

Anatomy of the Crocodilian Spinal Vein

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ABSTRACT The crocodilian spinal vein is remarkably robust yet historically overlooked. Using corrosion casting, we describe the anatomy of this vessel and its connections with the caval and hepatic venous systems in representatives from four crocodilian genera. The spinal vein arises from an enlarged occipital sinus over the medulla and extends the entire length of the vertebral column. Unlike in squamate reptiles, the spinal vein is single (nonplexiform), voluminous, and situated dorsal to the spinal cord, and plexi lateral to the cord span between emerging intercostal veins. The connections with the other venous systems are otherwise similar to those in other tetrapods. The overall anatomy of this vessel and its abundant connections with the other venous systems indicate it likely plays a primary role in returning blood to the heart from all parts of the body. Preliminary studies of function suggest that this vessel could also play an adaptive role during basking and diving. *J. Morphol.* 258: 327–335, 2003. © 2003 Wiley-Liss, Inc.

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There are few publications on the anatomy of spinal veins in nonmammalian vertebrates. Zippel et al. (2001) described in snakes an elaborate vertebral plexus extending from the base of the skull to the tip of the tail and summarized much of the scant published information on spinal veins in other vertebrate taxa. Girgis (1962) described the venous system in an aquatic turtle (*Trionyx triunguis*), including the large intravertebral vein in the anterior cervical region. Of the extant archosaurs, birds are known to possess a robust spinal vein that forms a single, voluminous sinus dorsal to the spinal cord (Richards, 1968; Baumel, 1975, 1988; West et al., 1981). The nature of the spinal veins in crocodilians, on the other hand, has been essentially unexplored. Rathke (1866) made reference to the basic anatomy of the spinal vein in an unspecified crocodile, with emphasis on the more accessible connections with the caval veins. Beddard (1905, 1906) made several observations and clarifying comments regarding these connections. Neither investigator provided illustrations of the spinal vasculature. Subsequent works on crocodilian vascular anatomy have omitted the spinal veins entirely (e.g., Reese, 1914; Chiasson, 1962). Olson et al. (1975), reviewing sites for blood collection from reptiles, radiographically dem-

onstrated a vessel within the cervical neural canal of *Alligator mississippiensis*. This vessel is clearly the spinal vein but was erroneously referred to as the “internal jugular vein.”

Modern techniques such as corrosion casting and angiography allow easy access to, and observation of, these ensconced vessels (e.g., Zippel et al., 1998, 2001). Herein, we use these methods to elaborate on previous anatomical descriptions of the crocodilian spinal vein and its connections.

MATERIALS AND METHODS

Juvenile crocodilians of several species and mixed sexes were provided by a local zoo (Table 1). We housed the animals in glass aquaria or fiberglass tanks and fed them a prepared alligator chow (Burris Aquaculture Feeds, Franklinton, LA). Air temperatures were maintained between 24 and 26°C. The Institutional Animal Care and Use Committee of the University of Florida approved all research on these animals.

Resinous casts of the circulatory system were produced using Mercor (Ladd Research Industries, Burlington, VT) perfusions and macerative baths, as in Zippel et al. (1998). Injection sites included the ventral abdominal veins, the jugular veins, the carotid artery, and/or the aortic arches. Stopping the digestion process after the NaOH bath allowed us to study the relationships between blood vessels and bones before we went on to macerate the bone as well. Vascular casts of the head and neck of ratite birds with bones intact were borrowed from a colleague (J. Sedlmayr of the Witmer lab at Ohio University, College of Osteopathic Medicine) and examined for comparison.

A portion of the vertebral column was removed from one alligator cadaver and used to prepare histologic sections. Tissues were fixed in 10% neutral buffered formalin, decalcified in 5% acetic acid, and embedded in paraffin or plastic resin. Five-micron transverse sections were then generated and stained using routine Harris hematoxylin and eosin procedure.

Alligators (*Alligator mississippiensis*) used for fluoroscopy (Table 2) were sedated with 1.0 mg/kg xylazine IM (XYLA-JECT®; Phoenix Pharmaceutical, St. Joseph, MO) followed after 30 min with 20 mg/kg ketamine hydrochloride IM (Ketaset®; Fort Dodge Laboratories, Fort Dodge, IA) and 0.01 mg/kg glycopyrrolate IM (Robinul®; A.H. Robins Co., Richmond, VA). After an additional

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TABLE 1. Crocodilian species used for vascular casting

Species	N	Body mass (g)	SVL (cm)
<i>Alligator mississippiensis</i>	2	290, 1370	22, 38
<i>Caiman latirostris</i>	7	57–66	12–14
<i>Crocodylus siamensis</i>	3	60–700	14–30
<i>Osteolaemus tetraspis</i>	1	31	12

