THE CAROTID ARTERIES IN THE PROCYONIDAE

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INTRODUCTION

The present study is one of a series of investigations being made at Chicago Natural History Museum in conjunction with work on the giant panda. More information on the vessel patterns in the Carnivora is needed before the considerable data on the giant panda can be evaluated. The taxonomic value of the circulatory system, demonstrated by Davis (1941) and others, suggests the usefulness of further study on this aspect of carnivore anatomy.

The characteristics of the carotid circulation in the Felidae have been established (Davis and Story, 1943). The cats exhibit one extreme of specialization within the superfamily Feloidea (Aeluroidea of authors); the conditions in the other feloid families are too incompletely known to be used for comparison. The Canoidea (Arctoidea of authors), to which the giant panda belongs, have been little investigated, aside from the well-known work of Ellenberger and Baum (1891) on the domestic dog. Accordingly, work was begun on the arteries of the head in the raccoon, and extended to include the other members of the raccoon family available in the Museum collection of preserved specimens.

In order to broaden the scope of this paper, my notes on the arteries of the head of several members of the Canidae, Ursidae, and Mustelidae have been used to interpret the data on the Procyonidae. The Felidae, exemplifying the feloid carnivores, have been used to emphasize both contrasts and parallels. Unfortunately, a thorough comparison of the arteries of the head in the order Carnivora cannot be made without examination of many more genera than are now available for dissection.

Simpson's (1945) classification of the Carnivora is followed, with reservations due to certain difficulties pointed out below.

MATERIAL AND ACKNOWLEDGMENTS

The material examined included twelve representatives of the Procyoninae, and a lesser panda. Additional dissections were made on a coyote, two dogs, a ferret, and a weasel. Most of these animals were received from the Chicago Zoological Society, whose continued co-operation is greatly appreciated. Thanks are also due the General Biological Supply House of Chicago for the splendid embalming and injection done by Mr. Arnold Blaufuss. Mr. Ernest Siegfried of the University of Chicago prepared two domestic dogs. A few of the smaller individuals were preserved in our own laboratory. A 9-power binocular microscope was used for much of the dissection, making it possible to trace even the uninjected vessels to their termini.

Frequent reference was made to the Museum's osteological collection, from which several skulls had been selected and sectioned in a previous study. Special thanks are due Mrs. Dorothy Foss for careful cleaning of the foramina in key skulls.

I am deeply indebted to Mr. D. Dwight Davis, Curator of Vertebrate Anatomy in Chicago Natural History Museum, for his helpful advice and criticism. Mr. Bryan Patterson, Curator of Fossil Mammals, has given valuable assistance in criticizing the manuscript.

The illustrations are intended to show the relations of the arterial pattern to the topography of the skull. In most of the drawings, muscles have been omitted for the sake of clarity. Structures covered by bone or muscle are indicated by lighter shading than structures on the surface.

The specimens dissected were all adult. The data on their preparation are as follows:

C.N.H.M. no. 48578	*Bassariscus astutus* ♂	Gelatin injection
C.N.H.M. no. 1357	*Bassariscus astutus* ♀	Starch injection
C.N.H.M. no. 1304	*Procyon lotor* ♀	Starch injection
C.N.H.M. no. 1309	*Procyon lotor* ♀	Gelatin injection
C.N.H.M. no. 1358	*Procyon lotor* ♂	Starch injection
C.N.H.M. no. 1359	*Procyon lotor* ♀	Starch injection
C.N.H.M. no. 53935	*Procyon lotor* ♂	Latex injection
C.N.H.M. no. 1328	*Nasua narica* ♂	Latex injection
I. T. Sanderson no. 2720M	*Nasua narica* ♀	Uninjected
C.N.H.M. no. 48676	*Potos flavus* ♀	Starch injection
C.N.H.M. no. 48829	*Potos flavus* ♂	Starch injection
C.N.H.M. no. 55429	*Bassaricyon alleni* ♂	Uninjected
C.N.H.M. no. 50815	*Ailurus fulgens* ♀	Uninjected

All living procyonid genera except the only slightly distinct *Nasuella*, and *Ailuropoda* (on which detailed data were available), are represented.

Other carnivores examined are:

C.N.H.M. no. 1312	*Canis latrans* ♂	Latex injection
C.N.H.M. no. 1419	*Canis familiaris* ♂	Starch injection
C.N.H.M. no. 1420	*Canis familiaris* ♂	Starch injection
C.N.H.M. no. 49304	*Mustela novaboracensis* ♀	Gelatin injection
C.N.H.M. no. 50813	*Mustela putorius* ♀	Latex injection

CAROTID CIRCULATION IN THE RACCOON
(*Procyon lotor*)

The Common Carotid Artery

The common carotid arteries run forward on either side of the trachea as far as the middle of the thyroid cartilage to the level of the ventral crossing of N. hypoglossus. Each usually gives off no branches until its terminal bifurcation. In one specimen there is a minute twig to the sternothyroid muscle. In two cases out of six the anterior thyroid arose from the common carotid instead of from the external carotid. The common carotid artery is closely associated with the vagus nerve and the cervical sympathetic trunk throughout its course. At the level of the thyroid cartilage the common carotid divides into the external and internal carotid arteries, approximately opposite the posterior surface of the occipital condyles (fig. 82). The internal carotid is slightly less than half the caliber of the external carotid, bearing about the same relation to that vessel as in the bears and pandas. In a specimen of *Bassariscus astutus*, the internal carotid is three fourths the caliber of the external carotid, and thus is apparently the largest known among carnivores.

Variations: In one individual (C.N.H.M. no. 1304) the bifurcation of the left common carotid takes place far posterior, opposite the neck of the scapula. The right common carotid in this individual divides at the posterior border of the cricoid cartilage.

The Internal Carotid Artery

A. carotis interna runs diagonally anterodorsad beside the longus capitis muscle to the foramen caroticum posterius, which is situated midway between the condyloid and medial lacerated foramina. The internal carotid has a distinct enlargement, the carotid sinus, at its base. The average basicranial internal carotid exceeds the length of the bulla by 7 per cent. The internal carotid artery gives off no branches outside the skull. Accompanied by the plexiform internal carotid nerve and a small vein to the sinus cavernosus, the artery enters the anterodorsally directed carotid canal in the dorsomedial wall of the tympanic bulla, opposite the round window. The carotid canal arches dorsad and slightly laterad as it parallels the promontorium. Within the canal the artery gives off fine *Aa. caroticotympanicae* that accompany the two caroticotympanic nerves onto the promontorium and anastomose with the other tympanic arteries (fig. 83). The carotid canal arches ventrad at its anterior end, so that in its entirety it forms an S curve. Where the carotid canal communicates via the foramen caroticum anterior with the foramen lacerum medium (fig. 94), the internal carotid artery receives an anastomotic twig from the ascending pharyngeal artery, then bends sharply dorsad to reach the floor of the cranial cavity. The artery curves gently mesad to enter the posterior end of the sinus cavernosus, where it takes a straight course to the tuberculum sellae. At this point the internal carotid artery pierces the dura mater and terminates by participating in the circle of Willis.

The internal carotid supplies a threadlike branch to the dura mater overlying the inferior petrosal sinus. The anastomotic artery from the orbital branch of the internal maxillary artery joins the internal carotid opposite the dorsum sellae.

The Circle of Willis

The circle of Willis is hexagonal in outline, with considerable irregularity in caliber and bilateral symmetry, three out of five cases being asymmetrical. In one instance the circle took an ellipsoid form. The internal carotid contributes the strong anterior semicircle, and the slightly smaller basilar artery completes the circuit posteriorly (figs. 82 and 93).

Immediately after perforating the dura, the internal carotid gives off the extremely slender ophthalmic artery, then breaks up in the circle of Willis. *A. ophthalmica* (fig. 86) joins the strong median branch of the internal ethmoidal and the resulting "ophthalmic" artery runs forward on the lateral surface of the optic nerve into the orbit, where it terminates by anastomosing with the rete from the ciliary arteries midway to the eyeball. The central artery of the retina is absent.

Opposite the infundibulum the internal carotid enters the circle of Willis and divides into three vessels, the subequal anterior and middle cerebrals, and the smaller posterior communicating artery. There is no anterior communicating artery, but the anterior cerebrals unite to form a median vessel in the longitudinal sulcus.

A. cerebri anterior arches around the optic chiasma and gives off the internal ethmoidal[1] and minute twigs to the anterior perforated substance before it enters the longitudinal sulcus. The anterior cerebral at once unites with its fellow and runs as a median vessel around the genu of the corpus callosum. Here it turns backward over the body of the corpus callosum, then divides into right and left arteries that give off branches to the inner surfaces of the frontal and parietal lobes, their outer surfaces along the longitudinal fissure, and the corpus callosum, finally anastomosing near the splenium with the posterior cerebral artery. Just before the anterior cerebral ascends in the sulcus, it sends to the olfactory lobe a small branch, *R. bulbi olfactorii*, that divides into subequal branches, one supplying the ventral surface of the olfactory bulb, the other running in the longitudinal sulcus, giving off twigs to the adjacent olfactory areas.

A. ethmoidalis interna (figs. 87 and 88), a medium-sized vessel, arises from the anterior cerebral laterad of the optic nerve. The internal ethmoidal winds toward the midline, where it runs tortuously in the heavy dura beside its mate from the opposite side, anastomosing with it, as well as with the external ethmoidal, ventral to the olfactory lobe. The anastomosis between the two internal ethmoidals gives rise to a median vessel that turns backward to the optic nerves, where it divides. The resulting vessels run along the medial surface of the optic nerves into the orbit. The true ophthalmic joins this orbital branch.

A. communicans anterior is present as a minute vessel in one specimen. The anterior communicating artery is a slender connection between the anterior cerebrals, which form a median vessel in this raccoon as well as in the others. The constancy of the union of the anterior cerebrals eliminates the necessity for a communicating artery. In two individuals the median anterior cerebral divides at the genu of the corpus callosum, instead of farther posteriorly.

A. cerebri media is the largest branch of the circle of Willis. It winds dorsad between the pyriform lobe and the anterior perforated substance to the lateral fissure, where it ramifies to the lateral surface of the olfactory tract, the rhinal fissure, and the temporal, parietal, and frontal lobes. The small *A. chorioidea* is given off by the middle cerebral near its origin and passes backward on the cerebral peduncle

[1] For use of the term "internal ethmoidal" see Davis and Story, 1943, p. 24.

to the choroid fissure, where it terminates in the choroid plexus. In three cases the choroid artery took an additional root from the posterior communicating artery, and in one arose from it alone.

A. communicans posterior connects the internal carotid with the terminal bifurcation of the basilar artery, and gives rise regularly to one branch, *R. hippocampi*, to the hippocampal gyrus, besides an occasional root to the choroid.

Between the first and third cervical nerve roots the vertebral arteries form a plexus, the *Rete basilaris*. There is a large branch of the vertebral at the level of the third cervical nerve root, a minute branch at the second, and a second large branch at the first cervical nerve. The relative caliber of these branches varies considerably, but the rete has typically a modified diamond pattern. Posteriorly the rete gives off the threadlike *A. spinalis anterior* that runs on the ventral surface of the spinal cord, receiving anastomoses from the arteries at each spinal nerve. Anteriorly the plexus unites to form the basilar artery. The vertebrals sometimes unite at once, then divide again in forming the rete.

A. basilaris extends at the midline on the medulla oblongata, from the first cervical nerve to the anterior border of the pons, where it bifurcates. The terminal branches of the basilar, completing the circle of Willis, are continued into the posterior communicating arteries at the origin of the posterior cerebrals. In its course the basilar gives off several fine unnamed pontile rami, two pairs of inferior cerebellar arteries on each side, the superior cerebellar, and the posterior cerebral arteries. The basilar followed a tortuous path in one individual and in another was small in caliber, making the posterior half of the circle of Willis disproportionate to the large anterior half.

A. cerebelli inferior anterior is represented by two small arteries that arise on the pyramid opposite the root of the vagus nerve. *A. auditiva interna*, a minute artery to the inner ear, is given off as the inferior cerebellar approaches the cerebellum. *A. cerebelli inferior posterior*, smaller than its companions, also arises as two vessels, coming off either near the origin of the basilar or directly from the rete. The two pairs of inferior cerebellar arteries anastomose freely, supplying both the ventral and posterior surfaces of the cerebellum.

A. cerebelli superior arises at the anterior border of the pons and runs laterad to ramify on the anterior and dorsal surfaces of the cerebellum.

A. cerebri posterior arises at the level of the posterior perforated substance and promptly divides into anterior (central) and posterior (cortical) branches. The posterior cerebral supplies the cerebral peduncle and the posterior and inferior surfaces of the occipital lobe. The central and cortical branches arose independently in three instances. A small twig, *R. thalamica media,* supplies the thalamus.

The External Carotid Artery

The external carotid artery is the direct continuation of the common carotid trunk beyond the origin of the internal carotid artery. It runs forward to the level of the anterior border of the digastric muscle, around which it winds laterad to reach the postglenoid process. Here the superficial temporal is given off and the trunk is continued as the internal maxillary artery. Near the origin of the lingual artery the hypoglossal nerve crosses the external carotid. A branch of the superior cervical sympathetic ganglion, the external carotid nerve, accompanies the external carotid past the digastric muscle, and on to the internal maxillary plexus.

The external carotid gives rise to the following branches:

(1) *The Anterior Thyroid Artery*

The large anterior thyroid is the first branch. It supplies twigs to the laryngeal and hyoid musculature, and the sternomastoid muscle. The bulk of the vessel richly supplies the thyroid gland. A branch to the sternomastoid muscle and the cervical lymph gland usually arises opposite the thyroid cartilage, but may arise independently from the external carotid artery. *A. laryngea anterior* (superior) is a small branch that takes origin either directly from the external carotid, or from the anterior thyroid, these two origins often appearing in the same animal. The anterior laryngeal artery follows the nerve of the same name to supply the intrinsic laryngeal musculature. The anterior thyroid was absent on one side in one individual, but this vessel on the opposite side was compensatingly enlarged.

(2) *The Ascending Pharyngeal Artery*

A. pharyngea ascendens (fig. 82) arises in the angle of the bifurcation of the common carotid, where it crosses the anterior laryngeal nerve and is crossed by the spinal accessory nerve. The artery courses forward between the pharyngeal constrictor musculature and the bulla to the level of the hamular process of the pterygoid bone, where it divides into its terminal twigs. The ascending pharyngeal artery gives off the following branches:

(*a*) *R. muscularis* arises from the lateral wall of the ascending pharyngeal, opposite the hypoglossal nerve, and supplies the digastric and sternomastoid muscles.

(*b*) *R. lymphoglandulae* is given off opposite the above branch. It ramifies to the longus capitis muscle and the cervical lymph gland, and sends nutrient twigs to the vagus and sympathetic nerves.

(*c*) *A. occipitalis* is a small vessel that arises at the posterior border of the bulla, and gives off at once a strong branch that runs beside the spinal accessory nerve, supplying the nerve, the cleido-mastoid, rectus capitis lateralis, and complexus muscles. The occipital artery runs dorsad along the medial border of the digastric muscle to the paroccipital process, where it breaks up. This part of the vessel sends twigs to the digastric muscle and the superior cervical ganglion. The terminal twigs supply the walls of the transverse sinus, the atlanto-occipital capsule, and the deep axial musculature, in addition to an anastomosis with the posterior meningeal and vertebral arteries. In three out of ten cases, the posterior meningeal was a branch of the occipital artery. The occipital trunk was absent in one individual, but the branches arose from the ascending pharyngeal and were distributed as usual.

(*d*) *A. meningea posterior*, a vessel of variable caliber, takes origin at the level of the posterior lacerated foramen. After giving off the inferior tympanic as well as rami to Mm. longus capitis and rectus capitis ventralis, the bulk of the posterior meningeal anastomoses with the occipital and vertebral arteries. The terminal branch of the posterior meningeal, much diminished in caliber, enters the hypoglossal canal beside the twelfth nerve and the condyloid vein, supplying the walls of this canal, the adjacent dura, and nutrient twigs to the nerve. *A. tympanica inferior* enters the foramen lacerum posterior beside the internal jugular vein, runs between the bulla and the promontorium, sending a twig to the walls of the transverse sinus, and terminates on the promontorium by anastomosing with the other tympanic arteries; it supplies the periosteum of the bulla. The mastoid meningeal ramus of the posterior auricular trunk takes over the area of dura supplied by the posterior meningeal in *Felis domestica.*

The ascending pharyngeal supplies the longus capitis, rectus capitis ventralis, pharyngeal constrictor, tensor veli palatini, and

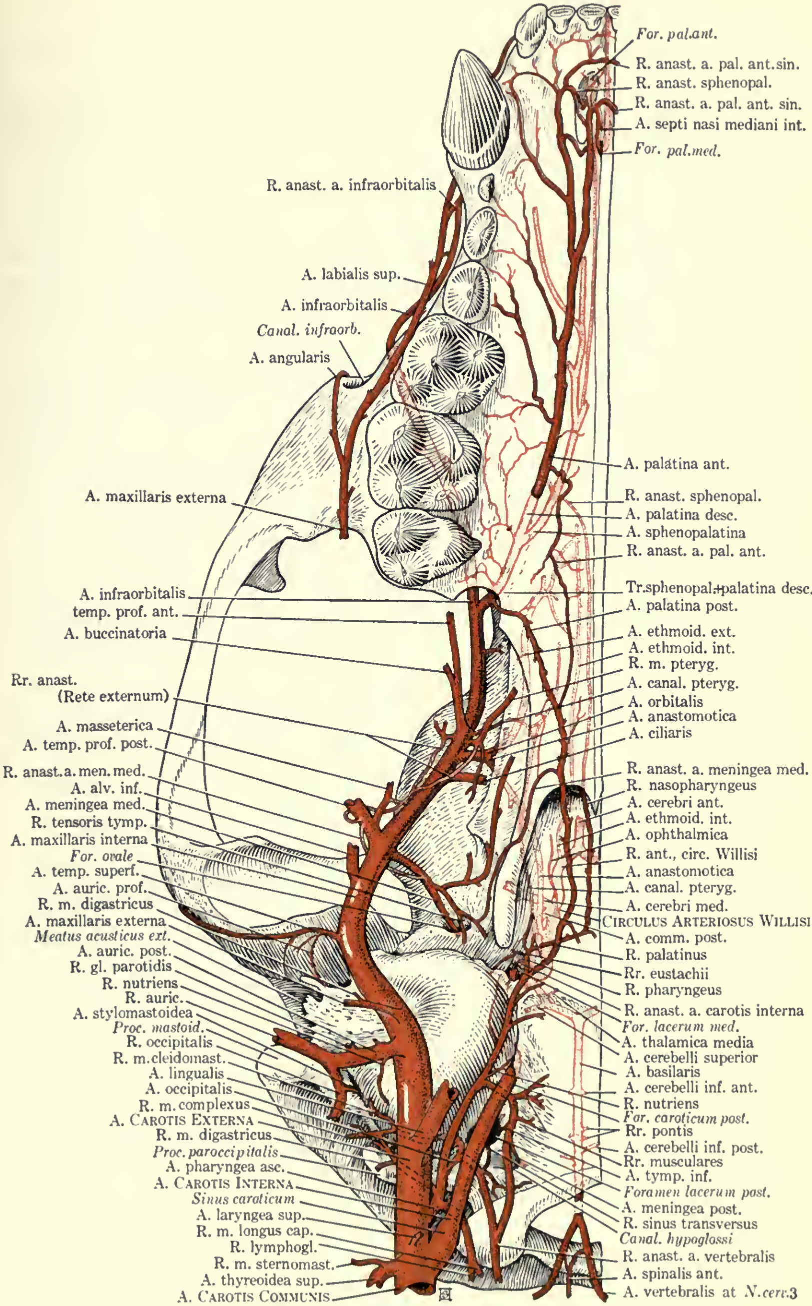


FIG. 82. Ventral view of the arteries of the head in the raccoon. × 1½.

levator veli palatini muscles, and nutrient twigs to the adjacent bone, as it lies beside the bulla.

At the posterior border of the hamular process of the pterygoid bone the ascending pharyngeal divides into its terminal branches, the palatine and pharyngeal rami.

(*e*) *R. palatinus* runs craniad between Mm. levator veli palatini and constrictor pharyngis anterior, giving off a twig to the velum palatinum. The palatine branch then ramifies in the glands of the soft palate, anastomosing with the tonsillar and posterior palatine arteries.

(*f*) *R. pharyngeus* ascends dorsolaterally to the auditory (Eustachian) tube, where it gives off several minute *Rr. tubarii*, the pharyngeotympanic artery, and a small anastomotic artery to the internal carotid (fig. 83). The above-mentioned small arteries may arise from a common trunk. The anastomotic artery is constant, and joins the internal carotid near the exit of the great deep petrosal nerve from the carotid canal. The pharyngeal branch gives off twigs to the pharyngeal tonsil, then spends itself in the mucosa of the nasopharynx, receiving an anastomosis from the sphenopalatine artery.

A. pharyngeotympanica enters the middle ear medial to the tendon of the tensor tympani muscle and anastomoses with the other tympanic arteries on the promontorium.

(3) *The Lingual Artery*

A. lingualis (fig. 95), the largest branch of the external carotid, is given off at the level of the stylohyal cartilage. It is accompanied by the hypoglossal nerve as far as the hyoglossal muscle, beneath which the artery turns, but the nerve remains on the lateral surface of the muscle. The lingual artery gives off the following branches:

(*a*) *R. m. digastricus* is the first branch. It supplies the posterior part of the digastric muscle.

(*b*) *R. tonsillaris posterior* arises at the level of the stylohyoid and winds between the anterior and middle pharyngeal constrictors to enter the soft palate. The posterior tonsillar artery is distributed to the posterior and middle surfaces of the palatine tonsil, and the adjacent glandular area of the soft palate. Twigs anastomose with the anterior tonsillar, the ascending pharyngeal palatine ramus, the posterior palatine, and the palatine branch of the middle meningeal trunk. This artery is accompanied by the tonsillar branch of the glossopharyngeal nerve. In one specimen the posterior tonsillar arose from the pharyngeal constrictor ramus of the ascending pharyngeal.

