Development of Intracranial Arterial Patterns in Turtles [1]

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ABSTRACT Observations on chelonian intracranial arteries are based primarily on the adult condition in *Pseudemys scripta* and on a series of *Chrysemys marginata* embryos. Those vessels which show major modifications are the anterior cerebral, posterior cerebral, cerebellar, and internal auditory arteries. The distal portion of the embryonic anterior cerebral is acquired by more medial vessels; from the proximal portion develops the middle cerebral which becomes the major source of supply for the lateral surface of the adult cerebral hemisphere. The posterior cerebral appears early in development and eventually supplies branches to the epiphysis, posterior portions of the hemisphere, olfactory regions, anterior face of the optic lobe, and choroid plexus of the third and lateral ventricles. The cerebellar and internal auditory arteries show similarities in development, each initially supplying the area immediately surrounding a nerve root and then acquiring larger areas of distribution by means of anastomoses with nearby medullary vessels.

Although the vascular system assumes a fundamental role in the ontogenetic history of the brain, relatively few studies have been directly concerned with the development of the intracranial arteries. Such accounts have been confined largely to mammals (Tandler, '02; Mall, '04; de Vriese, '05; Padget, '48) and to birds (Hafferl, '21; Hughes, '34). Grodzinski ('28, '47) has made some developmental studies of these arteries in the snake *Tropidonotus* and in fish.

For such investigations reptiles are particularly useful, since their brains show most of the intracranial arterial components present in more advanced vertebrates. Moreover, since the reptilian brain does not undergo drastic architectural modifications resulting from extensive cerebral overgrowth, the development of the intracranial arteries can be followed with less difficulty than is the case in mammals. The purpose of this paper, therefore, is to present observations on the ontogeny of these arteries as found in embryos of the turtle, *Chrysemys marginata*. A description of the adult condition in *Pseudemys scripta* will be included. In this study, attention is centered solely upon the surface vessels, and thus no mention will be made of intracerebral capillary beds. Occasional references to extracranial vessels, however, are obviously unavoidable.

The majority of studies on the chelonian intracranial arteries have been based on *Testudo*. Schepers ('39) gives fairly detailed descriptions of seven *Testudo geometrica* adults; other authors who have worked on this genus include Hofmann ('00), Beddard ('05), Shindo ('14), and Kappers ('33). The last also describes a few specimens of *Chelone midas* and *Damonia subtrijuga*, but his account is limited to the arteries of the forebrain. Descriptions of the intracranial arteries in *Emys europaea* may be found in the studies of Bojanus (1819–21) and Klinckowström (1890). All of these accounts are based on adult material; there seem to be no studies on the ontogeny of these vessels in turtles.

MATERIALS AND METHODS

Six single-injected specimens of *Pseudemys scripta* were used as representatives for the adult condition. The brains were removed with the arteries and nerve roots intact, and the vascular pattern was examined first macroscopically and then under a dissecting microscope at a magnification ranging from 25 × to 60 ×.

The embryonic material consisted of *Chrysemys marginata* embryos which were obtained from the Minot Embryological

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Collection of the Harvard Medical School. These embryos are listed in table 1. Serial sections in sagittal, transverse, and frontal planes were studied by means of a light microscope with a magnification of 17.5 × to 430 ×. Certain embryos were selected for graphic reconstructions which were made by tracing images projected onto transparent paper by means of a Promi projection microscope.

Since the intracranial arterial pattern was found to be essentially the same on both sides of the brain, only the vessels of the right side will be described, unless otherwise designated. In like manner, all of the plates depict the right side of the brain; the adult condition is represented by a free-hand drawing, and the diagrams of embryos are from reconstructions.

OBSERVATIONS AND RESULTS

Adult (fig. 1)

The distal portion of the internal carotid artery passes through the carotid canal in the floor of the basisphenoid bone. At the posterior limit of the sella turcica, the carotid sends off a tiny palatine branch which emerges from the canal by means of an anterolateral foramen. (The course of this artery was not traced beyond this point.)

The internal carotid then travels dorsally into the intracranial cavity where a strong post-hypophyseal anastomosis is formed with the corresponding artery of the opposite side. The internal carotid thereafter proceeds anterodorsally along the lateral wall of the hypophysis and gives off a slender orbital artery which extends

TABLE 1

Chrysemys marginata embryos from the Minot Collection. The following abbreviations are used for stains listed in column 5: AC, Alum cochineal; BC, Borax carmine; C, Cochineal; E, Eosine; LB, Lyons blue; OG, Orange G; S, Saffranine

Minot series number	Length	Plane	Thickness	Stain
	mm		μ	
1049	4.8	trans	6	BC and OG
1050	4.8	sag	8	BC and S
1056	5.0	sag	8	BC and OG
1475	5.1	front	8	BC and LB
1053	5.3	sag	6	BC and S
1057	5.5	front	8	BC and OG
1070	5.7	trans	8	BC and OG
1068	5.7	sag	8	BC and E
1071	5.8	sag	8	BC and E
1064	5.8	trans	8	BC and OG
1065	6.0	sag	8	BC and E
1059	6.1	sag	8	BC and E
2131	6.2	trans	10	C and OG
1062	6.5	sag	8	BC and OG
2132	7.0	trans	10	C and OG
1075	8.4	front	10	BC and LB
1074	8.6	sag	10	BC and E
1433	8.8	sag	10	BC and E
1085	9.0	sag	10	BC and OG
1079	9.6	trans	10	BC and OG
1478	9.7	sag	10	BC and E
1084	10.0	trans	10	BC and OG
1088	11.0	sag	10	BC and E
1479	11.5	sag	10	BC and E
1082	11.8	sag	10	BC and E
1090	16.8	trans	10	BC and OG
1091	17.4	sag	10	BC and E
1094	21.4	sag	10	BC and E
1099	26.4	sag	10	BC and E
1097	26.7	sag	10	BC and E
1101	31.7	sag	12	BC and E

anteriorly and which then emerges from the intracranial cavity through a foramen in the anterior region of the sella turcica. The orbital artery distributes several branches to the walls of the orbit and to the ocular muscles. Anterior to the origin of this vessel, the internal carotid (now referred to as the cerebral carotid) continues anterodorsally a short distance and bifurcates into anterior and posterior rami: the anterior and posterior encephalic arteries, respectively.

Anterior encephalic artery

The anterior encephalic passes ventral to the posterior pole of the hemisphere (the occipito-basal lobe of Herrick, 1891) and gives rise to the infundibular artery which travels ventrad, giving small twigs to the infundibulum and optic chiasma. The anterior encephalic next sends off the lateral choroidal artery which travels posteromedially behind the posterior pole of the hemisphere and then anteriorly along its medial wall. This artery sends several small vessels through the foramen of Monro into the choroid plexus of the lateral ventricle and then continues anterodorsally. The lateral choroidal next divides into several smaller vessels which form numerous anastomoses with branches of other arteries within the intercerebral fissure.