30 min, animals were generally tractable enough for intubation. They were induced with 5% isoflurane (IsoFlo®; Abbott Laboratories, North Chicago, IL) and maintained at 3%. We prepared a sterile field at various sites along the dorsal midline for catheter insertion and administration of iodinated contrast medium. Catheters were introduced into the spinal vein with 18 gauge Seldinger-type needles, either a modified Cournand style needle (length = 2 1/16") or a modified Seldinger needle (length = 2 3/4") (Universal Medical Instrument Corp., Ballston Spa, NY). We secured emerging catheters with tissue adhesive and a ligature to the skin (Fig. 1). Catheters were then plugged with blocked needles (tissue adhesive in the hub), and flushed periodically with heparinized (2 units/ml) saline (0.9%). Animals were placed in large glass aquaria and allowed at least 24 h to recover. For injection of contrast medium, we replaced the plug needle with a needle that had the plastic hub removed, i.e., just the metal shaft. This allowed a catheter to be attached to both ends, and in this way the implanted catheter could be extended to reach out of the tank. Blood flow through the spinal vein was fluoroscopically imaged in lateral and dorsal-ventral planes using a C-arm fluoroscope (as in Zippel et al., 1998) during air-breathing (31 injections in five animals), "voluntary" submergence in a depth of water equivalent to twice the height of the animal (18 injections in three animals; see comments in Discussion regarding "voluntary" dives in captive vs. free-ranging animals), and during exposure to radiant heat on the dorsum from a 250 W heat lamp placed 50–100 cm away (39 injections in four animals).

RESULTS

Vascular Casts

The general vascular anatomy of crocodilians has been documented elsewhere (Reese, 1914; Chiasson, 1962); readers should refer to these sources for detailed descriptions of the vessels mentioned below in connection with the spinal vein. Because of the many similarities between crocodilian and avian vascular anatomy, readers are also referred to Richards (1968), Baumel (1975, 1988), and West et al. (1981) for details of the spinal veins of birds.

An extensive occipital sinus covers the dorsal and lateral surfaces of the crocodilian brain and drains posteriorly through the foramen magnum into a voluminous cervical sinus (Fig. 2A,B). These sinuses are likely derived from the fusion of paired posterior cerebral veins, which persist as thickened lateral channels in each sinus. There is a transverse widening of this vasculature at the foramen magnum where the sinuses are confluent with the jugular vasculature. The cervical sinus continues caudally as the extradural spinal vein, a broad vessel wider than the jugulars, and remains dorsal to the spinal cord for the entire length of the vertebral column (Fig. 2C). A lateral plexus of smaller vessels is present on each side of the cord (Fig. 2D). This basic

anatomic arrangement also obtains in the ratite materials observed by us.

The crocodilian spinal vein has numerous branches throughout its length, dorsally (interspinals), ventrally (basivertebrals), and laterally (intervertebrals). The anteriormost interspinal vein is unpaired and drains the occipital region of the skull and neck caudally into the cervical sinus (Fig. 3A). Posterior to this, the interspinal veins usually arise in quartets with two cranial and two caudal branches. The contralateral pairs pass dorsally, uniting with their mate before joining the ipsilateral pair, forming a vertical vascular ring between the neural spines in the plane of the longitudinal axis (Fig. 3B). A thin longitudinal, subcutaneous vessel (perhaps the homolog of Baumel's supraspinous vein) joins these circles at their summits, where it receives a pair of lateral branches; this arrangement is most prominent in the thoracic spine. Occasionally, however, the interspinal arises again as a single, median, laterally compressed vessel (Fig. 3C), as in the occipital region. The interspinal veins are markedly longer in the cervical region where the vertebral column curves ventrally and is therefore further from the dorsum. Here, the interspinals form small vascular beds penetrating the ventral surface of the cervical osteoderms (Fig. 3D).

Two small ventral branches, one per side, are produced at each intervertebral junction (Fig. 4A). These vessels pass anteriorly and meet beneath the cord halfway to the next junction, giving rise to the basivertebral vein that penetrates the centrum below. This arrangement is most prominent in the cervical region. The basivertebral veins collectively form dense vascular beds that clearly outline the vertebral bodies in the completely macerated casts (Figs. 2A,B, 3C, 4B).

The lateral branches, or intervertebral veins, arise between each pair of vertebrae. They produce three branches: a dorso-cranial branch, which sometimes unites with its serial homologs to form a longitudinal vessel on the dorso-lateral surface of the vertebral column; a ventro-cranial branch that wraps around the vertebral artery; and a lateral branch, which gives rise to the intercostal veins in the thorax. These vessels collectively form an extensive external plexus in the neck (Fig. 3C). Between

TABLE 2. Data for alligators (*Alligator mississippiensis*) used in fluoroscopy studies

Body mass (kg)	SVL (cm)	Catheter site*	Treatment
5.2	51	S1–2	air, water
10.3	66	C1–2, Ca3–4	air, heat, water
14.7	78	C1–2, L2–3, Ca3–4	air, heat, water
8.3	65	L2–3, Ca7–8	air, heat
5.1	65	L3–4, Ca9–10	air, heat

*Catheter sites between vertebrae; C, cervical; L, lumbar; S, sacral; Ca, caudal.

