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Anatomy of the vascular system of the head and neck of the helmeted guineafowl *Numida meleagris*

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(With 4 figures in the text)

The vascular anatomy of the head and neck of eight adult helmeted guineafowl (*Numida meleagris*) was investigated by latex injections and dissection, resin casting, and lipidol injections and X-ray photography. The vascular anatomy of these regions is similar to that of the domestic fowl *Gallus domesticus*, the main differences being in the helmet, wattle and cere vascularization, and the presence of a nape–cheek rete in *N. meleagris*. It is postulated that five vascular arrangements in the head and neck are important in brain temperature regulation. These arrangements are: the nape–cheek rete, the temporal rete, fine arterio-venous networks in the wattles and cere, and the cavernous sinus–intercarotid association. All but the last of these arrangements require pathways of blood flow to the brain other than the most direct route. Such pathways are discussed.

Contents

Introduction

The helmeted guineafowl *Numida meleagris* is a characteristic member of the African savanna avifauna (Chapin, 1932; Crowe & Snow, 1978). It is a widespread and polytypic species (Crowe, 1978*a*), and each of the various subspecies encounters a considerable range (up to 30·5°C) of environmental temperatures (Crowe, 1978*b*). High variation in environmental temperature presents an endotherm with acute thermoregulatory problems (Bartholomew, 1968). Therefore one would expect *N. meleagris* to have evolved anatomical, morphological, physiological and/or behavioural adaptations to deal with a fluctuating environmental temperature. Crowe (1978*b*) has shown that variation in certain phenetic characters in *N. meleagris* is statistically significantly related to variation in environmental temperature. For example, phenetic characters which measure the size of exposed structures of the head, i.e. helmet height, helmet area, helmet thickness, wattle length and cere structure thickness, tend to have lower values in hotter and/or drier localities. Crowe & Withers (in prep.) are investigating possible physiological mechanisms of temperature

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regulation in *N. meleagris*. The aims of the present study are to describe the major arteries and veins of the naked head and neck regions of *N. meleagris*, and to hypothesize as to how cervico-cephalic vascular arrangements may help this species in the regulation of brain temperature.

Materials and methods

Three techniques were used to locate and determine the exact positions of blood vessels in the head and upper neck regions of *N. meleagris*. The left common carotid artery and the right jugular vein of two adult male specimens were injected with differently coloured crystic resin monomers with an added catalyst and an accelerator (Thompsett, 1970). The head and neck of one of these birds was then macerated in a pancreatin solution (Thompsett, 1970), producing a resin cast of the vascular system in relation to the skull and the cervical vertebrae. The second specimen was macerated in hydrochloric acid, resulting in a cast minus the skull and cervical vertebrae. Three specimens, two adult males and one adult female, were similarly injected with lipidol, a radio-opaque dye, and examined by X-ray photography. Three specimens, two adult males and an adult female, were similarly injected with differently coloured latex, and the vessels dissected *in situ*. Nomenclature in both the text and figures follows Richards (1967, 1968) wherever possible. The abbreviations used in the figures are as follows:

Arterial system

AVC, anterior ventral cerebellar artery; B, basilar artery; CA, inter-carotid anastomosis; CC, common carotid artery; CCa, cerebral carotid artery; CO, cerebral ophthalmic artery; CW, circle of Willis; E, ethmoid artery; EC, external carotid artery; EF, external facial artery; EO, external ophthalmic artery; H, hyoid artery; IC, internal carotid artery; IO, internal ophthalmic artery; IOR, infra-orbital ramus; L, lingual artery; LIM, lower internal maxillary artery; MC, middle cerebral artery; MIM, middle internal maxillary artery; NC, nasal-cere artery; NCR, nape–cheek rete; O, Occipital artery; Oe, oesophageal artery; OR, ophthalmic ramus; OVA occipital artery-vertebral artery anastomosis; P, palatine artery; Ph, pharyngeal artery; PVC, posterior ventral cerebellar artery; S, sphenomaxillary artery; SL, supra-laryngeal artery; SOR, supra-orbital ramus; TR, temporal ramus; UIM, upper internal maxillary artery; V, vertebral artery; Va, vagus artery; VOL, ventral optic lobe artery; VS, ventral spinal artery; W, wattle artery.