A fairly large ophthalmic artery arises from the anterior encephalic just anterior to the origin of the lateral choroidal. The

Abbreviations

A. Cer., Anterior cerebral
A. Com., Anterior communicating
A. Enc., Anterior encephalic
A. Orb., Anterior orbital
A.R. Cereb., Anterior ramus of cerebellar
A.R. Mes., Anterior ramus of mesencephalic
Bas., Basilar
Cereb., Cerebellar
D. Sp., Dorsal spinal
Epi., Epiphyseal
Eth., Ethmoidal
I. Aud., Internal auditory
I.C., Internal carotid
Inf., Infundibular
L. Chor., Lateral choroidal
L. Med., Lateral medullary
L. Olf., Lateral olfactory
M. Cer., Middle cerebral
M. Olf., Medial olfactory
Mes., Mesencephalic
Oph., Ophthalmic
Orb., Orbital
P. Cer., Posterior cerebral
P. Enc., Posterior encephalic
P.H.A., Post-hypophyseal anastomosis
P.R. Cereb., Posterior ramus of cerebellar
P.R. Mes., Posterior ramus of mesencephalic
Pal., Palatine
Sp. 1, First spinal
V. Sp., Ventral spinal

EXPLANATION OF FIGURES 1–6

Continuous line, unshaded vessels lie medially and are not visible in lateral view; broken line vessels represent corresponding structures of the opposite side.

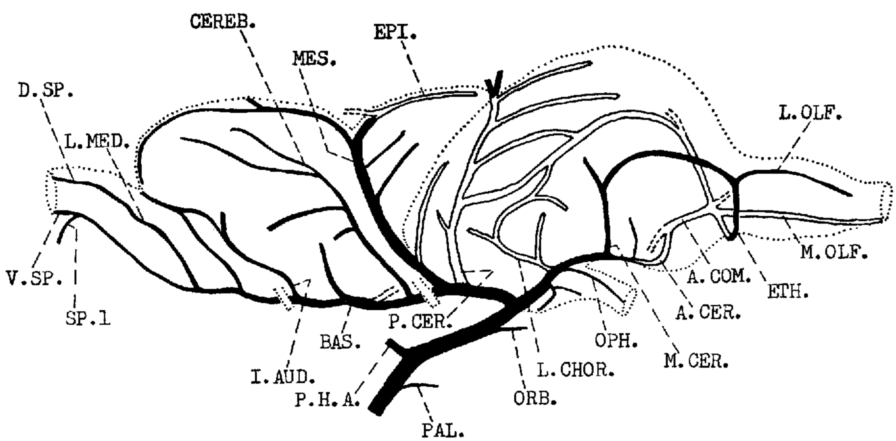

Fig. 1 Lateral view of brain in *Pseudemys scripta* adult.

ophthalmic travels along nerve II through the optic foramen; its course could not be followed beyond this point.

The anterior encephalic next begins to turn slightly mediad along the rim of the optic chiasma. Here several large vessels are sent dorsally along the lateral face of the hemisphere. The most prominent of these is the middle cerebral whose branches form anastomoses with neighboring arteries to provide a rich vascular network for this region of the hemisphere. (There is a certain amount of individual variation in the origin of the middle cerebral: in four cases this vessel arose anterior to the origin of the ophthalmic artery, while in two animals the middle cerebral originated immediately posterior to it.)

In addition to the branches which supply the lateral regions of the hemisphere, the middle cerebral also produces a long anterior ramus which continues anterolaterally and eventually is joined by the ethmoidal artery, to be described below. Beyond this junction the anterior ramus is designated as the lateral olfactory artery; this passes along the dorsolateral surface of the olfactory lobe and disappears near the origin of nerve I.

The anterior encephalic (now termed the anterior cerebral) continues mediad around the optic chiasma and passes into the ventral region of the intercerebral fissure, thus becoming completely hidden from a ventral view of the brain. Within this fissure the anterior cerebral unites with its mate from the opposite side to form the anterior communicating artery, which travels anteriorly between the two hemispheres to the region of the sulcus lobaris (coronal sulcus, Schepers, '39). This sulcus separates the hemisphere from the olfactory lobe.

The anterior communicating artery gives rise to a right and left ethmoidal artery. Each of these immediately sends forth a medial olfactory branch which travels anteriorly along the ventromedial aspect of the olfactory lobe and nerve. Each ethmoidal then continues laterad beneath the lobe, turns dorsally along its lateral face, and joins the anterior ramus of the middle cerebral. After giving rise to the right and left ethmoidals, the anterior communicating artery (still contained within the intercerebral fissure) turns dorsocaudally and merges with the fused portion of the two posterior cerebrals. The latter will be described presently.

Posterior encephalic artery

The posterior encephalic travels caudad and gives off the posterior cerebral artery, which passes beneath the posterior pole of the hemisphere and which continues along its mediodorsal aspect. In addition to numerous branches for this region of the hemisphere, the posterior cerebral also sends a branch to the epiphysis and to the choroid plexus of the third ventricle. The posterior cerebrals of both sides travel anteriorly in close association with one another and eventually unite to form a single median vessel. The latter then passes ventrad and merges with the anterior communicating artery.

Anastomoses are frequently found between the branches of the posterior cerebral and lateral choroidal arteries, since both vessels pass relatively close to each other in the posteromedial region of the hemisphere. From this intercommunicating network, branches originating from the posterior cerebral as well as from the anterior choroidal furnish blood to the choroid plexus of the lateral ventricle.

The next major outgrowth of the posterior encephalic is the mesencephalic artery. This large vessel originates anterior to nerve III and runs dorsoposteriorly between the optic lobe and cerebellum. The

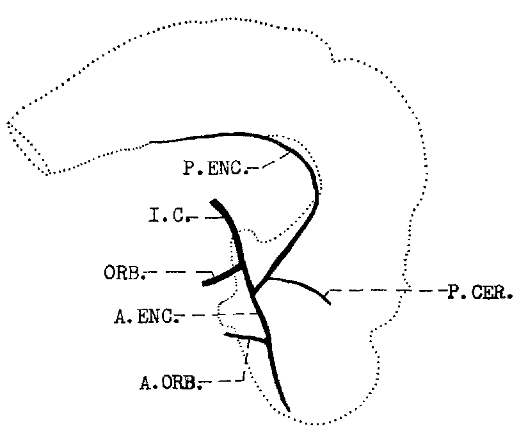

Fig. 2 Reconstruction of brain in *Chrysemys marginata* 5.1 mm embryo.

midbrain receives branches from the mesencephalic, and most of these travel obliquely upwards and somewhat parallel to one another. Some of these branches also pass onto the posteromedial surface of the hemisphere.

When the mesencephalic artery reaches the posterodorsal boundary of the midbrain, this vessel bifurcates into anterior and posterior branches. The anterior branch passes mediad and joins its counterpart from the other side to form the epiphyseal artery which proceeds anteriorly between the optic lobes. After sending branches to this region of the brain and to the choroid plexus of the third ventricle, this artery finally ends at the epiphysis.