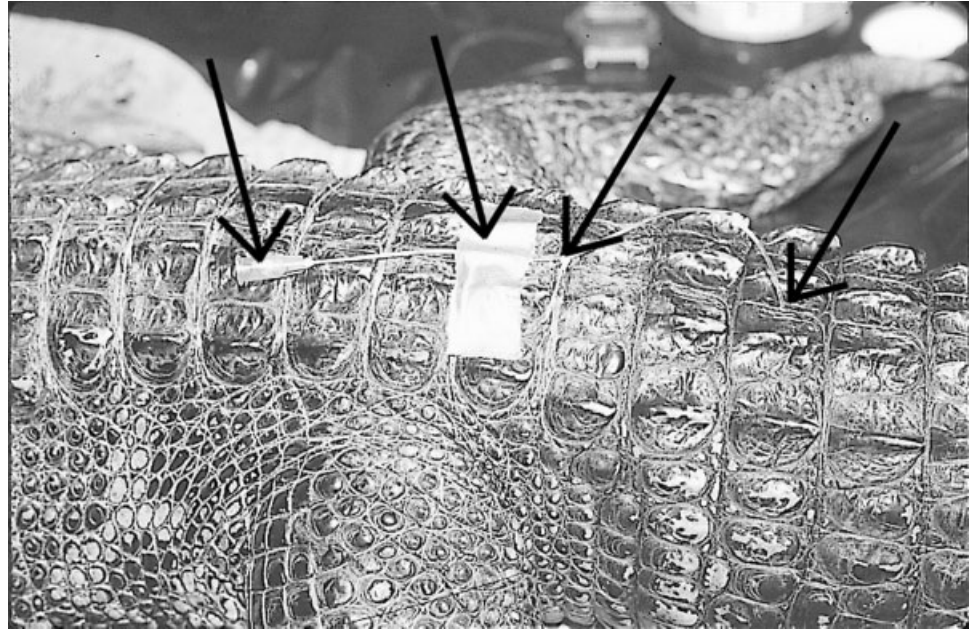


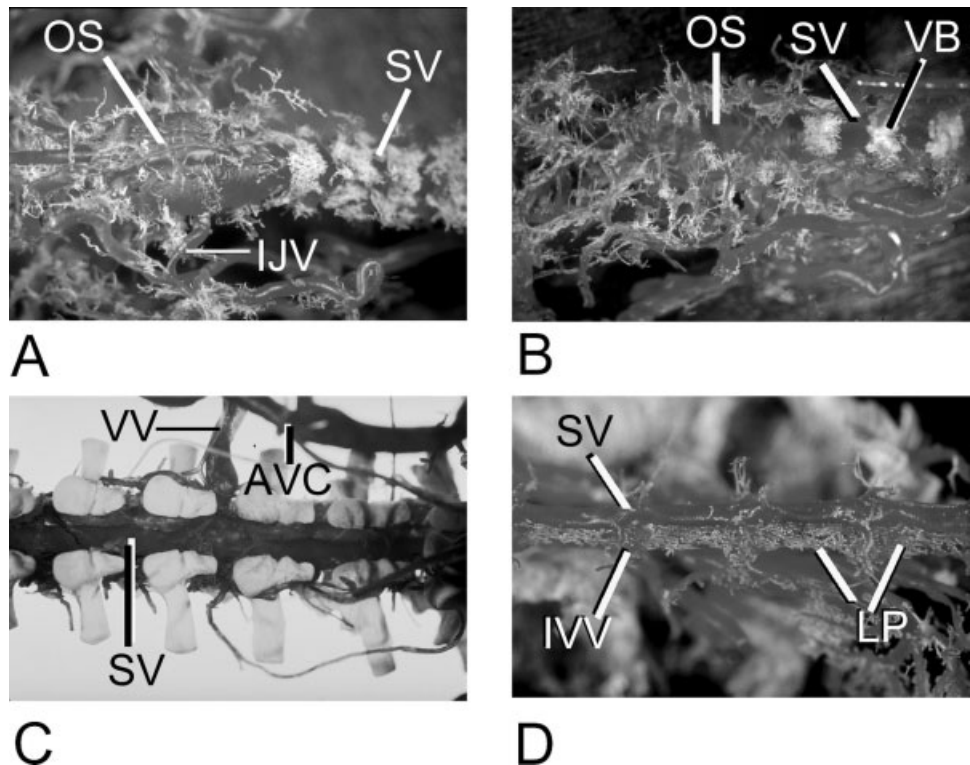
Fig. 1. *Alligator mississippiensis*. Emerging catheters used in fluoroscopy for the administration of contrast medium were (from right to left) secured at the site of emergence with tissue adhesive, looped over and ligated to the skin, taped to the skin, then plugged with a blunt hypodermic needle with tissue adhesive in the hub. Dorso-lateral view, anterior to the left.

the 3rd and 4th thoracic vertebrae, the intercostal veins form a pair of large anterior vertebral veins. The vertebrals pass from the vertebral column at the anterior end of the lungs and are equal in magnitude to the anterior caval veins into which they empty (Figs. 2C, 5A). In some specimens, the vertebral gives rise to anterior and posterior branchlets as it passes from the vertebral column, but these

seem to span no more than one segment in either direction. They were not observed to form longitudinal vessels along the column, as observed by Rathke (1866).