Venous system

AC, anterior cephalic vein; ACb, anterior cerebral vein; C, carotid vein; CFv, cutaneous facial vein; Cv, cervical sinus; DCO, dorsal cerebral ophthalmic vein; EF, external facial vein; Eoc, external occipital vein; Ev, ethmoid vein; IF, internal facial vein; IM, internal mandibular vein; IOC, internal occipital vein; J, jugular vein; Lv, lingual vein; MC, middle cerebral vein; MD, mid-dorsal sinus; Moc, median occipital vein; NCv, nasal-cere vein; Oc, occipital sinus; Op, ophthalmic vein; P, palpebral vein; PC, posterior cephalic vein; Rop, recurrent ophthalmic vein; S, supra-palatine vein; SC, sinus cavernosus; Sp, superior pharyngeal vein; T, temporal vein; TA, transverse anastomosis; Top, temporal ophthalmic vein; Tr, temporal rete; Vv, vertebral vein; Wv, wattle vein.

Results

A certain amount of individual variation in the origin and/or position of the blood vessels was found. Therefore, the results related here are a generalized picture, and only major variations are discussed.

The arterial system

The largest blood vessels which supply the head and neck regions in *N. meleagris* are the carotid arteries. Shortly after diverging from the innominate artery, the two common carotid arteries enter the hypophyseal canal of the cervical vertebrae, and continue, side by side, up the neck without fusing. At the base of the fifth cervical vertebra, the carotids emerge from the hypophyseal canal and continue relatively superficially to the base of the skull. At this level, each common carotid divides into two equal branches, the internal carotid, which is essentially a continuation of the main branch, and the external carotid.

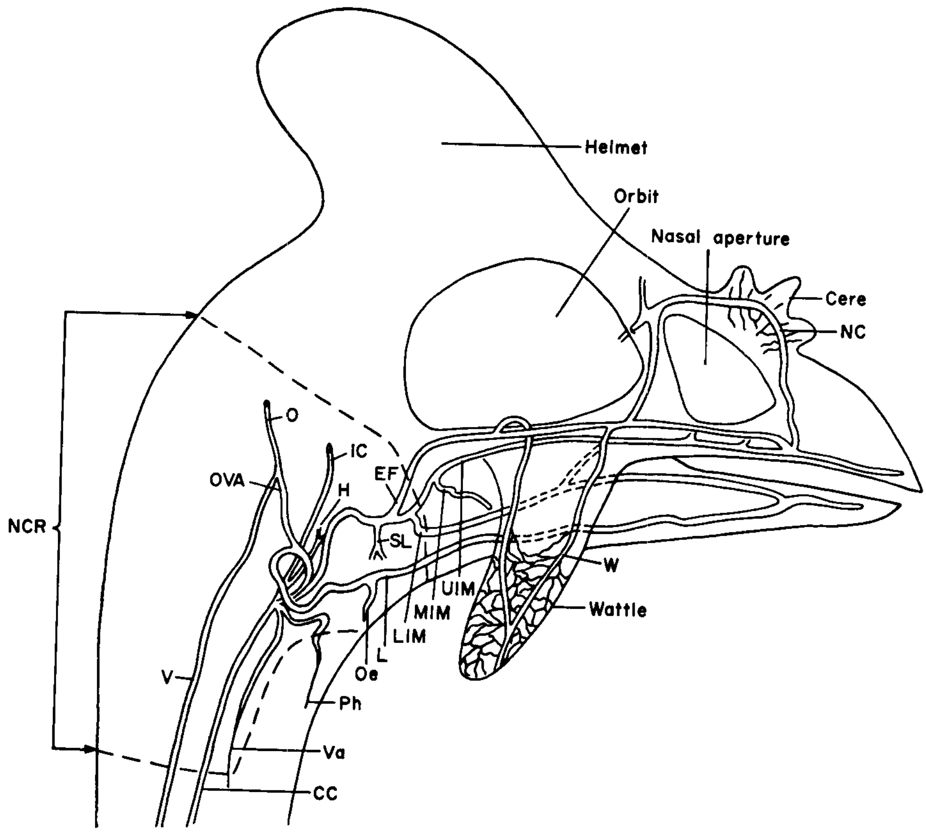

FIG. 1. A semi-diagrammatic lateral representation of the right external carotid artery and its branches. The nape–cheek rete is indicated by broken lines. For key to abbreviations, see p. 222.

