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Avian Cephalic Vascular Anatomy, Sites of Thermal Exchange, and the Rete Ophthalmicum

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ABSTRACT

The general anatomy of avian cephalic blood vessels is well known and there are published details of their role in physiological thermoregulation. Unfortunately, the finer details of vascular pathways to and from sites of thermal exchange are not well known. Additionally, the role of the rete ophthalmicum (RO), a vascular heat exchanger in the temporal region, has been investigated in terms of brain temperature regulation, yet only the arteries have received substantial attention. Without anatomical details of both the arterial and venous pathways, the role of blood vessels in physiological thermoregulation is incomplete. Cephalic vascular anatomy of multiple avian taxa was investigated using a differential-contrast, dualvascular injection technique and high-resolution X-ray microcomputed tomography. Sites of thermal exchange (oral, nasal, and orbital regions) and the RO were given special attention due to their known roles in cephalic thermoregulation. Blood vessels to and from sites of thermal

ABBREVIATIONS: aCC = Common carotid artery; aCerC = Cerebral carotid artery; aCLatNas = Caudal lateral nasal artery; aCMedNas = Caudal medial nasal artery; can = Common nasal artery; aCPlex = Plexus around choana; aCVNas = Caudal ventral nasal artery; aEC = External carotid artery; aET = Ethmoid artery; aFac = Facial artery; aIC = Internal carotid artery; aIO = Infraorbital artery; aLatNas = Lateral nasal artery; aLPal = Lateral palatine artery; aMan = Mandibular/intramandibular artery; aMax = Maxillary artery; aMedNas = Medial nasal artery; aMPal = Medial palatine artery; Anas = Anastomosis; aNas = Nasal artery; anasEtOpt = Anastomosis between ethmoid and ophthalmotemporal arteries; anasRORA = Anastomosis between RO and rostral auricular artery; anasROSM = Anastomosis between RO and sphenomaxillary artery; aOC = Occipital artery; aOM = Oromandibular artery; aOpt = Ophthalmotemporal artery; aOrbit = Orbital artery; aPal = Palatine artery; aPalM = Median palatine artery; aPM = Palatomaxillary artery; aPR = Profundus artery; aRA = Rostral auricular artery/auricular rete; aRLatNas = Rostral lateral nasal artery; aRMedNas = Rostral medial nasal artery; aRO = Arterial rete ophthalmicum; aRPalp = Rostral palpebral artery; aRVNas = Rostral ventral nasal artery; aSM = Sphenomaxillary; artery; aSO = Supraorbital artery; aSP = Sphenopalatine artery; aST = Stapedial artery; aTO = Temporoorbital artery; gNas, = Nasal gland; iJug = Interjugular anastomosis; PalPlex = Palatal plexus; RO = Rete ophthalmicum; sCav = Cavernous sinus; sDL = Dorsal longitudinal sinus; sOC = Occipital sinus; vCCeph = Caudal cephalic vein; vCerC = Cerebral carotid vein; vCN = Common nasal vein; vCVNas = Caudal ventral nasal vein; vDPalp = Dorsal palpebral vein; vFac = Facial vein; vIO = Infraorbital vein; vJug = Jugular vein; vLatNas = Lateral nasal vein; vLPal = Lateral palatine vein; vMan = Mandibular vein; vMax = Maxillary vein; vMedNas = Medial nasal vein; vMPal = Medial palatine vein; vOM = Oromandibular vein; vOph = Ophthalmic vein; vOpt = Ophthalmotemporal vein; vOrbit = Orbital vein; vPalM =

Median palatine vein; vPO = Postorbital vein; vPR = Profundus vein; vRA = Rostral auricular vein/auricular rete; vRCeph = Rostral cephalic vein; vRPalp = Rostral palpebral vein; vRVNas = Rostral ventral nasal vein; vRO = Venous rete ophthalmicum; vSO = Supraorbital vein; vSP = Suprapalatine vein; vST = Stapedial vein; vTM = Temporomandibular vein; vTO = Tempororbital vein

This article includes AR WOW Videos. Figure 3-D1 is a 3-D image that is viewable in the online "Interactive 3-D PDF."

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exchange were investigated to detect conserved vascular patterns and their ability to deliver cooled blood to the RO and dural venous sinus. Sites of thermal exchange were supplied by arteries directly and through collateral pathways. Veins were found to offer multiple pathways that could influence the temperature of neurosensory tissues, as well as pathways that would bypass neurosensory tissues. These results question the paradigm that arterial blood from the RO is the primary method of brain cooling in birds. A shift in the primary role of the RO from brain cooling to regulating and maintaining the temperature of the avian eye should be further investigated. Anat Rec, 299:1461–1486, 2016. © 2016 Wiley Periodicals, Inc.

Key words: blood vessels; avian; cephalic; vasculature; thermoregulation

Research into avian cephalic vasculature has at times been very active. The literature spans at least 150 years, from general studies by Neugebauer (1845; turkeys), Baumel (1975, 1993; domestic fowl), Sedlmayr (2002; ducks and other Galloanseres), and Holliday et al. (2006; flamingos) to more focused studies on, for example, avian encephalic arterial patterns (Aslan et al., 2006; Verduzco et al., 2009; Nazer and Campos, 2011). This research includes both vascular anatomy and its role in thermal biology, which is critical to the understanding of avian physiological thermoregulation. In 1970, Richards (1970) reported a temperature differential between the brain and body in chickens, with the hypothalamic region of the brain being roughly 1° C cooler than colonic temperatures. Shortly after this publication, the results of similar physiological experiments were published that showed that rheas (Kilgore et al., 1973), nighthawks, mallards, pigeons, ravens, roadrunners (Kilgore et al., 1976, 1979), helmeted guinea fowl (Withers and Crowe, 1980), and bobwhite quail (Kilgore et al, 1981) used the rete ophthalmicum (RO), a vascular heat exchanger in the temporal region, to establish and maintain a similar temperature differential. Following these results, the literature again grew to include descriptions of innervation (Midtgård, 1985), vascular anatomy and physiology of the RO in guinea fowl (Crowe and Crowe, 1979), jackass penguins (Frost et al., 1975), zebra finches (Bech and Midtgård, 1981), vultures (Arad et al., 1989), calliope hummingbirds (Burgoon et al., 1987), herring gull (Midtgård, 1984a), mallards (Midtgård, 1984b), Hawaiian seabirds (Pettit et al., 1981) and 48 other avian species (Midtgård, 1983).

Additional physiological experiments highlighted which regions of the head are important in thermal exchange. These sites were shown to employ evaporative cooling to lower blood temperature, which was then shunted to the RO (Bernstein et al., 1979a). The nasal region was found to be important in penguins (Murrish, 1973) and pigeons (Bernstein et al., 1979a; St-Laurent and LaRochelle, 1994), the oral region was found to be important in mallards (Hagan and Heath, 1980) and panting pigeons (Bernstein et al., 1979a; Peltonen, et al., 1989; St-Laurent and LaRochelle, 1994), and the orbital region was found to be important in penguins (Frost et al., 1975) and pigeons (Bernstein et al., 1979a; Pinshow et al., 1982; St-Laurent and LaRochelle, 1994). Despite all the work that went into the characterization, function, and support of the RO, there were few studies that clearly documented the arterial anastomotic connections between the RO and the cerebral vasculature that were thought to support the brainbody temperature differential. Studies that discussed these connections (Richards, 1970; Midtgård, 1984a,b; Arad et al., 1987; Arad, 1990) cited only anastomotic connections between the orbital and ethmoid arteries.

Few publications explained the role of the RO in supporting the thermal environment of the eyeball (Frost et al., 1975; Midtgård, 1983, 1984a; Arad and Midtgård, 1984), and focused mainly on the role of the RO in brain cooling. Birds are well known to have large eyes that generate considerable metabolic heat (Pinshow et al., 1982), require strict thermal tolerances (Parver, 1991), and are often exposed to dramatic environmental and thermal changes as flying birds change altitude, migrate, etc. The vessels of the RO supply or drain blood directly from the eyeball (Hossler and Olson, 1984), and thus blood reaching the brain from this route must occur through connections via the orbital and ethmoid arteries. Potentially, according to advocates of this route (Richards, 1970; Midtgård, 1984a,b; Arad et al., 1987; Arad, 1990), these connections would have to supply the brain via retrograde flow, somehow against the pressure gradient produced by the heart. Unfortunately, these investigations into the RO have provided little research into the location and function of other physiological thermoregulatory capabilities, which highlights a gap in the knowledge of the vascular anatomy of the RO and its physiological function.

Most recently, Sedlmayr (2002) described a series of interconnected arterial vascular physiological devices that may also support avian brain cooling, and potentially the auricular rete (Ghetie, 1976; Sedlmayr, 2002) may also support RO function in Galliformes. Much of the research surrounding the RO and related vascular anatomy occurred from the late 1970s through the late 1980s, with a few anatomical publications more recently on Galloanseres (Sedlmayr, 2002), flamingos (Holliday et al., 2006), and night herons (Ninomiya, 2002). A vast majority of the publications cited here regard the role of the cephalic venous system as simply a way to deliver cooled blood to the RO. Unfortunately, the preferred *in vivo* pathways for cooled blood in a thermoregulating bird are still completely unknown. Veins might deliver cooled blood to the dural sinuses to cool the brain directly (Sedlmayr, 2002; Caputa, 2004). Cooled blood flowing through the dural sinus system has the potential for brain cooling by influencing the temperature of cerebrospinal fluid surrounding the brain and spinal column (Zenker and Kubik, 1996).

With the recent increase in the use of computed tomographic (CT) scanning as a means of visualizing soft tissues such as blood vessels (Holliday et al., 2006; Porter and Witmer, 2015) and other soft tissues (Metscher, 2009), another look at the vascular anatomy of the RO and its supporting sites of thermal exchange is appropriate. Therefore, this study focused on the vascular anatomy within three major sites of thermal exchange and the potential patterns and pathways leading to the brain and RO. The goals were (1) to specifically investigate the vascular anatomy found in sites of thermal exchange, (2) to detect conserved anatomical patterns and routes of blood flow and pathways from areas of thermal exchange, and (3) to incorporate them into a physiological framework to better understand the role of blood vessels in avian thermoregulatory strategies. Wild turkeys were selected as the primary exemplar, with data from other species brought in when relevant.