Where the spinal vein passes over the liver (thoracic vertebrae 8–12), the intercostal veins form large hepatico-parietal vessels exiting the vertebral column bilaterally (Fig. 5B,C). These veins drain the

Fig. 2. Vascular casts of crocodilian spinal veins. **A:** *Caiman latirostris*. Full maceration of the head and neck; dorsal view showing the extensive occipital sinus covering the brain. **B:** *Caiman latirostris*. Full maceration of the head and neck; ventral view. **C:** *Crocodylus siamensis*. Partial maceration of vertebral column; ventral view, anterior to the left, vertebral bodies removed. The spinal vein is clearly seen coursing along the dorsal wall of the neural canal. **D:** *Crocodylus siamensis*. Full maceration of vertebral column; lateral view, anterior to the left. Small lateral plexi span the distance between emerging intervertebral veins. AVC, anterior vena cava; IJV, internal jugular vein; IVV, intervertebral vein; LP, lateral plexus; OS, occipital sinus; SV, spinal vein; VB, vasculature of the vertebral body; VV, vertebral vein.



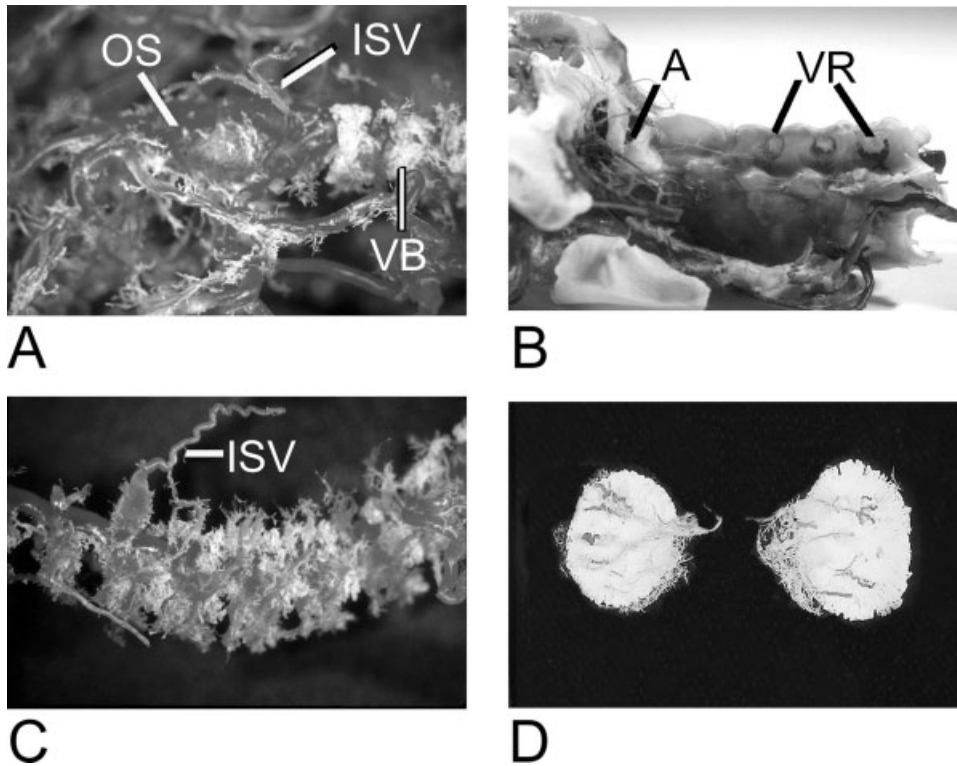


Fig. 3. Crocodilian vascular casts. **A:** *Caiman latirostris*. Full maceration of the head and neck; dorso-lateral view, anterior to the left. **B:** *Alligator mississippiensis*. Partial maceration of head and neck; lateral view, anterior to the left. **C:** *Caiman latirostris*. Full maceration of the neck; lateral view, anterior to the left. **D:** *Alligator mississippiensis*. Partial maceration; ventral view of cervical osteoderms. A, atlas-axis junction (for reference); ISV, interspinal vein; OS, occipital sinus; SV, spinal vein; VB, vasculature of the vertebral body; VR, vascular ring.

spinal vein into the posterior margin of the liver. The exact number and their point of egress from the column are as variable intra- as interspecifically, and even vary bilaterally within a specimen. The hepatico-parietals generally number one to three per side, sometimes forming longitudinal vessels along the vertebral column, but they usually unite as they pass to and into the liver (Fig. 5C). They wrap all the way around the posterior margin, sometimes separating and reuniting with themselves, sending occasional branches penetrating into the liver lobes. The hepatico-parietal veins are continu-

ous with the ventral abdominal (a.k.a., epigastric) veins on the ventral surface of the liver.