The posterior branch of the mesencephalic distributes vessels over the dorsal region of the cerebellum. In the mid-region of the cerebellum, an anastomosis is formed between the posterior branches of both sides; each branch then continues along the caudal convexity of the cerebellum and enters the choroid plexus of the fourth ventricle.

After giving rise to the mesencephalic artery, the posterior encephalic passes medial to the root of nerve III, continues ventrally beneath the medulla, and gives rise to a large cerebellar artery just anterior to the origin of nerve V. The cerebellar ascends the lateral wall of the medulla and gives off branches to its anterior region, as well as a trigeminal ramus to nerve V. Some branches also pass over the flocculus and continue dorsoposteriorly along much of the cerebellar surface. These cerebellar rami frequently form anastomoses with outgrowths from the posterior branch of the mesencephalic.

Posterior to the origins of the cerebellar arteries, the two posterior encephalics turn medially and fuse with each other to form the basilar artery lying ventral to the medulla. This fused basilar was found in five of the six *Pseudemys* adults; in the remaining case, there was a cross-connection between the two posterior encephalics at the level of nerves VII-VIII, but the "basilar" remained paired throughout the length of the medulla.

In those specimens where the basilar is single, the exact site of fusion is highly variable. The two encephalics usually join immediately posterior to the origin of nerve V, although in one case the fusion occurred at the level of nerves VII–VIII. In another specimen, the basilar again became double beyond the origin of nerve X. In some of these adults, small arteries arise from this vessel, run parallel to it, and then reunite with it. For these reasons the adult basilar is a structure which is generally difficult to define.

The basilar artery sends a series of vessels dorsolaterally along each side of the medulla. Some of these medullary branches form anastomoses with each other. The major medullary vessels are usually given off in pairs (i.e., one member for each side), although occasionally one will originate just anterior to its mate.

Anterior to the root of nerve VI, the basilar gives off a prominent internal auditory artery. The latter travels posterodorsally and sends a branch to nerve VIII, after which point several anastomoses are formed with nearby medullary arteries from the basilar. The internal auditory also sends a ramus into the choroid plexus of the fourth ventricle.

The remaining medullary arteries sent along the lateral surface of the medulla often form connections with one another and, as mentioned above, with the internal auditory. The basilar then sends off the lateral medullary artery which travels posterodorsally and somewhat parallel to the other vessels. Near the posterodorsal boundary of the medulla, each lateral medullary turns directly posteriorly through the foramen magnum and joins the appropriate dorsal spinal artery which travels along the dorsolateral surface of the spinal cord. (Contrary to the condition of the ventral spinal artery, the dorsal spinals remain paired throughout their course along the spinal cord.)

Posterior to the origin of the lateral medullary artery, the basilar continues along the ventral side of the medulla. This artery then passes through the foramen magnum to become continuous with the ventral spinal artery. The single condition of the ventral spinal was found in all six specimens used in this study.

Immediately posterior to the foramen, the first pair of spinal arteries unites with the ventral spinal. These rather weak spinal arteries originate from the vertebrals on either side of the vertebral column. Although the spinal cord receives its supply by means of these vertebral and spinal arteries, the carotids serve as the primary source of blood for the brain.

Development

The following description is based on four developmental stages of *Chrysemys marginata*. The embryos were arbitrarily grouped into these stages on the basis of the condition of the brain, degree of intracranial arterial development, and extent of chondrification and ossification.

Stage I (4.8 mm–5.5 mm)

The five embryos of stage I range in length from 4.8 mm to 5.5 mm. On the basis of brain development, the 5.3 mm embryo actually appears to be the youngest of the group, followed in age respectively by the 4.8 mm, 5.0 mm, 5.1 mm, and 5.5 mm embryos. The intracranial pattern of the 5.1 mm embryo will serve as the basis for the following description.

The internal carotid artery extends anteriorly from the dorsal portion of the first aortic arch. In the region of the hypophysis, the internal carotid gives rise to an orbital artery which proceeds laterally toward the ventral region of the optic cup (fig. 2). The internal carotid (cerebral carotid) then passes anterodorsally along the lateral aspect of the infundibulum. At approximately the anterior limit of this structure, the cerebral carotid bifurcates into the anterior and posterior encephalic arteries.

The anterior encephalic extends forward along the ventrolateral walls of the brain and turns slightly dorsad in order to pass over the optic stalk. A short distance beyond the stalk, the anterior encephalic gives rise to a small anterior orbital artery which travels to the anterodorsal rim of the optic cup. The anterior encephalic then continues its course along the ventrolateral walls of the telencephalon and eventually disappears near its anterior limits.

The posterior encephalic artery travels caudad along the ventrolateral wall of the diencephalic region. A slender artery is sent dorsad and probably represents the precursor of the posterior cerebral artery. The posterior encephalic then bends along with the cranial flexure at the mesencephalon and continues its posterior course medial to the nerve roots. The artery becomes progressively thinner until it finally disappears at the level of nerves VII–VIII. Although the posterior encephalic sends several tiny vessels a short distance up the side of the midbrain and hindbrain, no prominent branches as yet supply these regions.

The anterior portion of the ventral spinal artery may be found in the posterior region of the hindbrain. This vessel extends along the spinal cord but is very weakly developed. The ventral spinal arteries of both sides apparently do not fuse with each other nor is there as yet any connection with the distal ends of their respective posterior encephalic arteries.

Stage II (5.7 mm–8.6 mm)

The following description is based on the 6.0 mm embryo. The internal carotid artery travels dorsomedially and reaches the posterolateral margin of the hypophysis. Here the internal carotid sends mediad a small vessel which fuses with its counterpart from the other side (fig. 3). This delicate post-hypophyseal anastomosis is present in 10 of the 11 embryos of this stage. In the remaining specimen, each internal carotid sends a short vessel medially, but no connection between the two could be found.

The internal carotid continues anterodorsally and gives off the orbital artery near the ventral rim of the infundibulum. This artery proceeds laterally toward the posterior part of the orbit. The internal carotid (cerebral carotid) extends a short way up the side of the infundibulum and then divides into the anterior and posterior encephalic arteries.

The anterior encephalic artery first gives rise to a small posteroventral twig, the infundibular artery, which supplies the infundibular and hypothalamic regions. At the posterior margin of the optic stalk, the anterior encephalic next sends off a weak ophthalmic artery, which can be more easily identified in the later embryos of this stage.