MATERIALS AND METHODS

Salvage bird specimens from the Ohio University Vertebrate Collections (OUVC), which are legally held under the terms of Permit 14-2762 issued by the Ohio Division of Wildlife, were used. No live animals were collected, obtained, used, or euthanized for any aspect of this study. Bird specimens used in this study include three adult Phasianus colchicus (captive pheasant; OUVC 10441, 10601, 10442), four Meleagris gallopavo (wild turkey; OUVC 10443, 10444, 10599, 10610), two Struthio camelus (captive ostrich; OUVC 10519, 10664), three Phalacrocorax auritus (wild cormorant; OUVC 10401, 10644, 10645), one Morus bassanus (wild northern gannet; OUVC 10434), two Gavia immer (wild loon; OUVC 10407, 10462), two Phoebastria immutabilis (wild Laysan albatross; OUVC 10408, 10448), one Ara severus (captive chestnut-fronted macaw; OUVC 10306), and one Megaceryle alcyon (wild belted kingfisher; OUVC 10643) were studied using vascular injection, μ CT scanning, and gross dissection.

The vascular anatomy of Galliformes is well known in the literature (Neugebauer, 1845; Baumel, 1975, 1993; Crowe and Crowe, 1979; Richards, 1967, 1968, 1970; Sedlmayr, 2002; Aslan et al., 2006) and serves as a wellknown model with which to compare more derived taxa. Turkeys are large-bodied birds with unfeathered heads, hold a broad range with varying temperatures and environmental conditions, and display vascular features useful for thermoregulation (Buchholz, 1996). The vascular anatomy of the suliform sample (gannets and cormorants) is undocumented in the literature and the clade displays a morphological and ecological disparity that offers the potential for insights into the relative importance of sites of thermal exchange. These taxa display a keratinized palate, nostrils that are secondarily closed by hornified epithelium (rhamphotheca), a highly reduced nasal region (Bang, 1971), and are underwater visual-pursuit predators (Owre, 1967; Strod et al., 2004).

Each specimen was CT-scanned prior to vascular injection at the Ohio University MicroCT Scanning Facility (OUµCT) on a GE eXplore Locus in vivo Small Animal MicroCT scanner at 45 and 90µm slice thicknesses, 80kV, $450 \ \mu A$ (Figs. 1 and 2). This pre-injection scan allowed the bony skull to be cleanly segmented (i.e., digitally extracted) from the full soft-tissue dataset. This step is necessary because the vascular densities of the injected dataset typically exceed that of the bone, making digital extraction of a clean skull virtually impossible. The two datasets-pre- and post-injection-are then registered to each other, allowing more flexibility in visualization and analysis (Fig. 3). For example, the vessels can be viewed in isolation or together with the skull, or the skull can be made semitransparent to view the internal course of the vessels. All specimens were frozen for variable periods of time prior to analysis and subsequently thawed prior to injection. None were embalmed or otherwise fixed. With regard to the injection process, the common carotid artery and jugular veins were cannulated with a 20-gauge cannula (Becton Dickinson and Co., Franklin Lakes, NJ) and injected with a solution of latex (Ward's, Rochester, NY) and barium (E-Z-EM, Westbury, NY) using the Differential-Contrast Dual-Vascular Injection (DCDVI) method of Holliday et al. (2006). Injection pressures were not measured, but care was taken not to over-pressurize the blood vessels by applying a constant, but light, pressure on the syringe plunger. Several specimens were injected with Permaflow V2 (Dodge Chemical, Billerica, MA) or One Point (Pierce Companies, Dallas, Texas) prior to latex injection to aid perfusion by attempting to break up any blood clots. To better understand the arterial or venous system, one specimen each of pheasant, turkey, and cormorant were injected via the carotid artery or jugular vein exclusively; the remaining specimens were injected via both the carotid artery and jugular vein concomitantly using DCDVI. The post-injection scan was done at the same settings as the pre-injection μ CT scan. CT datasets are available at http://dx.doi.org/10.5061/ dryad.61dr5. Digital segmentation was completed using Avizo 7 (FEI Visualization Sciences Group, Burlington, MA) on a Dell T3400 Workstation with 8GB of RAM and an nVidia Quadro FX 4600 video card running Microsoft Windows 7 Enterprise. Segmented blood vessels were then imported into Maya (Autodesk, San Rafael, CA) from Avizo. Maya was used to overlay 3D surfaces representing the blood vessels, using the segmented blood vessels from Avizo as templates. Using this process, the CT datasets from different turkey specimens were composited into a single model within Maya, allowing the strengths of each dataset to be represented and a more complete model generated. The outcome of this process was the generation of a diagrammatic and interactive 3D PDF digital illustration (Fig. 3-D1) that allows detailed manipulation by the user/reader. The model in the 3D PDF can be freely rotated and zoomed, structures can be made visible, invisible, or transparent, and the vessels can be identified simply by clicking on them and reading the bolded name at left in the Model Tree.

After µCT scanning and segmentation was complete, specimens were dissected to verify the digital results. Multiple dried skulls of *Phoebastria immutabilis* (Laysan albatross), *Scolopax minor* (American woodcock), *Phalacrocorax auritus* (cormorant), *Meleagris gallopavo* (turkey), *Ardea herodias* (great blue heron), *Bubo virginianus* (great horned owl), *Gavia immer* (loon), *Struthio camelus* (ostrich), *Pygoscelis adeliae* (Adelie penguin), *Larus*



Fig. 1. Volume renderings of four bird specimens in right lateral view showing blood vessels of the head. (A) *Phalacrocorax auritus* (wild cormorant; OUVC 10645) arteral injection; (B) *Meleagris gallopavo* (wild turkey; OUVC 10599) arterial and venous injection; (C) *Phalacrocorax auritus* (wild cormorant; OUVC 10644) venous injection; and (D) *Meleagris gallopavo* (wild turkey; OUVC 10610) arterial and venous injection. See Abbreviations for vessel names.

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Fig. 2. CT slice of *Meleagris gallopavo* (wild turkey; OUVC 10610) showing arteries and veins highlighted using the differential contrast dual vascular injection technique. Veins were injected with a less concentrated barium solution, resulting in a region with less intensity in the CT scan slice, see VRCeph. The arteries were injected with a solution containing a higher concentration of barium, resulting in a more intense region in the CT scan slice, see aRO. D indicates dorsal and R indicates right side. The inset shows a transparent skull and vascular isosurface rendering to indicate slice location and orientation. See Abbreviations for vessel names.

delawarensis (ring-billed gull), and *Gallus gallus* (domestic chicken) were observed to record vascular osteological correlates (Witmer, 1995a) and include a wider taxonomic sample (Fig. 4). Vascular nomenclature primarily follows Baumel's (1993) vascular system chapter in *Nomina Anatomica Avium*. When nomenclature pertaining to specific sub-segments of blood vessels are necessary (as noted in the text), Sedlmayr (2002) is followed. Blood vessels will be described within three specific regions of the head, termed sites of thermal exchange, consisting of the nasal, oral, and orbital regions.

RESULTS

Detailed vascular anatomy will be described within known sites of thermal exchange in birds: the oral, nasal, and orbital regions. The blood vessels of each region will be reported in the context of anastomotic connections to other blood vessels (both within and between sites of thermal exchange), collateral blood supply and drainage pathways, and blood flow to and from the RO and neurosensory tissues (e.g., brain and eye). The major blood vessels that supply or drain the head will not be discussed in great detail, as these anatomical details have been well reported elsewhere in the literature. These larger blood vessels are mentioned in the context of smaller blood vessels branching from or draining into them. The course of each blood vessel is related to nearby bony landmarks and special attention is given to vascular osteological correlates. The arteries and the veins are described based on the direction of blood flow (i.e., arteries in a caudal to rostral direction and veins rostral to caudal).

Orbital Region

Overview. The main arterial blood supply to the orbit is through the terminal branches of the stapedial artery, which is itself a branch of the internal carotid artery.

Arteries. The temporoorbital artery (the rostral continuation of the external ophthalmic artery [Midtgård, 1984a,b; Baumel, 1993]), a branch of the stapedial artery, supplies the orbit by ramifying into the infraorbital, ophthalmotemporal, and supraorbital arteries. These arteries share several anastomotic branches with encephalic and nasal region arteries. Collateral routes of blood supply to the orbit are through the sphenopalatine, sphenomaxillary, and orbital arteries, which are branches of the cerebral carotid artery.

Veins. The veins of the orbit follow the respective arteries of the same name. The ophthalmic vein, a large vein in the medial aspect of the orbit receives the ethmoid, ophthalmotemporal, and orbital veins, and then drains into the maxillary vein to form the rostral cephalic vein (Midtgård, 1984b; Baumel, 1993). The ophthalmic vein is thought to contain smooth muscle fibers that allow for venodilation (Midtgård, 1984b) to direct blood through the orbit and to the brain or RO. Routes of venous blood through the orbit have direct access to the dural venous sinuses, the RO, or the rostral cephalic vein.

Supraorbital artery (Figs. 5-9). In Galliformes, the supraorbital artery branches from the profundus artery (Sedlmayr, 2002) on the rostrodorsomedial aspect of the RO, medial to the postorbital process, along the caudolateral aspect of the orbit. The supraorbital artery takes a tortuous course along the dorsal aspect of the orbit, within the suture between the frontal and laterosphenoid bones, often creating osseous grooves along its course. In dry skulls of great horned owls, woodcocks, and ostriches, most of the course of the supraorbital vessels can be demonstrated with osseous grooves. Next, the supraorbital artery courses rostrodorsomedially and anastomoses with the ethmoid artery once the latter traverses the ethmoid foramen into the orbit (Baumel, 1975, 1993; Sedlmayr, 2002). The supraorbital artery contributes branches that pass dorsally through foramina and/or wrap around the dorsolateral edge of the frontal bone (passing through the supraorbital membrane), where they then exit onto the dorsal surface of the frontal to supply the skin (Baumel, 1975). These branches often leave discernible grooves on the dorsal surface of the frontal bone in dry skulls. In turkeys and chickens, so many blood vessels pass through the supraorbital membrane near the edge of the frontal bone and onto its dorsal aspect that the dorsal margin of the orbit is highly rugose, and in some specimens a large notch was formed. In dry skulls of Laysan albatross, loon, and Adelie penguin, numerous foramina in the frontal transmitted blood vessel into the dorsally located fossa



Fig. 3. *Meleagris gallopavo* (wild turkey; OUVC 10603) in lateral and ventral views and *Phalacrocorax auritus* (wild cormorant; OUVC 10645) displaying blood vessels within sites of thermal exchange (oral, nasal, and orbital regions). Each taxon displays high degrees of vascularization in the orbital region, showing the ophthalmic rete, a known

heat exchanger. The turkey displays a high degree of vascularization in the nasal and oral regions as well, with plexuses in the nasal region and palate. The cormorant shows a reduced nasal region and modified nasal vasculature. The different colors of the turkey arteries indicate individual named blood vessels.



