New Vascular System in Reptiles: Anatomy and Postural Hemodynamics of the Vertebral Venous Plexus in Snakes

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ABSTRACT Using corrosion casting, we demonstrate and describe a new vascular system—the vertebral venous plexus—in eight snake species representing three families. The plexus consists of a network of spinal veins coursing within and around the vertebral column and was previously documented only in mammals. The spinal veins of snakes originate anteriorly from the posterior cerebral veins and form a lozenge-shaped plexus that extends to the tip of the tail. Numerous anastomoses connect the plexus with the caval and portal veins along the length of the vertebral column. We also reveal a posture-induced differential flow between the plexus and the jugular veins in two snake species with arboreal proclivities. When these snakes are horizontal, the jugulars are observed fluoroscopically to be the primary route for cephalic drainage and the plexus is inactive. However, head-up tilting induces partial jugular collapse and shunting of cephalic efflux into the plexus. This postural discrepancy is caused by structural differences in the two venous systems. The compliant jugular veins are incapable of sustaining the negative intraluminal pressures induced by upright posture. The plexus, however, with the structural support of the surrounding bone, remains patent and provides a low-pressure route for venous return. Interactions with the cerebrospinal fluid both allow and enhance the role of the plexus, driving perfusion and compensating for a posture-induced drop in arterial pressure. The vertebral venous plexus is thus an important and overlooked element in the maintenance of cerebral blood supply in climbing snakes and other upright animals. J. Morphol. 250:173–184, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: vertebral venous plexus; reptile; snake; vascular or corrosion cast; fluoroscopy; posture; gravity; siphon; circulation; brain

Plexiform spinal veins have been documented previously only in mammals (Batson, 1957; Barnett et al., 1958). The anatomy of this peculiar vascular arrangement, typically referred to as the vertebral venous plexus, has been thoroughly described in certain mammals (reviews in Worthman, 1956a; Batson, 1957; Barnett et al., 1958; Harris, 1964; Groen et al., 1997). In humans, the plexus originates anteriorly from the inferior petrosal and ventral occipital dural sinuses forming several valveless, longitudinal venous chains spanning the length of the vertebral column, extradurally, intraosseously, and paravertebrally (Bowsher, 1954; Batson, 1957). The extradural system, or internal venous plexus, is the most extensive and voluminous component and is therefore the most easily demonstrable. It consists of two longitudinal pairs of vessels lying within the column, one smaller pair dorsal (posterior in the human anatomy literature) and one larger pair ventral (anterior) to the spinal cord. Segmental anastomoses between vessels of each pair create a ladder-like appearance in which the 'rungs' are formed beneath the vertebral arches by the anastomotic cross-branches and the spaces occur where the intervertebral discs bulge into the spinal canal (Bat-

son, 1957). The dorsal portion of the internal plexus is less robust than the ventral and is more variable in form along the length of the column (Théron and Djindjian, 1973; Groen et al., 1997). The basivertebral veins form a second system, coursing through the intraosseus cavities of the vertebrae. The paravertebral system, or external venous plexus, forms a third network, running along the vertebral spines, around the column, and deeply penetrating the muscles of the dorsal parietes. Where they ascend through the transverse foramina of the cervical vertebrae, the vertebral arteries are also surrounded by a plexiform extension of this system (Harris, 1964; Dilenge et al., 1975).

Numerous transverse connections exist among these three longitudinal networks in mammals, especially in the cervical region (Eckenhoff, 1971). The plexus also has many anastomoses with caval and

TABLE 1. Snake species, body measurements, and treatments used

Species	Number	Body Mass (g)	SVL (cm)	Treatment
Colubridae				
Coluber constrictor	1	62	68	Vascular cast
Elaphe obsoleta quadrivittata	3	230–503	90–118	Fluoroscopy, vascular cast
E. o. quadrivittata	2	427, 481	105, 113	Vascular cast
E. o. quadrivittata	1	525	121	Histology
E. o. spiloides	1	432	103	Fluoroscopy, vascular cast
Nerodia fasciata fasciata	1	112	52	Vascular cast
Opheodrys aestivus	1	27	52	Vascular cast
Boidae				
Boa constrictor	1	1811	144	Vascular cast
Python molurus bivittatus	2	152, 213	52, 58	Fluoroscopy, vascular cast
P. m. bivittatus	2	115, 201	48, 57	Vascular cast
Python regius	1	232	57	Vascular cast
Viperidae				
Crotalus adamanteus	1	255	61	Vascular cast

portal veins in the cranium, neck, thorax, abdomen, and (if present) the tail. Blood is thought to flow freely through the valveless plexus in multiple directions as a function of prevailing pressures (Batson, 1940, 1957; Herlihy, 1948; Tomlinson, 1956; Eckenhoff, 1970; but see Groen et al., 1997, re: functional valves). In essence, the vessels of the plexus both connect and functionally bypass the portal, pulmonary, and caval veins, and the vertebral veins are collectively recognized as the fourth venous system (Batson, 1940; Worthman, 1956b).