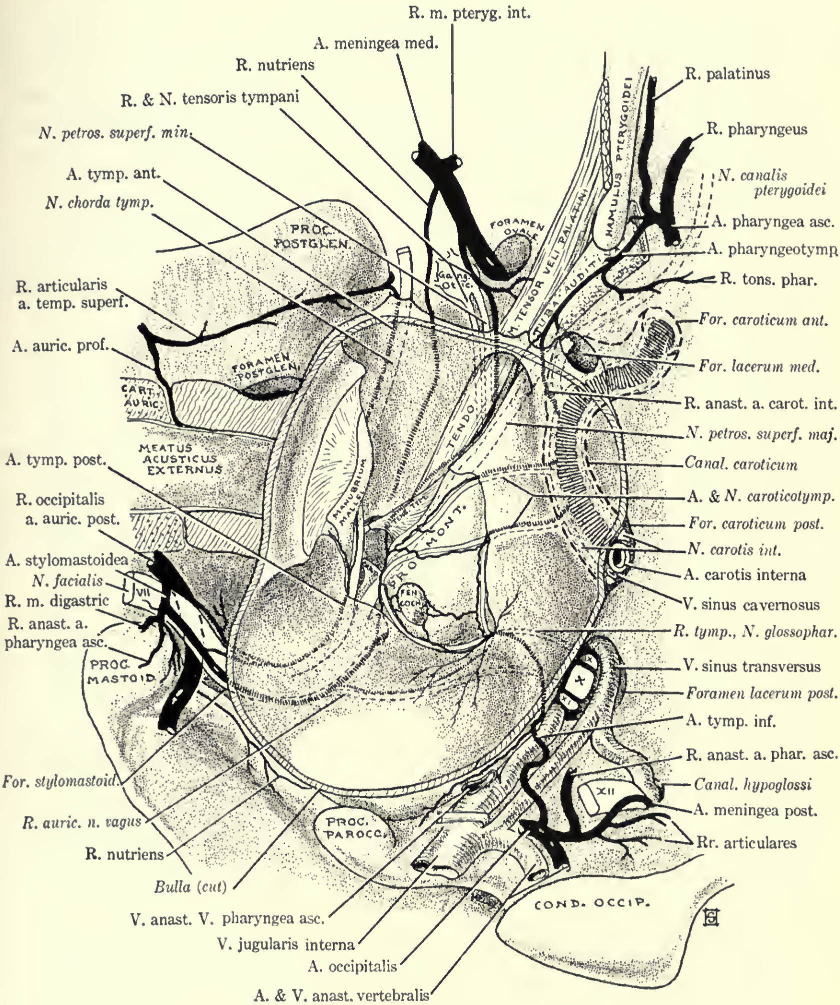


FIG. 83. Arteries of the right auditory region in the raccoon. The floor of the bulla and external auditory meatus have been removed. × 4.

(c) *R. tonsillaris anterior* arises opposite the styloglossal muscle, to which it sends twigs, then arches mesad to reach the anterior margin of the palatine tonsil, where it enters the rich arterial plexus of the tonsil.

(*d*) *R. m. mylohyoideus* arises at the posterior margin of the mylohyoid muscle, which it supplies, finally anastomosing with the submental artery from the external maxillary.

(*e*) *R. geniohyoideus* leaves the lingual anterior to the body of the hyoid, mesad of the hyoglossal muscle, and after sending twigs to the adjacent muscles, anastomoses with its mate from the opposite side. The trunk thus formed runs forward, supplying the geniohyoid muscles, to terminate at the symphysis by anastomosis with the sublingual artery.

(*f*) *Rr. dorsales linguae* are given off at irregular intervals as the lingual artery lies between the genio- and styloglossal muscles. These arteries richly supply the dorsum of the tongue, their course roughly paralleled by branches of the hypoglossal nerve.

A few millimeters beyond the entrance of the lingual nerve, the lingual artery breaks up into its terminal branches, the sublingual and deep lingual arteries. The smaller vessel, (*g*) *A. sublingualis,* joins the duct of the sublingual gland, and supplies the genioglossal muscle on its course to the symphysis. Much diminished in caliber, the artery sends a minute twig to the frenulum, then anastomoses with the geniohyoid branch of the lingual, and with the incisive branch of the inferior alveolar.

(*h*) *A. lingualis profunda,* the larger branch, accompanied by terminal twigs of the lingual nerve, enters the ventral surface of the styloglossal muscle, coursing near the midline, approaching the inferior surface of the body of the tongue. From the anterior border of the genioglossus, the deep lingual lies beside the narrow lyssa (cartilaginous median supporting rod of the tongue). The artery breaks up into numerous small branches that go to the tip of the tongue, forming minute anastomoses with its fellow and with twigs derived from the dorsal lingual.

(4) *The External Maxillary Artery*

A. maxillaris externa[1] (fig. 85) arises at the posterior border of the external pterygoid muscle, opposite the external acoustic meatus, immediately beyond the posterior auricular artery. The external maxillary runs first laterally, then anteriorly between the digastric and internal pterygoid muscles, and crosses the submaxillary duct, emerging near the middle of the digastric in company with an anastomotic loop between the mylohyoid and buccal nerves. The artery follows the anteroventral border of the masseter muscle as

[1] In all other procyonid genera this artery precedes the posterior auricular.

far as the posterior angle of M. buccinator, where the vessel bifurcates into inferior and superior labial arteries. A small sympathetic nerve from the external carotid nerve accompanies the external maxillary artery. In one case the posterior auricular followed the origin of the external maxillary.

The branches of the external maxillary follow:

(*a*) *R. m. digastricus* is the first branch given off by the external maxillary. It supplies the posterior part of the digastric muscle.

(*b*) *R. glandulae submaxillaris* arises near the lateral border of the digastric and passes ventrad to enter the submaxillary gland. This vessel arose from the occipital trunk in one specimen, and from the submental in another.

(*c*) *A. submentalis,* a large branch, comes off near the anterior border of the internal pterygoid muscle. The artery parallels the duct of the submaxillary gland and the mylohyoid nerve as it runs anteriorly between the mylohyoid and digastric muscles, which it supplies. The submental artery continues along the ventromedial border of the mandible as far as the symphysis, where it anastomoses with its fellow of the opposite side. A delicate twig follows the lateral border of the digastric muscle to its insertion.

(*d*) *R. lymphoglandulae* ramifies to the sub-maxillary lymph nodes.

(*e*) *Rr. m. masseterici* are several twigs to the ventral border of the masseter muscle.

(*f*) *A. labialis inferior* is given off opposite the third molar, and, joined by the inferior buccal nerve, runs along the ventral border of the buccinator muscle and the alveobuccal gland, to which it supplies numerous twigs. The inferior labial artery terminates in the skin of the lower lip, anastomosing with its fellow of the opposite side.

(*g*) *A. labialis superior* is the continuation of the external maxillary artery beyond the point at which the inferior labial arises. The superior labial artery, in company with the superior buccal nerve, follows the posterodorsal border of the buccinator muscle, supplying that muscle and the platysma, and terminates by anastomosing with a branch of the infraorbital artery in the vicinity of the third premolar. The strong artery resulting from this union follows the margin of the upper lip, anastomosing with the artery of the opposite side, and other infraorbital twigs, and gives off a branch to the outer surface of the septum. *A. septi nasi* [externi] anastomoses with septal branches of the ethmoidal, sphenopalatine, and anterior palatine arteries (figs. 85 and 88). *A. angularis*,[1] a large branch of the superior labial, arises opposite the first molar, ramifies in the superficial muscles, sends a twig toward the lateral angle of the eye to join the lateral palpebral, and anastomoses in front of the infraorbital foramen with twigs from the medial palpebral and transverse facial arteries. Terminal twigs of the angular artery accompany the external nasal nerve.

(5) *The Posterior Auricular Artery*

A. auricularis posterior is a large branch arising from the anterior part of the external carotid (fig. 84), opposite the mastoid process, and at its origin associated with the posterior auricular nerve. The following branches are given off:

(*a*) *R. mm. pterygoidei et masseterici*, the small first twig, arises from the anterior wall of the posterior auricular. In one case this artery anastomosed with the digastric ramus from the lingual artery.

(*b*) *R. nutriens* is given off at the same level as the muscular twig but from the opposite wall of the trunk. It supplies one twig to the digastric, runs along the posterior border of the bulla, supplying the adjacent musculature, and enters a small foramen at the paroccipital process.

(*c*) *R. parotideus* arises opposite the mastoid process and richly supplies the parotid gland, as well as sending an anastomotic twig to the superficial temporal. The parotid ramus gives off a slender branch that parallels the parotid duct, supplying it and anastomosing with the transverse facial and superficial labial arteries.

(*d*) *R. occipitalis* is a large trunk given off at the anteromedial border of the mastoid process. *A. stylomastoidea*, the first branch of the occipital ramus, joins the facial nerve, along which it runs, giving nutrient arteries to the nerve and to the surrounding bone. The stylomastoid artery gives off first the *A. tympanica posterior*, which accompanies the chorda tympani, supplying the inner surface of the tympanic membrane and anastomosing with the anterior tympanic branch from the internal maxillary. Before reaching the genu facialis, the stylomastoid sends an anastomotic twig to the inferior tympanic. The vessel breaks up opposite the round window of the cochlea, supplying the outer surface of the secondary tympanic membrane, the stapedial muscle, the adjacent mastoid bone, the

[1] This artery is homologous to the angular artery of human anatomy. Its thread-like dimensions in the cat caused it to be overlooked in our preceding study. The angular artery in that paper was a misnomer for the medial palpebral.

great superficial petrosal nerve, and the proximal portion of the facial nerve, anastomosing with the internal auditory artery and with the arterial plexus on the promontorium.

The occipital branch winds mesad around the mastoid process between the insertions of the digastric and the sternomastoid muscles,

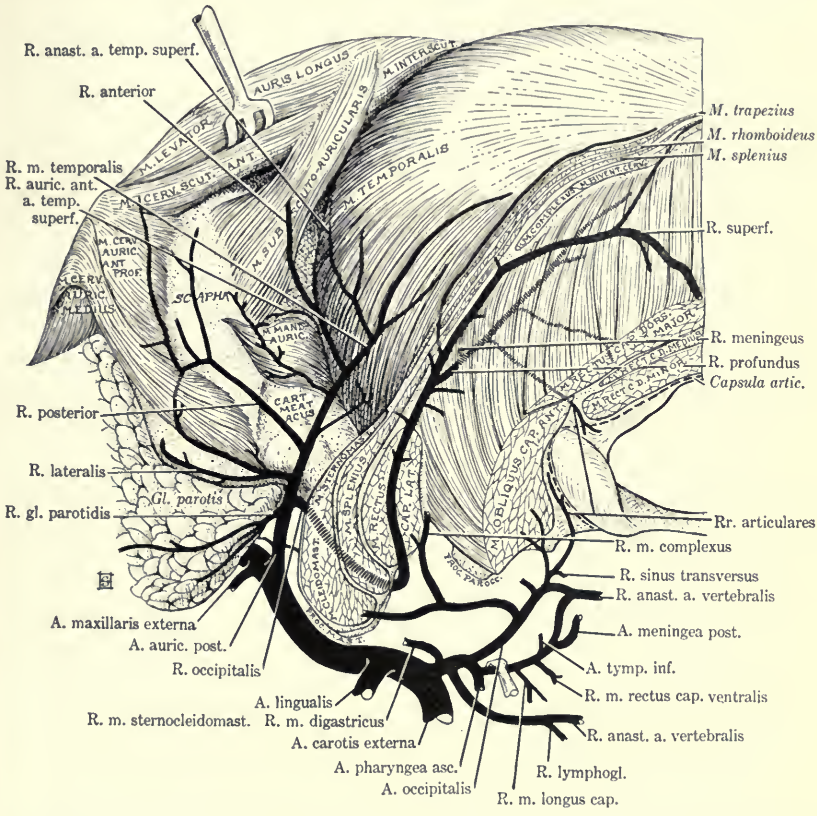


FIG. 84. The posterior auricular and occipital arteries in the raccoon. The left external ear has been retracted anterolaterally. × 1½.

to which it sends twigs, and continues postero-dorsad through the insertion fibers of M. rectus capitis lateralis. The occipital branch runs underneath the complexus, across the obliquus capitis anterior and the biventer cervicis to the midline, where it anastomoses with its fellow of the opposite side. A deeper branch courses through the M. obliquus capitis anterior to the rectus capitis dorsalis complex, one twig perforating the insertion tendon of the complexus to emerge on the lambdoidal crest along which it runs almost to the midline.

Twigs are supplied to the surrounding axial musculature, in addition to a well-developed *R. meningeus* that accompanies a large vein through the mastoid foramen into the skull, where it supplies the dura mater of the posterior cranial fossa. The occipital ramus has taken over the distribution of the main occipital trunk of *Felis domestica* and *Homo*.[1]

(*e*) *R. auricularis posterior* is the continuation of the main trunk of the posterior auricular after the origin of the occipital ramus. A medium-sized branch is distributed to the free lateral surface of the auricle; then a larger branch supplies the posterior margin and associated muscles. A small branch ramifies to the medial surface, penetrating the cartilage after giving off muscular twigs. A strong *R. auricularis anterior* runs between the pinna and the temporal muscle to the anterior border of the pinna, where it ramifies in M. intermedius scutulorum. The posterior auricular terminates in several superficial and deep branches to the posterior part of the temporal muscle, one twig anastomosing with the middle temporal branch of the superficial temporal.

(6) *The Superficial Temporal Artery*

A. temporalis superficialis (fig. 85) is the comparatively small last branch of the external carotid. It takes origin at the level of the postglenoid process, and runs in close association with the auriculotemporal nerve all the way to the orbit. The superficial temporal artery winds laterad around the temporomandibular joint, then arches anterodorsally across the zygoma and the temporal fascia to the posterior margin of the orbital ligament, where, covered by the scalp musculature, it divides into its terminal frontal and parietal branches.

The superficial temporal supplies the following branches:

(*a*) *R. articularis* arises at the level of the postglenoid process and supplies the capsule of the mandibular joint. *A. auricularis profunda*, a minute medial twig from the articular ramus, runs between the cartilaginous and bony parts of the meatus and supplies the external surface of the tympanic membrane, as well as part of the skin of the meatus. The deep auricular artery sends a slender branch, *A. tympanica anterior*, through the petrotympanic fissure, where it joins and supplies the chorda tympani, anastomosing with the posterior tympanic artery.

[1] For a discussion of the occipital trunk in the domestic cat and man, see Davis and Story, 1943, pp. 13–14.

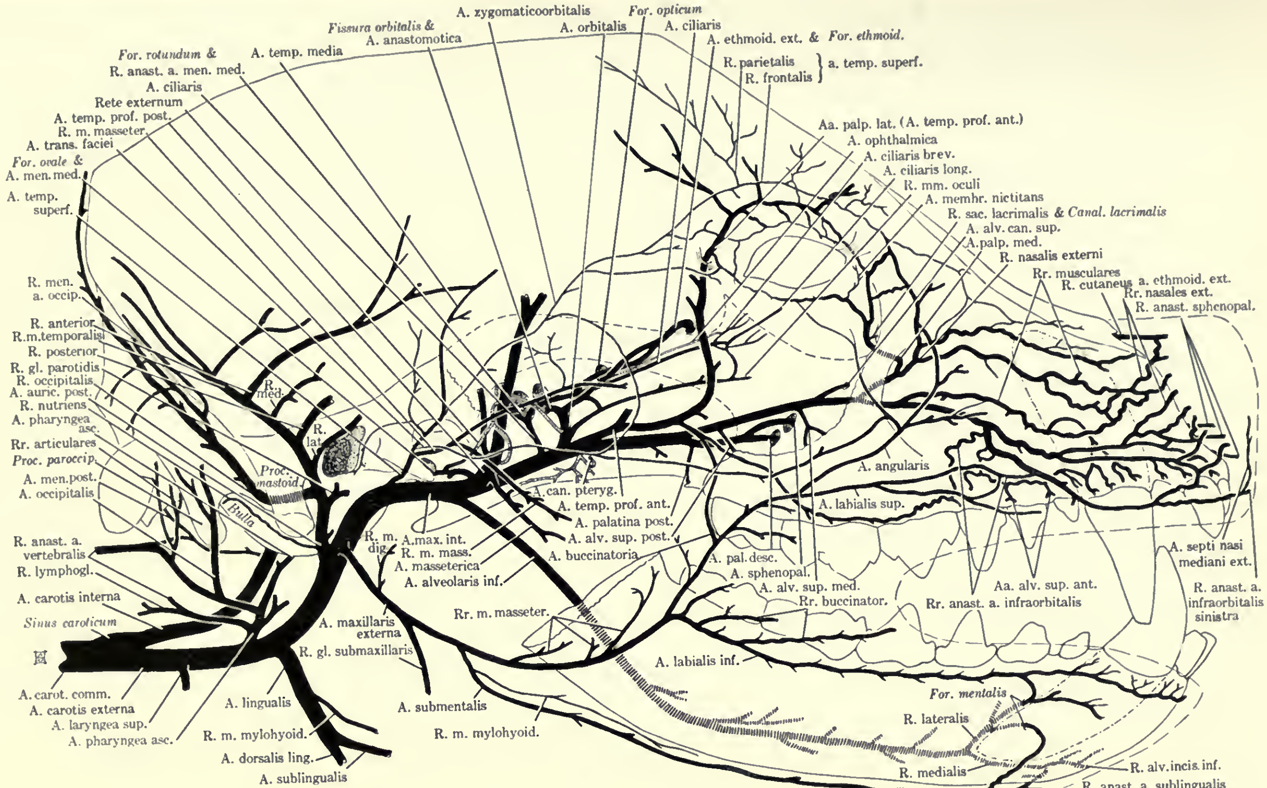


FIG. 85. Lateral view of arteries of raccoon head. External rete indicated as stippled anastomosing arterioles.

(*b*) *R. massetericus,* the largest branch, arises at the mandibular condyle and runs deep in the masseteric muscle, one branch (*R. dorsalis*) following the curve of the zygoma, the other (*R. ventralis*) turning toward the ventral border of the masseter. Twigs anastomose with the external maxillary, masseteric, and buccinator arteries.

(*c*) *A. transversa faciei,* a slender vessel, arises just beyond the masseteric ramus and runs forward across the masseter muscle, giving twigs to the superior buccal nerve. It supplies the superficial layer of the masseter, and anastomoses with a twig of the angular artery external to the infraorbital foramen.

(*d*) *A. auricularis anterior* comes off opposite the transverse facial artery and is hidden by the parotid gland throughout its course. The anterior auricular supplies twigs to the parotid gland and to the anterior surface of the pinna, besides anastomosing with a small parotid twig from the posterior auricular artery.

(*e*) *A. temporalis media,* the second largest branch, takes origin at the articular tubercle. It accompanies a temporal branch of the auriculotemporal nerve directly dorsad, crossing the root of the zygoma, and piercing the temporal aponeurosis to ramify in the temporal muscle. The middle temporal artery receives an anastomosis from the anterior auricular branch of the posterior auricular artery. As the superficial temporal follows the zygomatic arch it sends arterioles to the periosteum, forming a minute zygomatic rete that is paralleled by companion venules. Near the center of the zygomatic arch a twig loops across to join the transverse facial artery.

(*f*) *A. zygomatico orbitalis* is given off several millimeters after the superficial temporal reaches the anterior part of the temporal muscle, and is a minor anastomotic nutrient branch that follows the zygomaticoorbital nerve and joins the lateral palpebral artery at the lateral angle of the eye.

Shorter twigs from the superficial temporal pass to the orbital region as the artery arches posterior to the orbital ligament. *R. parietalis,* the posterior terminal branch, ramifies in the temporal fascia in the parietal region, reaching almost to the vertex. The anterior terminal branch, *R. frontalis,* winds past the medial angle of the eye to break up into small twigs that supply the frontal periosteum and anastomose with the medial palpebral artery.

The Internal Maxillary Artery

Beyond the origin of the superficial temporal artery the external carotid is continued, without diminishing in size, as the internal

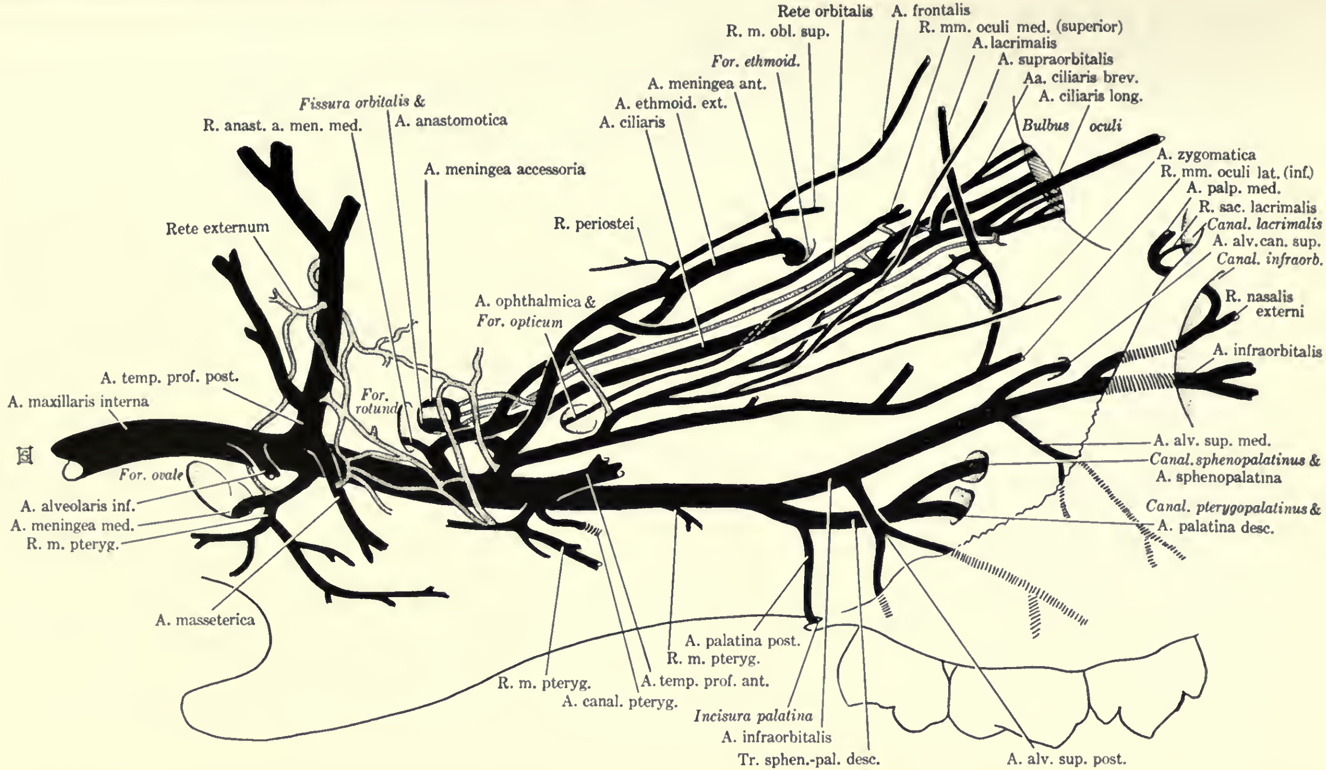


FIG. 86. Branches of the right internal maxillary artery in the infratemporal fossa in the raccoon. Anastomotic arterioles are stippled; the orbital branches are spread apart.

maxillary artery. *A. maxillaris interna* joins the auriculotemporal nerve at the postglenoid process and winds around the medial extremity of the mandibular condyle into the infratemporal fossa (fig. 86). Here the internal maxillary crosses the anterior part of N. mandibularis, runs between the external and internal pterygoid muscles and is crossed dorsally by N. masticatorius (to masseter, temporal, pterygoid and buccinator muscles). Beyond the foramen rotundum the artery rests upon the dorsal surface of the internal pterygoid muscle, and accompanies the maxillary nerve. At the level of the palatine notch the internal maxillary terminates by dividing into the infraorbital and sphenopalatine-descending palatine trunks. An incipient rete surrounds the internal maxillary in the infratemporal fossa. Many of the arteries of this region are closely associated with branches of the cranial nerves.