Fig. 3-D1. A 3-Dimensional model of the skull and blood vessels of a turkey. To activate the model, click on the turkey skull in the center of the page. The model can then be freely manipulated and structures can be rendered transparent by right clicking the object. The names of the blood vessels can be found simply by clicking on them and reading the bolded name at left in the Model Tree. In the center of the Model Tree, on the left side of the page, a list of clickable views that

housing the salt gland. These vessels supply the salt gland, along with anastomotic branches from the facial artery, via the rostral and dorsal palpebral branches. In Galliformes, the supraorbital arteries are known to give branches that supply the lacrimal gland and extrinsic eye muscles (Baumel, 1975, 1993; Sedlmayr, 2002). In cormorants, the supraorbital artery sends a single branch that wraps around the frontal and ramifies across its dorsal surface, supplying the skin and anastomosing with the rostral palpebral artery.

Infraorbital artery (Figs. 5–9). The infraorbital artery branches off from the temporoorbital artery in a rostroventral direction and receives numerous anastomotic connections along the rostroventral edge of the RO, which can give the appearance that the artery is a coalescence of RO arteries. The infraorbital artery courses rostrally to supply the ventral and anterior aspect of the eyeball in ducks (Hossler and Olson, 1984) and the lower eyelid in chickens (Baumel, 1975). This artery left no discernible osteological correlates in the specimens observed.

Ophthalmotemporal artery (Figs. 5-9). Along the rostromedial border of the RO in Galliformes, the ophthalmotemporal artery branches off from the profundus artery along with the supraorbital artery. The ophthalmotemporal artery then turns dorsally for a short distance, and then quickly turns ventromedially along the caudal aspect of the orbit, closely appressed to the laterosphenoid. The artery then passes between the dorsal and lateral rectus muscles (SedImayr, 2002). The artery then courses ventral to the optic nerve and along the medial aspect of the eyeball (Baumel, 1975, 1993). The artery gives off branches that supply the medial aspect of the eyeball, including the choroid and ciliary will orient the model to the same position as the figures found in the text. To open Fig. 3-D1 in a floating window that will remain open throughout the document, after the 3D PDF is activated (click to activate), right click (or control-click) on the model, then click View in Floating Window. The 3D PDF will remain open in a resizable floating window as the user advances through the pages.



Fig. 4. Phylogenetic relationships of all birds sampled for this study. Modified from Jarvis et al. (2014). Key: (i) indicates birds that were injected with a barium-latex solution and CT scanned; (b) indicates bony specimens that were investigated using dried skulls.

capillary beds, as well as the pecten (Hossler and Olson, 1984). On both the rostral and caudal aspect of the optic nerve, the ophthalmotemporal artery receives PORTER AND WITMER



Fig. 5. *Meleagris gallopavo* (wild turkey; OUVC 10599) in left rostrolateral view displaying arteries of the orbital region. The major arteries of the orbit are the supraorbital, infraorbital, ophthalmotemporal, and intramandibular arteries. The anastomotic connections between the ophthalmotemporal and ethmoid arteries and the orbital and ophthal-

motemporal arteries are thought to aid in brain cooling, yet these connections are fairly small. An anastomotic connection found between the rete ophthalmicum and the rete auricularis, may allow both the RO and RA to supply blood to the orbit. See Abbreviations for vessel names.

anastomotic connections (Figs. 5 and 6). On the caudal side, it anastomoses (Fig. 6B) with the small orbital artery (Sedlmayr, 2002) and, on the rostral side of the optic nerve, it receives a branch from the ethmoid artery (Fig. 6C). The orbital artery (internal ophthalmic artery of Baumel, 1993) in turkeys, pheasants, cormorants, and ostriches was a small branch of the cerebral carotid artery that branches off within the pituitary fossa as the cerebral carotid turns dorsally and before the gives off the rostral and caudal cerebral arteries. This artery is present in chickens (Sedlmayr, 2002; Baumel, 1975, 1993), ducks (Hossler and Olson, 1984), and gulls (Midtgård, 1984a), and in all specimens the artery passes through the internal ophthalmic foramen ventrolateral to the optic foramen. Once it exits the foramen, the orbital artery anastomoses with the ophthalmotemporal artery caudal to the optic nerve.

The anastomosis between the ophthalmotemporal artery and the ethmoid artery can include multiple arteries in turkeys, pheasants, chickens (Baumel, 1975, 1993), ducks (Hossler and Olson, 1984; Sedlmayr, 2002), and gulls (Midtgård, 1984a). In turkeys and chickens, the anastomotic connection branches off in a dorsoventral direction; the ventral connection is just rostral to the optic nerve, and the dorsal part anastomoses with the ethmoid artery caudal to the anastomosis between the supraorbital and ethmoid arteries (Baumel, 1975, 1993; Sedlmayr, 2002). In cormorants, this branching pattern was different from that in turkeys and pheasants in that the ethmoid artery did not exit the endocranial cavity through a named foramen, but rather through a membrane covered, large osseous opening in the rostral wall of the braincase surrounding the unfused laterosphenoid bones (Fig. 8) The ethmoid artery gives off the single anastomotic branch to the ophthalmotemporal artery in a rostroventrolateral direction. Loons demonstrated a similar vascular pattern, and the rostral wall of the braincase is more complete, but the ethmoid artery still passes through a large opening found just dorsal to the optic nerve.

Ophthalmic vein (Figs. 10 and 11). The ophthalmic vein forms caudal to the olfactory foramen with the union (Fig. 11A) of the ethmoid and supraorbital veins (Fitzgerald, 1969; Baumel, 1975). In turkeys, pheasants, and chickens (Baumel, 1975) a tributary of this vein passes through an unnamed foramen caudodorsal to the olfactory foramen and dorsal to the ethmoid foramen and passes into the endocranial cavity to anastomose with the olfactory venous sinus, and ultimately the dorsal longitudinal sinus. The ophthalmic vein then takes a sinusoidal course ventrally, along the medial aspect of the



Fig. 6. Left lateral view of a turkey diagrammatically showing the arteries of the head. (A) Anastomosis between the ethmoid and supraorbital arteries. (B) Anastomosis between the orbital and ophthalmotemporal arteries. (C) Anastomosis between the ophthalmotemporal artery and a branch from the ethmoid artery. (D) Anastomosis between

laterosphenoid, passing between the dorsal and medial rectus muscles (Fitzgerald, 1969; Baumel, 1975). The vein then passes caudal to the eyeball, rostral to the optic nerve, and receives the ophthalmotemporal and ciliary veins (Fig. 11B) that drain the eyeball (Fitzgerald, 1969; Baumel, 1975) and ventral rectus muscle (Sedlmayr, 2002). The ophthalmic vein then courses ventrally between the lateral and ventral rectus muscles (Sedlmayr, 2002). The ophthalmic vein curves caudally and passes lateral to the parasphenoid rostrum and dorsal to the ptervgoid bone, where it joins the maxillary vein.

Ophthalmotemporal vein (Figs. 10 and 11). The ophthalmotemporal vein courses in close opposition to the ophthalmotemporal artery and anastomoses with the venous component of the RO along its medial aspect. The ophthalmotemporal vein anastomoses with the ophthalmic vein (Fig. 11B) about halfway along its length and ventral to the optic nerve. A variable tributary of the ophthalmic vein was found to join the ophthalmotemporal artery and vein just dorsal to the optic nerve. This condition results in the ophthalmotemporal artery being in close apposition to a vein on both its dorsal and ventral aspects. This condition was not noted in ducks (Midtgård, 1984b), gulls (Midtgård, 1984a), quail (Fitzgerald, 1969), or turkey vultures (Arad et al., 1989), but was noted in chickens (Baumel, 1975; Ghetie, 1976) and helmeted guinea fowl (Crowe and Crowe, 1979) where it was called the temporal ophthalmic vein or the recurrent temporal ophthalmic vein. Crowe and Crowe (1979) noted that this situation provides two anastomotic connections from the ophthalmic vein to the RO.

the caudal ventral nasal artery and the medial nasal arteries. (**E**) Anastomosis between the rostral ventral nasal artery and the lateral nasal artery. (**F**) Anastomosis between the caudal ventral nasal artery and the sphenopalatine arteries. See Abbreviations for vessel names.

Ghetie (1976) also noted this condition, but named both veins the ophthalmotemporal vein.

Orbital vein (Fig. 11). The orbital vein is a small tributary of the ophthalmotemporal vein (Fig. 11C) that passes through the internal ophthalmic foramen (Midtgård, 1984a) and drains into the cavernous sinus (Fig. 11D).

Supraorbital vein (Figs. 10 and 11). The supraorbital vein parallels the tortuous course of the supraorbital artery from the union of the ethmoid and ophthalmic veins to the RO. The supraorbital vein enters the venous component of the RO lateral to the supraorbital artery. The vein travels along the dorsal aspect of the orbit, rostral to the artery. In a specimen of *wild turkey* (OUVC 10610), the supraorbital vein passed rostral to the supraorbital artery and caudal to the branches of the supraorbital artery that course laterally along the frontal. In cormorants, the supraorbital vein receives a large tributary that wraps around the caudodorsal aspect of the frontal. This vein drains the skin of the dorsal aspect of the head.

Infraorbital vein. The infraorbital vein courses closely apposed to the infraorbital artery. The infraorbital artery is a tributary of the profundus vein dorsal to the orbital process of the quadrate.

Suprapalatine vein (Fig. 10). The suprapalatine vein (Ghetie, 1976) is a vein that courses from the rostrodorsomedial aspect of the orbit, where it is a tributary of the nasal vein, to the caudoventral aspect of the orbit

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Fig. 7. *Phalacrocorax auritus* (wild cormorant; OUVC 10645) in right ventrolateral view showing arteries of the orbit and palate. The palatine arteries do not branch into medial and lateral branches and course dorsal to the palatal process of the premaxilla and maxilla. The left palatine artery was found to be more robust than the right in both

where it joins with the rostral cephalic vein rostral to the ophthalmic vein. This vein was found only in turkeys and Ghetie (1976) named it the suprapalatine vein. This vein has the potential to drain venous blood from the nasal region, straight to the jugular and completely bypass the orbital veins.

Stapedial artery in regards to the rete ophthalmicum (Figs. 1 and 6). The stapedial artery branches from the internal carotid artery in the parabasal fossa and enters the stapedial canal (Figs. 1 and 6). Within the canal, the artery courses dorsal to the tympanum and exits into the temporal fossa. The artery then passes medial to the capitulum of the quadrate and through the cranioquadrate canal. The stapedial artery gives off a dorsally directed branch, an occipital artery (Baumel, 1993), and continues rostrally as the temporoorbital artery (Sedlmayr, 2002). Four large arteries that supply the orbital region branch off from the temporoorbital artery within the substance of the RO (Figs. 6 and 9). The caudal border of the RO is found in the caudolateral aspect of the orbit along the rostral border of the otic process of the quadrate and

cormorants with an arterial injection. A plexus found lateral to the choana branches from the palatine artery and anastomoses with the arteries of the nasal region. Inset above indicates view for image below. See Abbreviations for vessel names.

the rostral face of the laterosphenoid, medial to the postorbital process.