External carotid artery (Fig. 1)

At about 5 mm from its point of origin the external carotid divides into five major, unequal arteries. The thickest of these gives rise to the internal maxillary and external facial arteries. In one male specimen, this artery gave rise to a supra-laryngeal artery before bifurcating. In the others, the origin of the supra-laryngeal artery is from the lower internal maxillary. The other four major arteries are the occipital artery, the lingual artery, the hyoid artery and the auricular artery.

Internal maxillary artery (Fig. 1)

The internal maxillary artery feeds the upper and lower jaws, the nasal and buccal areas and the cere.

The *upper internal maxillary artery* has branches to the pharynx, and anastomoses with the palatine artery and the ethmoid artery of the internal carotid. Anterior to the nasal cavity, the upper internal maxillary bifurcates, sending one large branch the nasal-cere artery, upwards to the cere, and another smaller branch to the end of the premaxilla, where it anastomoses with the same branch from the upper internal maxillary of the opposite side. The nasal-cere artery gives off a network of fine vessels in and around the cere. In two specimens fine branches of the upper internal maxillary were given off to the wattles.

The *middle internal maxillary artery* is approximately the same thickness as the upper internal maxillary. It supplies the salivary glands of the lower jaw and ultimately connects to the spheno-maxillary of the internal carotid.

The *lower internal maxillary artery* is the smallest branch of the internal maxillary, and supplies the salivary glands and the superficial areas of the mouth.

External facial artery (Fig. 1)

The external facial artery gives rise to a variable number of branches to the lower jaw and to the superficial areas of the face, including the nasal areas. This artery runs along the quadratojugal and the jugal bones, and, at the level of the wattle, gives rise to the wattle artery. The *wattle artery* passes behind its parent branch into the inner side of the wattle, and has connections with branches of the upper internal maxillary artery. Examination of the resin casts revealed that the wattle artery divides extensively, while within the wattle, to form a network of fine vessels. Farther along, another small branch of the external facial artery passes dorsally upwards anterior to the orbit. This branch feeds the superficial skin of the eye and the area surrounding the nasal aperture and divides into branches serving the cere area. In two male specimens, another branch, the nasal-cere artery, was observed to enter the cere and pass ventro-laterally anastomosing with a branch of the upper internal maxillary artery.

Occipital artery (Fig. 1)

The occipital artery is the second of the five major branches of the external carotid. This artery passes posteriorly upwards, giving off branches to the neck muscles and to the base of the skull. It also bifurcates to form a fine artery, which feeds the base of the skull, and a much larger artery, the vertebral artery, which curves caudally. At the level of the atlas, the vertebral artery enters the transverse canal of the cervical vertebrae. Therein it passes caudally, giving rise at regular intervals to numerous smaller branches which feed the cervical muscles and vertebrae. This vessel continues caudally, and gives off one or two additional branches to the common carotid before joining that vessel 15–20 mm above the carotid–innominate bifurcation. Additional branches of the vertebral artery are associated in a fine network (from approximately the fourth cervical vertebra upwards) with similar branches from the occipital, common carotid, lingual, and the internal maxillary arteries to form the arterial portion of what we call the nape–cheek rete. In two specimens, a fine branch of the posterior ventral cerebellar artery connected to the arterial vessels of this rete. It is possible that this vessel was destroyed in other dissections. Within the nape–cheek rete, near its origin, the occipital artery gives rise to the vagus artery and a small artery which feeds the pharynx.

Lingual artery (Fig. 1)

The lingual artery is the third branch of the external carotid artery. This artery supplies the tongue musculature, oesophagus and pharynx. The main branch of this artery continues to the distal end of the lower jaw, where it connects to branches of the lower internal maxillary artery. A smaller branch, the oesophageal artery, feeds the oesophagus.

Hyoid artery (Fig. 1)

The hyoid artery is the fourth and smallest branch of the external carotid. This artery gives rise to several smaller arteries which terminate in the hyoid muscles and in the muscles surrounding the jaw hinge. This artery also has fine branches which contribute to the nape–cheek rete.

Auricular artery (Fig. 1)

The auricular artery varies in size from specimen to specimen. It feeds the muscles surrounding the ear. Small branches feed the inner ear, and a large branch of this artery feeds the temporal muscles.

Internal carotid artery (Fig. 2)

At the base of the basisphenoid, the internal carotid divides into two unequal vessels. The larger is the external ophthalmic artery, and the smaller is the cerebral carotid artery.