Vascular casting conducted in our laboratory to demonstrate the arteries of the head and neck in the rat snake *Elaphe obsoleta* (Zippel et al., 1998) indicated the presence of a vertebral plexus. As this system was previously known only in mammals, we here describe the anatomy and function of the plexus for the first time in a nonmammalian taxon.

MATERIALS AND METHODS

Snakes of mixed sexes representing multiple taxa (Table 1) were shipped by air from a supplier in central Florida or donated by a local zoo. To study the anatomy of the circulatory system, we injected methyl methacrylate (Mercox; Ladd Research Industries, Burlington, VT) into the vessels of fresh cadavers and digested the flesh and bones in corrosive baths to isolate resinous casts of the circulatory system (as in Zippel et al., 1998). A portion of the vertebral column was removed from one cadaver and used to prepare histologic sections. Tissues were fixed in neutral buffered formalin, decalcified in 5% acetic acid, and embedded in paraffin. Six-micron sections were then generated and stained using routine Harris hematoxylin and eosin procedure.

We also used fluoroscopy to visualize postural effects on patterns of venous return from the head in six animals (see Zippel et al., 1998, for details of surgical and radiographic techniques). Polyethylene catheters were surgically introduced into selected blood vessels and secured nonocclusively. After a

minimum 24-h recovery period, contrast medium was introduced through a carotid artery catheter (n = 5), as the carotid is the primary artery supplying blood to the head (Zippel et al., 1998), or through a pulmonary vein catheter (n = 1) so that any pressure artifacts induced by contrast injection could be dissipated during passage through the heart. Patterns of blood flow were then observed using a C-arm fluoroscope (OEC-1; OEC Diagnostics, Salt Lake City, UT). Snakes were restrained in transparent acrylic tubes slightly larger than their girth, and posture was changed repeatedly (three times per animal) by tilting the tubes from horizontal to vertical head-up positions. In one animal we also imaged venous return during vertical head-down tilting. The Institutional Animal Care and Use Committee of the University of Florida approved all research on these animals.