Arterial component of the rete ophthalmicum (Fig. 9). Most of the blood passing through the RO supplies the eyeball and associated tissues (Ninomiya, 2002). This vascular physiological device has been the subject of much scrutiny regarding avian brain cooling. In Galliformes (Fig. 9A), all of the arteries forming the RO are ultimately branches of the temporoorbital artery, the rostral branch of the stapedial artery, although other anastomotic connections (e.g., with the sphenomaxillary artery) that could supply the RO have been found, confirming Baumel's (1975) identification of this condition in chickens. After entering the temporal fossa, the temporoorbital artery bifurcates into the intramandibular and profundotemporal arteries (Sedlmayr, 2002) at roughly a 45° angle. The intramandibular artery courses rostroventrally and passes rostral to the orbital process of the quadrate. The profundotemporal artery gives off the lateral temporal artery and continues rostrally as the profundus artery (Sedlmayr, 2002). The profundus artery

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Fig. 8. *Phalacrocorax auritus* (wild cormorant; OUVC 10645) in left lateral view displaying arteries found within the orbital region. Cormorants show an arterial branching pattern similar to Galliformes, yet the rostrocaudal length of the RO is much longer. Inset above indicates enlarged region for region below. See Abbreviations for vessel names.

courses rostrodorsally and is the main artery passing through the RO and it also acts as a bypass of the RO arteries (Ninomiya, 2002). Most of the arteries forming the RO were found to occur as branches passing between the ventrolateral aspect of the profundus artery to the intramandibular arteries and the anastomotic connection from the auricular rete (RA). A few of these branches pass dorsal to the profundus artery along its lateral aspect. Rostrally, the supraorbital artery branches from the profundus artery and takes a dorsal course along the rostroventral aspect of the laterosphenoid. The supraorbital artery contributes a few arteries that anastomose with the profundus artery and the anastomotic connections of the RA. After the bifurcation of the profundus artery into the supraorbital and ophthalmotemporal arteries, the latter makes a sharp turn medially and then, after a short distance, turns dorsally to pass ventral to the lateral rectus muscle. The ophthalmotemporal artery does not give off any arteries after the medially directed sharp turn. The infraorbital artery branches off from the temporoorbital artery and shares numerous anastomotic connections with RO arteries.

In ostriches (Fig. 9B), the morphology of the RO shares the basic patterns of turkeys and pheasants but with some key differences. The numerous arteries forming the RO ramify laterally from the lateral aspect of the profundus artery, sending few anastomotic branches to the infraorbital artery. The profundus artery courses rostrodorsally, similar to the galliform sample, but when the supraorbital artery branches off along a nearly dorsal course, the ophthalmotemporal artery makes a sharp turn ventromedially and then makes another, more gradual turn in a more medial direction. Between these curves, the arteries of the RO coalesce to become three large arteries. In the case of an ostrich specimen (OUVC 10519), these arteries anastomoses with the arteries of the RO. The supraorbital and infraorbital arteries send few arteries into the RO in the ostrich sample.

In the sampled cormorants (Fig. 9C), the RO was found to be greatly elongated when compared to turkeys (Fig. 3). The arterial branching patterns were very similar to those of the turkey and pheasant, but the relative rostrocaudal length of the RO was much greater. Cormorants are underwater pursuit predators and have evolved highly developed jaw musculature (Goodman and Fisher,



Fig. 9. (A) Medial view of the RO of *Meleagris gallopavo* (wild turkey; OUVC 10599), (**B**) *Struthio camelus* (captive ostrich; OUVC 10519), (**C**) *Phalacrocorax auritus* (wild cormorant; OUVC 10645), (**D**) *Gavia immer* (wild loon; OUVC 10462) displaying branching patterns. All of the efferent vessels of the RO supply the eyeball and other orbital tissues. Inset indicates direction and taxon for each rete figured. See Abbreviations for vessel names.

1962; Owre, 1967). The jaw adductor musculature became so enlarged that the caudal portion of the adductor mandibulae externus muscle attaches to the occipital style, a neomorphic bone projecting caudally from the occiput (Goodman and Fisher, 1962). This elongation is likely due to the evolution of increased jaw musculature.

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In the loons (Fig. 9D) and kingfisher sampled, the RO was elongate when compared to turkeys, but not to the extent observed in cormorants. Instead of giving off

arteries laterally from the profundus artery, they branch in a ventral direction and anastomose with the infraorbital artery. These arteries then coalesce and anastomose with the ophthalmotemporal artery as it curves ventrally to course along the caudal aspect of the orbit. These branching patterns have also been seen in night herons (Ninomiya, 2002), mallards (Midtgård, 1984b), and, according to Kilgore et al. (1976), in roadrunners, lesser nighthawks, pigeons, white-necked ravens, and mallards.



Fig. 10. *Meleagris gallopavo* (wild turkey; OUVC 10610) in left lateral view. (**A**) Anastomotic connections between the frontal vein and rete auricularis. Veins from within the eyelid, a potential site of thermal exchange, also drain into the RO and RA. (**B**) Veins of the orbit with scleral ossicle removed. The venous drainage of the orbital region dis-

plays numerous anastomotic connections that would allow blood to flow through the ophthalmotemporal vein and then potentially to the eye, brain, rete ophthalmicum, and auricular rete. See Abbreviations for vessel names.

Venous component of the rete ophthalmicum (Figs. 2–11). In pheasants and turkeys, the named tributaries of the RO closely followed arteries with the same name. Once the named veins enter the RO, they ramify into numerous veins that anastomose so often that determining the course of these veins within the RO was challenging. The ophthalmotemporal vein enters the RO along its rostromedial pole, medial to the lacrimal gland, where it ramifies. The veins draining the lacrimal gland drain into the ophthalmotemporal veins, giving the rostral aspect of the RO a large appearance on μ CT scans. The supraorbital vein passes caudomedial to the lacrimal

gland, receiving veins from it, and then continues to ramify into veins that join with the ophthalmotemporal veins. The veins from the RA enter the RO ventral to the lacrimal gland and ramify into veins that anastomose with the RO (Fig. 10). This highly anastomotic venous component of the RO courses caudally, mostly lateral to the arterial component of the RO (Sedlmayr, 2002) although the arteries and veins intermingle, making descriptions of relative locations somewhat imprecise.

The venous component of the RO is drained by two veins, the stapedial vein and an unnamed vein that is a tributary of the maxillary vein. The stapedial vein



Fig. 11. Left lateral view of a turkey showing the diagrammatic veins of the head. (A) Anastomosis between the ethmoid and nasal veins. (B) Anastomosis between the ophthalmic and ophthalmotemporal arteries. (C) Anastomosis between the ophthalmotemporal and orbital veins. (D) Anastomosis between the orbital vein and cavernous sinus.

(E) Anastomosis between the caudal ventral nasal vein and the medial nasal vein. (F) Anastomosis between the rostral ventral nasal artery and the lateral nasal veins. Pink dots indicate locations of smooth muscle in the ophthalmic vein found by Midtgård (1984b). See Abbreviations for vessel names.

parallels the stapedial artery through the stapedial canal, to drain into the maxillary vein (Baumel, 1975). The unnamed vein courses along the ventral aspect of the venous component of the RO, then curves in a rostroventromedial direction to anastomose with the lateral aspect of the maxillary vein, just rostral to the location where it accepts the ophthalmic vein. Another tributary of the venous component of the RO is the transversooccipital sinus (caudal petrosal sinus of Kaku [1959] and Baumel [1993]). Sedlmayr (2002) described the profundus vein in birds traveling through the "middle meningeal" foramen to connect to the cerebrotectal sinus (sphenotemporal sinus of Baumel [1993]). This condition was found in turkeys and pheasants, although this connection could not be verified in cormorants.

In cormorants, the venous component of the RO has fewer, larger-diameter veins than those found in the Galliformes sample. This may have consequences for heat transfer between the arteries and veins. Ventral to the frontal portion of the postorbital process, the ophthalmotemporal vein courses laterally and makes a caudal turn. At this location, the ophthalmotemporal vein accepts the dorsal palpebral vein. In turkeys and pheasants, the dorsal palpebral vein is a tributary of the auricular rete (Fig. 10). The ophthalmotemporal vein also accepts the supraorbital vein at this location. The ophthalmotemporal vein ramifies into about a dozen anastomosing veins that form the RO. These veins course caudally to coalesce into the stapedial vein and enter the cranioquadrate passage and, farther caudally, the stapedial canal. Loons had a similar morphology to cormorants, with the major difference being the rostrocaudal length. The loon rete was much shorter and had an increased dorsoventral length. There were numerous fine veins that were arranged in a dorsoventral stack.

Auricular rete (Figs. 5-10). Another rete mirabile, the auricular rete (RA), was figured by Neugebauer (1845) and Ghetie (1976) in turkeys and was described by Sedlmayr (2002) as the postorbital plexus in chickens. The RA was found in pheasants and in a much reduced form in loons. In the galliform sample, the auricular rete was found lateral to the guadrate, and potentially supplied the RO in a parallel manner. The arterial supply to the RA stems from the external carotid artery by the branching of the rostral auricular artery. This artery courses rostrally and curves around the caudal aspect of the quadrate. The artery then ramifies into a rete lateral to the quadrate. Along the ventral border of the RA, the facial artery (palatomaxillary of Sedlmayr [2002]) sends fine branches that anastomose with the RA. The number of anastomotic connections was found to be higher in pheasants than in turkeys. Rostrally, the arteries coalesce into a single vessel that curves around the lateral aspect of the postorbital process, then turns medially to anastomose with the RO. The venous blood supply to the RA originated within the eyelids (Fig. 10). The dorsal and ventral palpebral veins course through the eyelids, which are important sites of thermal exchange (Bernstein et al.,

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Fig. 12. *Meleagris gallopavo* (wild turkey; OUVC 10599) in ventral view. Inset with red arrow indicates direction of view. The palatine artery branches into a medial and lateral branch that give off numerous anastomotic connections between them, creating a large plexus and surface area for thermal exchange. See Abbreviations for vessel names.

1979a; Pinshow et al., 1982; St-Laurent and LaRochelle, 1994), and drain into the rostral pole of the RA.

Summary of the orbital region. The orbital region could be the most important region for the avian physiological thermoregulatory strategy, as it could direct both arterial and venous blood flow into the dural sinuses or the RO. The arteries of the orbital region are thought to provide cooled blood from the RO to the encephalic arteries through the orbital and ethmoid arteries (Arad et al., 1987; Arad, 1990; Midtgård, 1984a,b; Richards, 1970). The venous drainage of the orbit receives the ethmoid vein from the nasal region, where it drains into the ophthalmic vein and dural sinuses. The ventral portion of the ophthalmic vein has the possibility to drain cooled blood from the orbit and the nasal region dorsally through the skull and into the dural venous and cavernous sinuses or laterally into the RO.