Anastomoses between the spinal and caval veins are essentially segmental posterior to the liver, with some connections being more robust than others. The gonads have a large connection, usually bifid, with the spinal vein just anterior to the kidneys (Fig. 5D). The ventral abdominal veins are also confluent with the spinal vein immediately thereafter, and the renal vasculature forms a third major axis of communication between caval and spinal veins in the region of the posterior

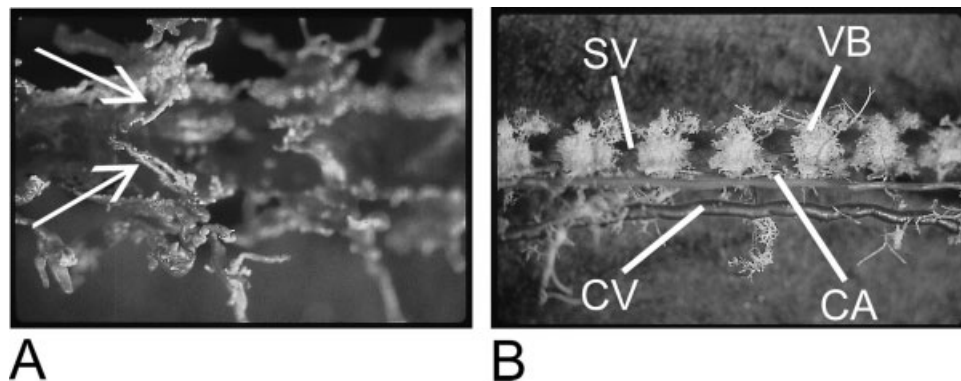


Fig. 4. Crocodilian vascular casts. **A:** *Crocodylus siamensis*. Full maceration of the cervical vertebral column; ventral view, anterior to the left. Note the paired ventral branches of the spinal veins. **B:** *Caiman latirostris*. Full maceration of the tail; ventro-lateral view, anterior to the left. The basivertebral veins form a dense vascular bed outlining the vertebral bodies. CA, caudal artery; CV, caudal vein; SV, spinal vein; VB, vasculature of the vertebral body.

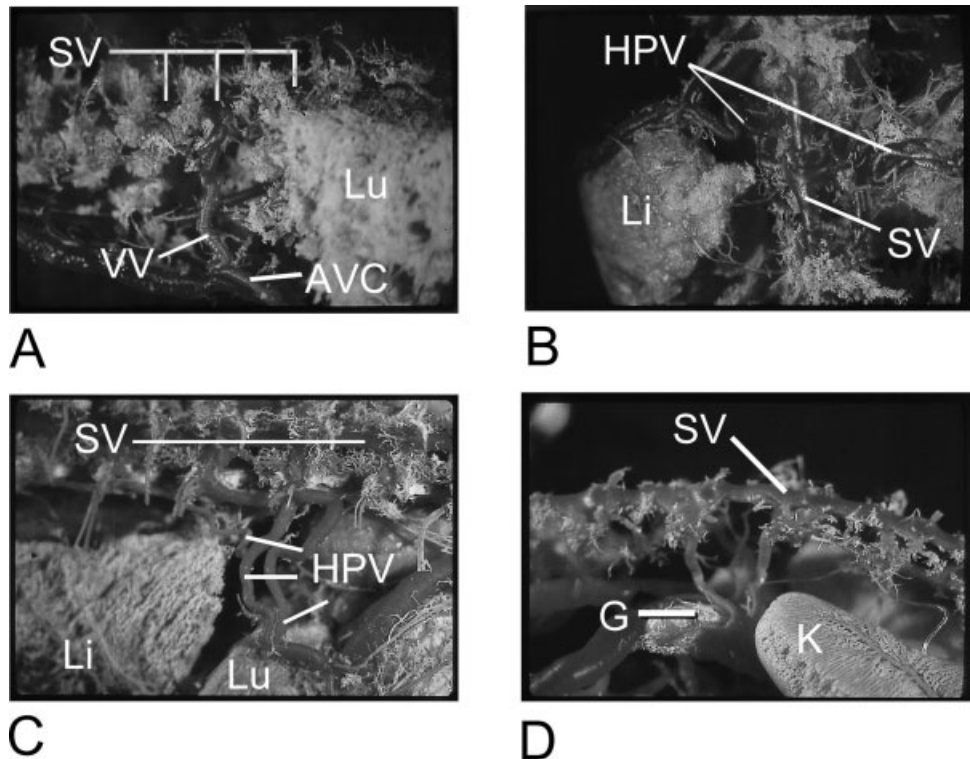


Fig. 5. *Caiman latirostris*. Vascular casts, full maceration. **A:** Thorax; lateral view, anterior to the left. Some lung casting has been removed to facilitate viewing the vertebral veins. **B:** Thorax/abdomen; dorsal view, anterior down. **C:** Thorax/abdomen; dorsal view, anterior to the left. **D:** Abdomen; lateral view, anterior to the left. AVC, anterior vena cava; G, gonad; HPV, hepatic-parietal vein; K, kidney; Li, liver; Lu, lung; SV, spinal vein; VV, vertebral vein.

lumbar vertebrae. Between the sacral vertebrae, the pelvic veins form robust connections between the caval veins (where the caudal bifurcates into renal efferents) and the spinal vein; segmental connections between the spinal and caudal vein commence posterior to the sacrum and continue posteriorly to the tip of the tail (Fig. 6).