ASSOCIATED NERVES AND ARTERIES OF THE HEAD IN PROCYON LOTOR

Artery	Nerve
A. carotis communis	accompanies vagus nerve; sympathetic cervical trunk
A. carotis interna	accompanies N. carotis interna (sympathetic)
A. ophthalmica	accompanies optic nerve
A. ethmoidalis interna	accompanies olfactory nerve
A. spinalis anterior	nutrient to spinal cord and spinal nerves
A. auditiva interna	facial and auditory nerves
A. carotis externa	crossed by hypoglossal nerve; paralleled by sympathetic cervical
A. laryngea anterior	accompanies N. laryngeus anterior
A. pharyngea ascendens	crosses N. laryngeus anterior; crossed by glossopharyngeal nerve
A. meningea posterior	nutrient to hypoglossal nerve
A. occipitalis	constant nutrient ramus to spinal accessory nerve
A. lingualis	accompanies hypoglossal nerve; crossed at base by ramus digastricus; sympathetic cervical ganglion
A. maxillaris externa	mylohyoid nerve anastomoses with N. buccalis inferior
R. m. digastricus	accompanies ramus digastricus; sympathetic cervical ganglion
A. submentalis	accompanies mylohyoid nerve for a few mm.
A. labialis inferior	accompanies N. buccalis inferior (facial nerve)
A. angularis	terminal twigs join N. nasalis externi
A. labialis superior	accompanies N. buccalis superior (facial nerve)

Artery	Nerve
A. auricularis posterior	N. auricularis posterior (facial nerve) at origin and for a few mm.
A. stylomastoidea	nutrient to ramus auricularis; vagus nerve and facial nerve in stylomastoid foramen
A. temporalis superficialis	accompanies N. auriculotemporalis all the way to orbit (facial nerve)
A. transversa faciei	nutrient to N. buccalis superior (facial nerve)
A. temporalis media	accompanies ramus temporalis, N. auriculotemporalis of facial nerve
A. zygomatico-orbitalis	nutrient to ramus zygomaticus, N. zygomatico-orbitalis (facial nerve)
A. maxillaris interna	accompanies N. auriculotemporalis from postglenoid process to foramen ovale, there crosses N. mandibularis and is crossed by motor root of N. trigeminus, then accompanies N. maxillaris
Rete externum	surrounds N. trigeminus, nutrient to N. maxillaris
Rete internum absent	
Ramus temporalis profundus medius	N. temporalis profundus medius
A. temporalis profunda posterior	N. temporalis profundus posterior
A. masseterica	N. massetericus
A. meningea media	N. mandibularis; nutrient to ganglion semilunare
R. m. pterygoideus internus	accompanies N. m. pterygoideus internus from N. mandibularis
R. anastomoticus cum A. meningea media	accompanies and nutrient to N. maxillaris
Aa. ciliares longae	accompanies N. ciliares longi on bulb
A. ciliaris	N. opticus
A. orbitalis	crosses N. maxillaris
Rete orbitalis	surrounds N. maxillaris and N. opticus
A. zygomatica	accompanies nutrient to N. zygomaticus
A. lacrimalis	accompanies and nutrient to N. lacrimalis
A. frontalis	accompanies and nutrient to N. frontalis
A. anastomotica	accompanies N. maxillaris; nutrient to N. ophthalmicus and N. maxillaris
A. canalis pterygoidei	nutrient to N. canalis pterygoidei from ganglion sphenopalatinum
A. temporalis profunda anterior	accompanied at origin by N. buccinatorius
A. temporalis profunda media	accompanies N. temporalis profundus medius (N. mandibularis)
A. buccinatoria	accompanies N. buccinatorius
A. infraorbitalis	accompanies N. infraorbitalis
A. alveolaris superior posterior	accompanies N. alveolaris superior posterior
A. palpebralis media	accompanies N. nasalis externi
A. alveolaris superior anterior	accompanies N. alveolaris superior anterior

Artery	Nerve
A. palatina posterior	accompanies N. palatinus posterior
A. palatina descendens	accompanies N. palatinus anterior
A. palatina anterior	each branch accompanied by ramus of N. palatinus anterior
A. sphenopalatina	N. sphenopalatinus from ganglion sphenopalatinum
Terminal twigs of A. sphenopalatina	accompanies N. nasalis posterior superior lateralis and N. nasalis posterior superior medialis

The External Rete

From the foramen ovale to the orbital fissure the branches of the internal maxillary are looped together by slender anastomotic vessels. The loose network, or *Rete externum*, thus formed, is intermeshed with the venous pterygoid plexus. The chief arteries involved are the posterior deep temporal, orbital, meningeal anastomotic, middle meningeal, ciliary, proper anastomotic, and pterygoid; the ramifications of these vessels are described below.

The external rete is hidden ventrally by the internal pterygoid muscle and dorsally by the external pterygoid muscle, the most dorsal and medial arterioles lying between this muscle and the sphenoidal periosteum. The mandibular and masticatory divisions of the trigeminal nerve pass through the rete posteriorly, and the maxillary nerve pierces the anterior part. Periorbita separates the rete from the ophthalmic division of the fifth cranial nerve, but this division is joined by the main trunks of the rete as it enters the apex of the orbital cone to become continuous with the orbital rete. The external rete in *Procyon* is the same type as that found in the domestic cat (Davis and Story, 1943), the difference being one of degree. The basic pattern in *Procyon* foreshadows the complex specialization found in *Felis domestica.* There is no internal rete in the raccoon.

The Branches of the Internal Maxillary Artery

(1) *A. alveolaris inferior* arises at the anterior border of the postglenoid process, and runs forward dorsad of the internal pterygoid muscle. The inferior alveolar artery is accompanied by the vein and nerve of the same name as it passes laterad of the tendon of M. mylohyoideus into the mandibular foramen. The artery courses through the mandibular canal, at first directed diagonally ventrad, to the vicinity of the root of M_1, there crossing to the

medial side of its companion nerve, to parallel the lower margin of the corpus mandibulae. Within the canal the inferior alveolar artery gives off twigs to the sockets and pulp cavities of the teeth and to the adjacent bone, as well as nutrients to N. alveolaris inferior. The artery divides at the apex of the canine root into lateral and medial branches. The large lateral branch breaks up into rami that emerge via the several mental foramina, with accompanying nerves and veins, onto the external surface of the jaw, to terminate in anastomoses with the inferior labial and submental arteries. The smaller medial branch by-passes the canine to approach the inner surface of the mandible, sending rami to the incisors, their alveoli, and the surrounding bone, anastomosing at the symphysis mentis with the corresponding vessel from the other side, with the sublingual artery, and, after passing through small foramina below the incisors, with the inferior labial. Twigs from these anastomoses supply vibrissae and superficial musculature of the lower jaw.

(2) *A. temporalis profunda posterior* is a large branch that comes off opposite the lingual nerve. The much weaker masseteric artery is the first branch of the posterior deep temporal. *A. masseterica* joins the masseteric nerve and winds around the medial end of the mandibular condyle to the posterior margin of the coronoid process. Here the masseteric artery divides into lateral and medial branches that ramify in the deep fibers of the masseteric and temporal muscles on their respective surfaces of the coronoid process. Twigs anastomose with both branches of the transverse facial, with the external maxillary, and with the anterior and posterior deep temporal arteries.

The posterior deep temporal sends a large branch to the posterior part of the temporal muscle, and to the temporomandibular joint. The bulk of the artery runs anterodorsally along the medial surface of the coronoid process, supplying the temporal muscle. Twigs arising at intervals from the main trunk anastomose with the masseteric, anterior deep temporal, orbital and anastomotic arteries (fig. 86). The delicate arterial network surrounds the internal maxillary artery and the external pterygoid muscle, partially paralleling the convolutions of the elaborate pterygoid venous plexus.

(3) *A. meningea media*[1] (figs. 96 and 97) arises just anterior to the posterior deep temporal, from the ventral wall of the internal maxillary. The middle meningeal artery follows the posterior border

[1] The intracranial distribution of the meningeal arteries was checked on dry skulls C.N.H.M. nos. 49227 and 47386 and found to be essentially the same as in the preserved specimens.

of the mandibular nerve into the foramen ovale. Midway between its origin and its entry into the cranial cavity, the artery crosses the chorda tympani nerve. At this level the strong *R. m. pterygoidei interni* is given off to the massive internal pterygoid muscle, one twig anastomosing with an internal pterygoid branch farther forward and another accompanying N. mylohyoideus, to anastomose with A. submentalis. This muscle branch supplies a minute palatine twig that accompanies the tensor veli palatini muscle ventrad onto the hamular process of the pterygoid. The palatine twig ramifies in the periosteum of the hard palate, anastomosing with the posterior palatine, tonsillar, and ascending pharyngeal arteries. The middle meningeal artery gives off a nutrient twig to the bulla and a branch, *R. tensoris tympani*, that crosses diagonally over the tendon of the tensor veli palatini to run along the medial surface of that tendon to reach the tensor tympani muscle and anastomose with the tympanic arterial network.

Within the cranium the middle meningeal runs posteriorly along the lateral surface of the semilunar ganglion to the tentorium, which the main vessel parallels as it sends branches to the dura mater of the posterior half of the middle cranial fossa. The branches of the middle meningeal extend to the level of the anterior limb of the ectosylvian gyrus, where they anastomose with the well-developed accessory meningeal artery. The main branches occupy grooves in the parietal bone, supplying this bone as well as the temporal. *R. petrosus superficialis* arises at the level of the hiatus facialis, which it enters beside the great superficial petrosal nerve. *A. tympanica superior* is a small vessel that is given off a short distance laterad of the petrosal branch. The superior tympanic runs between the tentorium and the periotic, which it supplies.

The middle meningeal receives anastomotic vessels from the large anastomotic branch of the internal maxillary and from the small anastomotic branch of the ciliary. These few slender anastomoses are the only indication of intracranial rete formation. Numerous small perforating arterioles communicate with terminal twigs of the temporal and posterior auricular arteries.

(4) *A. orbitalis* (fig. 86) is a large trunk that arises at the point where the buccinator nerve crosses the internal maxillary artery. Outside the periorbita the orbital artery sends its first small branch, *R. temporalis*, to the ventral part of the temporal muscle and to the external rete, anastomosing with the posterior deep temporal. The orbital artery arches mesad, pierces the periorbita, and breaks

up into the following terminal branches at the apex of the orbital muscle cone:

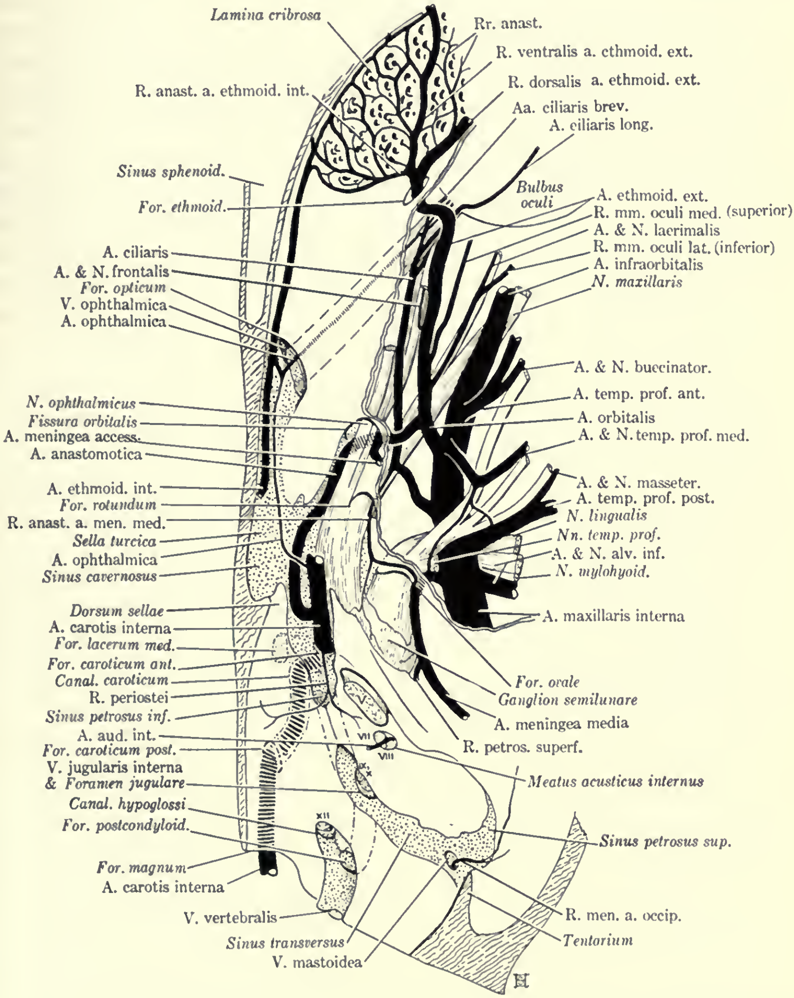


FIG. 87. Intracranial view of infratemporal and orbital branches of the internal maxillary artery in the raccoon, seen from above. The dissected skull is tipped slightly ventrad, toward the right. $\times$ 2.

(*a*) *R. muscularis lateralis* (corresponding to the inferior muscular ramus of human anatomy), supplies the lateral, inferior, and medial recti, and part of the retractor oculi. Opposite the optic foramen the muscular branch gives off a secondary branch that accompanies the optic nerve, participates in the loose orbital rete, and gives off the zygomatic, supraorbital and lacrimal arteries. The zygomatic and supraorbital arteries arise from a slender common trunk a few millimeters anterior to the optic foramen and accompany the zygomatic nerves to the orbital ligament. *A. zygomatica*, the lateral vessel, pierces the orbicularis oculi at the lateral corner of the eye, where it anastomoses with the orbital branch of the anterior deep temporal. *A. supraorbitalis*, the medial vessel, emerges from the orbit near the middle of the upper eyelid, and terminates by joining the anterior deep temporal. *A. lacrimalis* takes origin from the orbital rete anteriorly, sends nutrient twigs to N. lacrimalis, and exhausts itself in the substance of the lacrimal gland. The lateral palpebral, from the lacrimal in *Felis domestica*, comes from the anterior deep temporal in *Procyon lotor*.

(*b*) *A. anastomotica* (fig. 87) is the largest branch of the orbital artery before the origin of the external ethmoidal. A long slender branch of the anastomotic vessel follows the optic nerve to join the orbital rete near the bifurcation of the ciliary artery; other twigs anastomose with the external ethmoidal and the base of the ciliary. An accessory meningeal artery, half the caliber of the middle meningeal, is given off just outside the orbital fissure, through which it runs along the ophthalmic division of the trigeminal nerve posteriorly, supplying the dura of the anterior half of the middle cerebral fossa and anastomosing with the middle meningeal at the ectosylvian gyrus as well as in the vicinity of the semilunar ganglion. The accessory meningeal sends nutrient twigs to the frontal bone, in addition to perforating anastomoses to the temporal arteries. The anastomotic trunk turns posteriorly to enter the orbital fissure, and runs backward into the sinus cavernosus. The artery extends to the level of the posterior lacerated foramen, then doubles back upon itself to anastomose with the internal carotid artery, thus contributing to the circle of Willis. Opposite the dorsum sellae the anastomotic artery sends several minute twigs, *Rr. hypophysei*, to the hypophysis cerebri. The hypophyseal branches may arise from the combined trunk of the internal carotid and anastomotic arteries.

(*c*) *A. ciliaris* usually arises opposite the orbital fissure and runs forward with the ophthalmic nerve, first giving off a small anastomotic ramus. In three dissections out of ten, the ciliary arose from the internal maxillary independently, at the anterior border of the external pterygoid muscle. The first branch of the ciliary artery, *R. anastomoticus*, turns posteriorly, out of the orbital cone, to run along the lateral surface of the maxillary nerve, sending nutrient arteries to this nerve and to the semilunar ganglion. The anastomotic branch terminates by uniting with the middle meningeal artery at its entry to the cranial fossa.

The ciliary artery immediately sends a strong anastomosis to the external ethmoidal artery and crosses the ophthalmic nerve and the lateral and superior recti muscles, then curves beneath the M. levator palpebrae superioris to reach the dorsal surface of the optic nerve. Fine anastomotic twigs unite the ciliary with the other orbital vessels, forming a loose network or *Rete orbitalis* (fig. 86) within the orbit. The ciliary has three terminal branches:

A. ciliaris longa medialis is given off a few millimeters beyond the ethmoidal foramen and courses forward outside the eyeball. Anterior to the insertion of the medial rectus the medial long ciliary artery pierces the sclera to supply the ciliary process and the iris.

A. ciliaris longa lateralis is distributed on the lateral surface of the eyeball in like manner to its mate. The long ciliary arteries are accompanied by the nerves of the same name.

A. ciliaris brevis medialis arises a short distance anterior to the medial long ciliary, and is followed by the lateral long and short ciliaries. The short ciliary arteries perforate the sclera around the entrance of the optic nerve to supply the choroid coat, their branches radiating from the margin of the optic papilla to the retina, taking over the area usually supplied by the A. centralis retinae, absent in raccoons.

(*d*) *A. ethmoidalis externa* (figs. 87 and 88), the continuation of the orbital artery, arches across the ocular muscles, nerves, and vessels, to the ventral surface of the medial rectus, which it parallels as far as the ethmoidal foramen. The external ethmoidal receives anastomotic twigs from the inferior muscular ramus and the great anastomotic artery, then gives off the superior ocular muscular ramus, corresponding to the "superior" of human anatomy. *R. muscularis medialis* supplies both the superior and the medial recti, the levator palpebrae superioris and part of the retractor oculi. Opposite the levator palpebrae superioris the external ethmoidal gives rise to the small frontal artery, which joins and gives nutrient twigs to the nerve of the same name. Near its origin *A. frontalis* gives off a twig to the periosteum, then the *R. trochlearis*, opposite the ethmoidal foramen, to supply the superior oblique muscle and anastomose with the supraorbital artery near the trochlea. The frontal artery, with

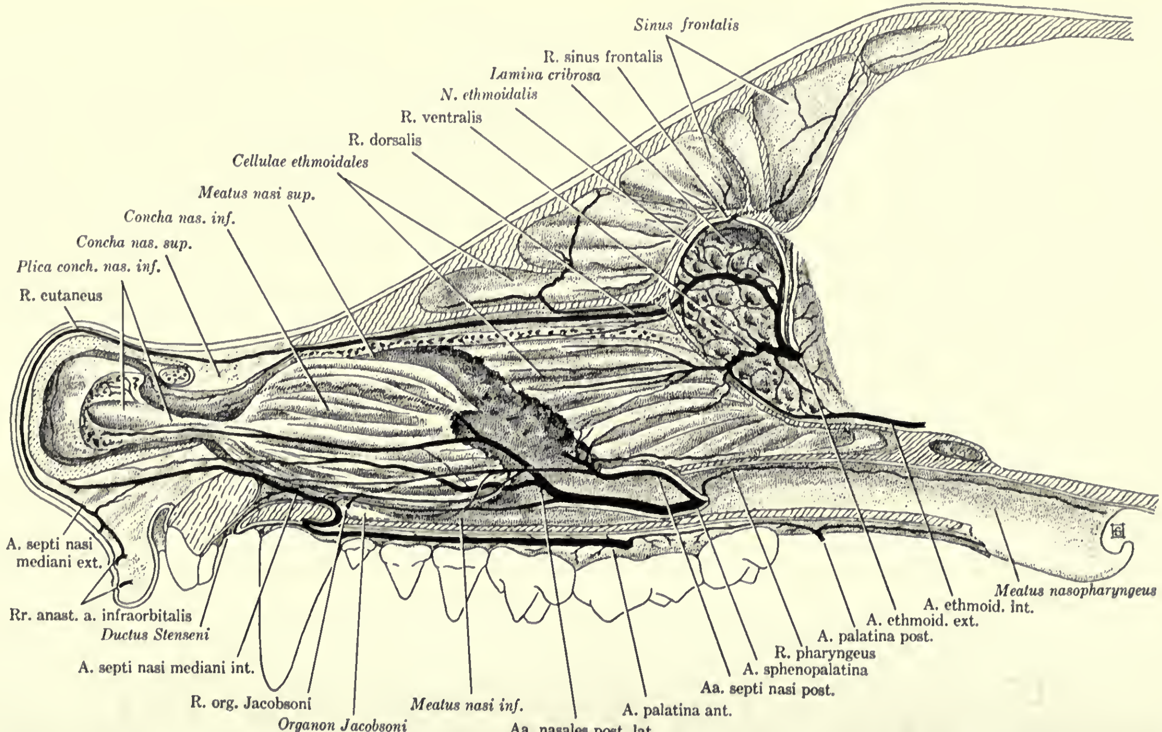


FIG. 88. Arterial supply of the internal nose in the raccoon. Median longitudinal section of the nasal cavity, with ethmoidal cells partially removed. $\times 1\frac{1}{2}$.

the nerve and vein of that name, emerges at the medial angle of the eye and unites with the orbital branch of the anterior deep temporal.