Oral Region

Overview. The vascular anatomy of the palate is well known in the literature (Ghetie, 1976; Midtgård, 1984b; Baumel, 1975, 1993; Sedlmayr, 2002), and the importance of the oral vasculature in thermoregulation has been shown by multiple studies using pigeons (Bernstein et al., 1979a; Peltonen, et al., 1989; St-Laurent and LaRochelle, 1994) and mallards (Hagan and Heath, 1980).

Arteries. The arterial supply to the palate is via the external carotid arteries and its branch, the palatine artery. The palatine artery in Galliformes splits into medial and lateral palatine arteries, with numerous branches spanning between them. In other birds, like cormorants, the palatine arteries do not bifurcate into medial and lateral branches. The palatine arteries show anastomotic connections to the nasal cavity through the rostral and caudal ventral nasal arteries. The palatal region can receive collateral blood flow from the cerebral carotid artery via the sphenopalatine and sphenomaxillary arteries.

Veins. The veins of the palate follow the arteries of the same name and share connections to the nasal region through the rostral and caudal ventral nasal veins.

Palatine arteries (Figs. 3–13). Blood supply to the palate is mainly supplied by the external carotid artery, with collateral supply from the cerebral carotid arteries. In turkeys and pheasants, the common carotid artery ramifies into internal and external carotid arteries ventrolateral to the occiput and m. rectus capitis ventralis and medial to m. depressor mandibulae. Just rostral to this bifurcation, the external carotid artery gives off the oromandibular artery rostroventrally and the occipital artery caudodorsally, all in close proximity to each other (Baumel, 1975, 1993; Sedlmayr, 2002). After the external carotid gives off the oromandibular PORTER AND WITMER



Fig. 13. *Phalacrocorax auritus* (wild cormorant; OUVC 10645) in left lateral view, with semitransparent skull showing arteries of the nasal region. Despites the nasal region being highly reduced, the blood vessels within show conserved patterns, yet cormorants show an apo-

morphic condition with rostral and caudal sections of the medial and lateral nasal vessels. The arterial plexus found along the lateral aspect of the choana can be seen. Inset indicates region of magnification in the lower image. See Abbreviations for vessel names.

artery, the rostrally directed continuation of the external carotid artery is named the maxillary artery (Baumel, 1975, 1993). The maxillary artery courses rostrally along the ventral surface of the palatine bone and bifurcates lateral to the choana into the medial and lateral palatine arteries (Baumel, 1975, 1993; Midtgård, 1984a,b). The medial and lateral palatine arteries pass along the palatine bones and anastomose ventral to the premaxilla to form the median palatine artery ventral to the premaxilla (Baumel, 1993). Numerous submucosal ramifications were seen anastomosing between the medial and lateral palatine arteries, increasing the surface area of blood vessels within the palate, facilitating thermal exchange (Midtgård, 1984b). In mallards, Midtgård (1984b) described these anastomoses between the medial and lateral palatine arteries, but made no mention of the extent to which these anastomoses occur in Galliformes.

Medial to the nasal process of the maxilla, the median palatine artery send a dorsally directed branch, the caudal ventral nasal artery (Fig. 6D), that initially courses in a caudodorsal direction, then curves sharply rostrally along the ventral aspect of the middle concha. This artery anastomoses with both the medial and lateral nasal arteries within the nasal region. Rostral to the formation of the median palatine artery, the rostral ventral nasal artery branches in a dorsal direction that initially courses in a rostrodorsal direction. This artery anastomoses with the dorsal and ventral branches of the lateral nasal artery and sends a rostrally directed branch that courses through the premaxilla, to supply the rhamphotheca (Midtgård, 1984b).

The arteries of the palatal region in cormorants (Fig. 13) display a more conservative condition when compared to Galliformes. The maxillary artery travels rostrally along the ventral surface of the large m. pterygoideus ventralis and caudal to the choana, where it curves dorsally to assume a position just ventral to the palatine-maxilla articulation. The palatine artery fails to divide into medial and lateral branches, similar to mallards (Midtgård, 1984b), and, in two arterially injected specimens (OUVC 10401, 10645), the right palatine artery was reduced compared to the left. Lateral to the choana, the palatine artery sends numerous dorsally directed fine branches along the lateral aspect of the airway instead of a single caudal ventral nasal artery. The two palatine arteries unite and form the median palatine artery, which then travels dorsal to the palatal process of the maxilla through a foramen located between the palatine bones. The foramen transmitting the palatine arteries was offset to the left side in many dry cormorant skulls, possibly reflecting the dominance of the left palatine artery. The median palatine, the union of the right and left palatine arteries, continues rostrally, where it anastomoses with the lateral nasal artery. The median palatine artery sends branches to the palate through dorsoventrally oriented canals in the maxilla.

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Fig. 14. *Meleagris gallopavo* (wild turkey; OUVC 10610) in ventral view showing veins of the palate. The maxillary vein receives the lateral palatine vein as a tributary, and the medial palatine vein is received by the veins accompanying the maxillary artery. These veins

show numerous anastomotic connections, creating a large plexus and surface area for thermal exchange that are in close contact with the palatine arteries, allowing thermal exchange or the establishment of a thermal gradient. See Abbreviations for vessel names.

These arteries exit the canals along the medial side of the medial ridge and form laterally directed grooves in the bone. These arteries may be the remnants of a palatal plexus that provide nourishment to the keratinous palatal region. Herons, loons, and albatross show osseous grooves indicating the presence of a plexus that may be more for the nourishment of the rhamphotheca than for heat exchange, although toucans can shed heat through a keratinous bill by adjusting the blood flow deep to it (Tattersall et al., 2009), so these plexuses may still serve a thermoregulatory role.

In loons, the arteries of the palate showed patterns similar to both cormorants and Galliformes. The palatine artery branches into a robust medial palatine artery and a much smaller lateral palatine artery that is located ventral to the palatine veins. The medial palatine arteries course rostrally just ventral to the palatine bones as two closely apposed vessels that unite into a median palatine artery about halfway between the naris (we follow Clark [1993] for use of the term naris for the fleshy nostril) and the choana. The lateral palatine arteries did not participate in the formation of the median palatine artery. The lateral palatine arteries continue rostrally, beyond the formation of the median palatine artery and course along the medial edge of maxillapremaxilla articulation. The median palatine artery courses rostrally and continues to send numerous anastomotic branches to the lateral palatine artery forming a palatal plexus similar to that in Galliformes that extends the entire length of the palate from the tip of the bill to the choana.

Sphenomaxillary and sphenopalatine arteries (Figs. 5-12). The sphenomaxillary and sphenopalatine arteries (Baumel 1967, 1975, 1993; Sedlmayr, 2002) are anatomically positioned to provide collateral blood supply to the palate. These two arteries travel though the rostral and caudal orbital canals lateral to the base of the parasphenoid rostrum (Baumel, 1993) in chickens (Sedlmayr, 2002), turkeys, and pheasants. The sphenopalatine artery branches off from the cerebral carotid and courses through the caudal orbital canal, travels ventrolaterally along the parasphenoid rostrum, then rostroventrally to the pterygoid-basipterygoid articulation, often leaving a groove (Sedlmayr, 2002). The artery then courses medially between the pterygoid and palatine bones, to anastomose with both the medial palatine artery and its caudal ventral nasal ramus. The sphenomaxillary artery then passes medial to the maxillary vein (Midtgård, 1984b; Sedlmayr, 2002) and dorsal to the pterygoid bone, then dorsolateral to the palatine bone, and ventral to the eyeball. The sphenomaxillary artery then anastomoses with the maxillary artery just caudal to its bifurcation into the palatine arteries.

Veins of the palatal region (Fig. 14). In the Galliformes sample, the medial and lateral palatine veins course through the palate in close apposition to their corresponding arteries. Similar to the arteries, the veins send numerous anastomotic connections between each other, and a few to the facial vein. The lateral palatine vein courses caudally to anastomose with the lateral nasal vein, just caudal to the maxillary process of the

nasal. It then courses ventrally to the antorbital sinus. Within the rostroventral orbital region, the palatine vein receives a tributary from the facial vein to form the maxillary vein (Baumel, 1975, 1993). The medial palatine vein courses caudally just ventral to the palatine bone and forms the venae comitantes of the maxillary artery (Fig. 14). These continuations of the medial and lateral palatine veins course caudally along the medial and lateral aspect of the maxillary artery, respectively. The two large veins of the venae comitantes of the maxillary artery drain into the rostral cephalic vein separately, just rostral to the interjugular anastomosis, with the lateral vein entering more caudally than the medial vein (Baumel, 1993). This condition bypasses the RO and prevents temperature-regulated (cooled) blood from the palatal region from reaching the RO.

Midtgård (1984b) reported that in order for blood from the palate to have any influence on brain temperature, it must be shunted through the nasal cavity. This alternative pathway, which Midtgård (1984b) reported and Baumel (1975) mentioned in one sentence, is via branches from the palatine veins that direct venous drainage into the medial and lateral nasal veins. Blood from the palatal region can then pass through the nasal cavity and into the orbit. The medial palatine vein shares an anastomotic connection that ultimately anastomoses with the lateral nasal vein just caudal to the naris. This vein passed ventrolateral to the middle concha, then medial to the antorbital sinus and dorsal to the nasal process of the maxilla. The lateral palatine vein also accepts a large anastomotic connection with the lateral nasal vein through a laterally directed branch of the ventral branch of the nasal vein (Baumel, 1975), providing multiple drainage pathways between the nasal cavity and palatal region.

In cormorants, the jugular anastomosis accepts the common rostral cephalic vein. Just rostral to this union, the maxillary vein courses rostrally for a short distance before it ramifies into two or three veins that accompanied the maxillary artery. These veins anastomose along the ventral surface of m. pterygoideus ventralis to travel as a single vein dorsomedial to the palatine artery. Rostral to m. pterygoideus ventralis, the palatine vein crosses dorsal to the palatine bone to course along the midline of the maxilla. Caudal to the choana, the palatine veins course caudally just ventrolateral to the palatine bones, then dorsal to the keratinous palate, creating grooves along the medial ridge of the maxilla.

In loons, the veins showed patterns similar to those found in the Galliformes sample. The palatine veins are located dorsolateral to the palatine arteries and have numerous anastomotic connections between the medial and lateral palatine veins. These anastomotic connections were found to be in close apposition to the arteries of the palate. Similar to the Galliformes samples, the medial palatine vein continues caudally as a tributary to the rostral cephalic vein and the lateral palatine veins course along with the maxillary veins as venae comitantes.