External ophthalmic artery (Fig. 2)

The external ophthalmic artery passes through the tympanic cavity. In places, it runs in a shallow groove in the mastoid bone. After emerging from the tympanic cavity, this artery divides into two branches, a branch which gives rise to the temporal and inferior alveolar arteries, and a branch which gives rise to the orbital and ophthalmic rami. In the area anterior to the tympanic cavity these arteries and their branches give rise to a network of small vessels. This network is termed the temporal rete (Richards, 1967), and is connected to the external carotid circulation via anastomoses with the sphenomaxillary.

The *temporal artery* passes out dorsally and laterally giving off relatively large branches to the temporal muscles, and smaller ones to the masseter muscles. This artery then continues to the helmet where it divides into smaller vessels which feed the keratinaceous sheath and the bone of the helmet. Fine branches also feed the eyelid.

The *alveolar artery*, a very much smaller vessel, arises from the temporal artery near its origin. This artery has connections with the temporal rete.

The second of the larger external ophthalmic branches gives rise to the supra-orbital ramus, the infra-orbital ramus and the ophthalmic ramus. The supra-orbital ramus and the ophthalmic ramus originate from the same branch. Between all three branches there are connections contributing to the temporal rete.

The *supra-orbital ramus* is the largest of the branches. It curves laterally and dorsally around the posterior surface of the eye, where it gives off branches to the eye musculature and a branch which anastomoses with the cerebral ophthalmic artery to form the ethmoid artery.

The *ethmoid artery* supplies the internal nasal cavities and the frontal regions, and has connections with external facial artery in the cere area.

The *infra-orbital ramus* arises from much the same position as the supra-orbital ramus. This artery curves below the optic nerve and divides into a number of small branches which feed the eye muscles. The infra-orbital ramus also has connections with the alveolar artery and the supra-orbital ramus.

The *ophthalmic ramus* is essentially a large branch of the supra-orbital ramus. This artery also feeds the eye musculature, and is connected to the internal ophthalmic artery of the cerebral carotid artery.

Cerebral carotid artery (Fig. 2)

The cerebral carotid artery passes through a canal in the basisphenoid. After passing unbranched for about 10 mm, this artery gives rise to the palatine and sphenomaxillary arteries.

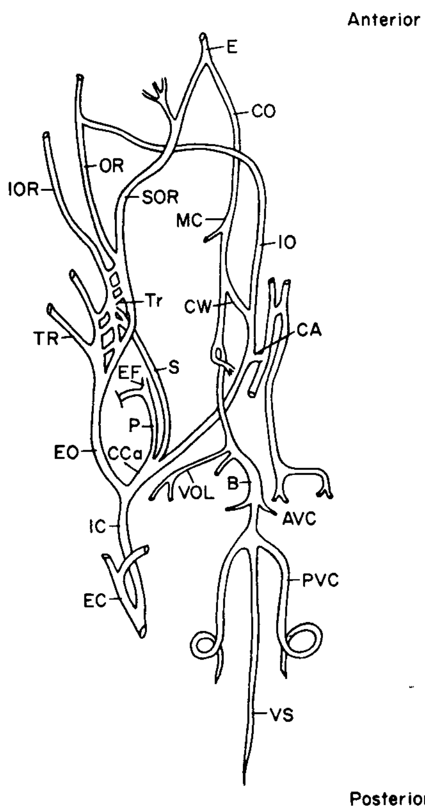

FIG. 2. A diagrammatic representation of the left internal carotid artery and its branches from the dorsal aspect. For key to abbreviations, see p. 222.

The *palatine artery* passes ventro-laterally before dividing into two branches. One branch anastomoses with a branch of the external facial artery, and the other ramifies to form small branches which feed the palate area. The palatine artery leaves the bony portion of the skull through a foramen.

The *sphenomaxillary artery* is larger than the palatine artery, and separates from the internal carotid anterior to the origin of the palatine. It passes through bone via the same foramen as the palatine artery. The sphenomaxillary has branches which anastomose with branches of the external ophthalmic artery.

Having given off these two branches, the internal cerebral carotid continues through the carotid canals until it forms an H-shaped anastomosis with the internal carotid of the opposite side. This anastomosis is formed caudal to the sella tunica or hypophaseal fossa. The connection between the two internal carotids is fine and short.