RESULTS
Vascular Casts

The anatomy of the vertebral veins in all snakes examined is similar enough to allow a general description. Blood from the brain can drain ventrally through the oblique palatine vein, laterally through the median cerebral veins, or dorsally through the longitudinal cerebral vein (see Bruner, 1907, or O'Donoghue, 1912, for a detailed description of cranial vascular anatomy). The two median cerebrals pass into the longitudinal vein above the medulla and the longitudinal then bifurcates, giving rise to two posterior cerebral veins (Fig. 1A). These vessels exit the cranium at the lateral edges of the foramen magnum. Between the occipital bones and the atlas, the posterior cerebrals communicate dorsally with each other via an arch over the spinal cord and laterally with small communicating vessels to the right and left lateral cephalic veins (branches of the jugular veins). Caudal extensions of the posterior cerebral veins enter the vertebral column, forming two lateral vessels within the atlas that unite ven-
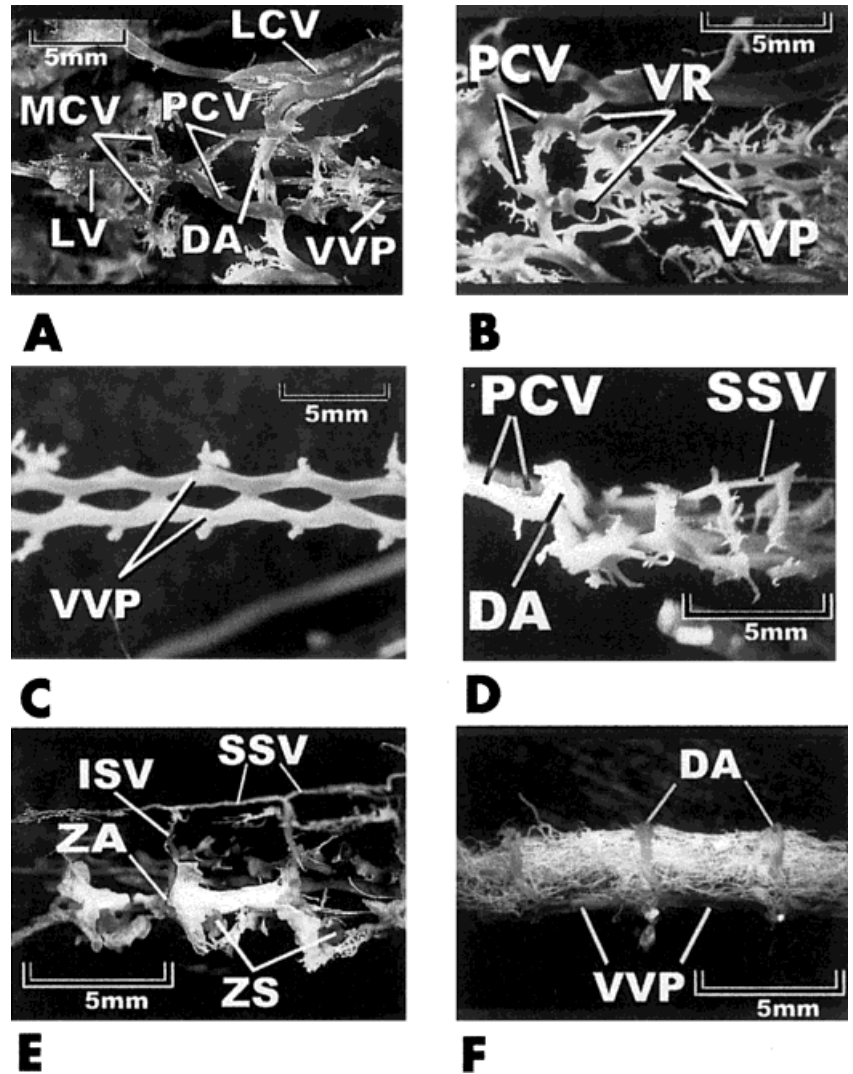
Fig. 1. Corrosion casts of the cervico-cephalic vasculature; anterior to the left. **A:** *Elaphe obsoleta:* cranial origin of the vertebral venous plexus from the posterior cerebral veins at the base of the skull; dorsal view. **B:** *Elaphe obsoleta:* cranial origin of the plexus with demonstration of the vascular rings at the atlanto-axis joint; ventral view. **C:** *Elaphe obsoleta:* isolated vessels of the internal plexus showing symmetry and lozenge or ladder-like structure of the internal plexus; dorsal view. **D:** *Elaphe obsoleta:* a supraspinous vein connects the dorsal arches of the internal plexus; lateral view. **E:** *Elaphe obsoleta:* posterior to the first several cervical segments, the supraspinous vein arises from segmental interspinous veins. A zygopophyseal sinus lies medio-caudal to the articulation of the bony zygapophyses; lateral view. **F:** *Python molurus:* a fine mesh of veins surrounds the spinal cord; lateral view. DA, dorsal arch of the internal plexus; ISV, interspinous veins; LV, longitudinal vein; LCV, lateral cephalic veins; MCV, median cerebral veins; PCV, posterior cerebral veins; SA, spinal artery; SSV, supraspinous vein; VR, vascular rings; VVP, vertebral venous plexus; ZA, zygopophyseal articulation; ZS, zygopophyseal sinus.

trally within the axis by way of some peculiar vascular rings (Fig. 1B) to form the internal vertebral plexus. The longitudinal vessels of the internal plexus extend caudally within the vertebral column to the tip of the tail, bifurcating at each intervertebral joint and reuniting intravertebrally, creating the typical ladder-like formation (Fig. 1B,C).

Only the single, ventral pair of longitudinal vessels was demonstrated in the internal plexus; however, a dorsal arch connects these vessels above the spinal cord at each vertebral joint (Figs. 1A,D,F, 2C). Beginning at the atlas-axis junction, a single, median, longitudinal vessel (the supraspinous vein) connects these arches dorsally (Fig. 1D). It arises directly from the peak of the arches in the first several cervical segments, but from vertical interspinous veins thereafter, forming a longitudinal, subcutaneous, supraspinous vein (Fig. 1E). A small sinus arises from the internal plexus caudal to each venous arch; it lies mediocaudal to the articulation of the zygapophyses (Fig. 1E). This zygopophyseal sinus gives rise to a thin vessel that passes dorso-

laterally between the vertebrae and into the musculature. A fine network of vessels was demonstrated around the spinal cord in several species, but it is unclear if these invest the dura or the surface of the cord itself (Fig. 1F).