Summary of the oral region. The arteries of the oral region directly supply the tissues of the palate and have connections to the nasal region. The palatine veins

may also drain blood to the nasal region, where cooled blood can enter pathways to neurosensory tissues. The most direct route of venous drainage, however, is through the rostral cephalic vein. Midtgård (1984b) showed that smooth muscle fibers in the maxillary vein (Fig. 11) could venoconstrict, which would force blood through the nasal region. If this were to happen, blood cooled in the palatal region would pass into the nasal region and the two regions would function as heat exchangers in series.

Nasal Region

Overview. The nasal region was found to be highly derived in some of the taxa examined. Despite this disparity, consistent patterns emerged.

Arteries. The avian nasal cavity is supplied by the ethmoid artery, which is a branch of the rostral cerebral artery, and from branches of the palatine arteries (Baumel, 1975, 1993; Sedlmayr, 2002). The ethmoid artery exits the endocranial cavity and enters the dorsomedial aspect of the orbit where it anastomoses with the supraorbital and ophthalmotemporal arteries in the orbit. The ethmoid artery is renamed the common nasal artery after it anastomoses with the supraorbital artery. The common nasal artery bifurcates into medial and lateral nasal branches that pass through the medial and lateral orbitonasal foramina, respectively (Baumel, 1975, 1993; Witmer, 1995b; Sedlmayr, 2002). The medial nasal artery supplies the conchae, and then anastomoses with the caudal ventral nasal artery from the palatine artery. The lateral nasal artery is found outside the nasal cartilages and anastomoses with the rostral ventral nasal artery. Collateral blood supply is from the palatine and sphenopalatine arteries.

Veins. The veins of the nasal region travel closely with their respective arteries. The medial and lateral nasal veins ultimately drain into the ethmoid vein, which anastomoses with the dural venous sinuses at the dorsal aspect of the ophthalmic vein, delivering blood cooled in the nasal region to the encephalic cavity.

Lateral nasal artery (Figs. 6–15). The lateral nasal artery travels along the medial side of the maxillary process of the nasal bone where it bifurcates into dorsal and ventral branches (Baumel, 1975) that arc along the dorsal and ventral aspects of the naris and anastomose with each other rostrally. This conjoined artery then courses medially and anastomoses with the rostral ventral nasal branch of the median palatine artery (Fig. 6E).

Medial nasal artery (Figs. 6–15). In turkeys, the medial nasal neurovascular bundle does not travel through a proper osseous canal within the ectethmoid, contrary to what has been observed in ducks and geese (Witmer, 1995b, Sedlmayr, 2002), because the ectethmoid is poorly ossified in turkeys (Maxwell, 2008). The medial nasal bundle travels in a shallow groove (some taxa have deeper grooves, e.g., gulls) within the mesethmoid, dorsal to the nasal cartilage and dorsomedial to the caudal concha. The medial nasal vessels continue rostrome-dially along the rostral border of the mesethmoid, then



Fig. 15. Dorsomedial view of the left side of a sagittally-sectioned skull of a turkey displaying blood vessels of the nasal region. (A) Anastomotic connections between the nasal and palatal regions would allow the passage of cooled blood from the palatal region to drain

through the nasal region and into the orbital region. (**B**) The nasal cavity is supplied via the ethmoid arteries and rostral and caudal ventral nasal arteries that anastomose with the medial and lateral nasal arteries. See Abbreviations for vessel names.

course rostroventromedially along the nasal septum. The medial nasal artery then sends branches that course ventrally and send numerous branches that supply the rostral and middle conchae. This is similar to the condition found by Sedlmayr (2002) in ducks. These arteries also anastomose with the caudal ventral nasal arteries. The medial nasal artery courses rostrally along the nasal septum and comes into close apposition with its contralateral partner, which creates the dorsal aspect of the anastomosis between the palatine and ethmoid arteries. In turkeys and pheasants, the median palatine artery gives off the rostral ventral nasal branches (Fig. 6E) along its dorsal margin, along the nasal process of the premaxilla. Caudally, the medial palatine artery branches off the caudal ventral nasal arteries caudomedial to the palatine process of the maxilla. Both right and left rostral and caudal ventral nasal arteries travel dorsally in close apposition, appearing as one artery in the µCT scan data, and supply the ipsilateral ventromedial region of the nasal cavity (Midtgård, 1984b). The caudal ventral nasal arteries travel rostrally along the septum of the nasal capsule and then turn sharply caudally about halfway along the nasal septum. Between these two legs of the artery, numerous fine anastomotic connections were found.

Sphenopalatine artery (Figs. 5–15). Anastomotic connections from the sphenopalatine artery have the potential to contribute collateral blood flow to the nasal region. Once the sphenopalatine artery emerges from the caudal orbital foramen, it bifurcates. One branch joins the maxillary artery just rostral to the branching of the facial artery. A second branch proceeds rostrally and joins the caudal ventral nasal branch of the palatine artery (Fig. 6F) and is in a position to supply both the nasal and oral regions. These arteries thus provide the nasal cavity with at least three sources of blood supply: (1) nasal arteries from the palatine artery, and (3) the sphenopalatine artery.

Comparisons of avian nasal vascular anatomy (Figs. 6-15). The arteries of the nasal region of cormorants exhibited a superficially very different vascular morphology than Galliformes, no doubt because of the obliteration of the nostril in cormorants and the concomitant changes in the structure of the nasal cavity (Fig. 13). Despite this disparity, a conserved branching pattern was still detectable. As in the Galliformes sample, the blood supply to the nasal cavity in cormorants originates in the orbital and oral regions, via the ethmoid and palatine arteries. In the rostrodorsal portion of the orbit, the nasal artery courses rostrally along the ventral aspect of the olfactory tract, through the orbitonasal foramen to enter the nasal region. The medial and lateral nasal arteries in cormorants are each separated into two parts, a rostral and caudal branch, joined together by what appears to be the continuation of the large nasal artery. The rostral and caudal branches of each artery cover the same territory of the respective artery in other birds. The nasal artery curves medially around the rostral surface of the mesethmoid and sends a ventrally directed branch, the caudal medial nasal artery, that courses ventrally along the rostral surface of the thin and laterally directed ectethmoid and anastomoses with the sphenopalatine artery just caudal to the nasal cavity. The caudal medial nasal artery sends branches laterally that anastomose with a plexus found along the lateral aspect of the choana. Just slightly rostral to the caudal medial nasal artery, the nasal artery sends a

rather large rostroventrolaterally directed branch that enters the caudodorsal aspect of the nasal gland and supplies it. This artery exits the rostroventral aspect of the gland and begins to ramify into a large plexus covering the ventrolateral aspect of the nasal cavity, the lateral aspect of the choana, and the medial side of the keeled bony palate. Branches of this plexus course rostroventrally, giving off numerous arteries that anastomose with the palatine artery along its ventrolateral surface. Along its rostral aspect, the palatal and choanal plexuses give off a smaller, dorsal branch that courses through the obliterated nostril and anastomoses with branches of the facial artery. Rostral to the caudal medial and lateral nasal arteries, the nasal artery continues rostrally along the dorsal aspect of the olfactory region of the nasal cavity, and, dorsal to the middle concha (Bang, 1971), the nasal artery divides into a ventrally directed rostral medial nasal artery and a rostroventrally directed rostral lateral nasal artery. The medial nasal artery travels ventrally, and at the level of the middle concha, the artery bifurcates into rostrally and caudally directed branches. The caudally directed branch anastomoses with the sphenopalatine artery and contributes to the choanal plexus. The rostrally directed branch of the rostral medial nasal artery sends branches caudally along the lateral aspect of the nasal cavity that anastomose with the palatal and choanal plexuses. This branch is likely the caudal ventral nasal artery branching from the palatine artery, as found in Galliformes. The rostral lateral nasal artery continues rostrally along the suture between the premaxilla and maxilla to anastomose with the palatine artery about halfway along the length of the maxilla. The rostral lateral nasal artery sends a rostrally directed branch before its anastomosis with the palatine artery, the rostral ventral nasal artery, which sends branches into the articulation between the premaxilla and maxilla that course through the bone to supply the tissues of the rhamphotheca. Grooves for these arteries can be found on the lateral surface of these bones. In summary, cormorants have a highly derived nasal cavity anatomy, yet still demonstrate traditional avian vascular patterns. Despite the reduced nasal cavity, the blood vessels that pass through it still have to supply tissues rostrally. In cormorants, the development of an elongate bill and reduced nasal region likely applied disparate pressures on the nasal blood vessels (i.e., supplying a long structure with blood vessels that pass through a reduced structure), which caused the medial and lateral nasal arteries to separate into rostral and caudal branches.

In loons, the vasculature of the airway showed similarities to the vascular patterns found in both turkeys and cormorants, although loons lack the highly reduced nasal cavity of the latter clade. The sphenopalatine artery in loons was found to anastomose with the medial palatine artery along the caudal aspect of the airway. The medial nasal artery is more similar to cormorants in that its course was rostroventrally directed along the nasal septum and anastomoses with the palatine artery, without the rostrocaudal loop of Galliformes. In OUVC 10642, both right and left caudal ventral nasal arteries branched from the left palatine artery, just caudal to the union of the paired palatine arteries into the median palatine artery. Dorsal to the anastomosis with the caudal ventral palatine artery, the medial nasal artery sends a rostrally directed branch that anastomoses with the rostral ventral nasal artery. This condition was not seen in cormorants, but was observed in the Galliformes sample. The lateral nasal artery takes a very similar course in loons as it does in Galliformes. The lateral nasal artery sends a branch that travels ventral to the middle concha and anastomoses with the palatine artery. Rostrally, the lateral nasal artery then branches into dorsal and ventral branches encircle the naris, as in galliforms. These branches anastomose with the rostral ventral nasal artery, again similar to the condition found in the Galliformes sample.

Loons also displayed a vascular feature found in pheasants but not cormorants. The facial artery courses along the dorsal aspect of the jugal, then turns rostrodorsally rostral to the orbit. It then turns rostroventrally to course along the dorsal aspect of the nasal bone and nasal process of the premaxilla, deep to the rhamphotheca. These arteries ramify into a large plexus that covers the entire region between the naris and the orbit, even sending branches ventral to the nasal bones. These arteries anastomose with the lateral nasal arteries and drain into the lateral nasal veins. This may be an emphasized plexus in loons, as it exposes blood vessels close to the skin between the nostril and orbit.