Histology

Transverse sections through the cervical vertebral column of the alligator revealed the relation between the spinal vein and the other soft and bony tissues of the vertebral column. The single, voluminous spinal vein courses dorsal to the spinal cord

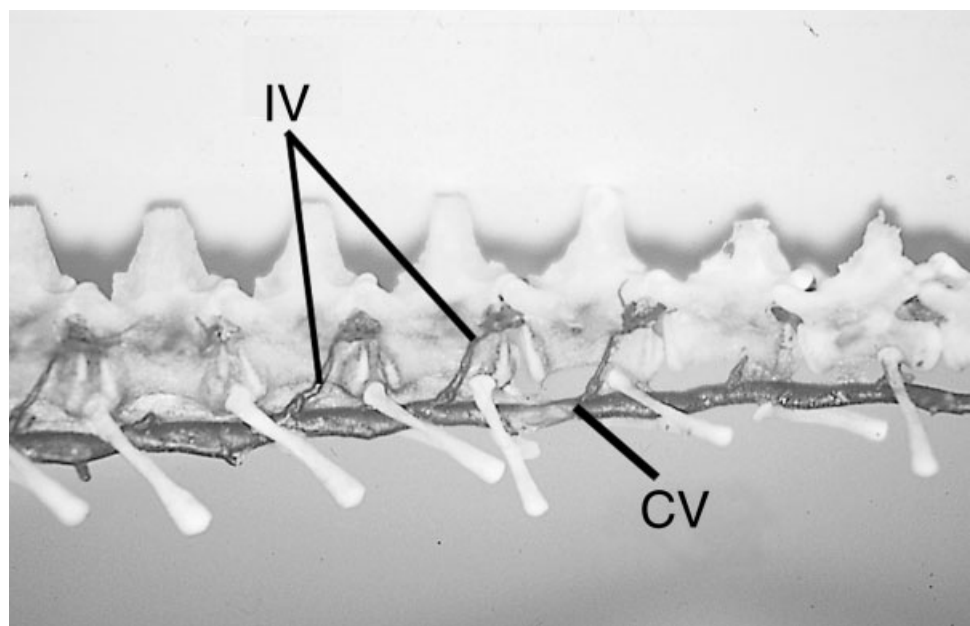


Fig. 6. *Crocodylus siamensis*. Vascular cast of tail, partial maceration; lateral view, anterior to the left. Segmental intervertebral veins connect the caudal vein to the spinal vein. CV, caudal vein; IV, intervertebral veins.

within the neural canal and it is equal to or greater in caliber than the cord (Fig. 7).

Fluoroscopy

Contrast medium in the cervical spinal vein (18 injections) always flowed caudally, regardless of treatment, and passed out into the vertebral veins anterior to the heart and into the hepatico-parietal veins above the liver. With the animal in air, medium injected in the lumbar spinal vein (nine injections) flowed cranially to the hepatico-parietal veins, but in two injections it flowed as far cranial as the anterior vertebral veins. In the sacral region (four injections), medium in the spinal vein flowed no more than one or two segments longitudinally before passing out the pelvic veins into the ventral abdominal veins. Medium in the caudal spinal vein flowed cranially to the hepatico-parietal veins (13 injections), but four of those times also flowed into the caudal vein via the intervertebral veins, where it continued anteriorly into the ventral abdominal veins.

Submergence in water caused few changes to the pattern seen in air. Medium in the lumbar spinal vein still flowed cranially to the hepatico-parietal veins, but a considerable amount flowed through the segmental intervertebral veins and into the ventral abdominal veins (two injections). In the sacral region, contrast medium again flowed right through the pelvic veins and into the ventral abdominal veins (three injections). Medium injected into the caudal spinal vein (six injections) again flowed cranially to the hepatico-parietal veins, often (three injections) passing also into the caudal vein and continuing anteriorly.

The application of radiant heat to the dorsum caused more considerable changes. When the heat source was directed over the abdomen, medium in the lumbar region flowed cranially as in air, but with more emphasis on passage of blood into the ventral abdominal veins via the intervertebral veins (eight injections). In one case, blood flow was reversed, passing caudally in the spinal vein out the pelvic veins and into the ventral abdominal veins where it then continued anteriorly. Heat over the abdomen also caused changes in blood flow in the tail. Half the time blood in the caudal spinal vein flowed caudally (three injections, one animal), and half the time it flowed cranially (three injections, another animal), passing out into the caudal and into the pelvic veins, both of which empty into the ventral abdominal veins.

Moving the heat source to a position over the tail, we found that medium in the lumbar spinal vein flowed cranially as in air (seven injections), but in two cases (one animal), blood flow was reversed, passing caudally in the spinal vein out the pelvic veins and into the ventral abdominal veins, where it then continued anteriorly. Caudal heat application

also changed caudal blood flow. Contrast in the caudal spinal vein flowed cranially (seven injections), partially filling the caudal vein as often as not, yet in one instance returning primarily through the caudal vein, and in either case, draining into the ventral abdominal veins at the pelvis. However, in six injections contrast flowed caudally in the spinal vein for as many as seven segments before passing into the caudal vein and flowing anteriorly.