Beyond the origin of the frontal artery the external ethmoidal is markedly increased in caliber by a strong anastomotic branch from the ciliary artery. Just before entering the cranial cavity the external ethmoidal gives off the small anterior meningeal. *A. meningea anterior* enters the skull through a minute foramen, to supply the dura of the anterior cranial fossa, and anastomose with the accessory meningeal artery. The external ethmoidal artery and nerves pass through the large ethmoidal foramen to the floor of the olfactory fossa. Here the artery winds dorsad around the olfactory lobe, giving off numerous twigs to the lamina cribrosa, and two large dorsal and ventral branches. *R. dorsalis* arches across the cribriform plate to pass into the nasal fossa at the angle formed by the frontal with the ethmoidal, and courses forward between the bony roof and the mucosa of the superior nasal meatus, emerging on the nose between the nasal bone and cartilage. This artery gives off twigs to the dorsal ethmoidal cells, the anterior part of the nose and the skin, a cutaneous twig anastomosing with the external artery of the septum (from the infraorbital). *R. ventralis* tortuously crosses the lamina cribrosa to enter the nasal cavity near the center of the ethmoturbinals and immediately fans out to supply the olfactory region, anastomosing with the posterior septal branch of the sphenopalatine.

On the dorsal surface of the olfactory lobe the much diminished external ethmoidal anastomoses with the slender internal ethmoidal (from the circle of Willis), and the terminal twigs from this anastomosis supply the dura and ethmoid cells of the frontal sinus.

(5) *R. m. pterygoidei interni*, a small vessel, springs from the internal maxillary opposite and slightly anterior to the orbital artery. The branch supplies the central part of the extensive internal pterygoid muscle, sends a twig to the external pterygoid, and anastomoses with the orbital, masseteric, and posterior deep temporal arteries.

(6) *A. canalis pterygoidei* is given off ventrally immediately after the muscular branch. It runs beneath the maxillary nerve to the minute pterygoid canal, through which it continues posteriorly beside the Vidian nerve, to anastomose with a twig of the ascending pharyngeal near the auditory tube. This vessel supplies nutrient arteries to the nerves in the pterygopalatine fossa and contributes to the external rete.

(7) *A. temporalis profunda anterior* is a well-developed trunk arising at the same level as the A. canalis pterygoidei, but from the dorsal wall of the internal maxillary. The anterior deep temporal runs forward parallel to the internal maxillary artery and with N. buccinator as far as the orbital gland. *A. temporalis profunda media,* the first branch, runs mesad with the nerve of the same name to supply the deep anterior part of the temporal muscle. *A. buccinatoria,* a small vessel, arises at the posterior border of the orbital gland, across which it runs, in company with the buccinator nerve. The buccinator artery sends twigs to the orbital gland, the molar alveoli, and the buccinator muscle, and anastomoses with the superior labial artery. Beyond the buccinator artery the anterior deep temporal ascends along the posterior border of the infraorbital fat cushion to the orbital ligament, supplying the adjacent part of the temporal muscle. After piercing the orbital ligament at the external angle of the eye, the anterior deep temporal gives off the lateral palpebral arteries, then runs along the orbital ligament, sending numerous branches to the superior tarsal arch, the adjacent superficial musculature and the scalp. Much diminished in caliber, the anterior deep temporal terminates by anastomosing with the medial palpebral, frontal and superficial temporal arteries at the internal (medial) angle of the eye.

Aa. palpebrales laterales ramify along the free borders of the eyelids, their twigs forming a thick network, the tarsal arches, with other twigs of the anterior deep temporal. These arteries anastomose with the somewhat smaller medial palpebrals, from the infraorbital artery, near the internal angle of the eye. In two cases the anterior deep temporal supplied twigs to the lacrimal gland.

A small branch of the anterior deep temporal, or of its buccinator branch, arches around the lateral border of the infraorbital fat cushion, supplying it and the walls of the large deep facial vein.

(8) *R. m. pterygoidei interni* is given off midway between the anterior deep temporal artery and the internal pterygoid muscle.

The Terminal Branches of the Internal Maxillary Artery

The internal maxillary artery divides into its terminal branches opposite the posterior palatine notch. The larger, or lateral, branch supplies structures external to the skull and the medial branch structures within the skull.

(9) *A. infraorbitalis* (fig. 85), the lateral branch, which is the continuation of the internal maxillary, accompanies the infraorbital

nerve across the internal pterygoid muscle and the maxillary tuberosity to the infraorbital foramen. Within this foramen, the infraorbital artery in ramifying profusely over the external surface of the maxilla gives rise to the following branches: *A. alveolaris superior posterior* arises opposite the second molar and is distributed to both molars. *A. alveolaris superior media* is given off at the level of the pterygopalatine canal, and supplies the first molar and the fourth premolar. An additional alveolar artery arises a few millimeters farther forward, and passes through a foramen into the maxillary sinus, where it ramifies to the fourth premolar. A large alveolar artery and nerve enter a canal that runs to the canine alveolus. The alveolar arteries are accompanied by the nerves of the corresponding name. Inside the infraorbital foramen the infraorbital artery divides into dorsal and ventral branches.

The dorsal branch,[1] *A. palpebralis medialis*, ramifies together with N. nasalis externi over the side of the nose, anastomosing with the angular branch of the external maxillary and with the orbital branch of the anterior deep temporal. Before emerging from the infraorbital foramen the vessel gives rise to a trunk that divides at the lacrimal canal into the medial palpebral arteries proper that pass on each side of the medial palpebral ligament to enter the superior and inferior tarsal arches. *Aa. palpebrales mediales* supply the superficial muscles at the internal angle of the eye, as well as the lacrimal sac and the nictitating membrane. One of these twigs may reach the arterial plexus on the nasal mucoperiosteum. The medial palpebral arose from A. ciliaris in one case.

The ventral branch, the continuation of the infraorbital artery, runs forward in the muscles of the upper lip, to richly supply the musculature of the snout in addition to an external septal (philtral) branch. Twigs anastomose with the superior labial artery, the sphenopalatine, the septal branch of the anterior palatine, and with the infraorbital from the opposite side. *Aa. alveolares superiores anteriores* (fig. 85) are given off to the premolars, canine and incisors,

[1] Davis and Story (1943) called this vessel "A. angularis" in *Felis domestica*. This term can not be used, for a careful review of dissections of the external maxillary in the cat reveals a thread-like angular artery from the external maxillary in addition to the so-called "A. angularis" from the infraorbital. In man, unnamed rami from the infraorbital supply the lower eyelid and adjacent structures, but the medial palpebral arteries proper are derived from the enormous ophthalmic artery. The vessel in carnivores reaches the same structures that are supplied by the two anastomosing channels in man, but the infraorbital is enlarged and the other source dwindled. Because of this shift of proportions in carnivores an exact homology with man is not possible. The term "medial palpebral artery" seems most appropriate to use in the following pages.

and are accompanied by the nerves of the same name, derived from N. maxillaris.

The medial terminal branch of the internal maxillary, the combined trunk of the descending palatine and sphenopalatine arteries, is a longer vessel than in the cat and only one half the caliber of the infraorbital. It gives off the posterior palatine artery at its base, then crosses the body of the maxilla to reach the pterygopalatine canal, where it divides into the subequal descending palatine and sphenopalatine arteries.

(10) *A. palatina posterior* is a small vessel that accompanies the posterior palatine nerve and large palatine vein through the posterior palatine notch onto the hard palate. It ramifies in the palatine glands and anastomoses anteriorly with the anterior palatine artery, posteriorly with the palatine ramus of the ascending pharyngeal and posterior tonsillar branch of the lingual artery.

(11) *A. palatina descendens,* a slightly smaller vessel than the sphenopalatine, accompanies the anterior palatine nerves through the pterygopalatine canal, giving off several small twigs, *Aa. palatinae minores,* that pass through minute foramina and are nutrient to the palatine nerves as well as the palate. The descending palatine artery emerges on the hard palate through the posterior palatine foramen opposite the middle of the first nerve, and from this point takes the name *A. palatina anterior* (fig. 82). It gives off an anastomotic twig to the posterior palatine artery, then runs forward in a groove on the hard palate to the incisive (anterior palatine) foramen. The anterior palatine supplies the mucoperiosteum of the hard palate, and terminates in an anastomotic network with its fellow from the opposite side and with a branch of the sphenopalatine at the incisive foramen. Twigs from the network circle around the cartilage of Jacobson's organ and supply the mucosa of that structure, as well as the lining of Stenson's duct, anastomosing with the posterior septal artery. A large median trunk, *A. septi nasi mediani,* is formed by the coalescing anterior palatine arteries at the incisive foramen. This vessel arches posteriorly to enter a well-developed median incisive palatine foramen, and doubles back upon its course as it reaches the inferior nasal meatus. The median septal artery then runs forward, between the cartilaginous septum and the incisive bone, to terminate in the rich arterial plexus supplying the snout (fig. 88).

(12) *A. sphenopalatina* enters the nasal cavity through the sphenopalatine foramen, and immediately gives off the posterior

nasal septal artery and a pharyngeal twig. The sphenopalatine artery runs forward along the lateral wall of the inferior nasal meatus, accompanied by N. nasalis posterior superior lateralis, to the posterior border of the maxilloturbinals, where it breaks up into its terminal branches, the lateral posterior nasals and the anastomotic branch to the anterior palatine (fig. 88). *A. nasalis posterior septi* gradually crosses over to the septum, then ramifies to the ethmoturbinals, the septum, and the vomeronasal (Jacobson's) organ, anastomosing with the ethmoidal and anterior palatine arteries. *R. pharyngeus* supplies the mucous membrane of the nasopharyngeal meatus, anastomosing with the ascending pharyngeal. The nasal mucoperiosteum is supplied by a rich plexus of interlacing blood vessels from the above-named anastomosing arteries and their companion veins, forming a spongy tissue similar to that of the corpus cavernosus. *Aa. nasales posteriores laterales* are three or four vessels of almost equal caliber that run forward upon the mucous membrane lining the maxilloturbinals and the nasal meati, anastomosing with branches of the ethmoidal, anterior palatine, and infraorbital arteries, all providing high vascularization to the snout. A branch coursing along the floor of the inferior nasal meatus, supplying the lining of that cavity, reaches the incisive foramen, where it enters a rich plexus from the anterior palatine arteries.

The topographical relationships of the arteries of the head to other structures associated with the skull is indicated by the following list of the contents of the cranial foramina.

CONTENTS OF CRANIAL FORAMINA OF CARNIVORA

(All openings of the skull in approximate order from anterior to posterior)

Anterior palatine (paired)

Nerve: Nasopalatine from sphenopalatine ganglion
Artery: Anastomosis of anterior palatine with sphenopalatine
Vein: Anastomosis of anterior palatine with sphenopalatine
Remarks: Stenson's duct, confluence of nasal and buccal cavities

Median anterior palatine

Nerve: None
Artery: Median septal (anastomoses with septal artery of infraorbital)
Vein: V. comitans
Remarks: Foramen absent in Canidae and Felidae, large in Ursidae

Infraorbital

Nerve: Maxillary
Artery: Infraorbital; medial palpebral in some forms
Vein: Venules
Remarks: Occasional subdivision for middle palpebral artery and external nasal nerve

Accessory infraorbital (unnamed)
Nerve: None
Artery: Middle palpebral
Vein: None
Remarks: Opens inside infraorbital foramen, leads to lacrimal; presence variable

Canine alveolar canal (unnamed)
Nerve: R. dentis canini
Artery: Alveolaris superior media to canine
Vein: None
Remarks: Position variable

Alveolar canals (in maxillary tuberosity; unnamed)
Nerve: R. sinus maxillaris; Nn. alveolares superiores post. and med.
Artery: Alveolares superiores post. and med.
Vein: V. comitans
Remarks: Variable in number

Lacrimal
Nerve: Lacrimal ramus of ophthalmic division of trigeminal
Artery: Branch of middle palpebral
Vein: None
Remarks: Lacrimal sac

Sphenopalatine (internal orbital)
Nerve: Lateral posterior superior nasal branch from sphenopalatine ganglion
Artery: Sphenopalatine
Vein: V. comitans
Remarks: Sometimes confluent with pterygopalatine canal

Pterygopalatine canal
Nerve: Descending palatine
Artery: Descending palatine
Vein: None

Small posterior palatine foramina (*minor*)
Nerve: Anterior palatine
Artery: Minor palatine
Vein: None
Remarks: Also arteries nutrient to nerve branches

Posterior palatine (*major*)
Nerve: Anterior palatine
Artery: Anterior palatine
Vein: None visible at 12×.

Palatine notch (*incisura palatina*)
Nerve: None
Artery: Posterior palatine
Vein: Anterior palatine (groove in palate)
Remarks: Closed by ligament to form foramen

Fenestrae cribrosae
Nerve: Olfactory; ethmoidal (from ophthalmic)
Artery: Many twigs of internal ethmoidal
Vein: V. comitans

Ethmoidal
Nerve: External ethmoidal (from ophthalmic)
Artery: External ethmoidal
Vein: External ethmoidal

Optic
Nerve: Optic
Artery: Ophthalmic
Vein: Ophthalmic

Orbital fissure (lacerum anterior; sphenorbital)
Nerve: Oculomotor; trochlear; trigeminal; abducens
Artery: Accessory meningeal; anastomotic artery
Vein: Orbital
Remarks: Sometimes confluent with foramen rotundum

Rotundum
Nerve: Maxillary branch of trigeminal
Artery: Small anastomosis to middle meningeal
Vein: Venules

Pterygoid (Vidian) canal
Nerve: Canalis pterygoideus from sphenopalatine ganglion
Artery: Canalis pterygoideus
Vein: V. comitans
Remarks: Exit lateral to orbital fissure; entrance near foramen lacerum medium

Median basisphenoid canal
Nerve: None
Artery: None
Vein: Branch to sinus cavernosus
Remarks: At suture with presphenoid; enters cranial fossa at tuberculum sellae

Alisphenoid canal
Nerve: None
Artery: Internal maxillary
Vein: None
Remarks: Sometimes confluent with foramen ovale; present in Canidae, Ursidae, *Ailurus*, Viverridae

Ovale
Nerve: Mandibular; motor root of trigeminal
Artery: Middle meningeal
Vein: Venules

Canalis musculotubarius
Nerve: Minor superficial petrosal; R. tensoris tympani
Artery: Arterioles
Vein: Venules
Remarks: Auditory tube in medial half; tendon of M. tensor veli palatini in lateral half

Lacerum medium
Nerve: None
Artery: Anastomotic artery with internal carotid
Vein: Large vein from inferior petrosal sinus, draining to pharyngeal and pterygoid plexuses

Anterior carotid (intracranial exit of carotid canal)
Nerve: Internal carotid, division to cavernous plexus
Artery: Internal carotid
Vein: Branch from sinus cavernosus

Postglenoid
Nerve: None
Artery: None
Vein: Internal facial, from superior petrosal sinus

Internal auditory meatus
Nerve: Facial; acoustic
Artery: Internal auditory
Vein: Nutrient venules

External auditory meatus
Nerve: Small branches of auriculotemporal (V_3); small branches of auricular ramus of vagus
Artery: Deep auricular
Vein: Venules

Stylomastoid
Nerve: Facial; auricular ramus of vagus
Artery: Stylomastoid; posterior tympanic
Vein: Venules
Remarks: Sometimes confluent with fossa for tympanohyal bone

Caroticum posterium (extracranial)
Nerve: Internal carotid (both divisions)
Artery: Internal carotid
Vein: Branch from sinus cavernosus
Remarks: Situated midway between foramen lacerum posterium and basisphenoid

Lacerum posterium
Nerve: Glossopharyngeal, vagus, and spinal accessory
Artery: Inferior tympanic
Vein: Branch from transverse sinus

Jugular
Nerve: None
Artery: R. sinus transversi
Vein: Internal jugular
Remarks: Enters inferior petrosal sinus at confluence with transverse sinus

Condyloid (hypoglossal)
Nerve: Hypoglossal
Artery: Posterior meningeal
Vein: Anastomotic branch from vertebral vein
Remarks: Confluent with foramen lacerum posterium in Hyaeninae

Postcondyloid (intracranial)
Nerve: None
Artery: None
Vein: Vertebral
Remarks: Empties from transverse sinus, posterolaterad to condyloid foramen

Mastoid
Nerve: None
Artery: Meningeal ramus from occipital branch of posterior auricular
Vein: Branch from transverse sinus

Magnum
Nerve: Spinal cord
Artery: Vertebral
Vein: Vertebral

CAROTID CIRCULATION IN OTHER PROCYONID GENERA

Because of the basic similarity in the arterial pattern of the following specimens, only those vessels that present differences from *Procyon* will be described.

Bassariscus astutus (fig. 89)

The common carotid artery bifurcates at the middle of the thyroid cartilage, approximately opposite the foramen magnum, slightly farther forward than in *Procyon*. The internal carotid artery is three fourths the caliber of the external carotid.

In the region of the carotid sinus, the internal carotid gives off a fine arteriole to the carotid body, and another to the superior cervical ganglion. The basicranial internal carotid is slightly shorter than in *Procyon*, being approximately 65 per cent of the length of the bulla. Within the carotid canal the artery arches gently anterodorsad, without deviating laterally toward the promontorium, and then bends sharply dorsad to enter the sinus cavernosus. A caroticotympanic artery is given off near the foramen lacerum medium. The bone-enclosed portion of the internal carotid is greater than in *Procyon*, as the carotid canal extends from the level of the posterior border of the promontorium to the foramen lacerum medium.

The internal carotid gives off the ophthalmic artery before entering the circle of Willis. The ophthalmic is a small vessel, but relatively much larger than that of *Procyon*. It gives off several small hypophyseal twigs, and receives the anastomotic artery from the internal maxillary, but does not give rise to a central artery of the retina.

There is no anterior communicating artery.

The internal ethmoidal arteries remain as two vessels as far as the anterior surface of the olfactory lobe, where they anastomose with the external ethmoidal. There is no median anastomosis of the internal ethmoidals.

The circle of Willis is nearly identical in pattern to that figured for *Procyon*, but with the posterior half of the circle of larger caliber. The terminal part of the posterior communicating artery has a diminished caliber as it joins the internal carotid.

There is no collateral middle cerebral. The olfactory area is supplied by rami from the middle cerebral instead of from the external ethmoidal.

At the root of the third cervical nerve, the vertebral artery gives off a large branch that joins its fellow at the midline in a diamond-shaped anastomosis. Two large parallel arteries run forward, receiving small twigs from the vertebral at the second cervical nerve, and medium-sized terminal vertebral branches at the first nerve. Here the arteries form a second diamond, then continue as one

Bassariscus astutus—continued

vessel, the basilar artery, with a caliber greater than the internal carotid.

The common carotid gives off a branch (from the ascending pharyngeal in *Procyon*) to the sternomastoid muscle and the large cervical lymph gland before its bifurcation.

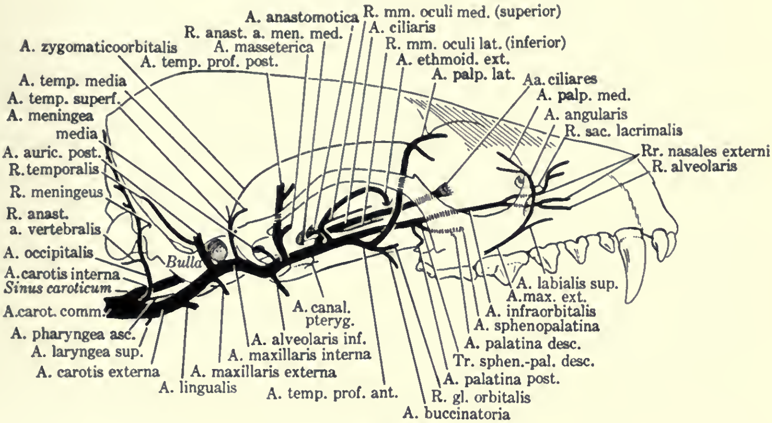
The external carotid gave off the anterior laryngeal artery at its base in one specimen, but in the other the vessel arose from the lingual artery. As the external carotid crosses the recessus meatus, it sends a twig through a foramen in the floor of the meatus, to supply the external surface of the tympanic membrane.

The ascending pharyngeal is small, with much of its usual distribution taken over by twigs of the occipital. The ascending pharyngeal gives a nerve nutrient twig that completely encircles the nerves emerging from the foramen lacerum posterius. The terminal *R. pharyngeus* sends two small arteries into the foramen lacerum medium, one of them to anastomose with the internal carotid as well as supply the great deep petrosal nerve as it enters the Vidian canal, the other twig being nutrient to the basisphenoid bone. The other terminal branch, *R. palatinus*, gives off the small pharyngeotympanic artery.

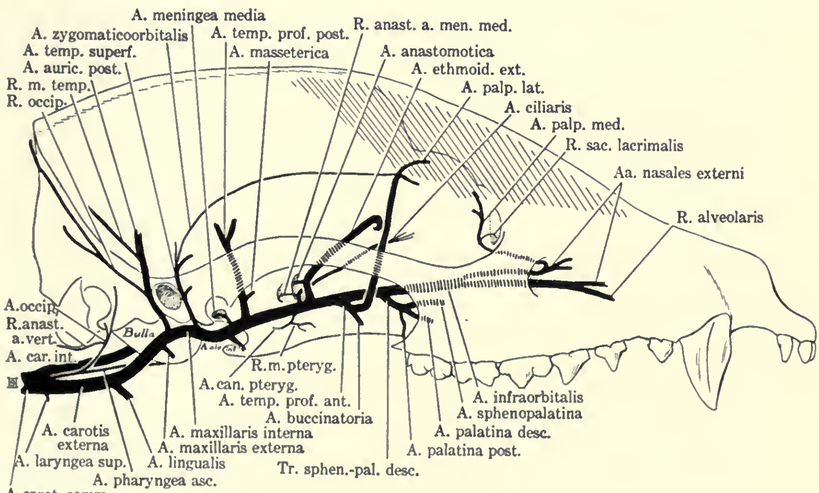
The occipital artery is relatively large and has complete occipital distribution, supplying the splenius, the biventer cervicis and the intrinsic axial musculature. The inferior tympanic branch also gives off R. lymphoglandulae and R. mm. longus capitis and digastricus. R. sinus transversus also sends a nutrient twig to the carotid canal. Only a small part of the posterior meningeal artery enters the condyloid foramen. The bulk of the posterior meningeal anastomoses with the vertebral, with a smaller anastomosis with the ascending pharyngeal, and a twig to the M. longus capitis.