The *internal ophthalmic artery* is given off before the main trunk of the cerebral carotid, the *circle of Willis*, passes dorso-laterally. This artery passes anteriorly in association with the optic nerve, and gives rise to branches which link up with the cerebral ophthalmic artery and the external ophthalmic artery. It also has connections with the ethmoid artery.

Having given off the internal ophthalmic artery, the circle of Willis divides into an anterior branch, the cranial ramus, and an incomplete posterior branch, the caudal ramus.

The *cranial ramus* supplies the cerebrum and optic lobes. It gives off the ventral optic lobe artery which ramifies, supplying the ventral surface of the optic lobe, and has connections with the anterior ventral cerebellar artery. The cranial ramus then passes antero-laterally around the cerebrum to give rise to four branches:

(a) The *posterior cerebral artery* was most developed on the right hand side of the head in the three specimens in which the brain was dissected. It gives rise to branches which feed the cerebellum and the dorsal surface of the optic lobe.

(b) The *middle cerebral artery* comes off the cranial ramus anterior to the origin of the posterior cerebral artery. This artery passes laterally around the cerebral hemispheres toward the olfactory lobes. It gives off numerous small vessels along the way.

(c) The *cerebral ophthalmic artery* arises from the same point as the middle cerebral artery. This vessel passes antero-medially through the dura mater. It receives branches of the external ophthalmic artery after entering the orbit via the foramen ethmoidale (Hoffman, 1900; Richards, 1967). Together, the external ophthalmic artery and the cerebral ophthalmic artery form the ethmoid artery, which has connections with the upper internal maxillary, and external facial arteries of the external carotid.

(d) The *anterior cerebral artery* is the finest of the four branches of the cranial ramus. It passes in a medial direction, and appears to enter the dura mater.

In two specimens, the *caudal ramus* of the circle of Willis, or basilar artery, was well developed on the left hand side and rudimentary on the right hand side. The reverse was found in a third specimen. In one of the specimens with a "left-hand" basilar artery, a fine connection occurs between the rami of the two sides before the anterior ventral cerebellar arteries are given off. The caudal ramus passes posteriorly along the medial ventral surface of the medulla, gradually decreasing in size. It gives off two large, and many smaller lateral vessels along the way.

(a) The *anterior ventral cerebellar arteries* feed the cerebellum.

(b) The two *posterior ventral cerebellar arteries* arise in the vicinity of the medulla, and feed the lateral flocculus and the dorsal surface of the cerebellum. These arteries have numerous connections with the anterior ventral cerebellar artery and, in two specimens, fine connections with the nape–cheek rete.

(c) The *ventral spinal artery* originates from the basilar artery. This vessel passes along the ventral surface of the spinal cord as a single vessel. We were unable to trace vessels which may have passed from this artery to the dorsal surface to form the dorsal spinal artery (Richards, 1967).

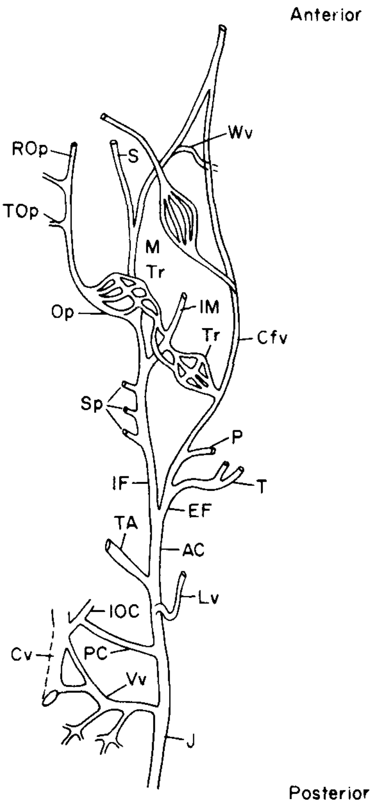

FIG. 3. A diagram of the right jugular vein and its branches from the dorsal aspect. For key to abbreviations, see p. 222.

The venous system
(Figs 3 and 4)

The largest vessels which drain the superficial head and neck regions are the jugular veins. The right-hand jugular is considerably larger in diameter than the left. The jugulars pass down the neck in a ventral superficial position. Near the base of the skull, they connect via the transverse anastomosis, which slopes caudally towards the right-hand side. In two specimens, branches from anterior regions of the head fed into the transverse anastomosis. We recognize five major veins, or categories of veins, which drain into the jugulars.