There is apparently no intraosseous component to the vertebral plexus of snakes. Occasionally, small vessels do pass ventrally through the vertebral bodies, but no basivertebral veins were found to course longitudinally within the bone of the vertebral column. An external plexus was present, insofar as numerous diminutive vessels course around the column, connecting the internal plexus with the dorsal musculature and caval veins. At each convexity of the internal plexus, where it gives rise to the dorsal arch and the zygopophyseal sinus, a lateral intervertebral vein passes between the vertebrae. The intervertebral receives a small parietal vein from the dorsal musculature, a caudal branch from the paravertebral lymphatic vessels, and continues ventrolaterally as an intercostal vein (Fig. 2A). Other vessels permeate the musculature and surround the
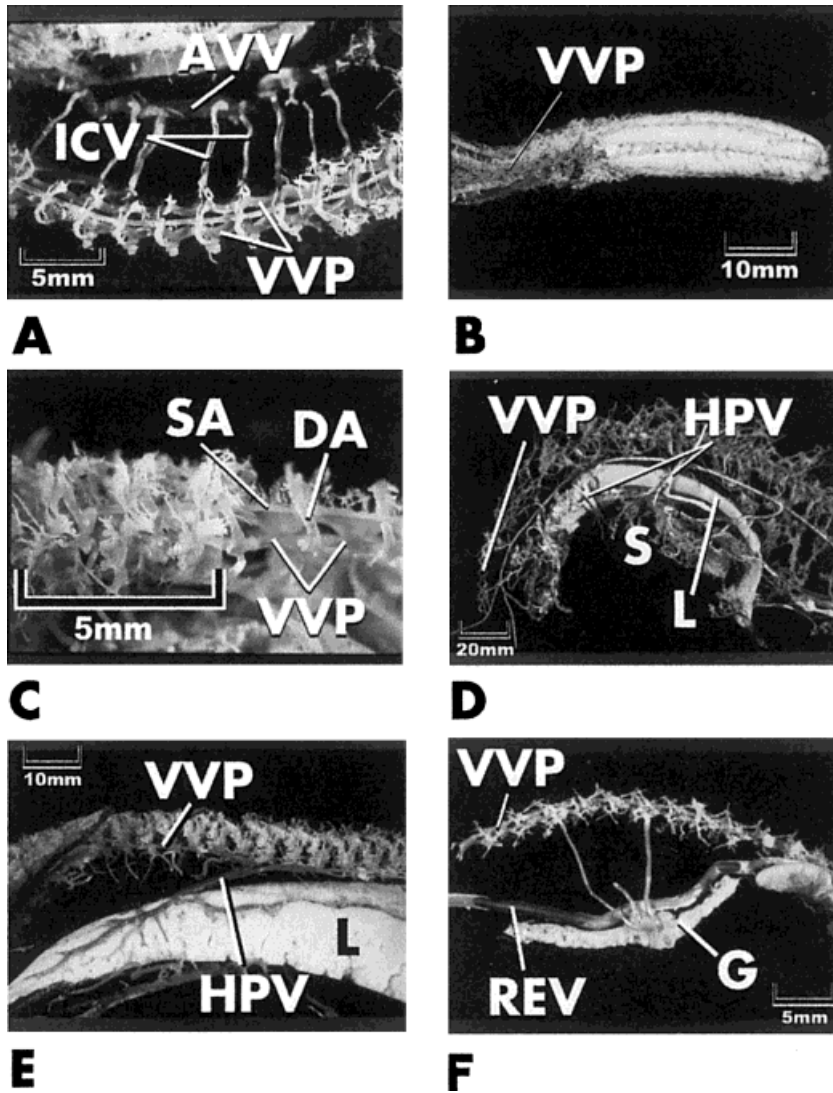
Fig. 2.   Corrosion casts; anterior to the left. **A:** *Elaphe obsoleta:* numerous anastomoses connect the anterior vertebral vein and the venous plexus via the intercostal veins; dorsal view. **B:** *Crotalus adamanteus:* the caudal plexus lying on the dense capillaries of the shaker muscle; dorsal view. **C:** *Python molurus:* the external plexus and lymphatic vessels have been removed posteriorly to reveal the internal plexus; lateral view. **D:** *Crotalus adamanteus:* robust hepatico-parietal veins connect the portal and spinal veins; ventral view. **E:** *Python molurus:* numerous hepatico-parietals form longitudinal vessels that anastomose extensively with the plexus; lateral view. **F:** *Opheodrys aestivus:* the renal efferent veins, where they lie adjacent to the gonads, typically have robust connections with the plexus; ventral view. AVV, anterior vertebral vein; DA, dorsal arch of internal plexus; G, gonad; HPV, hepatico-parietal vein; ICV, intercostal vein; L, liver, REV, renal efferent vein; S, vasculature of the stomach, which sits in the crescent of the liver; SA, spinal artery; VVP, vertebral venous plexus.

column; these are remarkably dense in the epaxial musculature of *Coluber constrictor* and in the shaker muscle of *Crotalus adamanteus* (Fig. 2B). Many of the terminal vessels external to the vertebral column of snakes are small in caliber and some might be components of, or connectives with, the lymphatic system (Fig. 2C).