The digastric branch of the lingual artery also supplies the submaxillary gland and an adjacent lymph gland.

The rather large external maxillary arises before the posterior auricular in both specimens, and differs from the artery in *Procyon* in having a large buccinator ramus, which anastomoses with the small inferior labial artery and gives off the medial palpebral, a vessel of less than half the size of the lateral palpebral. This origin of A. palpebralis media occurs in no other carnivore examined. A twig from the external maxillary artery crosses the zygoma, sends a nutrient twig to the parotid duct, and anastomoses with a terminal twig of the superficial temporal.



Bassariscus



Nasua

FIG. 89. Main branches of the external carotid circulation in the cacomistl, *Bassariscus astutus* (× 1), and in the coati, *Nasua narica* (× ¾). The extent of the frontal sinus is indicated by diagonal lines.

Bassariscus astutus—continued

The posterior auricular artery is very large, with its main branch subequally dividing to supply the temporal muscle and the auricle. The occipital ramus is represented by a slender vessel that runs along the lambdoidal crest and by a branch to the sternomastoid muscle. The branch to the anterior surface of the auricle is small.

The middle temporal branch is the largest one from the superficial temporal artery. The masseteric ramus comes off opposite the deep auricular muscle. In one individual the deep auricular artery arose from the external carotid. The transverse facial gives a fair-sized ramus to M. platysma, and anastomoses with the zygomatic branch of the external maxillary.

The external rete follows the same arrangement as in *Procyon* but the anastomotic vessels are smaller in proportion to the internal maxillary artery. There is no internal rete.

The palatine twig of the middle meningeal is relatively twice the caliber of that branch in the raccoon. Intracranially, the middle meningeal[1] runs parallel to the tentorium to the level of the posterior limb of the ectosylvian gyrus, where it runs vertically, giving branches that extend to the region of the Sylvian fissure. Here terminal twigs of the meningea media anastomose with the large accessory meningeal.

The ciliary artery arises immediately posterior to the orbital fissure, giving muscular, short and long ciliary rami. The short ciliaries, which form a complex rete at the distal third of the optic nerve, enter the optic papilla at its periphery, giving off six radially arranged rami that supply the retina. A recurrent anastomotic ramus from the short ciliary artery, halfway to the eyeball, is nutrient to the optic nerve. There is no central artery of the retina. Near its base the ciliary gives off a very small anastomotic ramus that is nutrient to the ophthalmic division of the trigeminus and anastomoses with the middle meningeal near the semilunar ganglion. In one individual the ciliary trunk was doubled after the origin of the anastomotic twig.

The orbital artery is a large trunk of the same caliber as the ciliary, and arises a short distance anterior to that vessel. The orbital artery gives off the anastomotic artery, the A. canalis pterygoidei, the lateral muscular ramus, and the lacrimal artery, after which the trunk is continued as the external ethmoidal. The

[1] The pattern of the meningeal arteries was checked on dry skull C.N.H.M. no. 46013 and found to be identical with the preserved specimens.

Bassariscus astutus—continued

lacrimal artery gives off the medial muscular ramus, the supraorbital and the zygomatic arteries. The ethmoidal rete gives off the small anterior meningeal artery at the dorsal surface of the olfactory lobe, as in *Felis domestica*.

At the emergence of the ophthalmic nerve from the orbital fissure the orbital artery gives off the A. anastomotica, which is distributed mostly as the accessory meningeal (exceeding the middle meningeal in caliber), but with a slender anastomosis with the ophthalmic branch of the internal carotid artery and another with the middle meningeal. There is reciprocal variation between the anastomotic artery and the accessory meningeal, with the former being the larger in two out of four cases. The accessory meningeal supplies the area of dura between the coronal sulcus and the Sylvian fissure, which its main branch parallels (fig. 96).

The anterior and middle deep temporal arteries are very large. The buccinator artery is a small branch of the former vessel. The lateral palpebrals, from the anterior deep temporal, greatly exceed the medial palpebrals in size and distribution.

The internal maxillary terminates opposite the orbital fissure at the origin of the orbital artery, in a rather weak infraorbital and the subequal sphenopalatine-descending palatine trunk.

The most dorsal of the external nasal rami of the infraorbital artery sends a recurrent twig through a small foramen to supply the lacrimal sac. The infraorbital fat cushion is supplied by a branch of the fourth and last of the series of posterior superior alveolar arteries.

The anterior palatine artery emerges on the hard palate opposite the anterior border of the first molar, slightly farther forward than in *Procyon*.

Nasua narica (fig. 89)

The common carotid artery bifurcates at the middle of the thyroid cartilage, approximately at the level of the occipital condyles, exactly as in *Procyon*. The internal carotid is slightly more than half the caliber of the external carotid. The basicranial internal carotid is relatively long, exceeding the length of the bulla by 72 per cent. The carotid canal is shorter than in *Procyon*, arching more sharply, with a slight lateral flexure toward the promontorium. The two caroticotympanic arteries are given off opposite the anteromedial border of the promontorium.

Nasua narica—continued

After piercing the dura mater, the internal carotid gives off the *R. hypophysis,* then enters the circle of Willis. The true ophthalmic artery, from the hypophyseal ramus, is a threadlike nutrient twig to the optic chiasma, terminating by anastomosis with the recurrent loop of the internal ethmoidal.

The pattern of the circle of Willis is nearly identical with that of *Procyon,* but the anterior half of the circle of Willis is more elongated, as the large common trunk of the anterior and middle cerebral arteries divides equally at the anterior border of the optic chiasma. The posterior communicating artery is slightly smaller than the middle cerebral. There is no anterior communicating artery.

The vertebral artery gives large branches at the third and first cervical nerves, forming a basilar rete of asymmetrical diamond shape. The basilar artery thus formed is two thirds the caliber of the internal carotid. The posterior inferior cerebellar artery is a single small vessel. The anterior inferior cerebellar is a large artery.

The external carotid gives off the anterior thyroid artery opposite the second tracheal ring, farther anterior than in the raccoon. The sternomastoid branch comes from the occipital artery.

The anterior laryngeal artery, from the external carotid, sends an anastomotic branch to the ascending pharyngeal artery near the superior cervical ganglion.

The ascending pharyngeal, larger than the occipital artery, gives off a nutrient artery to the accessory nerve. The anastomotic branch to the internal carotid at the foramen lacerum medium is small and very tortuous.

The occipital artery, from the ascending pharyngeal at the mastoid process, takes over the R. lymphoglandulae and R. mm. digastricus and sternomastoideus supplied by the parent vessel in *Procyon.*

The external maxillary artery arises at the lateral border of the digastric muscle, before the posterior auricular artery, and from its origin sends a branch across the external pterygoid muscle to the orbital gland. The submental artery is a branch of the external carotid just beyond the lingual artery. The terminal branches of the external maxillary are of small caliber but anastomose in exactly the same way as in *Procyon.*

The posterior auricular artery gives off the occipital ramus laterad of the mastoid process, but the stylomastoid artery was given off medially in one individual.

Nasua narica—continued

The middle meningeal artery[1] has a smaller intracranial distribution than in *Procyon*. Its branches extend only as far forward as the posterior Sylvian gyrus.

The internal maxillary and external rete are nearly identical with the arrangement in *Procyon*. The ciliary artery arose beyond the orbital trunk in one specimen. The anastomosis between the ciliary and the ophthalmic artery takes place at the distal third of the optic nerve.

The accessory meningeal artery from the ciliary trunk has a more extensive distribution than in *Procyon*. It ramifies to the dura mater from the level of the Sylvian (lateral) fissure as far as the presylvian fissure, thus exceeding the area supplied by the middle meningeal (fig. 96).

The orbital artery is a large trunk that divides at once into two main branches. The first branch gives off the lateral muscular ramus, the subequal anastomotic artery, and a small zygomatic artery. The other branch of the orbital gives off the supraorbital, the lacrimal, the medial muscular ramus, and the frontal artery and terminates as the very large external ethmoidal. In one individual the external ethmoidal was doubled. The increased size of the external ethmoidal is characteristic of *Nasua*. The other orbital branches could not be traced on the Sanderson specimen because of unsatisfactory preservation. The anastomotic artery is convoluted in the sinus cavernosus. It does not run past the hypophysis but joins the internal carotid just inside the cranium.

The internal maxillary terminates opposite the posterior superior alveolar process, the larger division continuing as the infraorbital; the smaller division forms the sphenopalatine-descending palatine trunk.

Before bifurcating, the sphenopalatine-descending palatine trunk gives off a branch to the internal pterygoid muscle, in addition to the posterior palatine artery.

The descending palatine is one third the caliber of the sphenopalatine, and emerges as the anterior palatine opposite the second molar.

In all other respects *Nasua* closely follows the arterial pattern of *Procyon*.

[1] The meningeal arteries followed this same pattern in two dry skulls examined, C.N.H.M. nos. 41196 and 14011.

Potos flavus (fig. 91)

The common carotid artery bifurcates at the anterior border of the thyroid cartilage, at the level of the foramen lacerum posterius. The internal carotid is more than half the caliber of the external carotid. The basicranial internal carotid is extremely short (56 per cent of the length of the bulla), despite the anterior location of the posterior carotid foramen, since the artery originates at the level of the posterior lacerated foramen. In the anteromedial wall of the bulla, the internal carotid runs almost vertically until it levels off as it approaches the foramen lacerum medium. Here the artery receives an anastomosis from the ascending pharyngeal, then turns sharply dorsad to enter the sinus cavernosus. Within its canal the internal carotid gives off the caroticotympanic artery opposite the anterior border of the promontorium.

In one specimen the internal carotids were united subdurally by an anastomotic artery posterior to the hypophysis. The internal carotid gives off a tortuous, small, but well-defined ophthalmic artery and a separate twig to the hypophysis. The ophthalmic enters the optic foramen on the lateral side of the optic nerve, makes a turn around the nerve and runs medially inside the orbit, anastomosing with the ciliary artery near the distal end of N. opticus.

The circle of Willis is the reverse of the pattern in *Procyon,* with the posterior half large in caliber and elongated (fig. 93). The anterior cerebral is half the caliber of the main middle cerebral artery. There is a doubling of the middle cerebral, with a small secondary middle cerebral of the same distribution, arising from the anterior cerebral above the optic nerve. The internal ethmoidal artery is given off near the base of the secondary middle cerebral, and anastomoses with the external ethmoidal without uniting with its fellow from the opposite side. There was an anterior communicating artery in one *Potos,* with the union of the anterior cerebrals farther forward than in the other specimen.

The posterior communicating artery is only slightly smaller than the main middle cerebral artery.

The basilar rete is in the pattern of two triangles with their bases juxtaposed. Smaller anastomotic triangles occur along the anterior spinal artery as it receives twigs from the vertebrals at each nerve root.

The basilar artery is smaller than the internal carotid. The anterior inferior cerebellar artery is represented by one large vessel and several small pontine rami.

Potos flavus—continued

The external carotid gives off the anterior thyroid artery and the lingual artery opposite the foramen magnum. The anterior laryngeal artery arises beside A. lingualis, but in one specimen was from a trunk that gave rise to the anterior thyroid artery and submaxillary ramus. The submaxillary ramus came from the sternomastoid artery in one case.

The ascending pharyngeal is small, with its usual cervical branches taken over by the occipital but its terminal branches the same as in *Procyon*. The ascending pharyngeal came from the base of the internal carotid on one side of the first specimen, and on the second, the R. m. longus capitis came from that vessel. Two newborn specimens (both females), C.N.H.M. nos. 52428 and 0-1333, were examined in this region only, and the ascending pharyngeal was found to arise from the internal carotid. This condition is seen also in *Ailuropoda* and in *Mustela* but not in other carnivores.

The occipital artery is large, but does not reach the occiput. Instead it breaks up at the foramen lacerum posterius into branches to M. longus capitis and anastomoses to the vertebral artery. In addition it gives off a nutrient branch that crosses the bulla to enter the floor of the external meatus. The posterior meningeal artery anastomoses with the vertebral, and does not reach the dura of the posterior cranial fossa. A small branch of this artery runs beside N. hypoglossus to supply the walls of the large anastomotic veins of the foramen magnum, in addition to the atlanto-occipital joint. The occipital arose from the base of the internal carotid in both newborn specimens mentioned above.

The external maxillary artery is weak, and most of its terminal area of distribution is taken over by the large buccinator artery. The submaxillary ramus of the external maxillary anastomoses with the above-mentioned branch of the superior laryngeal. The bulk of the external maxillary supplies the masseter muscle. In one specimen the external maxillary arose from the base of A. submentalis.

The submental artery is a branch of the lingual artery, anastomosing with the sublingual artery and supplying the symphysis mentis.

The posterior auricular artery gives off a strong occipital ramus that runs laterad of the mastoid process to a typical distribution.

The superficial temporal artery (fig. 95) is a powerful vessel that runs with its companion vein, between the temporal fascia and

Potos flavus—continued

muscle above the zygomatic arch, to emerge at the lateral angle of the eye. The bulk of the artery continues as the lateral palpebral arteries. The masseteric ramus is large, but the transverse facial is quite small, anastomosing with both the external maxillary and the buccinator arteries. The zygomatico-orbital is a short anastomotic branch to A. zygomatica of the orbital circulation. On one specimen the superficial temporal gave off the superior labial artery (as seen in *Bassaricyon*).

The external rete of the internal maxillary artery is represented by a few anastomotic arterioles that loop through the pterygoid and deep temporal muscular rami.

The inferior alveolar artery has a long straight course before it reaches its foramen, which is situated far anterior in the mandible, only a few millimeters posterior to the last molar.

The posterior deep temporal is a very large artery that also gives off the middle deep temporal. Rami to the internal pterygoid muscle arise independently from the internal maxillary, the anastomosis with A. submentalis being rather large.

Intracranially, the middle meningeal artery[1] (fig. 96) is one large trunk that is distributed more anteriorly than in *Procyon*, running at right angles to the basis cranii, to supply the middle cranial fossa, extending well beyond the anterior limb of the ectosylvian gyrus.

The orbital artery is a powerful vessel equal in caliber to the remaining internal maxillary trunk. The first branch of the orbital is very small. It accompanies the maxillary nerve through the foramen rotundum and anastomoses with the middle meningeal at the semilunar ganglion. In one specimen the two ocular muscular rami came off a common trunk, with the lacrimal artery as a secondary branch of the medial muscular ramus. The external ethmoidal, one of the terminal branches of the orbital, gives off the frontal, the trochlear and the anterior meningeal before entering the skull. The orbital also gives off a large deep temporal ramus; in one specimen it also gives rise to the anterior deep temporal.

The larger division of the orbital artery, *A. ciliaris*, first gives off the small accessory meningeal artery. *A. meningea accessoria* runs through the orbital fissure to ramify over the dura of the

[1] Sectioned skulls C.N.H.M. nos. 41606 and 8611 were examined and the ramifications of the meningeal arteries were found to be identical with those in the preserved specimens.

Potos flavus—continued

anteroventral area of the anterior Sylvian gyrus. The ciliary artery then divides into the long and short ciliary arteries that anastomose with each other on opposite surfaces of the optic nerve, and with the ophthalmic artery on the lateral surface. The great size of the ciliary artery seems a compensation for the reduction of the nasal area along with its sources of supply, and for the large eyeball.

In the adult *Potos* dissected, the anastomotic artery is a minute twig from the orbital artery to the ophthalmic nerve. This tiny arteriole runs from the orbital fissure to the Gasserian ganglion and anastomoses with the internal carotid at the sella turcica. In the subadult specimen the anastomotic artery was slightly larger.

The artery of the pterygoid canal arises from the internal maxillary posterior to the orbital.

The buccinator artery is unusually large in *Potos*, taking over much of the external maxillary area, as it gives off both labial arteries and the angular. In one specimen the anterior deep temporal came from the base of the buccinator trunk. The internal maxillary artery terminates in three branches, the largest of which is the anterior deep temporal; the infraorbital and the sphenopalatine-descending palatine trunk are smaller.

The infraorbital artery breaks up at the level of the alveolar process of the second molar. The medial palpebral arteries anastomose with the frontal, superficial temporal, lateral palpebral, and angular arteries, in a complete circuit around the eye, in addition to supplying the lateral surface of the nose.

The short sphenopalatine-descending palatine trunk arises at the level of the buccinator artery opposite the pterygoid process of the superior maxilla and divides a few millimeters farther forward. The foramina for these arteries are situated much more anteriorly than in *Procyon* and the vessels are correspondingly elongated.

The main trunk of the sphenopalatine runs on the lateral wall of the nasal cavity, as in the raccoon, but the small septal branch arches across to the septum at once.

The posterior palatine artery, from the base of the descending palatine, is of medium caliber and sends several rami into the area of distribution of the anterior palatine artery, in addition to the usual posterior branch.

The descending palatine is slightly smaller than the sphenopalatine and emerges as the anterior palatine artery on the hard palate opposite the fourth premolar, farther forward than in *Procyon*.

Potos flavus—continued

The palatine anastomoses at the incisive foramen give off a minute artery, A. septi mediani, to the median incisive foramen.

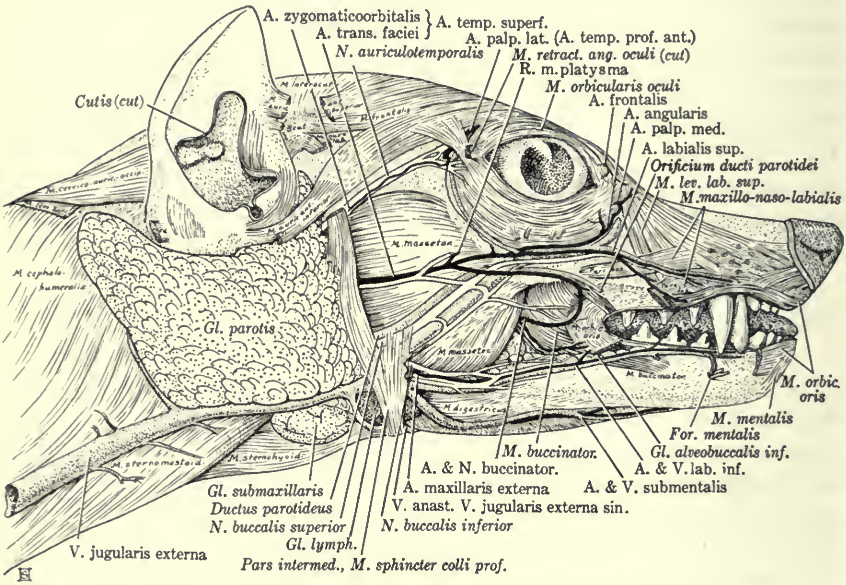


FIG. 90. Superficial arteries, veins, and nerves of the right side of the head in *Bassaricyon alleni*. Arteries are black, veins stippled and nerves unshaded. × 1.

Bassaricyon alleni (figs. 90 and 95)

Because of the rareness of this genus, our single embalmed specimen must serve several purposes. Only those arteries lying fairly near the surface could be observed for the present.

The common carotid artery bifurcates at the level of the middle of the thyroid cartilage. The internal carotid is one half the caliber of the external carotid, and takes a diagonal course to the posterior carotid foramen, which is situated midway between the posterior and medial lacerated foramina. The extracranial internal carotid is somewhat shorter than in *Procyon*, but not as short as in *Potos*.

The occipital artery arises from the base of the external carotid, and supplies basicranial muscles and an anastomosis to the vertebral without reaching the occiput. The posterior meningeal has a relatively large caliber. The ascending pharyngeal is a small branch of the occipital, and gives off a minute twig to the internal carotid at the foramen lacerum medium.

Bassaricyon alleni—continued

The external maxillary is of medium caliber, the bulk of the vessel continuing as the submental artery, but the inferior labial is given off as a smaller branch and the superior labial is reduced to a minute arteriole to the superior buccal ramus of the facial nerve. The submental artery anastomoses with the sublingual and terminates at the symphysis mentis. A small branch from the lingual artery supplies the posterior part of the mylohyoid muscle.

The posterior auricular is a massive trunk that gives rise to *A. stylomastoidea* as well as a large *R. occipitalis* that supplies the occipital field.

The superficial temporal is larger than the external maxillary, and its branches are the same as in *Procyon* with the exception of the transverse facial, the largest branch. *A. transversa faciei* runs across the masseter beside R. malaris of N. auriculotemporalis and takes over the area usually supplied by the superior labial. A large branch anastomoses with the buccinator artery. Then the artery sends an anastomosis to the anterior deep temporal at the lateral angle of the eye, followed by *A. angularis,* which anastomoses with the medial palpebral, from the infraorbital, at the medial angle of the eye. The transverse facial terminates in two branches supplying the upper lip to the level of the canine tooth.

The middle meningeal and accessory meningeal arteries were examined on skull C.N.H.M. no. 29180. The middle meningeal is twice the caliber of the accessory, and supplies the dura posterior to the lateral fissure.

The large anterior deep temporal artery arises just posterior to the terminal bifurcation of the internal maxillary, and supplies the supraorbital region as well as the temporal muscle, giving off the lateral palpebral and anastomosing with the zygomatico-orbital twig of the superficial temporal and with the medial palpebral.

The internal maxillary terminates in the large infraorbital and somewhat smaller sphenopalatine-descending palatine trunk at the posterior border of the palatine bone.

A. infraorbitalis gives off the medial palpebral and superior alveolar arteries before passing through its foramen, where it bifurcates in rami to the face.

The long sphenopalatine-descending palatine trunk bifurcates opposite the pterygopalatine canal, the sphenopalatine being much the larger subdivision. The pterygopalatine canal opens as the

Bassaricyon alleni—continued

anterior palatine foramen opposite the posterior border of the fourth premolar in one skull, and at the posterior border of the first molar in the other.

The medial septal artery is large.