Lingual vein (Fig. 3)

The lingual vein runs alongside the lingual artery. It arises at the level of the second cervical vertebra, and collects blood from the branches which drain the oesophagus and the pharynx. The lingual vein enters the jugular vein midway between the entry of the posterior cephalic vein and the transverse anastomosis. Smaller branches which drain the neck muscles enter the lingual at intervals.

Anterior cephalic vein (Fig. 3)

The anterior cephalic vein is the portion of the jugular anterior to the transverse anastomosis. It receives vessels which drain the extra-cranial regions of the head. The two main branches feeding this vein are the external facial vein and the internal facial vein.

The *external facial vein* drains the skin and muscles of the face and jaw articulation. Three branches (two large, one small) converge to form this vein:

(a) The *cutaneous facial vein*, one of the large branches, drains blood from the skin, face and eye muscles, and the area of jaw articulation. Complex fine vessels from the nasal-cere vein, which drain the cere, pass down anterior to the orbit and the main branch of the cutaneous facial vein. The cutaneous facial vein has connections with branches of the internal facial vein and the maxillary vein. A vein originating from the ethmoid vein ramifies in the preorbital area before feeding into the cutaneous facial vein.

(b) The *palpebral vein* is the second of the two larger branches. This vein converges on the external facial vein together with the cutaneous facial vein and the temporal vein. It collects blood from the lower temporal areas, the eye and eyelids.

(c) The *temporal vein* is a considerably smaller vessel. The main branch of this vein is fed by numerous smaller vessels which drain the muscles of the temporal area.

Smaller branches between the cutaneous facial and the palpebral vein, as well as connections with the internal facial vein branches, form a part of the venous component of the temporal rete.

The *internal facial vein* is the larger of the two veins which unite to form the anterior cephalic vein. It is made up of vessels which drain the pharyngeal and palate areas, the tongue musculature, the eyeball and the superficial orbit. There are connections between this vein, the temporal rete and the cutaneous facial vein.

(a) The *superior pharyngeal veins* are the most posterior vessels which drain into the internal facial vein. These small vessels drain the ventral palate and dorsal pharyngeal areas. They also form a link between the left internal facial vein and the right internal facial vein. In both specimens in which they were observed, three of these veins were found to be present.

(b) The next veins which bring blood to the internal facial vein are small branches which link it to the temporal rete and the cutaneous facial vein.

(c) The *internal mandibular vein* is a large vein which collects blood from the lower jaw. It has connections with the cutaneous facial vein, the temporal rete and the ophthalmic veins.

Progressing anteriorly, the next vessels feeding the internal facial vein are the maxillary vein and the ophthalmic vein.

(d) The *maxillary vein* has branches which collect blood from the anterior buccal muscles, the tongue and the palate area. It also has small branches which drain sections of the nasal area and eventually contribute to the temporal rete. The supra-palatine vein is the largest of these branches. This vessel drains a network of small vessels which ramify between the palate mucosa. There is a direct connection between the maxillary vein and the cutaneous facial vein. A vein consisting of numerous smaller branches, the *wattle vein*, drains the wattle. It feeds into the maxillary vein after passing ventral to the cutaneous facial vein.

(e) The *ophthalmic vein* joins the maxillaiy median to the eyeball. This vessel gives off many small branches which spread over the eyeball. Together with the middorsal sinus, it is fed by the ethmoid vein, which drains the frontal areas. Two large branches, the temporal ophthalmic vein and the recurrent ophthalmic vein drain the orbit and the cerebral areas. The temporal ophthalmic vein has two anastomoses with the temporal rete. The recurrent ophthalmic vein has connections with the temporal vein. The complexity of such anastomoses could not be fully determined in our dissections. The temporal ophthalmic vein, however, was observed to communicate with the cerebral circulation via the anterior cerebral vein. Small vessels draining the helmet pass through foramina in the frontal bone before draining into branches of this vein.

Posterior cephalic vein (Fig. 3)

The posterior cephalic vein is the major posterior division of the jugular vein. It joins the jugular prior to the transverse anastomosis. This vein receives blood from both the dorsal and ventral brain sinuses.