Multiple anastomoses between the internal plexus and the caval veins exist along the length of the vertebral column. Anterior to the heart, the jugulars communicate with the plexus only at the foramen magnum (Fig. 1A), while the anterior vertebral vein shares numerous transverse connections with the plexus via the intercostal veins (Fig. 2A). Proceeding caudally, the plexus communicates with the anterior vena cava at the level of the heart, the posterior vertebral vein, the posterior vena cava, the hepatic portal vein, the renal efferent and renal portal veins, and the caudal vein, but with none as extensively as with the anterior vertebral vein. However, connections between the plexus and he-

patic portal vein, i.e., the hepatico-parietals, are noteworthy in *Crotalus adamanteus* and *Python molurus* at the level where the portal vein courses into the liver. Where the stomach overlies the liver, the hepatico-parietals are remarkably large in *C. adamanteus* (Fig. 2D). In *P. molurus*, the hepatico-parietals are abundant and frequently form longitudinal vessels within the dorsal musculature above the liver; these vessels anastomose extensively with the vertebral plexus (Fig. 2E). Robust connections between the caval veins, specifically the renal efferent veins, and the plexus are also usually prominent in the vicinity of the gonads (Fig. 2F).

Histology

Transverse sections through the vertebral column of the rat snake revealed the relation between the internal vertebral plexus and the soft and bony tissues of the spine. The two large channels of the
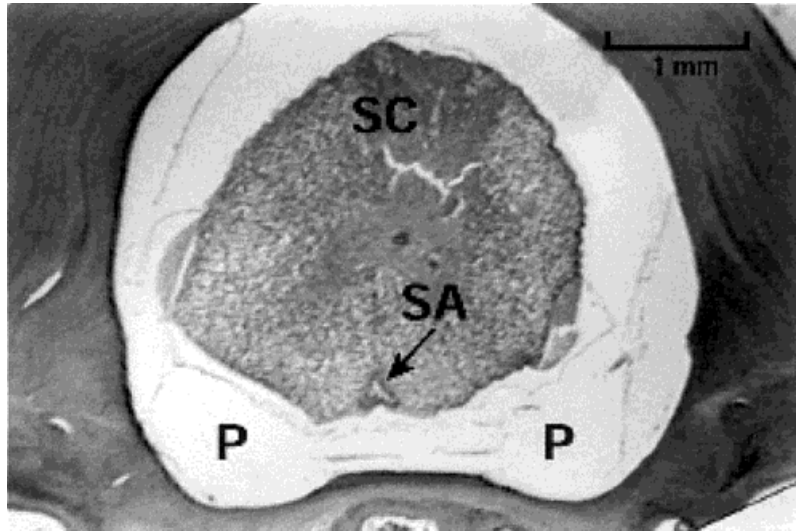
Fig. 3. *Elaphe obsoleta.* Histologic section through the vertebral column, prepared using routine Harris hematoxylin and eosin procedure; dorsal, up; SA, spinal artery; SC, spinal cord; P, venous channels of the internal plexus.

internal plexus lie beneath the spinal cord and spinal artery within the neural canal (Fig. 3). In some sections erythrocytes were clearly distinguishable, at higher power, within the vessels of the internal plexus.