Ailurus fulgens (fig. 91)

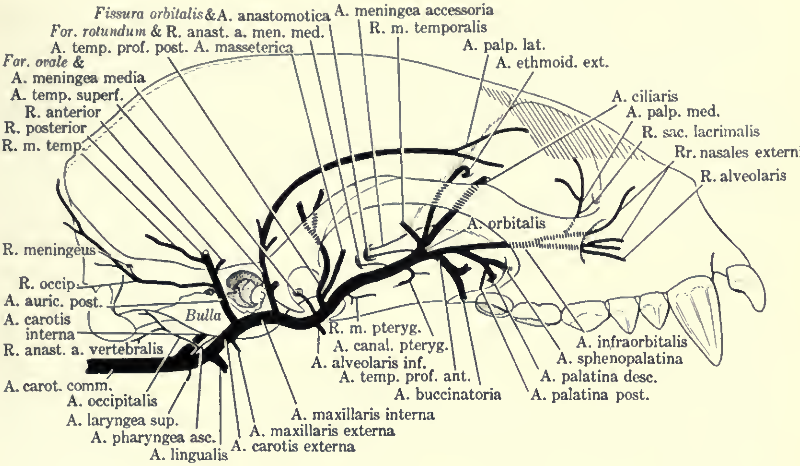
The common carotid artery bifurcates at the level of the thyroid foramen, opposite the atlas. The internal carotid is over half the caliber of the external carotid. The carotid sinus is a barely distinguishable small swelling at the base of the internal carotid. The slightly undulating basicranial portion of the artery is rather long, exceeding the bullar length by 6 per cent. The internal carotid running in its canal is longer than in any other genus examined, arching laterad in contact with the full length of the promontorium, turning ventrad as it approaches the foramen lacerum medium, then bending sharply dorsad to enter the sinus cavernosus. A caroticotympanic artery is given off at the anteromedial border of the promontorium, where it participates with the pharyngeotympanic in the tympanic plexus.

The internal carotid gives off a hypophyseal ramus subdurally, and a slender ophthalmic artery just after piercing the dura. The ophthalmic artery anastomoses with the ciliary artery at the distal third of N. opticus.

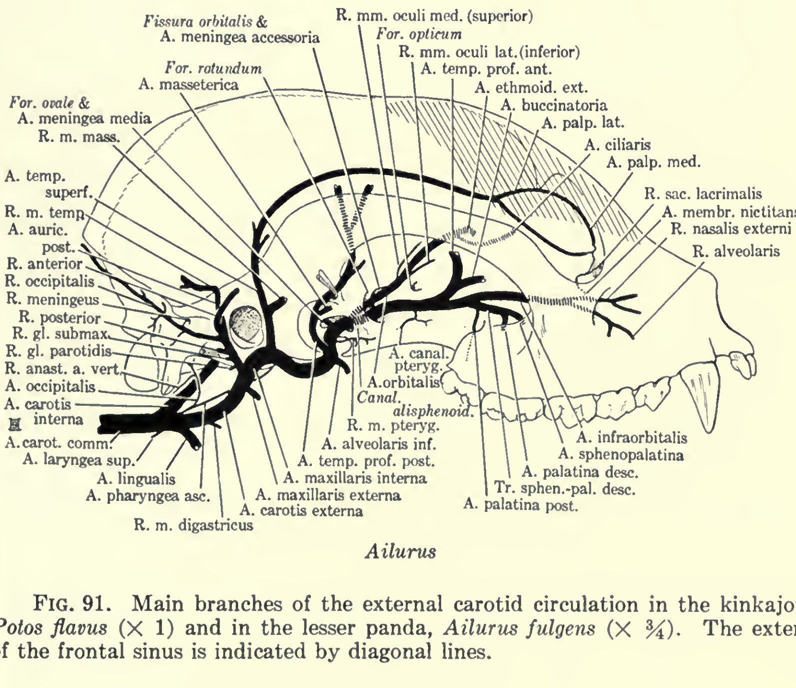
The circle of Willis is in the form of a semicircle anteriorly and a half-ellipse posteriorly. The anterior half of the circle slightly exceeds the other half in caliber. The combined anterior cerebral-middle cerebral trunk divides subequally at the optic chiasma. The middle cerebral is accompanied by a secondary, smaller vessel given off by the anterior cerebral. The internal ethmoidal arises from the anastomosis with the external ethmoidal without joining its fellow. There is no anterior communicating artery.

The posterior communicating artery is smaller than the main middle cerebral, and gives off large hippocampal rami, and the smaller posterior cerebral. The superior cerebellar arteries are doubled at their origin and an anastomotic vessel bridges the triangular space between them, giving off thalamic twigs.

The vertebral arteries give off small rami at cervical nerves II–IV, with a large branch at N. cervicalis III on the left side. The main branches of the arteries form the diamond-shaped basilar rete at the first cervical nerve. There is a small triangular anastomosis



Potos



Ailurus

FIG. 91. Main branches of the external carotid circulation in the kinkajou, *Potos flavus* (× 1) and in the lesser panda, *Ailurus fulgens* (× ¾). The extent of the frontal sinus is indicated by diagonal lines.

Ailurus fulgens—continued

where the anterior spinal artery arises, at the level of the third cervical nerve.

The basilar artery is large, subequal to the internal carotid, and gives off several pontine twigs in addition to a large anterior inferior cerebellar artery. The posterior inferior cerebellar artery arises from the anterior half of the basilar rete.

The external carotid artery gives off the anterior laryngeal at its base. The anterior thyroid is a branch of the common carotid artery.

The occipital artery is a medium-sized trunk that arises opposite the lingual artery and immediately sends a recurrent branch to the large cervical lymph gland and to the sternomastoid muscle. The artery divides at the condyloid foramen into lateral and medial branches. The lateral branch gives off rami to Mm. digastricus and rectus capitis lateralis, as well as to the inferior tympanic artery. The medial branch sends a twig to the transverse sinus, a nutrient twig to the internal carotid nerve, and gives off the small posterior meningeal artery and an articular and muscular ramus. It anastomoses with the vertebral artery. The posterior meningeal is a nutrient artery to the hypoglossal canal and does not enter the posterior cranial fossa.

The ascending pharyngeal, a small artery, arises just anterior to the occipital and sends an anastomotic twig to the internal carotid artery at the foramen lacerum medium before making its terminal bifurcation. The pharyngeotympanic artery is very minute. Opposite the carotid foramen the ascending pharyngeal gives off an arteriole that accompanies the inferior caroticotympanic nerve and participates in the arterial plexus on the promontorium. A similar vessel is present in the Tibetan bear and the giant panda, but was not found in any of the procyonines examined.

The external maxillary is a large artery that takes origin at the lateral border of the digastric muscle at the level of the mastoid process. The angular artery is given off opposite the fourth premolar and does not anastomose with the medial palpebral. The superior labial runs across M. buccinator widely separated from its companion vein and anastomoses with the infraorbital opposite the canine. A small collateral branch from the external maxillary accompanies the superior labial and anastomoses with the angular.

The posterior auricular is a very large vessel arising just anterior to the external maxillary. The stylomastoid artery is given off

Ailurus fulgens—continued

medial to the mastoid process. The strong occipital ramus is given off at the lower border of the sternomastoid muscle dorsolaterad of the mastoid process, supplies a well-developed meningeal ramus through the mastoid foramen, has the usual muscular rami and anastomoses with its fellow at the midline. The branch to the posterior surface of the auricle is given off before the occipital ramus, but the anterior auricular branch is given off at that level. After the occipital branch the main trunk of the artery continues as a temporal artery, as in the giant panda.

The superficial temporal artery is approximately two-thirds the caliber of the posterior auricular and the bulk of the vessel pierces the temporal aponeurosis to run between it and the temporal muscle fibers above the zygomatic arch, giving off several strong muscular rami in this part of its course. The masseteric and anterior auricular rami are large. The masseteric ramus divides into a large external branch (to the vertical part of M. masseter) that sends a slender transverse facial to anastomose with the superior labial, and a somewhat smaller internal branch to the deep fibers of the muscle, as in the giant panda. The superficial temporal supplies the medial as well as the lateral palpebral arteries.

The internal maxillary artery arches around the mandibular articulation and presses close against the skull as it crosses the foramen ovale and approaches the alisphenoid canal, through which it passes to the infratemporal fossa. Consequently only the base of the middle meningeal artery[1] is exposed extracranially, and the pterygoid rami usually from that trunk arise just anterior to it. Intracranially, the middle meningeal (fig. 96) divides into two main dural branches at the tentorium. The first branch supplies the middle cranial fossa, running diagonally anterodorsad as far as the anterior turn of the ectosylvian gyrus. Anastomoses with the accessory and anterior meningeal arteries are of extremely fine caliber. The second branch ramifies on the posteroventral margin of the cerebral dura, pressed between it and the tentorium. Skulls C.N.H.M. nos. 44875 and 36749 were examined and the former was found to have the tentorial branch subordinated, taking origin from the main branch. In the second skull, the ramifications followed the same pattern as in the embalmed specimen.

[1] The intracranial distribution of all meningeal arteries was checked on two dry skulls, C.N.H.M. nos. 36749 and 44875, and found to agree with the preserved specimen, except for a higher bifurcation of the middle meningeal in no. 44875.

Ailurus fulgens—continued

The external rete of the internal maxillary begins at the inferior alveolar artery and extends by delicate arterial loops to connect the posterior deep temporal, middle meningeal and pterygoid arteries. Twigs to the internal pterygoid arise from the anastomoses and from the internal maxillary itself opposite the otic ganglion. Unlike the Procyoninae, *Ailurus*' internal maxillary artery is crossed dorsally by both the mandibular and the masticator divisions of the trigeminal nerve.

The inferior alveolar has a long trunk external to the mandible, its foramen being situated far forward. The internal maxillary gives off separately the anterior tympanic and R. mm. tensor veli palatini and tensor tympani.

The orbital artery takes origin from the internal maxillary within the alisphenoid canal. The anastomotic artery, the small first branch of the orbital, runs through the orbital fissure and joins the internal carotid artery in the inferior petrosal sinus. The anastomotic artery gives off the accessory meningeal artery, which enters the skull through a small foramen just anterior to the orbital fissure. The accessory meningeal supplies the area of dura between the coronal sulcus and the anterior limb of the ectosylvian gyrus. The orbital next gives off the lateral muscular ramus, then the medial muscular ramus and continues as the external ethmoidal. The zygomatic artery comes from the lateral ramus, the lacrimal and supraorbital from the medial ramus. The zygomatic anastomoses with the superficial temporal, medial terminal branch. No separate zygomatico-orbital artery and no separate middle temporal are visible. The external ethmoidal gives off the small frontal artery and, just before entering the skull, the large ciliary artery. A. ciliaris supplies the lateral and inferior recti and the retractors as well as the usual ciliary branches, and anastomoses with the ophthalmic.

The small anastomotic ramus, from the ciliary in *Procyon*, is represented by a small nutrient artery to the maxillary nerve, at the terminal bifurcation of the internal maxillary.

The anterior deep temporal artery is given off as the internal maxillary emerges from the alisphenoid canal. The middle temporal branches, usually from the orbital, come from this trunk. The anterior deep temporal is a large artery but does not contribute to the circulation of the orbit, and is not as strongly developed as the adjacent sphenopalatine.

Ailurus fulgens—continued

The terminal bifurcation of the internal maxillary takes place at the posterior border of the superior alveolar process. The infraorbital artery exceeds the sphenopalatine-descending palatine trunk in caliber. The posterior and middle superior alveolar arteries are given off inside the infraorbital foramen. Here a branch of the infraorbital supplies the lacrimal sac, the nictitating gland, the orbicularis oculi and the adjacent bone, structures usually supplied by the medial palpebral, which in *Ailurus* comes from the superficial temporal instead of from the infraorbital artery. Then the infraorbital makes its division into a large anterior external nasal artery and a smaller alveolar. The alveolar trunk receives the terminal anastomosis of the superior labial artery opposite the canine tooth.

The sphenopalatine-descending palatine trunk supplies a branch to the internal pterygoid muscle as well as to the artery of the pterygoid canal. The posterior palatine is the next branch of the trunk, and besides its posterior branch has anterior palatine rami that anastomose with the main anterior palatine artery. The sphenopalatine-descending palatine trunk winds between the internal pterygoid muscle and the massive posterior alveolar process, to bifurcate into its components opposite the pterygopalatine canal. The descending palatine artery enters its diagonally directed canal and emerges on the hard palate opposite the space between the fourth premolar and the first molar, as the great anterior palatine. Several skulls have the anterior palatine foramen opposite the first molar. A. palatina anterior forms an anastomotic loop around the incisive foramen, is joined by a sphenopalatine branch, and sends a small branch through the median anterior palatine foramen.

The sphenopalatine artery gives a palatine ramus in addition to its usual branches. The posterior septal branch arches over to the septum at its origin, a short distance after the main artery emerges from its foramen.

THE PROCYONID CAROTID PATTERN

The preceding description of the arteries of the head in the procyonid genera has presented these vessels from the point of view of their differences from the most familiar genus, *Procyon*. The raccoon was selected for detailed description partly because of easily accessible specimens, but subsequent dissection of the other genera has shown the peculiar fitness of the raccoon to exemplify the family. Not only do the other genera bear a strong resemblance to *Procyon*, but features in which they differ from each other can be found combined in the collateral circulation of the raccoon.

The derivation of the characteristic patterns of each genus can be visualized as a blocking out of parts of essentially collateral arterial channels, compensated by an amplification of other channels. From a comparison of the condition in *Procyon* with the conditions of the other genera, it is possible to deduce the following schematic pattern (fig. 92), from which any of the procyonid generic patterns could have evolved. The relationships of the arteries to the cranial foramina and to the cranial nerves are constant.

Internal Carotid Circulation

The internal carotid is large, runs in a closed canal, and enters the circle of Willis directly. The ophthalmic is small, and anastomoses with the ciliary. There is no central artery of the retina. The anastomosis (via the foramen lacerum medium) of ascending pharyngeal with internal carotid is small. The anastomosis (via the orbital fissure) with the internal maxillary is of medium caliber.

External Carotid Circulation

The ascending pharyngeal and occipital arise from a common trunk. The occipital gives off three important branches before reaching the muscles of the occiput: (1) the posterior meningeal, (2) the anastomosis to the vertebral artery, (3) the meningeal ramus through the mastoid foramen.

The lingual artery is very large. It anastomoses with the ascending pharyngeal near the palatine tonsil and with the submental branch of the external maxillary at the symphysis of the mandible.

The external maxillary is small. It anastomoses with the buccinator, the transverse facial from the superficial temporal, and the infraorbital.

The external carotid is continued as the internal maxillary.

The posterior auricular is very large. It anastomoses with the occipital and the superficial temporal.

The inferior alveolar artery accompanies the nerve of the same name to the mandible, where it anastomoses with the submental artery.

The middle meningeal artery passes via the foramen ovale to the middle cranial fossa, its branches anastomosing with a large accessory meningeal artery from the internal maxillary via the orbital fissure. A nutrient artery accompanies the maxillary division of the trigeminal nerve through the foramen rotundum and anastomoses with the meningeal arteries.

The bulk of the internal maxillary is divided equally into branches supplying (1) the temporal muscle and supraorbital regions, (2) the orbital cone, (3) the nose, palate, and infraorbital regions. These trunks are linked by anastomotic arterioles.

(1) The superficial temporal and anterior deep temporal both reach the supraorbital region. The posterior deep temporal is the largest muscle branch.

(2) The orbital artery provides collateral circulation linking all three terminal regions, and gives off the anastomotic artery to the internal carotid. In addition to muscular rami the main orbital divides into the ethmoidal, which supplies the olfactory region, and the ciliary, which reaches the eyeball.

(3) The sphenopalatine supplies the internal nose; the infraorbital supplies the external nose and the infraorbital region. The descending palatine supplies the palate, and anastomoses with the preceding vessels. An additional communication is provided in a median septal artery at the median incisive foramen.

Differences from Basic Pattern

All procyonid genera follow this basic pattern, each with its particular variation, stated briefly below.

Procyoninae

Bassariscus is very similar to *Procyon,* but it differs in several ways. It has relatively the largest internal carotid, and a small anastomotic artery. It is the only procyonid exhibiting the primitive condition of basicranial origin of the large occipital artery (as in Canidae, Mustelidae and Felidae). The occipital ramus of the posterior auricular is very small, but the temporal ramus is large, as in the pandas. The external maxillary artery is of medium caliber, its angular branch giving off the medial palpebrals. The accessory meningeal artery exceeds the middle meningeal. The ciliary artery is exceptionally large, with a rete at its entrance to the eyeball. The ophthalmic is of medium caliber. The ethmoidal artery is smaller than the ciliary.

Procyon differs from the hypothetical pattern in the great size of the occipital branch of the posterior auricular. The true occipital does not go beyond the basicranium. The mastoid meningeal ramus of this trunk takes over the area supplied by the posterior meningeal. All the major vessels of the head are connected by anastomoses, providing collateral channels for every region. The external maxillary arises after the posterior auricular. The anastomotic artery is relatively large. The orbital artery is sometimes separated into independent ciliary and larger ethmoidal trunks.

Nasua follows *Procyon* almost artery for artery, the chief difference being in the enlarged caliber of the arteries supplying the olfactory apparatus. Arteries to the eye are relatively small. The accessory and middle meningeal arteries are equal in caliber.

Potos is farthest from the basic pattern and from *Procyon*, as evidenced in the shift of the internal maxillary flow to supply the temporal muscle and the orbit, with the olfactory trunks reduced. The extracranial trunk of the internal carotid is unusually short. The ophthalmic artery is well developed, but the anastomotic artery, smaller even than in *Bassariscus*, is a minute nutrient to the ophthalmic division of the trigeminal nerve. The accessory meningeal is small. The external maxillary is reduced, and has lost most of its usual distribution to the enlarged buccinator artery. The superficial temporal is large, running deep to the temporal fascia, as seen in *Ailurus*. The anterior deep temporal does not reach the supraorbital region.

Bassaricyon possesses a pattern in the buccal area intermediate between *Procyon* and *Potos*. The other accessible arteries follow *Procyon* closely, instead of *Potos*.

Ailurinae

Ailurus has more arterial characters in common with the giant panda *Ailuropoda* than with the Procyoninae, although it falls within the outlines of the general procyonid pattern. The giant panda (Davis, MS.) shares more arterial characters with the bears than with the lesser panda, and has far less resemblance to the Procyoninae. *Ailurus* resembles *Potos* in possessing a small accessory meningeal artery, a large superficial temporal artery, and a short descending palatine-sphenopalatine trunk. The anastomotic artery is very small, as in *Potos* and *Bassariscus*.

The Carotid Pattern in the Carnivora

The basic pattern of the arteries of the head (fig. 92) can best be appreciated if the head is subdivided topographically into regions,

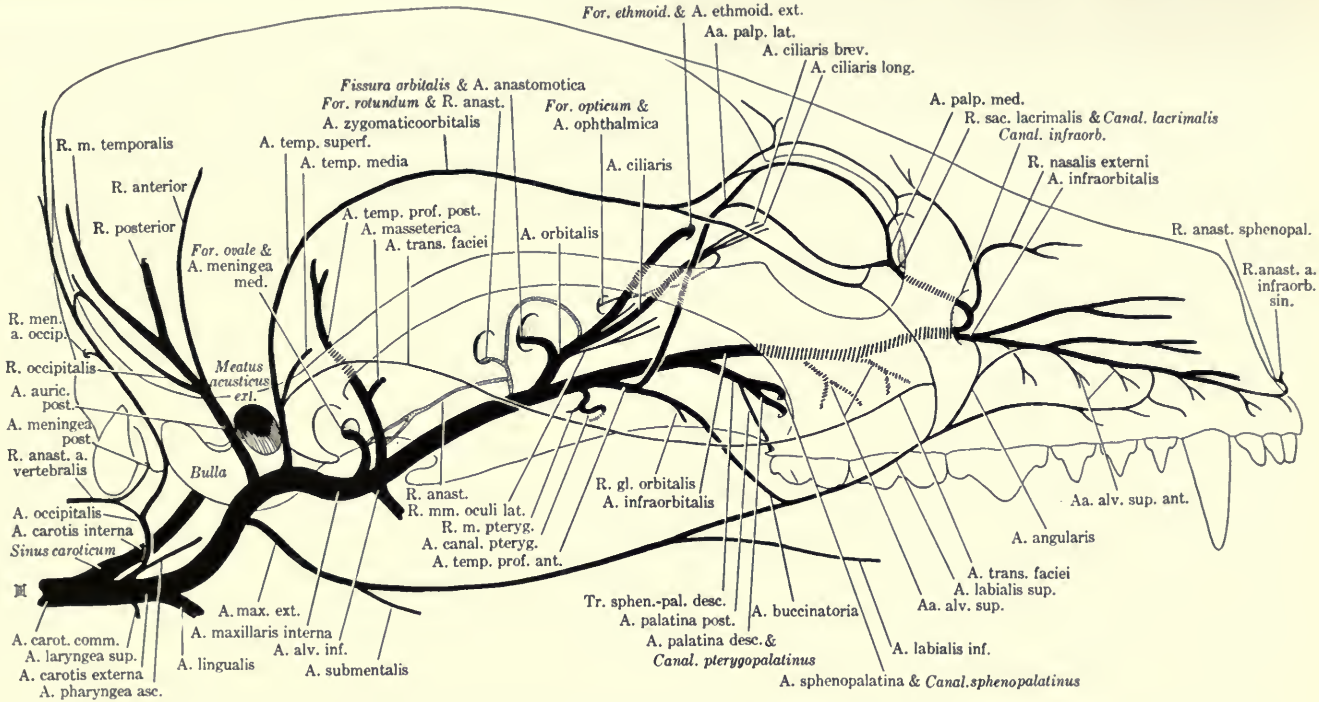


FIG. 92. Hypothetical basic arterial pattern from which any one of the procyonid patterns could have evolved. × 2.

each of which has more than one source of blood supply. The arteries providing collateral circulation to these regions of the head are as follows:

INTERNAL CAROTID CIRCULATION

Brain
- A. carotis interna
- A. anastomotica
- A. basilaris

EXTERNAL CAROTID CIRCULATION

Meninges
- A. meningea anterior
- A. meningea media
- A. meningea accessoria
- A. meningea posterior
- A. occipitalis, R. meningeus

Basicranium
- A. occipitalis
- A. pharyngea ascendens

Occiput
- A. occipitalis
- A. auricularis posterior, R. occipitalis

M. temporalis
- A. temporalis profunda posterior
- A. temporalis profunda media
- A. temporalis profunda anterior
- A. temporalis superficialis

M. masseter
- A. masseterica
- A. temporalis profunda posterior, R. masseter.
- A. temporalis superficialis, R. masseter.
- A. maxillaris externa, R. masseter.