The *auricular vein* is a small vessel which receives blood from the ear musculature. It feeds into the posterior cephalic vein at a point in common with the occipital vein. Very fine branches of the posterior cephalic vein, the occipital vein, and the vertebral veins form the extensive venous component of the nape–cheek rete. The fine branches of these veins drain into three to four larger branches on either side of the neck. These branches then feed into a large vertebral vein which feeds into the jugular vein.

The *carotid vein* completely surrounds the internal cerebral artery. This vein extends from the sinus cavernosus, which encloses the intercarotid anastomosis, and drains into the posterior cephalic vein.

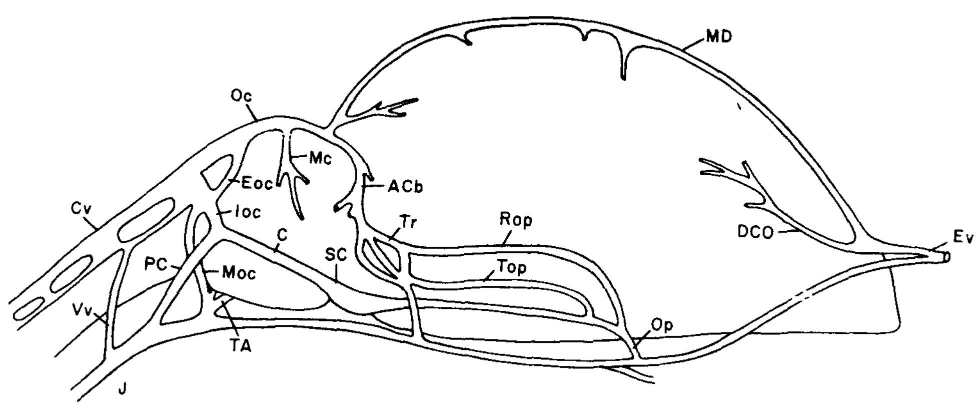

FIG. 4. A diagram of the lateral aspect of the brain showing the principle brain sinuses and their associated veins. For key to abbreviations, see p. 222.

The brain sinuses and occipital venous system (Fig. 4)

The dorsal cerebral ophthalmic vein and the ethmoid vein together feed into the mid-dorsal sinus. This fine vessel receives blood from the dorsal parts of the cerebrum. Near the junction of the cerebrum and the cerebellum, the anterior cerebral vein and the middle cerebral vein merge with the mid-dorsal sinus to form the occipital sinus. The anterior cerebral vein drains the area between the cerebrum and the cerebellum, as well as that between the cerebellar hemispheres. This vein has large connections with the temporal rete. The middle cerebral vein drains the cerebellum and the optic lobes, and has connections with the auricular vein.

The posterior cephalic vein and the carotid vein merge to form the internal occipital vein. This vessel connects dorsal and ventral components of the cerebellar brain sinuses. Near the origin of the middle cerebral vein from the occipital sinus, the external occipital vein branches off and connects to the internal occipital vein. The lateral occipital veins connect the internal occipital vein and the vertebral vein. At the point of fusion between the external occipital vein and the internal occipital vein, the middle occipital vein is given off. This vein passes ventrally around the cerebellum, and fuses with the same vein from the opposite side, before entering the transverse anastomosis. The ophthalmic vein fuses with the dorsal sinus to form the ethmoid vein. The vertebral vein connects to the internal occipital vein. This vein passes down the cervical canal, anastomosing with the cervical sinus, and the vertebral vein from the opposite side. It drains into the jugular vein level with the third or fourth cervical vertebra.

The cervical sinus is essentially an extension of the occipital sinus. It is connected to the jugular veins by two pairs of large veins, which we also call vertebral veins. Branches of these vertebral veins and those previously mentioned are fed by a network of small veins which form the venous component of the nape–cheek rete.

Discussion

The cervico-cephalic vascular system of *N. meleagris* is, in general, similar to that of *Gallus domesticus* (Richards 1967, 1968). Therefore, we will discuss only major differences between the two species.

In *N. meleagris* the upper internal maxillary artery gives rise to a nasal-cere artery, which feeds the cere and connects to the external facial artery. There is no comparable artery in *G. domesticus*. This could be due to the fact that the cere of this species lacks well-developed papillae which are often found on *N. meleagris* (Crowe, 1978*a*). The nasal-cere vein also has no counterpart in *G. domesticus*.