DISCUSSION

Spinal veins appear to be a trait common to most if not all extant vertebrates (Zippel et al., 2001). These vessels are an important component of the cervico-cephalic circulation in upright primates and snakes, in which they form a vertebral plexus and appear to facilitate cerebral perfusion. Spinal veins in mammals also serve as a collateral route of venous return to the heart after occlusion or ligation of various veins in the caval system and during transient increases in thoracic-abdominal pressure. Indeed, spinal veins appear to be the only route of venous return from the brain of pinnipeds and from the posterior extremities of sloths (Wislocki, 1928; Harrison and Tomlinson, 1956). Cursory studies had indicated the presence of a well-developed spinal vein in crocodilians (Rathke, 1866; Beddard, 1905, 1906; Olson et al., 1975). We have demonstrated that the crocodilian spinal vein is robust and serves as a collateral route for venous return to the heart. It remains unclear if the extent of this vessel's development in crocodilians represents convergence related to analogous function (diving), a synapomorphy of the archosaurian clade, or perhaps both.

Comparisons With Birds

The spinal vein has been observed to form a single, voluminous sinus dorsal to the spinal cord in columbiform (Baumel, 1988), galliform (Richards, 1968; Baumel, 1975), and ratite (this study) birds. The avian spinal vein also originates from expanded venous sinuses at the base of the skull and extends caudally, dorsal to the spinal cord, to the hip joints (Baumel, 1975). However, there is a diastema in the spinal vein within the lumbo-sacral vertebrae in birds where the spinal cord is enlarged and gives rise to a plexus of nerves, although the vein is continuous cranial and caudal to this point (Baumel, 1988). As in crocodilians, the spinal vein accepts the intersegmental veins throughout its length.

Baumel (1975) stated that blood in the avian spinal vein flows caudally from the head to the base of the neck, where a pair of large vertebral veins drains the spinal vein into the proximal jugulars. He also reported that blood flows cranially from the hip joint to the base of the neck and exits the vertebral canal through those same channels. Blood in the caudal spinal vein was reported to flow cranially into the

internal iliac veins. It is not stated how Baumel determined the directions of blood flow. This pattern, however, is essentially similar to what we observed in crocodilians, except a continuous spinal vein throughout the lumbo-sacral region in crocodilians allows for bidirectional flow in that region, presumably as a function of prevailing pressure gradients. For example, blood from the tail of a crocodilian can reach the heart without passing through the posterior caval veins by flowing anteriorly through the spinal vein. Under different circumstances, blood in the lumbar spinal vein can flow caudally and exit at the pelvis.

Comparisons With Diving Animals

Although the spinal vein of one semiaquatic turtle appears diminutive (Bruner, 1907), Girgis (1962) describes a voluminous, intravertebral vein dorsal to the cord in the cervical region of the fully aquatic, diving *Trionyx triunguis*. In this species, the jugular system is reduced (the left jugular does not even reach the head), and the robust spinal vein appears to be the primary avenue of venous return, at least from the head.

Nonplexiform spinal veins are also extensively developed in some cetaceans and sirenians, and especially in pinnipeds, where the jugular system is poorly developed and drains only extracranial tissues (Harrison and Tomlinson, 1956). Venous return through the spinal veins in these animals is thought to facilitate the supply of oxygenated blood to the brain during extended dives (Ronald et al., 1977). In seals, the spinal veins exiting the cranium are paired and lie ventral to the cord in the upper cervical region. These vessels pass laterally around the cord to unite dorsally in the lower cervical region, forming a large extradural vessel that extends to the second caudal vertebra (Harrison and Tomlinson, 1956; Ronald et al., 1977). Harrison and Tomlinson (1956) injected contrast medium into the lumbar portion of the spinal vein in an anesthetized seal; contrast passed anteriorly into the cranial sinuses and posteriorly out into the abdominal veins. Blood exiting the cranium of conscious seals passes primarily into the spinal veins and has been radiographically demonstrated to exit through the cervical vertebral venous system, an anastomotic complex of vessels draining the spinal veins into the vertebral veins and anterior vena cava (Ronald et al., 1977). Blood in the thoracic, lumbar, and sacral portions of the spinal vein drains anteriorly into the azygous vein by way of numerous intercostal veins before ultimately passing into the anterior vena cava. The lumbar and sacral portions also share communications with the posterior vena cava.

During a dive, there is a marked restriction of blood flow to all vascular beds except the heart and brain, and there is a reversal of flow in the posterior spinal vein (Harrison and Tomlinson, 1956). Blood

from the head gradually ceases to flow through the cervical vertebral venous system. Some continues to enter the anterior vena cava by way of the azygous vein, but it accumulates there with little entering the heart. The majority passes instead to the lumbar and sacral regions, where it drains into the distal posterior vena cava, and then into a greatly enlarged hepatic sinus, where it pushes relatively oxygen-rich blood forward. A caval sphincter at the level of the diaphragm meters out the "fresh" blood from this reservoir to the heart. In this way, all blood passes through the cerebral circulation once before any is recirculated, and the interventilatory period is extended (Ronald et al., 1977; but see Nordgarden et al., 2000). Some seals can dive for up to 60 min (Elsner et al., 1970), and whales for 2 h (Irving, 1939).