Fluoroscopy

Fluoroscopy in conscious snakes allowed direct visualization of fluid movement from the carotid vasculature of the head into the two venous systems. In the horizontal posture (Fig. 4A), blood drained from the head primarily through the jugular veins, while the plexus was only occasionally faintly indicated. In snakes tilted vertically head-up (Fig. 4B), the plexus became the principal route of cephalic venous drainage and the jugulars were only faintly indicated, if at all. In the relatively smaller pythons, the high pressure associated with injecting viscous
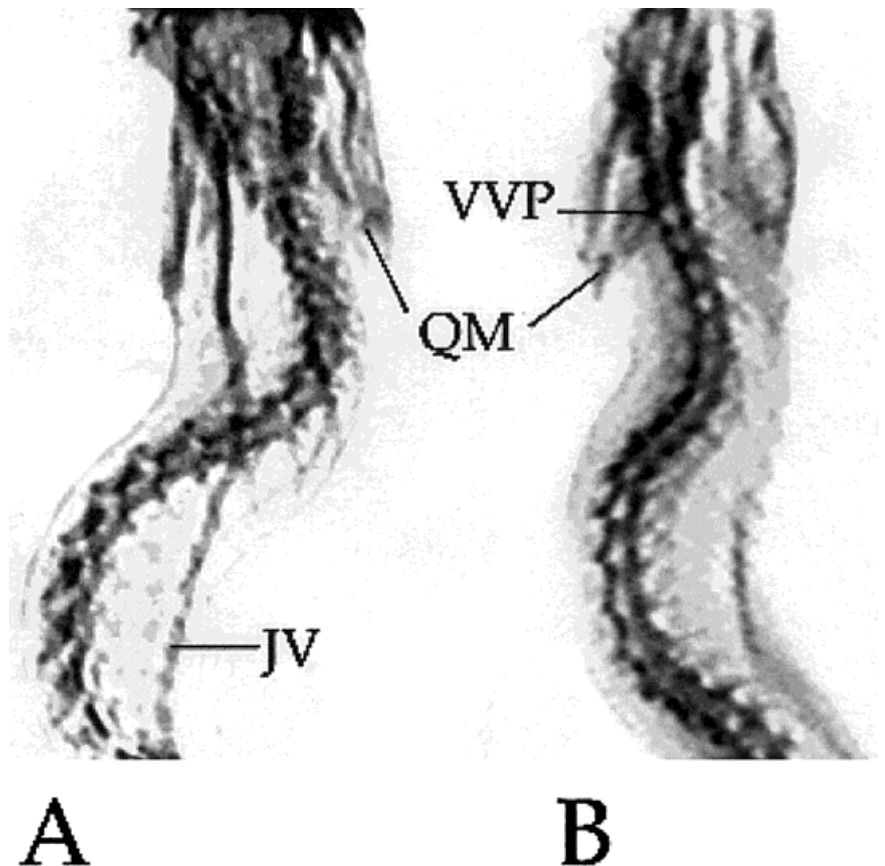

Fig. 4. *Elaphe obsoleta.* Fluoroscopic images showing postural effects on venous return from the head. **A:** In the horizontal posture, venous return occurs exclusively through the jugular veins. **B:** During head-up tilt, venous return is transferred to the vertebral venous plexus. QM, quadrato-mandibular articulation (for reference); JV, jugular vein; VVP, vertebral venous plexus.

contrast medium into small vessels was observed on several occasions to cause considerable jugular return in the vertical posture and, in one instance, retrograde flow in the vertebral artery. However, in the rat snake cannulated in the pulmonary vein, contrast passed through the heart and up the carotid, and no jugular return was evident. During vertical head-down tilt the jugular veins became greatly engorged and no venous return was evident in the vertebral column.

DISCUSSION

Longitudinal (nonplexiform) veins within the vertebral column, i.e., simple spinal veins, have been noted in the snake *Tropidonotus natrix* (= *Natrix natrix*) (Bruner, 1907; O'Donoghue, 1912). These paired vessels were described originating at the base of the head and entering the vertebral column, where they united beneath the spinal cord as a single, diminutive vessel that coursed caudally. However, these investigators failed to realize the magnitude and significance of the entire vertebral venous system. We have revealed that ophidian spinal veins form an elaborate vertebral plexus extending from the base of the skull to the tip of the tail (Fig. 5). This system has robust connections with the other venous systems and appears to play a critical role in postural hemodynamics.

Anatomic Considerations

The anatomy of the plexus in snakes is similar to that in mammals, with several notable exceptions. We did not detect a dorsal portion of the internal plexus, as has been done in several human studies (Groen et al., 1997; but see Hirabayashi et al., 1996). Worthman (1956a,b) did not detect any dorsal vessels in dogs, but rather observed direct dorsal connections between the ventral vessels, as we did in snakes. Geiger and Magnes (1947) found that the same arrangement obtains in the cat. Herlihy (1948) observed dorsal vessels in cats, but only in the upper portion of the cervical region, where in snakes we observed a single median vessel. The dorsal portion of the spinal veins is certainly well developed in pinnipeds and archosaurs. In seals, the dorsal vein is robust and the ventral portion is absent or present only as occasional ventral branches connecting the dorsal vessels (Harrison and Tomlinson, 1956). A similar arrangement is found in birds (Baumel, 1975, 1988) and crocodilians (Rathke, 1866).