The lateral choroidal artery arises from the anterior encephalic either at the origin

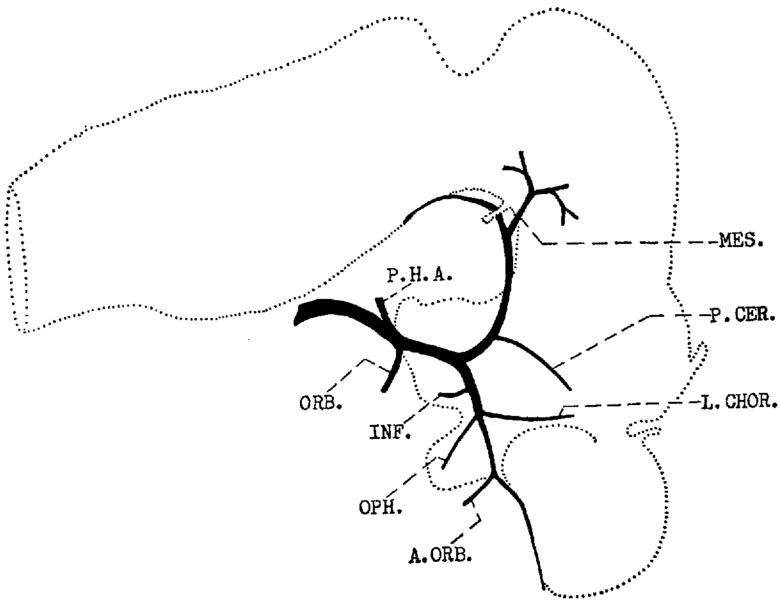

Fig. 3 Reconstruction of brain in *Chrysemys marginata* 6.0 mm embryo.

of the ophthalmic artery or slightly posterior to it. The lateral choroidal travels caudal to the posterior convexity of the hemisphere and extends dorsally toward the velum transversum. The length of this artery varies among the embryos of this series, but in all cases the lateral choroidal passes at least one half the distance up the side of the brain.

The anterior encephalic artery travels anterodorsally over the root of the optic stalk and continues along the ventrolateral aspect of the cerebral hemisphere. Just in front of the optic stalk, the anterior encephalic sends laterad an anterior orbital artery, which supplies a small anterodorsal region of the orbit.

Beyond the origin of the anterior orbital the anterior encephalic turns medially and gradually approaches its counterpart from the opposite side. At the midline each vessel turns directly anteriorly and continues ventrally along the remainder of the telencephalon. No fusion or cross-connection between these two arteries could be found.

As the posterior encephalic artery passes caudad along the diencephalon, a small posterior cerebral artery is sent anterodorsally toward the region of the choroid plexus of the third ventricle. At this stage, the posterior cerebral could not be traced all the way to the roof of the diencephalon. This artery sometimes arises as a complex of small interconnecting vessels, but usually there is one vessel which predominates as the definitive posterior cerebral artery.

The posterior encephalic continues along the floor of the diencephalon and mesencephalon. At the cranial flexure, this vessel gives rise to a short mesencephalic artery. The latter extends dorsad a short distance up the side of the midbrain and bifurcates into rudimentary anterior and posterior rami, each of which ends in a mass of small arteries and capillaries.

Beyond the origin of the mesencephalic artery, the posterior encephalic crosses beneath the oculomotor nerve and then follows closely the contour of the medulla. The subsequent course of this artery could not be followed in the 6.0 mm specimen.

In the 5.7 mm embryo the two posterior encephalic arteries pass ventromedial to the roots of the cranial nerves. An anastomosis may occasionally be found between the two posterior encephalics, but nowhere do they unite with each other. Each artery gradually becomes smaller until it joins the ventral spinal artery at the posterior region of the brain.

Stage III (8.8 mm–11.5 mm)

Although the embryos of stage III range in length from 8.8 mm to 11.5 mm, one 11.8 mm specimen has been included in this group. This embryo is much younger than the 11.0 mm embryo but corresponds generally in terms of development to the 8.8 mm and 9.7 mm specimens. The 9.7 mm embryo will be used as the representative of this stage (fig. 4).

Before entering the intracranial cavity, the internal carotid gives rise to a tiny palatine artery, which accompanies the palatine branch of the facial nerve. This artery could be followed anteriorly only a short distance. At the posterior region of the hypophysis, the internal carotid turns dorsally and enters the brain case.

Within the cranial cavity a strong posthypophyseal anastomosis is formed between the two internal carotids. The carotid then extends dorsolaterally and gives off an orbital artery. The latter emerges from the brain case through its own foramen and travels along with nerve III to the orbit. The cerebral carotid passes dorsolaterally and then divides into the anterior and posterior encephalic arteries.

Just anterior to the bifurcation, the anterior encephalic sends off a small infundibular artery, which turns caudad and furnishes twigs to the infundibular and hypothalamic regions. The anterior encephalic then continues along the lateral wall of the diencephalon and sends dorsally the lateral choroidal artery. The latter passes anterodorsally toward the velum transversum and breaks into a rich network of smaller vessels for the choroid plexus of the lateral ventricle. In the older embryos of this stage, well-defined choroidal rami extend into this plexus.

Immediately anterior to the origin of the lateral choroidal, the anterior encephalic gives rise to the ophthalmic artery. This vessel has increased in size and may now be traced, along with nerve II, through the optic foramen to the eye. In the later embryos, the distal portion of the ophthalmic supplies a fairly strong branch to the anterior regions of the orbit.

The anterior encephalic next gives rise to a short dorsolateral outgrowth representing the rudimentary middle cerebral artery. In some cases there are several of these vessels, and so it is often difficult to distinguish a definite middle cerebral at this stage.

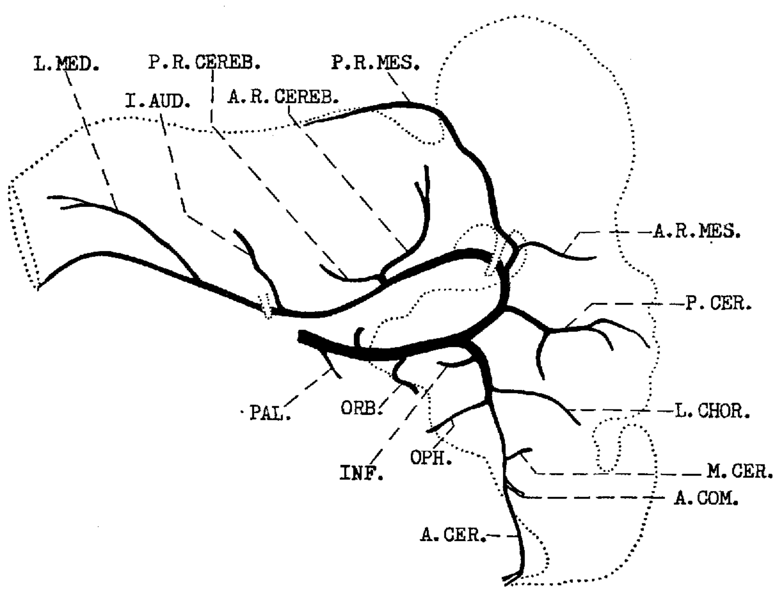

Fig. 4 Reconstruction of brain in *Chrysemys marginata* 9.7 mm embryo.

After giving rise to the middle cerebral, the anterior encephalic (anterior cerebral) sends mediad the rudiment of an anterior communicating artery around the anterior border of the optic chiasma. This vessel ends near the midline without forming any connections with its mate from the other side.