Crocodilians also have been observed submerging voluntarily for up to 60 min (Andersen, 1961). We have found that the anatomy of the spinal veins in crocodilians is convergent on that of diving mammals, with a voluminous spinal vein coursing dorsal to the spinal cord, uninterrupted for the length of the vertebral column. Crocodilians have been described as having voluminous sinuses around the liver (Rathke, 1866); similar sinuses in diving mammals have been interpreted as a reservoir for oxygenated blood. As in diving mammals, it has been demonstrated in crocodilians that there is a redistribution of blood during diving favoring cranial circulation over visceral (Axleson et al., 1991). Hypoxia-induced cerebral vasodilation might further augment this effect (Söderström et al., 1999). Unlike in mammals, the unique cardiac anatomy of crocodilians potentially allows them to bypass the pulmonary circulation to some extent while diving (Axleson et al., 1996), thereby sequestering much of the blood in an isolated heart-head circuit.

We have been unable to detect any consistent and significant changes in circulatory patterns of "diving" crocodilians indicating that they are taking advantage of their spinal veins, as do seals. Circulatory patterns under water were essentially identical to those in air. Although the animals were not forced underwater, their enclosures were essentially barren and surrounded by observers manipulating catheters and administering injections of contrast medium. It should be noted that some circulatory parameters (e.g., heart rate) observed during non-voluntary dives, and even in voluntary dives during disturbance from man, are considerably different from truly voluntary dives in free-ranging crocodilians (Smith et al., 1974). A similar situation might exist in pinnipeds (Nordgarden et al., 2000). Unfortunately, radiography and Doppler flowmetry do not lend themselves well to telemetry, and it remains to be determined if blood flow patterns through the vertebral vasculature change during undisturbed voluntary dives.



Fig. 7. *Alligator mississippiensis*. Histologic section through the cervical vertebral column; dorsal up. SC, spinal cord; SV, spinal vein; VB, vertebral body.

An alternative hypothesis to explain the extent of spinal vein development observed in diving vertebrates suggests that vessels encased in bone are protected from collapse, which might otherwise be induced by high external pressures experienced while diving at great depths (Hunter, 1787; Walmsley, 1938). Another hypothesis suggests that voluminous spinal veins might play a role in nitrogen absorption and protection against the bends (Fraser and Purves, 1954). However, since crocodilians have not been observed diving to significant depths, these explanations seem unlikely for this taxon. To the extent that crocodilians might depend on anaerobic energy production during either long dives or intense activity (Bennett et al., 1985), perhaps the venous capacity and architecture help to prevent acute hypercalcemia resulting from dissolution of ossified skeletal tissues when blood pH decreases as result of increased P_{CO_2} and lactate concentration (Ruben and Bennett, 1981).

Thermoregulatory Significance

Spinal veins and venous plexi have also been implicated as a vehicle of heat transfer in various mammals (Falk, 1990; Zenker and Kubik, 1996; Rommel et al., 1998). Considering their extensive development in numerous ectotherms, and especially their dorsal location and superficial course around the tissues of the central nervous system, it is conceivable that the hemodynamics through this large vascular bed could significantly affect heating and cooling. Some lizards have long been known to alter cutaneous blood flow to facilitate heating and delay cooling (Morgareidge and White, 1969; Bartholomew, 1982). Cutaneous vasodilation increases the circulation of heated blood from the warm body surface to the body core during heating, while vasoconstriction during cooling maintains that warm blood in the core. This response has been demonstrated in crocodilians also using measurement of heat flow across the skin (Smith, 1976), measurement of ^{133}Xe clearance half-times (Smith et al., 1978), and determination of heating and cooling curves (Smith et al., 1984).

Exposure of crocodilians in this study to radiant heat from above to simulate basking induced several minor changes in blood flow patterns involving the vertebral vasculature. There is a trend toward directing blood flow returning from the posterior extremities away from the spinal vein and over the viscera. In the tail, blood in the spinal vein has a greater tendency to flow caudally, thereby increasing its potential for heat capture. However, both of these observations could simply be the result of local vasodilation induced by the application of heat.

It is interesting to note the extensive vascularization associated with the cervical osteoderms. Seidel (1979) described the arterial supply of osteoderms and proposed that these islands of intermingling connective tissues act as thermal collectors in basking crocodilians. The bone and blood absorb heat that is then transferred to the body core through the blood vessels that permeate the bone. Increased arterial flow to the osteoderms during basking has since been reported using infrared cinematography (the Discovery Channel's "Ultimate Guide to Crocodiles"). The venous vascularization is equally well developed and would certainly allow for increased flow from these structures during basking (Fig. 2D). The system might also work as insulation during cooling, as dermal vasoconstriction would keep the heated blood beneath the barrier of bony skin (Seidel, 1979). Unfortunately, the radiographic techniques available to us do not allow resolution of blood flow patterns at such a fine level.

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