Veins of the nasal region (Figs. 10-15). The medial nasal vein courses along the lateral aspect of the nasal septum and then rostrally along the dorsomedial border of the middle concha. The medial and lateral nasal veins pass into the orbit through the orbitonasal foramina, and then combine to form the common nasal vein just ventral to the frontal and lacrimal joint. It is near this confluence that the rostral and dorsal palpebral veins anastomose with the lateral nasal vein. The lateral nasal vein courses along the lateral aspect of the caudal concha, and anastomoses with the much larger facial vein. Rostral to this anastomosis, the vein splits into dorsal and ventral lateral nasal veins; the dorsal lateral nasal vein is much larger than the ventral branch. The dorsal lateral nasal vein accepts branches from a plexus found between the orbit and the naris, draining the skin in this region.

Ventral to the middle concha, the medial palatine vein sends off a dorsally directed branch, the caudal ventral nasal vein. This vein subsequently bifurcates into two branches that continue into the nasal cavity. One branch courses rostrally, just ventral to the middle and rostral conchae to anastomose with the rostral ventral nasal vein (Fig. 11F). The other branch courses dorsally and anastomoses with veins in the mucosa of the middle concha, and anastomoses with the medial nasal vein along the caudodorsomedial aspect of the middle concha (Fig. 11E). The rostrally directed branch from the caudal ventral nasal vein anastomoses with the rostral branch from the caudal ventral nasal vein, yet, in some turkey specimens, this vein joins the medial palatine vein, and another rostrally directed branch from the medial palatine veins continues rostrally to anastomose with the rostral ventral nasal vein. The rostral ventral nasal vein also accepts the dorsal and ventral branches of the lateral nasal vein. The nasal vein travels through the orbitonasal foramen (Baumel, 1993; Witmer, 1995b; Sedlmayr, 2002) where it travels caudally closely apposed to the ethmoid artery within the orbit to anastomose with the supraorbital vein, ophthalmic vein, and olfactory sinus, a point at which blood can flow into the RO.

The arterially injected loon specimen OUVC 10642 provides insight into a potentially preferred pathway for venous blood flow. The palatine and lateral nasal veins were filled with latex and could be traced back into the orbit, through the ethmoid vein (and hence also into the rostrodorsal cerebral vein), into the ophthalmic vein, and into the RO via the ophthalmotemporal vein. This injection sheds some light on the venous drainage patterns of the nasal cavity in birds, indicating a potential brain temperature influencing pathway from the nasal cavity into the endocranial cavity and RO. This would indicate support for the ability to cool the brain directly from sites of thermal exchange and supply the RO to influence eye temperature, supporting Sedlmayr (2002) and Caputa (2004) that brain cooling may function independently of the RO.

Summary. The blood vessels of the nasal region show a highly conserved pattern, despite the apomorphic nasal cavity morphologies of some species. The nasal artery, the continuation of the ethmoid artery, bifurcates into the intracapsular medial nasal artery and an extracapsular (external to the nasal cartilages) lateral nasal artery. The medial nasal artery anastomoses with the palatine artery through the caudal ventral nasal artery. These conchal blood vessels are in the direct path of airflow, as the conchae are highly vascularized. The lateral nasal artery anastomoses with the palatine artery through the rostral ventral nasal artery, and the medial nasal artery anastomoses with the palatine artery though the caudal ventral nasal artery. The veins of the nasal cavity show a close relationship to their respective arteries, and can be tributaries to both the palatine and nasal veins. This arrangement would allow the veins of the nasal cavity, depending on pressure gradients, to flow into either the palatine veins without affecting neurosensory tissues, or into the dural sinuses and orbit, where there is a potential effect on the temperature of neurosensory tissues.

DISCUSSION

Vascular branching patterns in the heads of birds were found to be very distinct, yet conserved patterns were still detected. These conserved patterns shed light on the importance and function of sites of thermal exchange and how they support the role of the rete ophthalmicum (RO) in eye and selective-brain cooling. The arterial blood supply to all three sites of thermal exchange—oral cavity, nasal cavity, and orbit—each has a main source of blood directly supplying these areas, yet also have anastomotic connections that carry blood to and from other sites of thermal exchange, allowing these sites to function either in series or in parallel, creating a larger surface area for thermal exchange than if each site were to function independently.

Oral cavity. The oral cavity displayed conserved vascular patterns in the specimens studied. The anastomotic connections between the palatine arteries created a fine-caliber plexus, creating a large surface area for

heat exchange. Thus, the anatomical evidence supports the physiological findings that the oral cavity serves as a site of thermal exchange, such as Bernstein et al.'s (1979a,b) study showing that removing the oral cavity from the avian thermoregulatory strategy does have an impact on brain temperature regulation. The DCDVI injections of Galliformes and loons in the present study showed that veins are in close contact with the arteries supplying the palate, allowing the establishment of a thermal gradient via counter-current heat exchange (Arad et al., 1989) along the palate. Cormorants showed a somewhat different morphology when compared to Galliformes and loons, presumably due to the dramatic modifications associated with reduction of the nasal cavity. The palatine vessels did not branch into medial and lateral branches, and the palatal plexus was found to be largely absent, thus reducing the efficiency of the palate as a site of thermal exchange. However, a novel plexus, involving both arteries and veins, was observed in cormorants lateral to the choana, potentially indicating that a plexus of some kind associated with the oral region is critical for the support of brain cooling. The rostral and caudal ventral nasal vessels are large-caliber vessels that pass blood between the nasal and oral regions. These vessels were found in all of the taxa studied, with the rostral ventral nasal vessels anastomosing with the lateral nasal vessels and the caudal ventral nasal vessels anastomosing with the medial nasal vessels, potentially allowing blood to flow between the nasal and palatal regions.

Nasal cavity. The nasal cavity is a highly vascularized area, known to function well in thermal exchange, and is critical to the thermoregulatory strategy of birds (Murrish, 1973; Bernstein et al., 1979a; St-Laurent and LaRochelle, 1994). The nasal cavity is supplied by the medial and lateral nasal arteries, which are ultimately branches from ethmoid arteries. The lateral nasal artery supplies the lateral wall of the nasal cavity and creates a plexus at the nasal vestibule (Sedlmayr, 2002), setting up a volume of blood that is exposed to ambient airflow. The medial nasal artery supplies the nasal septum and the conchae of the airway. A third source of blood to the nasal cavity is via the sphenopalatine arteries. A branch of the cerebral carotid artery, it courses rostrally and anastomoses with the caudal ventral nasal arteries. In Kilgore et al.'s (1979) arterial occlusion study, the stapedial, sphenopalatine, and sphenomaxillary arteries were selectively occluded, and doing so stopped collateral blood flow to the orbital, nasal, and to a lesser degree, the palatal region, all of which are important sites of thermal exchange.

Similar vascular branching patterns in the nasal cavity were observed in nearly all of the birds, except in the suliform sample. The blood vessels within the cormorant nasal cavity were clearly separated into rostral and caudal segments that supply a large plexus surrounding the choana. This plexus may replace the nasal region as a site of evaporative cooling as airflow through the nasal cavity is blocked at the nostrils.

Auricular rete. The auricular rete (RA) was found in the same anatomical region as reported by Ghetie (1976) and Sedlmayr (2002), lateral to the body of the

quadrate. The RA occupied a more superficial position than the RO, yet offered anastomotic connections to the RO. The arteries of the RA ultimately coalesced and anastomosed with the RO, potentially supplying cooled blood to the RO. The venous drainage of the RA itself, however, is likely to have little direct influence on the head, due to the auricular vein emptying into the jugular vein. This anatomy would set up a physiologically interesting dynamic between the RA and the RO that has yet to be tested. The well-developed RA in turkeys and pheasants may function by using temperature gradients within the upper eyelid and skin near the external ear, and due to the connection with the RO, may indicate a particular need in Galliformes for an additional site of thermal exchange or an increase in the surface area for thermal exchange.

The thermophysiological implications of the RA are not currently known. Midtgård (1983) addressed the criteria for an ideal heat exchanger and, if we assume that the RO meets them, then we are able to review these requirements for the RA. The criteria listed by Midtgård are (1) the exchanger is completely insulated, (2) heat transfer is equally distributed throughout the exchange area, and (3) the heat transfer coefficient is constant throughout the exchange area. The RA was found in a mass of fat, thus likely meeting criterion (1). The other two criteria are beyond the scope of this paper, but (2)could be met as the arteries and veins appear to intermingle, possible indicating a consistent heat transfer. Requirement (3) could be met by the RA as it is made of similar arteries and veins as the RO and is likely to have a consistent heat transfer coefficient. Again, this anatomical finding merits physiological testing.

Orbit and rete ophthalmicum. In all of the taxa studied, the arterial supply to the orbital region passed through the RO to supply the eyeball and other orbital tissues via the supraorbital, infraorbital, ophthalmotemporal, and intramandibular arteries. The ethmoid artery anastomosed with the ophthalmotemporal and supraorbital arteries and then continued rostrally to supply the nasal region. The supraorbital artery also shared an anastomotic connection with the ethmoid artery, possibly providing cooled blood from the RO. Blood flow through these arteries was tested by experiments that occluded blood flow to the head and RO by Richards and Sykes (1967) and Kilgore et al. (1979), respectively, showing that alternate pathways are able to sustain some of the metabolic needs of cranial tissues.

The arterial blood from the RO has been reported to be critical in maintaining the selective temperature differential between the brain and body (Kilgore et al., 1973, 1976, 1979). Cooled blood from the RO is thought to supply the brain via anastomotic connections (Fig. 6A–C) between the ophthalmotemporal, orbital, and ethmoid arteries (Midtgård 1984a,b). All of these anastomotic connections, however, are relatively smalldiameter arteries that are unlikely to be able to influence the hot, body-temperature blood entering through the cerebral carotid artery.

When Kilgore et al. (1979) occluded the stapedial, sphenomaxillary, and sphenopalatine arteries, the ability to selectively regulate brain temperature was lost, producing results similar to those which experimentally blocked off sites of thermal exchange (Bernstein et al. 1979a,b; Pinshow et al., 1982). The temperature of the brain actually increased slightly above body temperature, providing evidence that these blood vessels are perfusing brain tissue and are critical to influencing brain temperature. All of these occluded arteries supply sites of thermal exchange, altering normal pathways of supply and drainage. The stapedial artery supplies blood to many tissues of the head. Occluding this artery would obliterate blood flow to eyeball, a significant site of thermal exchange. The ophthalmotemporal artery supplies the nasal cavity via the supraorbital artery. Collateral supply to sites of thermal exchange would also have been impacted by occluding the sphenomaxillary and sphenopalatine arteries. The sphenomaxillary artery provides collateral blood supply to the palate, and the sphenopalatine artery supplies both the palate and nasal region (Fig. 6F). Kilgore et al. (1979) stated that blockage of the sites of thermal exchange by tracheal cannulation (Bernstein et al., 1979a) showed the same results when these arteries were occluded, a brain temperature that was 0.4°C warmer than cloacal temperature. Restricting the amount of blood passing through the RO likely reduced the amount of blood to sites of thermal exchange. These experiments, however, may not have been truly testing the blood flow through the RO and whether it affects avian brain temperature, but rather how a lack of blood supply to sites of thermal exchange influences brain temperature. In other words, blocking the arterial supply to sites of thermal exchange prevents cooled venous blood from flowing from these sites, which negates the ability of birds to support brain cooling. Therefore, occluding arterial blood flow to the RO impacts more tissues than just the RO itself (e.g., nasal conchae, palatal plexus), and conclusions drawn from these experiments need further testing. Interestingly, calliope hummingbirds (Burgoon, et al., 1987) lack a sophisticated RO and are still able to sustain a moderate brain-to-body temperature differential, indicating the role and use of venous pathways from sites of thermal exchange to cool the brain, presumably via the dural venous sinuses and cerebrospinal fluid.

