the greater neopallial demands. Its supply to the tail of the caudate nucleus may be taken over by the anterior choroidal artery as Beevor has shown.

6. The basal ganglia have developed upon the lines laid down in lower Mammals. The palaeo-striatum has formed the medial part of the amygdaloid nucleus and the tail of the caudate nucleus (primitive amygdala), the globus pallidus and infero-medial part of the head of the caudate-putamen mass. The hypopallium has developed into claustrum, putamen, supero-lateral part of the head of the caudate-putamen mass, the body of the caudate nucleus and the antero-lateral part of the amygdaloid nucleus. The blood supply remains constant.

7. The blood supply of the internal capsule is the same as in lower Mammals, but it should be noted that the internal capsule has increased greatly in size and has a definite infralenticular part which has nearly cut off the amygdaloid nucleus from the rest of the basal mass. This has caused a considerable attenuation of the tail of the caudate nucleus (fig. 11).

8. Whenever the terminal arterioles enter the brain to reach their final area of distribution they become end-arteries. There is no evidence that subcortical arterial anastomosis ever occurs.

GENERAL SUMMARY

1. In Fishes the fore-brain is composed mainly of palaeo-olfactorium and is enveloped within a closed network of arteries. In this network two channels—the medial and lateral olfactory arteries—have become enlarged

to carry the main stream of blood. These channels run close to the grooves separating the palaeo- and neo-olfactoria and share equally the blood supply of both. The palaeo-olfactorium receives the richer supply.

2. In the frog the arterial network remains intact. The vessels reflect the regressive state of the brain but show an advance upon the condition of the Fish. The common ancestor of frog and Reptile probably possessed separate anterior, middle and posterior cerebral arteries, but the frog has only medial and lateral olfactory arteries. The medial olfactory artery is the same as in the Fish, but the lateral, having shifted its origin posteriorly, arises from one of the diencephalic vessels. It has three main sets of branches: hippocampal, pyriform and striatal. The striatal branch is the representative of the lateral olfactory artery of the Fish while the hippocampal and pyriform branches have evolved from the arterial anastomosis over the neo-olfactorium.

3. Reptiles have formed separate anterior, middle and posterior cerebral arteries from the arterial network. The anterior cerebral artery has developed from the medial olfactory artery but its main stream of blood has been diverted to the medial wall of the hemisphere, especially to the paraterminal body. The middle cerebral artery represents the combined pyriform and striatal branches of the lateral olfactory artery of the frog, but it has a direct connection with the cranial division of the internal carotid artery which is diminutive in the frog. The posterior cerebral artery has arisen from the lateral olfactory artery and is devoted mainly to the hippocampal region.

4. In lower Mammals the cerebral arteries have to cope with the demands of the growing neopallium. The dorso-posterior expansion of the hemispheres has caused the posterior cerebral artery to employ successively posterior stems of origin until it receives its blood through anterior mid-brain channels. The basilar artery enlarges to carry the increased supply. The posterior cerebral artery still supplies most of the hippocampal formation and has enlarged to meet the demands of its share of the neopallium. The anterior choroidal artery has evolved from the inferior cerebral artery, cf. *Sphenodon* (and its representative in other Reptiles) by the acquisition of choroidal branches from the posterior cerebral artery. The middle cerebral artery sends most of its blood to the pyriform lobe and neopallium but its old course and distribution in the anterior endorhinal fissure are subserved by small branches running forwards to the olfactory bulb. The anterior cerebral artery again sends most of its blood to the medial hemisphere wall to supply the paraterminal body and commissures, and the supracallosal hippocampus, and especially the neopallium. The three cerebral arteries anastomose at the periphery of their fields of supply and maintain the primitive vascular network.

5. In Primates the cerebral arteries complete the developmental tendencies of the sub-Primates. The posterior cerebral artery is usually constant in its mid-brain origin. The anterior choroidal artery has acquired some further choroidal branches. The middle cerebral artery observes the same course and

relations as in lower Mammals but has surrendered some of its supply to the anterior cerebral artery. The anterior cerebral artery has only altered in its acquisition of some of the middle cerebral field of supply. The primitive network is intact.

6. The evidence of vascular distribution supports the view that the hypopallium of Reptiles has formed the claustrum, putamen, body of the caudate nucleus, supero-lateral part of the head of the caudate-putamen mass and the lateral part of the amygdaloid nucleus. The palaeo-striatum has given rise to the infero-medial part of the head of the caudate-putamen mass, the globus pallidus, the medial part of the amygdaloid nucleus and the tail of the caudate nucleus. The tail of the caudate nucleus appears to be the incompletely split-off part of the primitive amygdala. The vascular supply of the various parts of the basal ganglia is constant from Fish to Mammal.

7. Heubner's artery is the survivor of the anastomoses over and around the palaeo-olfactorium. As this primitive vascular ring becomes crowded together with the closing up of the endorhinal fissure most of the channels revert to their originally diminutive condition, but one remains large. This vessel obtains most of its blood from the anterior cerebral artery but retains its old connection with the middle cerebral artery. It supplies most of the palaeo-olfactorium and the infero-medial part of the head of the caudate-putamen mass and the anterior part of the globus pallidus; from the middle cerebral artery it takes over the supply of some of the most anterior part of the corpus striatum.