Infratemporal fossa
- Aa. temporalis profunda, Rr. anastomotici
- Rr. mm. pterygoidei, Rr. anastomotici
- A. meningea media, Rr. anastomotici
- A. orbitalis, Rr. anastomotici

Orbit
- A. orbitalis, A. ciliaris, A. ethmoidalis, Rr. musculares oculi
- A. ophthalmica

Nasal and infraorbital regions
- A. ethmoidalis
- A. sphenopalatina
- A. infraorbitalis

Cheek and supraorbital regions
- A. maxillaris externa
- A. temporalis superficialis
- A. temporalis profunda anterior

Palate
- A. palatina anterior
- A. palatina posterior
- A. pharyngea ascendens

Tongue
- A. lingualis, A. sublingualis, A. dorsalis linguae
- A. submentalis

The terminal twigs of these main arteries anastomose freely. In the least specialized procyonid pattern, that of *Procyon,* all the anastomoses are present. When the effects of a specialization begin to show in the vascular system, some of the anastomoses disappear and one or another collateral artery begins to predominate. This potentiality of collateral circulations can be applied to the interpretation of most of the procyonid patterns. The elaboration of patterns upon a basic theme seems to be in accord with phylogenetic relationships. Fundamentally, alterations are designed to transfer the flow of blood from one area to another where basic physiological demands are greater. Massive muscle development requires larger-calibered, deep-lying conduits. Simplification of pattern in favor of larger-calibered vessels seems to go hand in hand with increased body bulk. The smaller carnivores examined usually have extensive collateral systems; the larger carnivores have simpler patterns.

The general trends of the arterial pattern of the procyonids are outlined below, in comparison with the conditions found in certain other carnivores.

The ground plan of the arteries of the head consists of two separate systems, the internal and external carotid circulations, united by an anastomotic vessel. The condition of the internal carotid circulation in the procyonids is essentially simple; a profusion of collateral channels makes the external carotid circulation more difficult to interpret.

Division of the primary common carotid trunk varies in location among carnivores. The common carotid artery bifurcates at the level of the middle of the thyroid cartilage in dogs, bears and procyonids, farther forward in cats and pandas. In mustelids the bifurcation is low on the trachea. Body proportions, especially length of neck, probably influence this condition.

Tandler (1899) analyzed the trend among feloid carnivores toward suppression of the internal carotid but paid less attention to the other side of the picture. The canoid carnivores observed by him included *Canis familiaris, Canis lupus, Ursus maritimus,* and *Meles* *taxus,* in which the internal carotid is well developed. This artery reaches its greatest caliber in the procyonids, in which it is always at least one half the caliber of the external carotid, often much larger, and in *Bassariscus* attains a caliber three fourths that of the

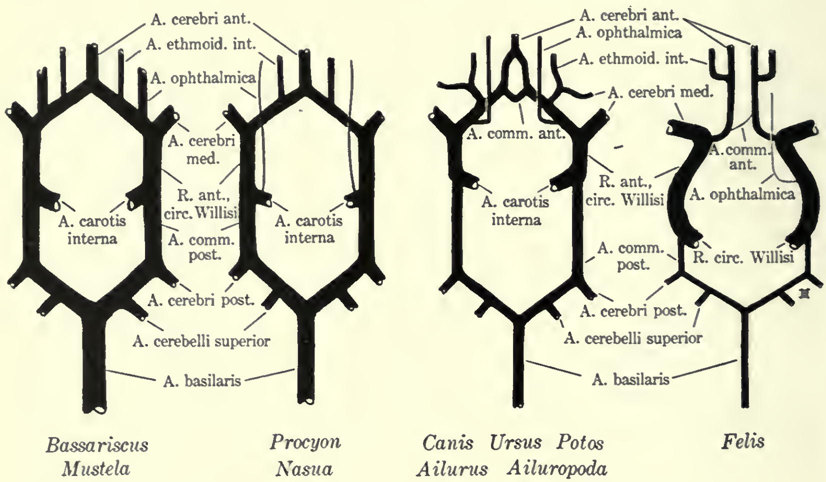


FIG. 93. Diagram showing four patterns of the circle of Willis in carnivores.

external. In pandas as well as bears and mustelids a large internal carotid is characteristic. In dogs the artery is weaker, its caliber varying in different breeds of the domestic dog, and somewhat better developed in the coyote. The specializations of the internal carotid in the feloid carnivores have been frequently discussed. It seems unfortunate that the extremely specialized domestic cat is used widely as a laboratory animal since it is far removed from the typical carnivore carotid pattern. In many ways a generalized form such as the raccoon would seem more suitable for studies involving head and neck regions.

The internal carotid supplies the major flow to the anterior half of the circle of Willis in the canoid carnivores. In those carnivores considered in this paper, the arrangement of the circle of Willis falls into four general patterns, ranging from a primitive canoid pattern to a specialized feloid pattern (fig. 93). The simpler patterns A and B have much in common, but pattern C is more complex and pattern D is definitely specialized. In pattern A, shared by *Bassariscus* and *Mustela,* the basilar exceeds the internal carotid in caliber, but both divisions of the circle are equal. The ophthalmic artery arises from the anterior cerebral in *Mustela*, but from the internal carotid in *Bassariscus*, *Procyon*, *Nasua*, *Potos* and *Ailurus*, although this could not be shown on all the diagrams. Pattern B, for *Procyon* and *Nasua*,

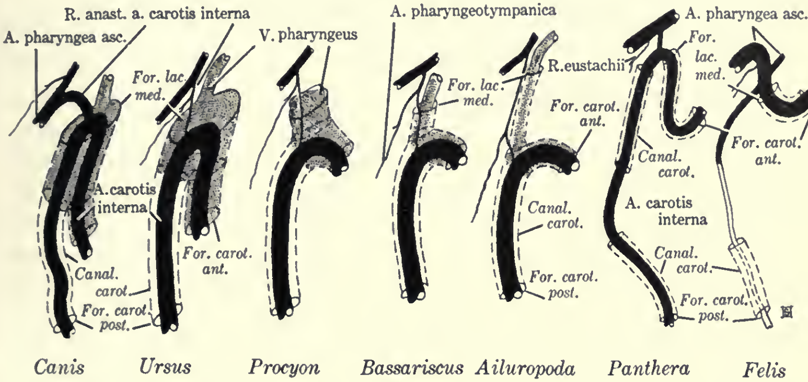


FIG. 94. Transition in form of the carotid canal and the foramen lacerum medium in carnivores. Stippled parts are occupied by venous sinuses; unshaded parts inside dotted outlines indicate space through which the internal carotid nerves pass. Various scales.

differs from A only in the relative caliber of internal carotid and basilar arteries, the latter being slightly smaller. In pattern C, approximated in *Canis*, *Ursus*, *Potos* and the Ailurinae, the anterior half of the circle of Willis is powerful, but much shorter than the smaller-calibered posterior division. The ophthalmic arises from the anterior cerebral in *Canis*, *Ursus* and *Ailuropoda*. The internal ethmoidal and collateral middle cerebral arteries arise by a common trunk from the anterior cerebral. In pattern D the specialized arrangement of *Felis domestica* is shown. The anterior half of the circle of Willis, supplied by the A. anastomotica, greatly exceeds the posterior division. The basilar artery is weak; the posterior communicating artery is short. The ophthalmic artery, if present, arises from the anterior division. The internal ethmoidal arises from the internal maxillary rete, but anastomoses with the anterior cerebral distad to the optic chiasma.

The anastomosis of ascending pharyngeal with internal carotid via the foramen lacerum medium[1] is present in procyonids, pandas,

[1] Weber (1927) defines the foramen lacerum anterior (=medium) as the foramen through which the internal carotid artery usually enters the skull cavity. The foramen lacerum medium is an opening situated at the anteromedial angle of the bulla, medial to the canalis musculotubarius, and communicates intracranially either directly or indirectly with the cavernous sinus.

and bears, but its insignificant caliber scarcely suggests its potentiality as a collateral channel to the brain circulation, in which it plays an important role in the Felidae. This anastomosis is well developed in the mustelids, and variable in the domestic dog, in which it may be large on one side, but absent on the other.

The topographical relationships of the foramen lacerum medium and the carotid canal undergo rather confusing alterations in carnivores (fig. 94). In dogs and bears the foramen lacerum medium is a large opening through which the sinus cavernosus communicates with the pharyngeal venous plexus. The internal carotid artery and nerves loop antero-ventrally almost to the roof of the pharynx at the foramen lacerum medium before turning abruptly dorsad to pass via the anterior carotid foramen into the sinus cavernosus. The cranial opening of the foramen lacerum medium is confluent with the distal part of the carotid canal in all arctoids observed. In procyonids and pandas the foramen lacerum medium lengthens to become a distinct canal, still transmitting a vein. On the other hand, no veins were seen in the narrow foramen lacerum medium and carotid canal of the felids. In the lion (*Panthera leo*) the second segment of the carotid canal is separated from the foramen lacerum medium by a short distance, bridged by the internal carotid artery on its way to the circle of Willis. In the cat (*Felis domestica*) the second segment of the carotid canal is no longer apparent, and the anastomosis of the ascending pharyngeal and internal carotid arteries runs through the foramen lacerum medium and the distal segment of the carotid canal to enter the sinus cavernosus via the foramen caroticum anterior.

The occipital and ascending pharyngeal arteries tend to vary reciprocally in procyonids, pandas and bears. In dogs, *Bassariscus*, mustelids, and cats, the basicranial occipital continues as the chief artery to the nape of the neck, in typical distribution, and there are collateral twigs from the posterior auricular to the occiput. If the occipital does not extend beyond the basicranium, the occiput is supplied by the posterior auricular artery. There is no apparent mechanical explanation for this condition. If this character has phylogenetic significance it links *Bassariscus* to a past shared with a common ancestor of dogs, mustelids, and cats; perhaps this is a primitive character once possessed by all fissipeds.

A resemblance between procyonines and pandas is seen in the reduced size of the posterior meningeal artery with the occipital meningeal branch, via the mastoid foramen, taking over supply of the posterior cranial fossa.

Changes in the buccal region in procyonids bring about a sharp reduction of the external maxillary, as the collateral terminal twigs of buccinator, transverse facial, and infraorbital become the important vessels reaching the external maxillary's area of distribution. This condition is found in none of the other carnivores dissected, although the terminal ramifications of the external maxillary in the dogs are rather small.

In the Procyoninae and Mustelidae (as far as our material goes) the superficial temporal is reduced in caliber, running as a slender vessel external to the temporal fascia, scarcely more than a nutrient to the accompanying zygomatico-orbital nerve. In the other carnivores studied this artery is powerfully developed, running beneath the surface of the temporal aponeurosis. *Potos*, like the pandas, has the deeper, larger trunk. The chief collateral vessel to this region is the anterior deep temporal. It varies reciprocally with the superficial temporal, taking over the external orbital region in procyonids and mustelids.

The temporal and masseter muscles receive their main blood supply from the posterior deep temporal artery in all carnivores, with the exception of the cats. In felids an independent masseteric artery exceeds the former vessel in caliber.

An indication of the method of origin of the external rete of the internal maxillary artery of the Felidae is to be seen in numerous anastomotic arterioles linking the main branches of this artery in the infratemporal fossa of procyonines and *Ailurus*. Few anastomoses occur in this region in dogs and mustelids, none in bears and the giant panda. Sheer muscle massiveness may be an unfavorable condition for rete formation, as the larger felids have less rete development than their smaller cousins.

The presence of the orbital branch of the internal maxillary in carnivores more than balances the small size of the ophthalmic artery (from the internal carotid), and in the procyonids leads to gradual suppression of the ophthalmic artery to mere nutrient dimensions.

Of the carnivores examined only the mustelids have a large ophthalmic artery. The central artery of the retina is absent in procyonids, bears, and pandas. In procyonids a tendency toward complexity in the orbital circulation, seen elsewhere only in feloid carnivores, brings about secondary division of the single orbital into two arteries, with an increased caliber in the one supplying the eye surface. This trend will be discussed further below.

Many fine-calibered anastomotic arterioles link the vessels of the orbit in dogs, procyonids, and cats. These vessels may be safeguards in case of injury to the main arterial supply, in addition to performing a hydrodynamic function as a means of raising or lowering blood volume to the area.

The anastomotic trunk from the external carotid to the brain circulation is relatively much smaller than the internal carotid in canoid carnivores, dwindling to little more than a nutrient to the trigeminal nerve in *Potos*, the Ailurinae, and *Ursus americanus*. Tandler (1899) does not mention the anastomotic artery in *U. maritimus* (*Thalarctos*). In *Canis familiaris* the anastomotic artery varies in caliber, sometimes exceeding the internal carotid artery in supply to the circle of Willis. The anastomotic artery in canoids appears to vary inversely with the caliber of the internal carotid.

The external carotid circulation reaches its terminus in the branches of the anterior part of the internal maxillary. In carnivores, such as *Canis latrans*, *Ursus americanus*, *Procyon*, and *Mustela*, with extensive nasal and infraorbital surface, the infraorbital and sphenopalatine trunks carry the major internal maxillary flow. These areas are much smaller and the flow is shifted to the orbital and anastomotic arteries in cats, and to deep temporal muscular rami in *Potos* and the pandas.

FACTORS INFLUENCING THE PROCYONID PATTERN

The shifting of importance among available collateral vessels has been discussed above, in procyonids and in other carnivores. Something more than the mere presence of alternate channels is needed to bring about pattern change. The circulatory system is functionally a passive supply system, carrying the products of metabolism throughout the body. The organ systems of the body wield final influence in determining the arrangement of the circulatory pattern; the kind of tissue being nourished places limitations upon its supply system. Thus the circulatory system can be best understood if approached from the functional standpoint.

It is apparent that vascular pattern is determined to a large extent by the functional purpose of the vessel, and by the degree of development of the functional unit supplied by the vessel.

Vessel distribution may be divided into three main categories:

(1) Branches supplying muscles and other soft parts.

(2) Branches supplying nerves, not necessarily the comitant vessels (most variable).

(3) Branches supplying periosteum and bone (least variable).

Of these, branches to bone are most conservative, a condition that reflects the slow nature of the modeling of bone. A structure established in bone is seldom subject to rapid change in adult mammals, aside from the ability, decreased with age, to repair direct injury. Rapid alterations in bone are associated with ontogeny and with the post-natal growth processes of young mammals. On the other hand, blood vessels supplying muscles and nerves are able to change rapidly in adult life.

Muscular branches are somewhat more plastic than other vessels, adapting readily to physiological and structural changes within a muscle, but always conforming to the demand for adequate supply to any area of muscle mass. Increased muscular activity develops a local oxygen deficiency. This oxygen loss is made up by increasing the blood volume to the area. The capillary bed of the muscle mass is the primary agent in providing additional blood, by means of widening the capillaries being used, and by opening other capillaries that are collapsed during quiescence. Frequent exercise of a muscle increases the size of its fibers; increased blood supply is a corollary of this physiological process (Abramson, 1944). Gradual increase in the caliber of capillaries either by expansion or coalescence brings them to the proportions of arterioles and venules; former arterioles attain the caliber of arteries and veins; minor arteries and veins become sizable trunks.

Although at first glance the small *Arteriae nutritiae nervi* may seem rather insignificant from the point of view of the comparative anatomist, their importance becomes apparent when they are followed through a series of genera. These minute vessels represent potential channels of pattern development.

As morphological changes in the muscle-skeleton-joint apparatus occur gradually with changing habits of an animal, alterations in the blood supply to the region become necessary. The minute collateral channels, already present as nutrients, are available for development into larger vessels of a pattern more useful to the transformed relationships of the functional unit. The basic work of Adams (1943) on the blood supply of the sciatic nerve in the rabbit has yielded the means and the proof of such alterations. He found that ligation of the inferior gluteal artery, main nutrient to the sciatic nerve, produced no change in the physiological state of the nerve. Ligation of all macroscopic sources of supply produced nerve degeneration in only two cases out of twelve. According to

Adams, these experiments indicate the ability of the intrinsic longitudinal anastomotic pathways of the sciatic nerve to accommodate by expansion and provide adequate circulation.

Wherever changes from a basic vascular pattern occur, it is advisable to consider what collateral channels previously existed. A good example of the perplexing differences that occur in one vascular pattern is shown by the external maxillary artery and its collaterals (fig. 95). At first glance, the pattern of *Procyon* seems widely separated from that of *Potos*. After observation of the intermediate pattern of *Bassaricyon* the transition between the vastly different patterns of *Procyon* and *Potos* can be recognized. The entire maze of collateral vessels is present in *Procyon*. In *Bassaricyon* the transverse facial, buccinator and submental arteries increase, the superior labial drops out, and the sublingual is reduced. The orbit in both *Procyon* and *Bassaricyon* is supplied by a large branch of the anterior deep temporal and a small zygomatico-orbital branch. In *Potos* the trunk of the external maxillary is feebly connected with its distal branches, which are taken over by the buccinator and the mylohyoid ramus of the lingual artery. The orbital branch of the anterior deep temporal has vanished, and the zygomatico-orbital dominates. The basic relationship between the two extreme patterns is apparent only after examining the intermediate.

An example of the influence that muscular development (as a result of changing food habits or other factors) may exert on vascular pattern is seen in the transformations in the superficial temporal and anterior deep temporal arteries. The superficial temporal is at first a large artery buried beneath the temporal aponeurosis, with a slender zygomatico-orbital branch accompanying the nerve of the same name to the orbit. The anterior deep temporal is a relatively small vessel terminating in the same region. The temporal muscle, in the role of most powerful agent for closing the jaws, is subject to the greatest demands for adaptability in response to changing food habits. Additional surface for origin of the temporal muscle is provided through growth of the sagittal and lambdoidal crests of the parietal, and dorsal and lateral expansion of the frontals. The latter process is accompanied by increase in the pneumatic space (so-called frontal sinus, figs. 88, 89, and 91) continuous through the frontal, maxillary and nasal bones. In elongated heads, increase in the mass of the temporal muscle tends to lie in the anteroposterior plane, but temporal expansion appears greater in the horizontal plane in short, broad skulls. Changes in the histological structure

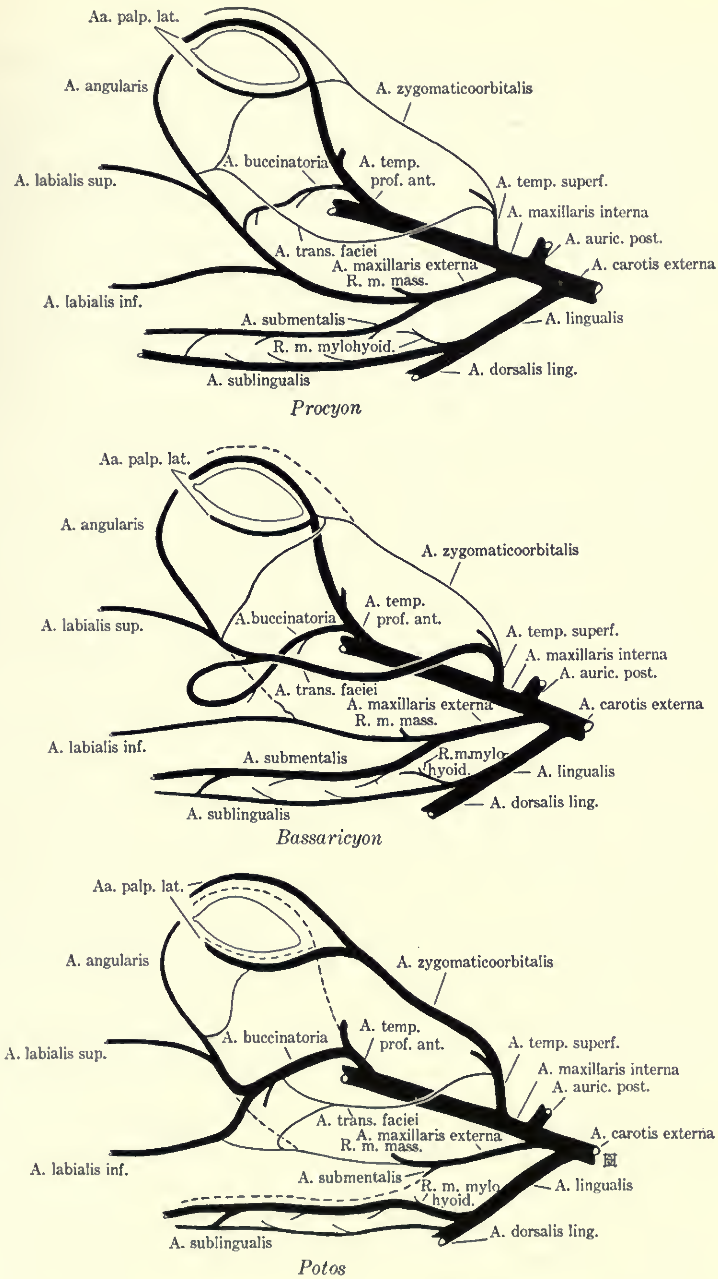


FIG. 95. Three arrangements of the external maxillary artery and its collateral vessels. Dotted lines indicate arteries that have disappeared as others increased in distribution.

of that part of the temporal muscle supplied by the superficial temporal may be correlated with the caliber of the artery. This part of the muscle is more tendinous than fleshy in those long-skulled carnivores (*Bassariscus, Procyon, Nasua, Mustela*), with a weak superficial temporal. The transition to tendinous fibers (resulting from changing stresses within the muscle) is accompanied by reduction of the superficial temporal in caliber; its main muscular branch no longer extends to the orbit, and the zygomatico-orbital branch, a weak vessel superficial to the temporal fascia, is the remaining link to the orbital circulation. Meanwhile, as deeper areas of the temporal muscle become bulkier, the anterior deep temporal increases its size to accommodate the enlarged fleshy fibers, and finally takes over the terminal orbital branches of the superficial temporal artery. The anterior deep temporal remains short in those carnivores (dogs, bears, *Potos*, pandas, and cats) in which the superficial temporal is a large artery supplying heavy fleshy fibers in the temporal muscle.