An external vertebral plexus was present in all snakes examined and is intimately associated with the paravertebral lymphatic system via myriad connectives. Numerous anastomoses connect the caval veins and the plexus; these are the intercostal veins of other authors (e.g., Beddard, 1904a,b, 1906; O'Donoghue, 1912). We did not detect an intraosseus

component of the vertebral plexus in any snake species.

Our findings are in opposition to those of previous works on the anatomy of the reptilian lymphatic system. One major treatise on reptilian anatomy (Ottaviani and Tazzi, 1977) portrayed lymph vessels within the vertebral column in an arrangement similar to what we observed with the venous plexus. Lymphatic vessels often accompany blood vessels, usually perivascularly in snakes (Chapman and Conklin, 1935). However, it seems unlikely that the authors would describe the lymphatic system in such detail without acknowledging an accompanying plexus of veins that was at that point unknown in reptiles. A more likely explanation is that the vertebral plexus was erroneously identified as a component of the lymphatic system. Other studies of snakes, humans, and tetrapods in general do not describe lymphatic vessels within the vertebral column, and the central nervous system is classically referred to as the only tissue without lymph drainage (Chapman and Conklin, 1935; Kampmeier, 1969; Gray, 1995). However, spinal veins of some form have been described in representatives of most major vertebrate lineages and seemingly represent a synapomorphy for the group. In chondrichthyans these vessels may be longitudinal (O'Donoghue, 1914), rhomboidal (Parker, 1886), or in the form of voluminous sinuses (Kampmeier, 1969). Some spinal vessels in teleosts have been described as lymphatic (Kampmeier, 1969), but spinal veins with distinct connections to the cardinal system have been identified in other osteichthyans (Owen, 1866). Some amphibians possess a simple longitudinal spinal vein dorsal to the cord (Francis, 1934; Millard, 1941), but the serpentiform salamander *Amphiuma means* has a ventral plexiform system similar to that of snakes (KCZ, pers. obs.). Bruner (1907) observed simple spinal veins in the lizard *Lacerta agilis* and in the turtle *Emys europæ* (= *E. orbicularis?*). A rudimentary plexus is demonstrable in iguanian lizards, but varanids possess an extensive plexus comparable to that of snakes, with the addition of major pelvic and pectoral branches (KCZ, pers. obs.). Columbiform, galliform (Baumel, 1975, 1988), and ratite birds (KCZ, pers. obs.), as well as crocodilians (Rathke, 1866; KCZ, pers. obs.), have voluminous spinal veins that originate from an enlarged occipital sinus and extend caudally dorsal to the cord. In mammals, spinal veins are found in the form of a ventral plexus, ventral sinus, dorsal sinus, simple paired dorsolateral vessels, and a dextral sinus (Barnett et al., 1958). Clearly, spinal veins are taxonomically widespread, while spinal lymphatics have only been tenuously identified in one group of advanced fishes (teleosts). Our studies of comparative anatomy, histology, and hemodynamics leave no doubt that the vessels we describe in snakes are indeed veins

Functional Considerations

Although the anatomy of the vertebral venous plexus has been well documented in a number of mammalian taxa, its function has not been so rigorously examined. The plexus has been observed to act as a collateral route of venous return to the heart after occlusion or ligation of various veins in the caval system (Batson, 1944, 1957; Worthman, 1956b, and references therein; Barnett et al., 1958, and references therein). In pinnipeds and sloths the spinal veins are normally the only avenue for venous return from some parts of the body (Wislocki, 1928; Harrison and Tomlinson, 1956). The plexus also acts as a vascular bypass during transient increases in thoracoabdominal pressure induced by coughing and defecation (Batson, 1957), micturition (Herlihy, 1948), lifting and the Valsalva maneuver (Batson, 1957; Eckenhoff, 1970), abdominal tumors (Pritchard et al., 1955; Scott, 1963), position of the viscera (Herlihy, 1948), pregnancy (Hirabayashi et al., 1996), activity of the abdominal muscles (Youmans et al., 1963), normal respiration (Reitan, 1941; Herlihy, 1948; Brecher, 1956; Eckenhoff, 1970), and the manual application of external pressure (Batson, 1940, 1957; Herlihy, 1948; Epstein et al., 1970; but see Worthman, 1956b). Under these various conditions, caval venous pressures rise sharply (e.g., Brigden et al., 1950; Scott, 1963) and blood is forced out of the thoracoabdominal veins and shunted into the plexus. Because of its vast connections throughout the body and lack of valves, the plexus has also been implicated in the multidirectional transfer of disease and air emboli between distant organs and systems (Batson, 1940, 1957; Eckenhoff, 1970). Radiographic and flowmetric studies have indeed verified different directions of flow through the spinal veins under various conditions in primates (Batson, 1940, 1957; Epstein et al., 1970; Dilenge and Perey, 1973; Dilenge et al., 1975), dogs (Herlihy, 1948; Tomlinson, 1956; Worthman, 1956b), cats, sheep, goats (Herlihy, 1948), and seals (Harrison and Tomlinson, 1956; Ronald et al., 1977; Nordgarden et al., 1998).