In the younger specimens of this period a delicate anterior orbital artery may still be given off from the anterior cerebral near the origin of the anterior communicating ramus. This anterior orbital artery is lacking in all of the older embryos (9.7 mm and later).

The anterior cerebral continues a short distance along the ventral region of the hemisphere and then assumes an anteromedial course, perpendicular to the olfactory nerve traveling dorsomedially from the nasal region. At the olfactory nerve, the anterior cerebral divides into several slender olfactory branches, which travel with the nerve to the nasal cavity.

The posterior encephalic artery passes posteriorly along the ventrolateral region of the diencephalon and gives rise to the posterior cerebral artery. The latter travels anterodorsally, supplies one or two branches to the wall of the diencephalon, and then ends dorsally in a network of vessels in the choroid plexus of the third ventricle.

The posterior encephalic continues caudad and follows the concave contour of the midbrain floor. Just anterior to the root of nerve III, a large mesencephalic artery is sent dorsally to supply the midbrain. The stem of this artery divides almost immediately into anterior and posterior rami.

The anterior ramus of the mesencephalic passes between the anteroventral convexity of the midbrain and the diencephalon. The posterior ramus is the longer of the two and extends dorsoposteriorly until it reaches the posterior boundary of the midbrain. This vessel turns directly caudad, travels across the fissure between the midbrain and cerebellum, and eventually disappears on the dorsal cerebellar surface.

Beyond the origin of the mesencephalic artery, the posterior encephalic crosses beneath the oculomotor nerve and continues its course ventral to the medulla. Just anterior to the root of nerve V, the posterior encephalic gives off a large cerebellar branch. This artery curves dorsolaterally around the side of the medulla and divides into the anterior and posterior rami. The anterior ramus travels anterolaterally and eventually reaches the anteroventral region of the cerebellum. The posterior ramus is quite short and travels caudad beneath the root of nerve V.

The posterior encephalics lie fairly close to each other as they continue their courses ventromedial to the nerve roots. Numerous cross-connections are present, and small portions of these two vessels occasionally fuse. There sometimes is a cross-connection or fusion at the level of nerves VII–VIII. Anterior to the origin of nerve VI, an internal auditory artery originates from the posterior encephalic, but it could be traced only a short way up the side of the medulla.

In the region of nerve X, a fairly large lateral medullary artery is sent off from the posterior encephalic. The lateral medullary travels posterodorsally and divides into several small branches, each of which ends near the posterior boundary of the medulla. Beyond the origins of the lateral medullary arteries, the two posterior encephalics join each other and become continuous with the single ventral spinal artery along the ventral region of the spinal cord.

Stage IV (16.8 mm–26.7 mm)

The arrangement of the intracranial arteries closely approaches the condition found in the adult. Although the 26.7 mm embryo has been chosen to represent this period of development, the following description will also include references to earlier stage IV embryos.

Although the hemisphere now completely conceals the lateral choroidal artery, a small proximal portion of the posterior cerebral is still visible in lateral view (fig. 5). The posterior cerebral artery supplies numerous rami to the posterior convexity of the cerebral hemisphere as well as to the epiphysis and to the choroid plexus of the third ventricle. Several of the anterior rami pass into the lateral choroid plexus, while others form anastomoses with posterior rami of the lateral choroidal artery. It thus appears that the

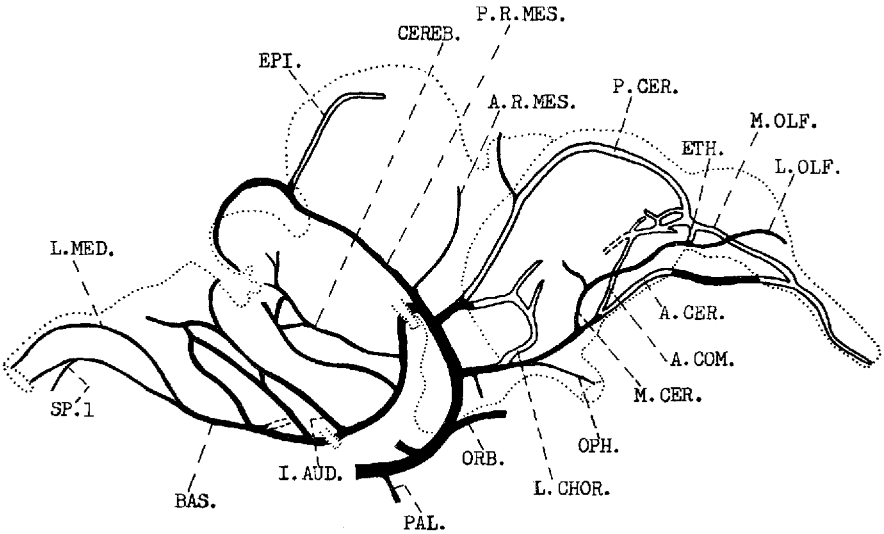

Fig. 5 Reconstruction of brain in *Chrysemys marginata* 26.7 mm embryo.

lateral choroid plexus is served by both the lateral choroidal and posterior cerebral arteries.

In the early embryos of this period the posterior cerebral continues along the dorsomedial wall of the hemisphere and disappears at about one half the distance to the olfactory lobe. In the later embryos, however, (e.g., 26.7 mm) this artery continues anteriorly until it reaches the sulcus lobaris. There the posterior cerebral turns posteroventrad and breaks into several smaller arteries which end in a mass of intercommunicating vessels. (Branches of the corresponding posterior cerebral also end in this network.)

Rudiments of the middle cerebral were already visible at stage III, but it is not until the latter part of stage IV that this vessel begins to provide a series of arteries for the lateral surface of the hemisphere. In the 26.7 mm embryo the middle cerebral sends an anterior ramus to the region of the sulcus lobaris. There this vessel is joined by the ethmoidal artery (to be described below) and then continues its course as the lateral olfactory artery along the lateral aspect of the olfactory lobe.

Beyond the origin of the middle cerebral, the anterior encephalic (anterior cerebral) turns slightly mediad and gives rise to an anterior communicating artery. This vessel travels medially into the intercerebral fissure and ends (along with its counterpart from the other side) in the median plexus into which the posterior cerebrals pass.

From this network a medial olfactory artery is sent along the ventromedial aspect of each olfactory lobe. At the origin of the olfactory nerves, each medial olfactory artery taps the blood stream in the anterior portion of the corresponding anterior cerebral.

Right and left ethmoidal arteries also originate in the anterior region of the median plexus. Each ethmoidal passes laterally onto the anterolateral region of the hemisphere and joins the anterior ramus of the middle cerebral.

After sending off the anterior communicating artery, the remainder of the anterior cerebral travels anteromedially toward the olfactory nerve. The anterior cerebral passes forward beneath the olfactory lobe but does not actually follow the contour of its ventral surface. Instead, this artery lies a short distance below the lobe and then becomes reassociated with the brain at the origin of nerve I. Here the anterior cerebral is joined by the medial olfactory artery (described above) and then continues along the ventromedial aspect of the nerve.