The anastomotic artery and the accessory meningeal often associated with it begin as nutritiae nervi and gradually increase in importance in many carnivores. The development of the anastomotic artery has already been discussed (Davis and Story, 1943) but the meningeal arteries (fig. 96) in carnivores have been neglected. The accessory meningeal may equal the middle meningeal in distribution, and in the extreme case of the giant panda may even take over completely. There may be some correlation between cranial form and the pattern of dural arteries, since longer crania tend to have two well-developed meningeal arteries, but shorter, more rounded crania are supplied by one main artery. The frontal bone always receives nutrients from the accessory meningeal; the parietal and temporal bones receive from the middle meningeal. The similarity in pattern among long-headed procyonids (*Bassariscus, Procyon, Nasua*) does not necessarily imply lack of relationship to other procyonids (*Bassaricyon, Potos*) for the basic pattern is still present in both, but altered to a degree conforming to the differing proportions. Endocranial casts of carnivores with elongated crania, such as the mustelids *Lutra, Tayra, Taxidea,* and *Mustela,* show the presence of two well-developed meningeal arteries. The dura of the shorter, more rounded brains of bears, pandas, and the brachycephalic dogs are supplied by one powerful artery, but even here a weak accessory meningeal is always present. The superficial resemblance of these arteries in *Potos, Ailurus,* and *Felis* cannot be regarded as more than coincidental due to the similar cranial proportions of these genera.

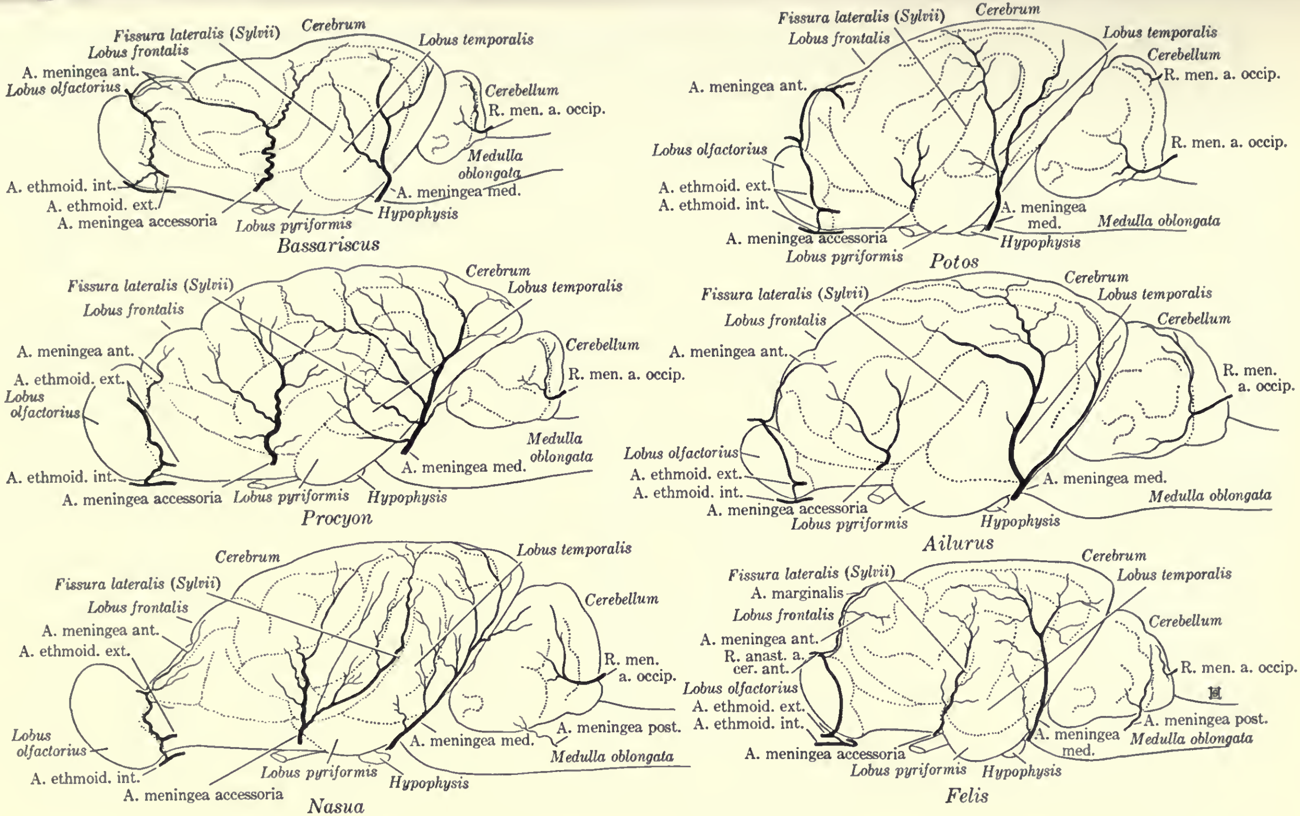


FIG. 96. The meningeal arteries of the raccoons, compared with those of the domestic cat. × 1.

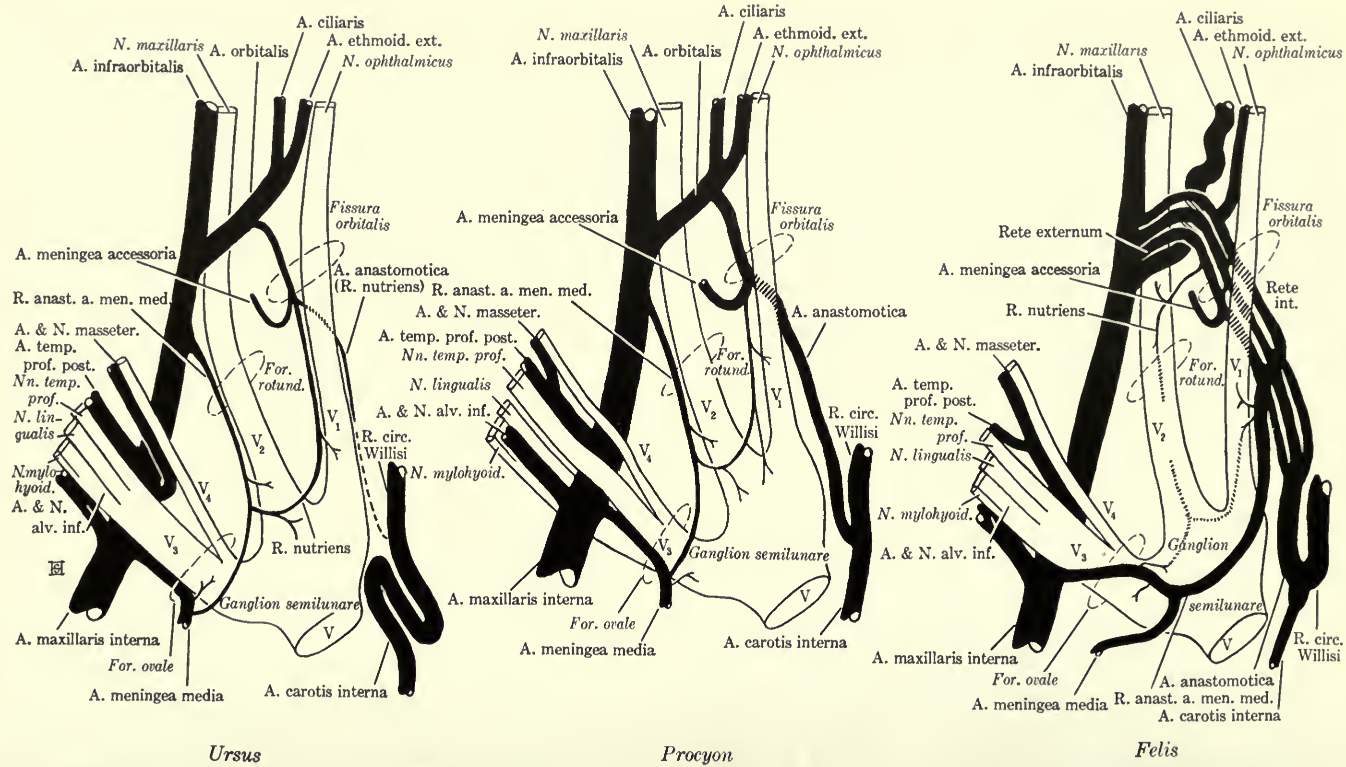


FIG. 97. Diagram of the meningeal and anastomotic arteries in association with the semilunar ganglion and main branches of the trigeminal nerve in *Ursus americanus*, *Procyon lotor* and *Felis domestica*.

The relations of the meningeal arteries with the fifth nerve, going hand in hand with the development of the anastomotic artery, are shown in the accompanying diagram (fig. 97). The necessity of adequate nutrition for the continued functioning of nerves appears to be an important factor in the constancy of the association of these arteries, regardless of their varying caliber, with the divisions of the fifth nerve as they leave the skull via their specific foramina; the ophthalmic division, via the orbital fissure, is accompanied by the anastomotic artery and the accessory meningeal; the maxillary division, via the foramen rotundum, is supplied by a nutrient anastomotic branch; the mandibular division, via the foramen ovale, is associated with the middle meningeal. All three arteries are linked by anastomoses surrounding the semilunar ganglion of the trigeminus. The extracranial relationships are constant also: N. ophthalmicus with A. orbitalis, N. maxillaris with A. infraorbitalis, N. mandibularis with A. alveolaris inferior, N. masticatorius with A. masseterica. These topographical relationships are constant in all carnivores seen; variation lies only in the caliber of the vessels. The anastomotic artery is essentially one of the nutrient arteries of the trigeminus, enlarged in *Procyon* to moderate importance, in *Felis domestica* to great size in order to perform a specialized function. In *Potos* and in *Ursus americanus* the anastomotic artery has not developed beyond its primary function of nutrition for the fifth nerve.

The proportions of the olfactory and masticatory apparatuses vary in the procyonids (fig. 98). Two divergent trends are present, one in the direction of nasal expansion, the other toward nasal reduction. In those forms with a large nasal development, such as *Procyon* and *Nasua*, the vessels to this region are powerfully developed; relatively weaker vessels supply the orbit. In the shorter-faced forms (*Bassariscus*, *Bassaricyon*, and *Potos*) the proportions of nasal versus orbital area are nearly reversed and vascular supply is likewise altered. The masticatory muscles (temporal, zygomatico-mandibular, masseter and pterygoids) are well developed in all the procyonids, but appear to increase in the horizontal plane in the shorter-faced forms. In the latter, the vascular supply to the nasal region is not extensive but the arteries to the masticatory muscles are very large. The variability of the arterial pattern of the face in procyonids may be due to functional necessities accompanying changes in facial proportions.

Ontogenetically, the eye and the olfactory apparatus are considered as parts of the brain; this primary relationship of olfactory and visual apparatuses accounts for the intimate association of the vascular trunks to these structures. The intracranial arteries (from internal carotid) to these sensory regions are augmented by a large trunk from the extracranial main vascular channel (external carotid).[1] The close approximation of the internal ethmoidal and (internal) ophthalmic arteries has already been mentioned by such authors as Hürlimann, Norris, and Tandler. The external ethmoidal and ciliary arteries (sometimes termed *external* ophthalmic) are juxtaposed branches of the external carotid. As the unequal growth of the sense organs brings a divergence in volume, functional demands change and a corresponding shift in the vascular supply occurs. Two sets of arterial channels are available for reciprocal variation: extracranial versus intracranial, and ethmoidal versus ciliary-ophthalmic. In mammals with a partially membranous orbit the extracranial channel tends to dominate. The relative caliber of ethmoidal and ciliary arteries varies with the relative size of the olfactory and visual apparatuses. In the Anthropoidea, which have a closed orbit, the intracranial channel takes over. The end stage of this trend is seen when a large ophthalmic from the internal carotid supplies the other orbital and ethmoidal structures in addition to the highly developed eye. Weidenreich has discussed the decisive role of the brain in the transformation of the primate skull. The structural modifications of the skull have rendered the phylogenetically earlier vascular channels untenable and a major shift in proportions of the main channels has taken place. Thus the factors operating upon skull transformation wield an influence on vascular supply.

The single orbital artery found in seven out of ten dissections of *Procyon*, and in *Potos* and *Ailurus*, represents the primitive condition, in which the olfactory and visual organs are nourished by a single large trunk that bifurcates distally into ciliary and external ethmoidal arteries. The single orbital artery is found also in the dogs, the bears and giant panda, and the mustelids. Among the dogs examined, the ethmoidal (olfactory) division considerably exceeds the ciliary (visual) division in *Canis latrans*, but the two divisions are equal in *Canis familiaris*. The skull of *C. latrans* is narrow and long-nosed, and the orbit small, but the shorter skulls of certain domestic breeds have larger orbits; the arterial pattern parallels these proportions. Correlation of skull form and vascular proportions is again apparent.

[1] The ontogeny of this region in man cannot be taken as a guide, for cranial expansion in primates has produced a wide difference from the basic mammalian pattern. The ontogeny of the arteries of the head has not been satisfactorily traced in a carnivore.

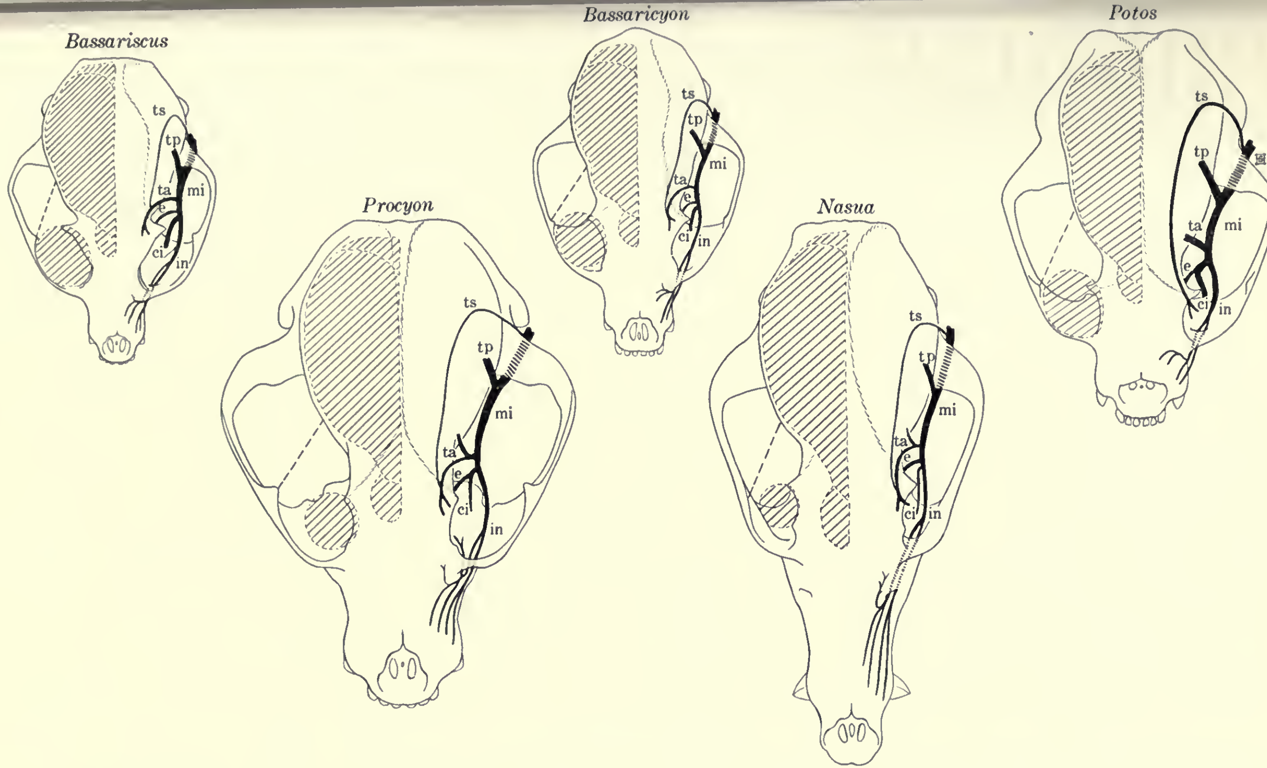


FIG. 98. The proportions of the internal maxillary artery to the skull and orbit in the Procyoninae. × 1½. Brain and eyeball are indicated by diagonal lines; a dotted line marks the posterolateral boundary of the orbit. Several large arteries are omitted. Abbreviations are: *mi*, internal maxillary; *ts*, superficial temporal; *tp*, posterior deep temporal; *ta*, anterior deep temporal; *e*, external ethmoidal; *ci*, ciliary; *in*, infraorbital.

In *Procyon* the orbit is in an unstable condition, the eyeball varying considerably in proportion to the volume of the orbit and in lesser degree relative to brain volume. The variability in the pattern of the orbital vascular supply of the raccoon, described above, reflects the dynamics of transformations in the orbital region of the skull. The basic pattern of a single orbital artery is gradually being changed to a duplex pattern in procyonines. The ciliary artery is separated from the original orbital (ethmoidal) trunk in *Bassariscus* and *Nasua* and is an independent vessel in three out of ten *Procyon* dissections. In *Bassariscus* the volume of the eye is greater in relation to brain volume than in *Procyon;* the ciliary, a powerfully developed vessel, slightly exceeds the combined caliber of the other orbital arteries. Among carnivores dependent on keen vision, this trend toward massiveness in the ciliary artery reaches a climax in *Felis domestica,* in which the eye is very useful. In *Felis* the huge ciliary artery maintains its strength and individuality through the complexity of the surrounding external rete that supplies all other vessels to the orbit.

Feeding habits and the masticatory apparatus as an influencing factor on skull form have been discussed recently by Sicher (1944). The influence of relative brain size on skull transformations has been brought out by Weidenreich (1941) and others. The relative proportion of facial area (olfactory, visual and masticatory apparatuses) to cranial area influences the vascular pattern of both main areas of the skull. Since there is a definite correlation between relative size of brain, mass of extracranial structures, and proportionately adequate vascular supply, trends in the vascular pattern within closely knit phylogenetic groups, such as the Felidae, clearly are associated with changes in skull contour brought about by facial and cranial development. In the Felidae a gradual shift in the source of blood supply to the brain has occurred (Davis and Story, 1943), with the external carotid taking over the functions of the internal carotid of other forms. The larger cats, with a powerful infraorbital artery supplying their facial area, show a diversion of part of the external carotid flow to reach the brain, but retain a functional internal carotid of small caliber. In the domestic cat, on the other hand, the facial region of the skull is relatively much smaller compared to the brain cavity. Extreme transformation in function of the carotids occurs in *Felis domestica,* in which only a moderate-calibered infraorbital artery supplies the facial area, with the balance of the external carotid going to the brain via the external rete; the true internal carotid is vestigial.

The Procyonidae are a less closely knit group than the Felidae, but there is apparent correlation throughout the family between general proportions of the head and vascular supply. The proportions of the internal and external carotid circulations are the reverse of the feloid condition and are probably nearer the primitive condition for carnivores. The extracranial structures, supplied by the external carotid, make up the greater part of the head. The brain is adequately supplied by the large internal carotid and the basilar artery (from the vertebrals); collateral sources of supply are not essential to maintain brain metabolism. The external and internal carotid circulations are thus nearly independent of each other, yet a slender connection through the anastomotic artery of varying caliber is always present, available as a collateral channel if functional demands change.

SUMMARY

The arteries of the head in the raccoon, *Procyon lotor*, are described in detail. In the other procyonid genera, *Bassariscus*, *Nasua*, *Potos*, and *Ailurus*, vessels differing from those in *Procyon* are described. Brief notes on *Bassaricyon* are included.

A basic similarity exists among all the procyonid genera. The arterial pattern of *Procyon* provides many collateral arteries to each region of the head, and in this respect approximates a hypothetical pattern from which any one of the procyonid generic patterns could have been derived.

The forces modelling the structure of the head in procyonids apparently influence the developmental trends of the passive circulatory system. Differences among the various genera have been brought about by shifts between available collateral vessels. Some of the factors involved in these shifts appear to be muscular development, nerve arrangement, skull proportions and size of brain and sense organs. None of these factors can with certainty be said to predominate, for there is a continuous interplay of influences. Perhaps some factors have been overlooked, but those enumerated above call for further investigation along comparative embryological as well as gross morphological lines.

The ground plan in the Procyonidae consists of a large internal carotid artery, with a small anastomotic artery connecting this intracranial trunk with the larger extracranial trunk, the external carotid. The extracranial trunk breaks up, in the infratemporal fossa, into

branches to the masticatory apparatus, the orbit, and the olfactory apparatus.

Two trends in head proportions are present in procyonids: (1) toward elongation of the olfactory and masticatory regions, with apparent reduction of the eye (*Procyon*, *Nasua*) and (2) toward shortening the olfactory and masticatory regions, with apparent increase in eye development (*Bassaricyon*, *Potos*). *Bassariscus* is intermediate, with little reduction in nasal area but with a large eye. Vascular changes parallel these transformations of skull contour.

Despite skull changes, arteries passing through cranial foramina and those accompanying nerves are constant in location; variations are in caliber.

Numerous arterioles anastomose around the internal maxillary artery in the infratemporal fossa of procyonids. This tendency may foreshadow, structurally, the external rete of the Felidae.

On the basis of arterial pattern, intergeneric relationships are indicated as follows: *Procyon* and *Nasua* are very close, *Bassariscus* and *Bassaricyon* intermediate between *Procyon* and *Potos; Potos* has some resemblance to *Procyon* but parallels *Ailurus; Ailurus* resembles *Ailuropoda* more than it does the other procyonid genera.

Many features shared with other carnivores are present in the raccoons, and it is difficult to point out a sharply delineated procyonid pattern. Limitations of material prevent a comprehensive comparison of the Carnivora, but the available data have been checked against the procyonids.

The Procyoninae (*Bassariscus, Procyon, Nasua*) share many characters with the Ailurinae, Mustelidae, Canidae, and Ursidae, in the order named. The Ailurinae (*Ailurus, Ailuropoda*) share characters with the Procyoninae, Ursidae, Canidae and Mustelidae. *Ailuropoda* shares more with the Ursidae than with *Ailurus* or the Procyoninae. *Potos* has more in common with *Ailurus* than with the Procyoninae. *Bassariscus* has fewer dog and bear characters than the other procyonines. Because the Procyonidae overlap the other canoid carnivores in their carotid circulation, the family gives a cross sectional view of this system in the Canoidea.

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