No vein and artery comparable to the wattle vein and artery in *N. meleagris* are described for *G. domesticus*. As with the nasal-cere artery and vein this is to be expected, since *G. domesticus* lacks a homologue for the cartilaginous wattle which hangs from the upper jaw of *N. meleagris* (Ghigi, 1936). In *G. domesticus*, wattles are fleshy structures which hang from the lower jaw (Lucas & Stettenheim, 1972).

The external facial artery in *G. domesticus* has a branch which feeds the comb. This branch is absent in *N. meleagris*. The helmet in *N. meleagris* is fed by a large branch of the temporal artery. The temporal artery in *G. domesticus* is much more reduced, and feeds mainly the temporal muscles. A number of vessels which drain the comb of *G. domesticus* empty into the cutaneous facial vein. In *N. meleagris*, vessels from the helmet feed into branches of the ophthalmic vein.

Tenuous connections between the occipito-vertebral and internal carotid systems occur in both species. In *N. meleagris* these connections are with the posterior ventral cerebellar artery, in *G. domesticus* with the ventral spinal artery. The ventral spinal artery in *N. meleagris* arises from the basilar artery, rather than from one of the posterior cerebellar arteries as it does in *G. domesticus*. Also, to the level of the fourth cervical vertebra, the ventral spinal artery of *N. meleagris* is a single vessel, whereas in *G. domesticus* it is, in some places, a double structure.

The most striking difference between the cervico-cephalic vascular systems of *G. domesticus* and *N. meleagris* is the presence of the nape–cheek rete in the latter. No rete in this area has been described for any other bird. It must be stressed that the complexity of the nape–cheek rete was apparent only in resin casts. Therefore, we cannot exclude the possible existence of similar retia in other species. However, Frost, Siegfried & Greenwood (1975), in the only other similar study of a bird, did not report a nape or cheek rete in their resin casts of the vascular system of the Jackass penguin (*Spheniscus demersus*).

There are five vascular arrangements in the head and neck of *N. meleagris* which we feel may be important in the regulation of brain temperature. These are the temporal and nape–cheek retia, the fine arterio-venous associations in the wattles and cere, and the intercarotid anastomosis-cavernous sinus association. The major problem in describing the possible ways in which these vascular arrangements could function in brain temperature regulation is understanding the alternative ways by which blood passing through these arrangements could reach the brain.

The most obvious direct route for blood to the brain is via the internal carotid artery and the caudal ramus of the circle of Willis. One alternative, less direct, route is via the anastomoses between branches of the external carotid and the palatine and sphenomaxillary branches of the internal carotid. Another pathway is from the vertebral artery via retrograde flow through the carotid bifurcation. Richards (1967) and Richards & Sykes (1967) have shown in *G. domesticus* that these routes of blood supply to the brain are able to maintain life indefinitely, in the absence of a direct route. Connections between the cerebral arterial circulation of the two hemispheres at the intercarotid anastomosis could allow lateral communication between the brain hemispheres.

Richards (1970) has discussed the feasibility and mechanisms by which relatively warm arterial blood on its way to the brain could be cooled in the temporal rete and in the intercarotid-cavernous sinus association. He, however, questions (Richards, 1970) the temporal rete as being the primary site of brain temperature regulation in *G. domesticus*. However, until more is known about intravascular temperatures, patterns of cervico-cephalic blood flow, and physiological responses of *N. meleagris* to varying temperature regimes we cannot demonstrate conclusively a thermoregulatory function for these vascular arrangements.

Summary

The anatomy of the cervical and cephalic arteries and veins of the helmeted guineafowl *Numida meleagris* was investigated by latex injections and dissection; by resin casting and maceration in pancreatin and hydrochloric acid; and by lipidol injections and X-ray photography.

The cervico-cephalic vascular anatomy of *N. meleagris* is similar to that of the domestic fowl *Gallus domesticus*. Major differences, particularly the existence of a nasal-cere and

wattle arteries, and an extensive arterio-venous rete in the nape and cheek regions of *N. meleagris*, are discussed.

Five vascular arrangements in the head and neck are postulated to be important in brain temperature regulation. These are: the nape-cheek rete, the temporal rete, fine arterio-venous networks in the wattles and cere, and the cavernous sinus-intercarotid anastomosis association. All but the last of these require arterial blood to flow to the brain via relatively indirect pathways. These pathways are discussed in the light of occlusion experiments carried out by other workers.

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