The olfactory arteries in the 17.4 mm and 26.4 mm embryos show basically the same arrangement except that there are two connections between the anterior cerebral and medial olfactory arteries. As in the 26.7 mm specimen, one communication occurs at the root of nerve I, but there is also an anastomosis between these two arteries near the sulcus lobaris.

The branches of the mesencephalic artery have grown considerably since the preceding stage. The anterior ramus follows along the anteroventral convexity of the optic lobe and disappears near the roof of the diencephalon. The posterior ramus passes along the caudal convexity of the optic lobe and supplies numerous anterior vessels to its lateral surface. In the dorsal region of the isthmus, the posterior ramus sends an anteromedial branch into the median fissure between the two optic lobes. This branch and its counterpart send off numerous small twigs forming a complex network of vessels within the narrow fissure. For this reason it was not possible to determine whether or not the two anteromedial branches had as yet formed the single epiphyseal artery found in the adult.

The posterior ramus of the mesencephalic next turns directly caudad and passes over the cerebellum into the choroid plexus of the fourth ventricle. Only a few short vessels are supplied by this artery to the cerebellum itself.

The cerebellum now receives numerous branches from the cerebellar artery. This vessel also forms anastomoses with closely associated branches originating from the posterior encephalic artery in this region of the medulla.

The internal auditory artery has become more elaborate in terms of size as well as distribution of subordinate branches. This vessel originates anterior to nerve VI, gives off rami to nerves VII–VIII, and sends a vessel into the choroid plexus of the fourth ventricle. In the 26.7 mm embryo, the internal auditory forms one or more anastomoses with nearby medullary arteries which run parallel to it.

In the early embryos of this stage (16.8 mm, 17.4 mm) the two posterior encephalic arteries first unite at the level of nerves VII–VIII, separate a short distance posteriorly, and finally reunite again to become continuous with the single ventral spinal artery. In the 26.7 mm embryo, the posterior encephalics fuse posterior to the root of the internal auditory artery and form a true basilar artery which remains unpaired throughout the rest of its course.

The basilar gives rise to several medullary vessels including a pair of lateral medullary arteries, each of which travels to the posterodorsal region of the medulla and joins the delicate dorsal spinal of the corresponding side. At the posteroventral boundary of the medulla the basilar receives the first pair of spinal arteries and continues caudad beneath the spinal cord as the ventral spinal artery.

A brief reference should be made to an extracranial feature which becomes modified during stage IV. The distal end of the internal carotid now travels along a slight groove (the rudimentary carotid canal) in the floor of the basisphenoid bone.

It is obvious that the intracranial arterial pattern of the 26.7 mm embryo conforms basically to the adult condition. Further changes are necessary, however, before the adult pattern is attained. These changes are as follows:

(1) The distal portions of the two posterior cerebrals fuse with each other and become continuous with a single median vessel formed by the arterial network in the anteroventral region of the intercerebral fissure.

(2) A segment of the anterior cerebral degenerates between the origin of the anterior communicating artery and the anastomosis with the medial olfactory artery.

(3) The mesencephalic arteries extend their areas of supply, while the anteromedial branches of the posterior rami develop into the single epiphyseal artery.

(4) The cerebellar arterial supply is increased by means of additional branches from the cerebellar arteries and from the posterior rami of the mesencephalics.

(5) The middle cerebral artery ramifies greatly in order to keep pace with the rapidly expanding cerebral hemispheres. (The final posterolateral enlargement of this region also ultimately conceals the posterior cerebral artery from a lateral view of the brain.)

DISCUSSION

Adult

Among the various previous studies on the adult condition, the greatest disagreement occurs with respect to the relationships of arteries lying within the intercerebral fissure. This is not surprising, since not only are these vessels hidden from external view and thus very difficult to follow, but also the proximity of the numerous branches often results in a great deal of individual variation.

A major difference between the *Pseudemys* material of this study and the *Testudo* adults of Schepers ('39) is that in the latter animals the anterior cerebrals of both sides supposedly do not form any cross-connections with each other. Therefore the circle of Willis is not closed anteriorly. In *Chelone midas,* Kappers ('33) states that no "distinct" communication was found between the two anterior cerebrals; however, one of his diagrams does show a thin cross-connection between these two vessels just anterior to the optic chiasma.

Direct references to an anterior communicating artery may be found in the studies of Bojanus (1819–21) and Klinckowström (1890) on *Emys europaea* and of Beddard ('05) on *Testudo vicina.* Hofmann's diagram of *Testudo graeca* ('00) shows a single median vessel formed by both anterior cerebrals, but he does not describe this in his text. The remaining workers do not mention whether or not this feature is present in their material.

The nomenclature for the posterior cerebral and lateral choroidal arteries presents another problem. The posterior cerebral artery of Schepers ('39) seems to correspond to the lateral choroidal artery of Kappers ('33). In Kappers' material, as well as in the *Pseudemys* adults used in the present study, the artery in question originates from the anterior encephalic, travels beneath the posterior pole of the hemisphere, and supplies portions of the posteromedial region of the hemisphere as well as the lateral choroid plexus. Since the "posterior cerebral" of Schepers shows the same origin and course, this vessel is most likely comparable to the lateral choroidal. Schepers' "diencephalic" artery originates from the posterior encephalic, travels behind the posterior pole, and gives branches to the epiphysis, choroid plexus of the third ventricle, and thalamic region. This artery probably corresponds to the posterior cerebral of other authors, although Schepers does not mention whether or not his "diencephalic" artery supplies any branches to the posterior regions of the hemisphere.

Bojanus (1819–21), Kappers ('33), and Schepers ('39) all state that a connection exists between the anterior or distal portion of the posterior cerebral artery and a medial branch of the anterior cerebral. However, since Schepers' "posterior cerebral" actually corresponds to the lateral choroidal of other authors, his findings would seem to be contradictory. An explanation for this may be obtained from the condition observed in the *Pseudemys* material where the posterior cerebral and lateral choroidal form anastomoses with each other. It is possible that in Schepers' specimens the lateral choroidal ("posterior cerebral") had acquired the distal ends of the posterior cerebral ("diencephalic").

Kappers ('33) remarks that in *Damonia subtrijuga,* the distal portions of the posterior cerebrals join each other to form a single, dorsal vessel in the midline. A comparable situation exists in *Pseudemys,* except that this vessel travels more ventrally within the intercerebral fissure.

Schepers ('39) states that in 80% of his material the "posterior cerebral" (lateral choroidal) originates from the anterior encephalic artery; in the remaining cases the origin is from the posterior encephalic. In all of the six *Pseudemys* adults as well as in those accounts which refer specifically to a lateral choroidal artery, this vessel originates from the anterior encephalic.