In order for the brain to receive arterial blood from the RO, blood must flow from the anastomotic connections within the orbit to the brain. Essentially, retrograde blood flow through the ethmoid and orbital arteries would be necessary. For blood to flow into the endocranial cavity, against the pressure of the cerebral carotid artery, pressures in the efferent vessels of the RO would have to be higher than that of the cerebral carotid artery, which seems unlikely, due to the pressure drop across the rete mirabile (Lluch et al. 1985). Ninomiya (2002) stated that because of the large diameter of the stapedial vessel passing through the RO, acting as a bypass to the finer arteries, and arterial sluice valves to ensure directional flow, the RO likely has the ability to influence blood flow direction and pressure. The pressure drop across the RO may be avoided by allowing blood to pass through fewer RO arteries, cooling less blood and then allowing cooled blood to mix with warmer blood on the rostral side of the arterial component of the RO. This flow pattern likely does not keep the brain temperature lower than the body during times of thermoregulation, and is likely for situations (e.g., escaping from predator or pursuit of prey) where nutritional blood flow to the eye is more important than regulating its temperature.

Because of small-diameter arterial anastomotic connections between the cerebral arteries and the RO, the primary role of the RO is likely to support not the brain, as commonly stated, but rather the eyeball (Frost et al., 1975; Midtgård, 1983, 1984a,c; Hossler and Olson, 1984). The function of the RO is likely separated into two roles, with the primary role being supporting the thermal environment of the eyeball, and a secondary role of supporting brain-temperature regulation through the small arterial anastomotic connections and venous anastomoses via a branch of the venous component of the RO that ultimately drains into the cerebrotectal venous sinus (see also Sedlmayr, 2002). Birds have large eyes that are exposed to dramatic thermal changes due to environment and altitude, and the largest efferent vessels of the RO directly supply the eyeball. The RO may serve a critical function in precisely regulating the temperature of the eye to mitigate excessive heat loss in cooler situations or allow heat loss in warmer situations, as the large eyes of birds also are known to be efficient sites of thermal exchange (Frost et al., 1975; Bernstein et al., 1979a; Pinshow et al., 1982; St-Laurent and LaRochelle, 1994). Maintenance of constant retinal temperature is known to be important to visual acuity in some non-avian taxa (Parver, 1991; Fritsches et al., 2005). Cormorants offer interesting insights into this explanation. Cormorants have a large RO and modified sites of thermal exchange. The nasal cavity is reduced and the nostrils are covered by hornified epithelium (Bang, 1971) preventing adequate nasal airflow to support evaporative cooling. There is no discernible palatal plexus, and they have a unique and emphasized plexus on the lateral wall of the choana. Even though these sites of exchange are reduced, cormorants can still maintain a temperature gradient across the RO as measured by Hudson et al. (1985). The large RO in cormorants, loons, kingfishers, and jackass penguins (Frost et al., 1975) likely establishes a thermal gradient that keeps the temperature of the eve relatively constant while submerged, indicating that the primary role of the RO is to support eye temperatures. Additionally, as an emphasis on visual acuity emerges, prey acquisition methods may factor into the size of the RO, in that, as this study has revealed, visual predators usually possess a larger RO. American kestrels (Falco sparverius) are small-bodied visual predators that possess a large RO, and a small bodied granivore, the zebra finch, has a small RO. Kestrels have about nine times more mass (119 g) than a zebra finch (13 g), yet kestrels have 43 times more arteries (260 vs. 6) and 37 times more veins (150 vs. 4) in its RO (Bech and Midtgård, 1981; Burgoon, et al., 1987). Chickens have a body mass of about 1,493 g (Arad and Midtgård, 1984) and demonstrate about 60 arteries and 40 veins in the RO. A similar-sized vulture weighs about 1,400 g and can have 100 arteries and 50 veins (Arad et al., 1989). These data suggest that in birds with similar body masses and very different RO morphology, the role of vision is linked to the size of the RO. Midtgård (1983) and Midtgård et al. (1983) indicated that body weight and other head parameters were not significantly correlated to body-to-brain temperature differentials. Midtgård (1983) looked favorably on the role of the RO supporting eyeball physiology, yet the role



Fig. 16. *Meleagris gallopavo* (wild turkey) in left rostrodorsolateral view indicating possible pathways for blood to drain from sites of thermal exchange. Red arrows indicate pathways that likely have little influence on neurosensory tissues. Blue arrows indicate pathways that likely have an influence on neurosensory tissues. See Abbreviations for vessel names.

of the RO in supporting brain temperature regulation is still not clear and has not adequately be tested for a role supporting the eyeball.

An additional physiological link between the RO and the eye was reported when oxygen was found to be transferred across the rete (Bernstein et al., 1984). Bernstein et al. (1984) was demonstrating a vascular connection between the RO and the brain vasculature, using the oxygen levels of the CSF as a proxy. That study also indicated, albeit indirectly, that blood supplied to the eyeball has an increased oxygen partial pressure, which would benefit a metabolically active retina that would require more oxygen, as Yu and Cringle (2001) found in mammals, and increase the oxygen delivery through the pectin to the avascular retina (Bernstein et al., 1984).

Although published studies report the importance of the arterial supply from the RO and its importance in establishing a brain-to-body temperature differential, the role of venous blood has been underemphasized. Occlusion studies (Kilgore et al., 1979) showing the importance of the stapedial artery in supporting the selective temperature difference between the brain and body made no considerations to the venous drainage coursing through the stapedial canal. Damage to this vein, by attempts to occlude the stapedial artery, may have had a detrimental impact on thermoregulation, by favoring one venous pathway over another. The anastomotic connections that the dural venous sinus share with the extracranial veins and the RO may indicate some function in whole brain cooling, versus the regional brain cooling the RO appears to provide to the anterior optic chiasm (Kilgore et al., 1973, 1976, 1979, 1981).

Venous drainage patterns from the sites of thermal exchange to the brain have numerous combinations of pathways that may influence brain temperature. Some pathways drain through the endocranial cavity or to the RO, and some bypass pathways leading to the endocranial cavity and empty into either the rostral cephalic vein or the jugular vein (Fig. 16). These pathways depend on the number, location, and direction of venous valves (Hossler and Olson, 1984; Hossler and West, 1988) and the actual pathways likely depend on the venoconstriction of the ophthalmic and maxillary veins (Midtgård, 1984a). Midtgård (1984b) tried to understand this key process by demonstrating the smooth muscles in key veins of the orbit that likely redirected venous blood to key neurosensory tissues.

The venous drainage of the nasal cavity displays numerous anastomotic connections, allowing multiple drainage pathways. A pathway that would have little influence on brain temperature would be cooled blood passing through the lateral nasal vein, through the rostral and caudal ventral nasal veins, and then though the palatine veins, allowing cooled blood to bypass the RO and flow into the jugular vein along with the blood in the palatine veins. If the dorsal portion of the ophthalmic vein was venoconstricted, and the maxillary vein was venodilated, this pathway may be preferred. The pathway for cooled venous blood to support the RO is through the medial and lateral nasal veins and then into the ethmoid vein. The ethmoid vein is a tributary to the olfactory sinus, which offers an additional pathway into the dural sinuses (Baumel, 1975), which surround the brain and may influence cerebrospinal fluid temperature (Zenker and Kubik, 1996). This pathway may be preferred if the maxillary vein was venoconstricted and the ophthalmic vein was venodilated, forcing cooled blood from the palate and nasal cavity to pass into the orbit through the ethmoid veins. The facial vein may also serve as a drainage route, although only the lateral nasal vein demonstrates direct anastomoses to the facial vein. Drainage from the medial nasal veins would have to pass through less direct pathways. This pathway would support the role of the RA as a vascular physiological device used in thermoregulation.

Venous drainage pathways within the orbit are likely important to the avian thermoregulatory strategy. The nasal veins have a direct connection to the ethmoid vein, olfactory sinus, and ophthalmic vein (Fig. 11A), allowing the cooled blood to pass through to the RO via the anastomotic connection with the ophthalmotemporal vein or via the supraorbital vein. The veins redirecting cooled blood from the palatal plexus (Baumel, 1975) into the nasal veins serve to deliver more cooled blood to the RO (Fig. 11E,F). Within the orbit, the ophthalmic vein is joined by the ethmoid vein and blood in the nasal cavity can drain along this vein, and in to the rostral cephalic vein. If the dorsal portion of the ophthalmic vein is venoconstricted and the ventral portion is not, the cooled blood is likely passed to the RO through the ophthalmotemporal vein, along with cooled blood from the eyeball and periocular tissues (eyelids). If the entire ophthalmic vein is vasoconstricted, along with the maxillary vein, the cooled blood within the ethmoid veins from the nasal cavity must drain through the dural venous sinuses, cooling the brain. If the entire ophthalmic vein is venodilated, the cooled blood can pass to the rostral cephalic vein and pass to the jugular vein without influencing brain temperature. Cooled blood can enter the endocranial cavity to join the rostral dorsal cerebral veins and the dorsal longitudinal sinus (Baumel, 1993). Again, cooled blood flowing through the dural sinus system has the potential for brain cooling by influencing the temperature of cerebrospinal fluid surrounding the brain and spinal column (Zenker and Kubik, 1996).

The thermoregulatory ability of birds has been well known, yet is still generating testable questions. This study found anastomotic connections that suggest pathways for blood to be shunted or diverted to specific regions, which would give birds an ability to control cephalic temperatures that may be unrivaled. These anatomical pathways leading from sites of thermal exchange into the endocranial cavity or RO, some described here for the first time, still need to be verified by studies focusing on favored pathways during times of thermal stress. Even during the research into function of the RO, preferred vascular pathways during thermoregulation were unknown (Kilgore et al., 1979; Arad et al., 1987). Until studies of blood flow reveal the preferred vascular pathways used during thermoregulation, we will not have a true understanding of the thermoregulatory abilities of birds.

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