8. The internal capsule has a composite blood supply. The anterior cerebral artery supplies the inferior half of the anterior limb, and the anterior choroidal the posterior two-thirds of the posterior limb to the upper level of the globus pallidus. The middle cerebral artery supplies the upper parts of both limbs and the posterior communicating artery the region of the genu.

9. However much cerebral arteries anastomose over the surface of the brain, they become end-arteries whenever they enter the brain substance. There is no evidence that sub-cortical anastomoses ever occur.

10. Every cerebral artery has evolved from a primitive vascular network enveloping the brain. From this net channels have become enlarged in response to the demands of the parts they supply. The principles which govern the formation of cerebral arteries are:

(*a*) Functional constancy: whenever a neural mechanism evolves an artery develops for its supply and this neuro-vascular mechanism remains constant throughout evolution.

(*b*) Economy of distribution: when two or more end-arteries lie close together they employ a common vessel of distribution.

(*c*) Convenience of source: if a distributing channel becomes separated from its source it obtains blood from a nearer source by the enlargement of existing anastomotic channels.

ACKNOWLEDGMENTS

REFERENCES

(1) HOFMANN, M. (1900). *Zeits. f. Morph. u. Anthrop.* Bd. II, S. 248.
(2) DE VRIESE, BERTHA (1904). *Arch. de Biol.* t. XXI, p. 357.
(3) SHELLSHEAR, J. L. (1920). *J. Anat.* vol. LV, p. 27.
(4) —— (1927). *J. Anat.* vol. LXI, p. 167.
(5) —— (1927). *J. Anat.* vol. LXI, p. 279.
(6) —— (1927). *Brain*, vol. L, pt. 2, p. 236.
(7) —— (1929). *Phil. Trans. Roy. Soc.* Ser. B, vol. CCXVIII, p. 1.
(8) —— (1930). *J. Anat.* vol. LXV, p. 45.
(9) ABBIE, A. A. (1933). *J. Anat.* vol. LXVII, p. 491.
(10) —— (1933). *Brain*, vol. LVI, p. 233.
(11) GUYOT, J. (1825). Quoted by Duret.
(12) DURET, H. (1874). *Arch. de Physiol.* No. 1, pp. 60, 316, 664, 919.
(13) KAPPERS, C. U. ARIËNS (1933). *Proc. Kon. Akad. v. Wetens.* vol. XXXVI, p. 52.
(14) SMITH, G. ELLIOT (1908). *Anat. Anz.* Bd. XXXIII, S. 513.
(15) —— (1910). *Lancet*, Jan. 1, 15, 22, pp. 1, 147, 221.
(16) DART, RAYMOND A. (1925). *Acta Zool.* Bd. VI, S. 224.
(17) —— (1920). *J. Anat.* vol. LV, p. 1.
(18) JOHNSTON, J. B. (1922–3). *J. Comp. Neur.* vol. XXXV, p. 337.
(19) —— (1923–4). *J. Comp. Neur.* vol. XXXVI, p. 143.
(20) SMITH, G. ELLIOT (1902). *Catalogue of the Museum of the Royal College of Surgeons*, vol. II, Physiol. Ser. pp. 107 and 123.
(21) KAPPERS, C. U. ARIËNS (1921). *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen*, S. 999. Haarlem.
(22) HERRICK, C. J. (1921). *J. Comp. Neur.* vol. XXXIII, p. 213.
(23) HINES, MARION (1922–3). *J. Comp. Neur.* vol. XXXV, p. 483.
(24) HERRICK, C. J. (1930). *Brains of Rats and Men*, p. 103. Chicago.
(25) KAPPERS, C. U. ARIËNS (1928). *Three Lectures on Neurobiotaxis and other Subjects*, p. 37. Copenhagen.
(26) EDINGER, L. (1896). *Abhandl. der Senckenberg. Naturforsch. Gesellsch.* Bd. XIX, S. 313.
(27) DENDY, A. (1909). *Phil. Trans. Roy. Soc.* Ser. B, vol. CC, p. 403.
(28) CROSBY, E. C. (1917). *J. Comp. Neur.* vol. XXVII, p. 325.
(29) SMITH, G. ELLIOT (1919). *J. Anat.* vol. LIII, p. 271.
(30) CAIRNEY, J. (1926). *J. Comp. Neur.* vol. XLII, p. 255.
(31) DURWARD, A. (1930). *J. Anat.* vol. LXV, p. 8.
(32) SONNTAG, C. F. and WOOLLARD, H. H. (1925). *Proc. Zool. Soc.* pt. 3, p. 1185.
(33) SMITH, G. ELLIOT (1894). *Proc. Linn. Soc. of N.S.W.* vol. IX, p. 635.
(34) —— (1897). *Trans. Linn. Soc. Lond.* vol. VII, p. 47.
(35) KOLISKO, A. (1891). *Ueber die Beziehung der Arteria choroidea anterior zum hinteren Schenkel der inneren Kapsel des Gehirnes.* Wien.
(36) HEUBNER, O. (1874). *Die luetische Erkrankung der Hirnarterien.* Leipzig.
(37) BEEVOR, C. E. (1909). *Phil. Trans. Roy. Soc.* Ser. B, vol. CC, p. 1.
(38) AITKEN, H. F. (1909). *Boston Med. and Surg. Journ.* vol. CLX, No. 18.
(39) CHARCOT, J. M. (1876–80). *Localisations dans les maladies du Cerveau*, p. 104. Paris.
(40) WILSON, S. KINNIER (1913). *Brain*, vol. XXXVI, p. 427.