Except for the lack of an anterior communicating artery in *Testudo geometrica* (Schepers, '39), the arrangement of the arteries in the olfactory region of the hemisphere generally agrees with that found in *Pseudemys.* The olfactory artery depicted in Bojanus' diagrams (1819–21) probably corresponds to the medial olfactory seen in *Pseudemys* and referred to by Schepers. Hofmann ('00) describes medial and lateral olfactory branches originating from the anterior cerebral near the midline. His lateral olfactory seems to represent the ethmoidal and lateral olfactory arteries found in *Pseudemys*. He also follows the anterior cerebral beyond the origin of the olfactory artery into the intercerebral fissure. As mentioned previously, he does not refer in his text to any communication between right and left anterior cerebrals. Further comparisons of these anterior vessels with those described in other studies cannot be made, since Schepers is actually the only author who includes sufficient details on their origin and distribution.

The ophthalmic artery of Shindo ('14), Kappers ('33), and Schepers ('39) corresponds to the orbital artery described in *Pseudemys*. These authors do not mention any artery originating from the anterior encephalic and passing into the orbit via the optic foramen. Bojanus (1819–21), however, refers to an orbital (originating from the cerebral carotid) and an ophthalmic (originating from the anterior encephalic). Both of these arteries are present and easily identified in *Pseudemys*.

In *Pseudemys* the condition of the cerebellar artery seems to agree with that found in other genera, although the trigeminal ramus may originate independently from the posterior encephalic. While it is difficult to compare individually the remaining medullary branches from the posterior encephalic and basilar arteries, at least one vessel goes to the choroid plexus of the fourth ventricle. This artery is usually associated with the internal auditory, which originates either anterior or posterior to nerve VI.

The lateral medullary artery of *Pseudemys* probably corresponds to the lateral spinal in Schepers' material ('39). Bojanus' diagram (1819–21) shows several medullary arteries whose distal ends coalesce near the posterior region of the medulla to form a longitudinal vessel passing dorsolaterally along the spinal cord. Hofmann ('00) describes a dorsal spinal artery but does not indicate whether or not it connects with the lateral medullary from the basilar.

The basilar varies greatly in form not only among different genera but also among individuals of the same species. The two posterior encephalics may fuse at any point from the region of nerve V to the posterior boundary of the medulla. In two-thirds of the *Pseudemys* specimens, the basilar originated at the level of nerve V; Bojanus' diagrams also show this to be the case in his material. Schepers found that the posterior encephalics do not fuse until they reach the posterior portion of the medulla, although cross-connections between the two may be seen posterior to the level of nerves VII–VIII. In two of Hofmann's four *Testudo graeca* adults ('00), the posterior encephalics become continuous with a pair of ventral spinal arteries which eventually fuse at the upper thoracic region; in the other two specimens the posterior encephalics fuse somewhere along the medulla. Beddard's observations ('05) indicate that in his material the posterior encephalics remain paired throughout their course beneath the medulla.

Since most of these authors begin their descriptions with the intracranial origin of the orbital artery, one usually cannot determine whether or not the palatine artery and the post-hypophyseal anastomosis are present. Shindo ('14), however, refers specifically to a small palatine artery which is given off just before the internal carotid enters the brain case; he also confirms the presence of an anastomosis between the two internal carotids posterior to the hypophysis.

Development

Since there is a lack of embryological studies on the intracranial arteries in turtles, it is difficult to determine those developmental features which may be peculiar to the genus used in the present study. However, a comparison of the intracranial condition in late stage *Chrysemys* embryos with that found in the adults of other chelonian genera reveals no gross differences, at least with regard to the general pattern, and so the following remarks on the development of *Chrysemys* may well apply to that in other turtles.

During the various developmental phases, the intracranial arteries which show the most significant modification are those found within the intercerebral fissure and between the olfactory lobes. During the third stage, each anterior cerebral artery sends mediad an anterior communicating artery which travels along the rim of the optic chiasma and into the anterior region of the fissure. By the beginning of stage IV each communicating artery breaks into a plexus of tiny inter-communicating vessels, thereby creating a direct connection between the anterior cerebrals of the right and left sides. (Many of the small arteries in this "anteroventral plexus" later coalesce to form the anterior communicating artery of the adult.)

During stage IV the anterior portions of the posterior cerebrals end in this network, and out of this mass of vessels two pairs of arteries are formed. The members of the first pair are the ethmoidal arteries, each of which travels laterally, turns dorsad onto the anterolateral region of the hemisphere, and joins the anterior branch of the middle cerebral. The second pair represents the right and left medial olfactory arteries. Each of these eventually joins the anterior end of the corresponding anterior cerebral.

The condition of the anterior cerebral was examined in one late *Chrysemys* embryo (31.8 mm). Although this vessel is still present, its distal portion has narrowed considerably. Thus during the later embryonic stages much of the blood for the olfactory region is being sent through the anterior communicating, ethmoidal, and medial olfactory arteries, instead of through the anterior cerebral. The posterior cerebrals are also sending blood to the olfactory area by means of their connections with the anterior communicating network of vessels. As a result, the anterior cerebral degenerates from the origin of the anterior communicating artery to the union with the medial olfactory artery. The most distal part of the medial olfactory artery is therefore the distal remnant of the embryonic anterior cerebral, while a major part of the adult anterior cerebral is derived from the anterior communicating artery of the embryo (fig. 6, C and D).

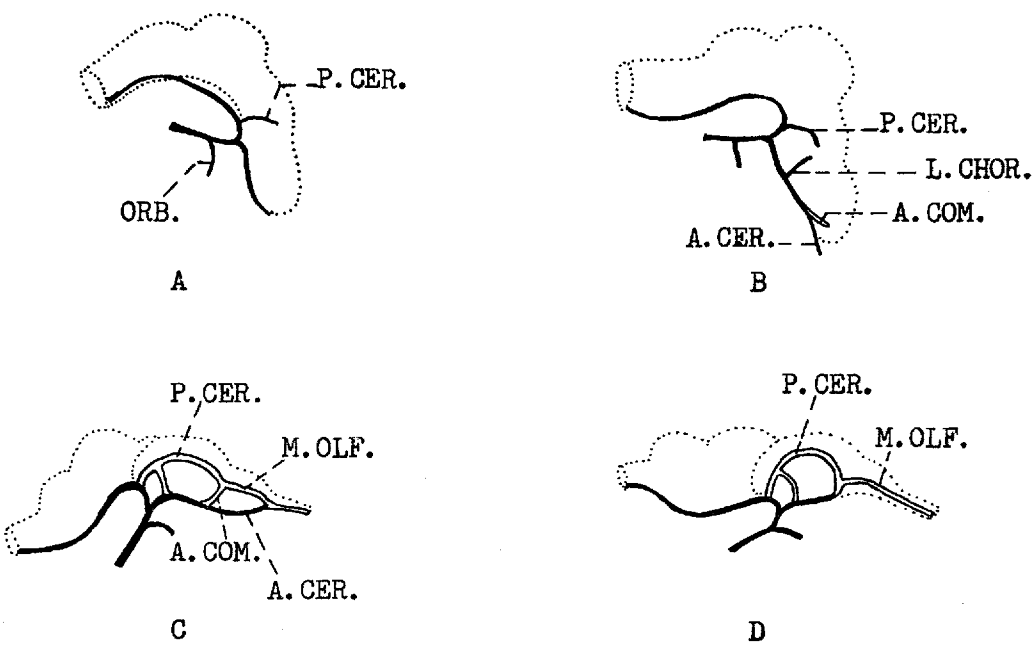

Fig. 6 Diagrammatic representation of modifications in chelonian forebrain arteries. A, posterior cerebral artery present at early stage; B, appearance of lateral choroidal and anterior communicating arteries; C, communications among posterior cerebral, lateral choroidal, and anterior communicating arteries, while medial olfactory develops in anterior region of brain and forms a connection with anterior cerebral; D, an intermediate portion of the anterior cerebral has degenerated, leaving its most distal end as part of the medial olfactory.

An anterior orbital artery appears in late stage I embryos and is present in all embryos through the early part of stage III. Since no anterior orbital could be found in any of the later stage III specimens, it is possible that this vessel completely degenerates or that some of its branches are taken over by the ophthalmic or even by the orbital artery. However, an examination of earlier embryos did not reveal any anastomoses between these vessels and the anterior orbital.

An interesting relationship exists between the lateral choroidal and posterior cerebral arteries. The lateral choroidal develops from the anterior encephalic artery; the posterior cerebral originates from the posterior encephalic. Both vessels pass dorsally into the anterior region of the diencephalon. During stage IV, anastomoses form between these two arteries so that it becomes difficult to distinguish their individual areas of supply.

The lateral choroidal artery appears during stage II, whereas the posterior cerebral is already present at stage I. The former, however, is the first vessel to supply branches to the lateral choroid plexus. As the posterior cerebral increases in size, it also begins to participate in the choroidal circulation, and by the end of stage IV, the posterior cerebral seems to have replaced the lateral choroidal as the primary source of blood for this plexus. The lateral choroidal artery is still retained in the adult, and indeed in Schepers' description of *Testudo* ('39) this artery is the only vessel serving the lateral choroid plexus. Consequently, either the posterior cerebral or the lateral choroidal may predominate as the main source of supply for this region of the adult chelonian brain.

The posterior cerebral shows a great deal of growth and differentiation. It not only participates in the lateral choroid plexus, but also develops branches for the epiphysis, posterior region of the hemisphere, anterior face of the optic lobe, and choroid plexus of the third ventricle. The posterior cerebral also extends forward and fuses with its mate to form a single channel which merges with the anterior communicating plexus and, as mentioned above, thereby sends some blood to the olfactory region as well.

The arteries supplying the optic lobe do not change much during embryonic development. Except for a few twigs from the posterior cerebral artery, the lobe receives its supply entirely from the large mesencephalic artery. This vessel is formed early in the second stage of development and soon bifurcates into anterior and posterior rami.

The relatively short anterior ramus of the mesencephalic travels over the ventrolateral face of the optic lobe, but even in the adult this artery never reaches any great size. The posterior ramus, however, becomes quite elaborate, and during stage IV this branch develops numerous anterodorsal rami traveling parallel to the anterior ramus. The posterior ramus also sends off a short anteromedial branch which passes between the optic lobes. This vessel and its counterpart eventually develop into the single epiphyseal artery of the adult.

At stage IV the anterior and posterior rami of the mesencephalic can still be easily distinguished, since neither the cerebellum nor the cerebral hemisphere has as yet reached its fullest development. In the adult, however, the cerebellum has pushed anteriorly against the optic lobes, and the posterior portion of the hemisphere has grown caudad over the anteroventral region of the midbrain. Much of the embryonic posterior ramus travels directly dorsad and thus becomes the stem of the adult mesencephalic. The embryonic anterior ramus is represented in the adult only by a small vessel traveling along the anteroventral convexity of the optic lobe and completely hidden from lateral view by the posterior pole of the hemisphere.

The cerebellar artery appears at stage III and at first supplies primarily the general area around nerve V and only a small portion of the rudimentary cerebellum. (Early in stage III the posterior region of the cerebellum is supplied by the posterior ramus of the mesencephalic artery.) As the cerebellum gradually expands during stages III and IV, the cerebellar artery sends a series of branches over its lateral surface, and in the later stage IV embryos connections are formed with branches of other medullary arteries. It is likely that many of these medullary vessels are taken over completely by the embryonic cerebellar, and the latter is thus transformed into the extensive adult cerebellar artery. In the adult a remnant of the early embryonic cerebellar is represented by the trigeminal ramus which travels laterad along with nerve V.

The cerebellum initially does not obtain much blood from the posterior ramus of the mesencephalic artery, for even in stage IV much of this vessel travels somewhat dorsal to the cerebellum. When the cerebellum further expands and is pushed against the optic lobe, the posterior ramus comes into closer contact with the anterior region of the cerebellum. Yet even in the adult the posterior ramus remains rather loosely associated with this area of the brain. Consequently, the posterior ramus seems to be intended primarily for the choroid plexus of the fourth ventricle and acts only to supplement the blood supply for the cerebellum.

At the third stage of development, the internal auditory artery originates anterior to nerve VI and passes toward the roots of nerves VII–VIII. During stage IV this vessel ramifies over the lateral region of the medulla and later sends a branch dorsoposteriorly into the choroid plexus of the fourth ventricle.

In most cases, anastomoses are formed between the internal auditory artery and nearby medullary arteries which originate posterior to nerve VI; these connections are usually retained in the adult. Occasionally the adult internal auditory originates posterior to nerve VI. In such instances a more posterior vessel probably has acquired distal branches of the embryonic internal auditory, while the proximal portion of the latter degenerates.

The cerebellar and internal auditory arteries show similarities in their embryonic development. Each of these initially supplies the area immediately surrounding a nerve root, i.e., nerve V for the cerebellar and nerves VII–VIII for the internal auditory. By means of anastomoses with nearby medullary vesels, each artery acquires a larger area of distribution, while only a small part of the original vessel actually supplies the nerve itself. (The internal auditory artery should probably therefore be renamed in order to indicate more accurately its area of supply. However, since the term "internal auditory" is used generally throughout most of the literature on the adult intracranial arterial system, it is convenient to retain this name for purposes of comparison.)

The lateral medullary artery does not undergo much modification. It is one of the most posterior of the medullary vessels given off by the basilar and is already easily distinguished at stage III. Although anastomoses may occasionally form between this and other closely associated medullary arteries, the lateral medullary generally does not give rise to many subordinate branches. During the early phase of stage IV this vessel unites with the dorsal spinal artery which extends along the dorsolateral region of the spinal cord.

Attention has already been called to the great variations in the form of the adult basilar artery. The embryos unfortunately do not offer many clues as to the manner in which this vessel develops. Anastomoses between the two posterior encephalics are often found in stage III embryos, but direct fusion between the two vessels is more frequently the case. The fusion or cross-connection usually first occurs at the level of nerves VII–VIII. The small outgrowths running parallel to the adult basilar may actually be unfused portions of the original posterior encephalic arteries, in which case these portions probably carry unequal amounts of blood. Thus one part might appear to be a small "collateral" of the other.

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