Blood flow through the vertebral plexus is also affected by gravitational stress induced by posture. In humans and other primates the plexus is a gravity-sensitive network and has been demonstrated radiographically to be the principal route of
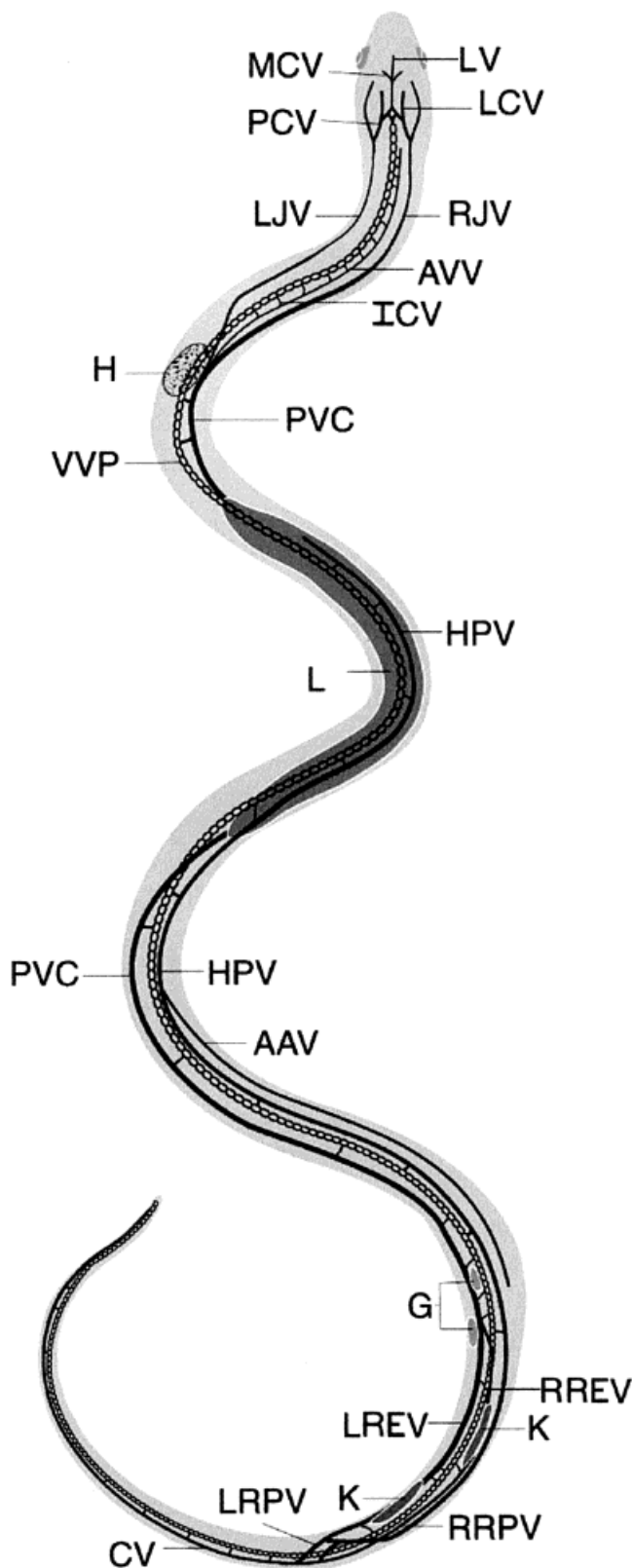

Fig. 5. Composite illustration of the vertebral venous plexus and its connections with the caval and portal veins. AAV, anterior abdominal vein; AVV, anterior vertebral vein; CV, caudal vein; G, gonad; H, heart; HPV, hepatic portal vein; ICV, intercostal vein; K, kidney; L, liver; LV, longitudinal vein; LCV, lateral cephalic vein; LJV, left jugular vein; LREV, left renal efferent vein; LRPV, left renal portal vein; MCV, median cerebral vein; PCV, posterior cerebral vein; PVC, posterior vena cava; RJV, right jugular vein; RREV, right renal efferent vein; RRPV, right renal portal vein; VVP, vertebral venous plexus.

cerebral venous drainage in upright subjects (Epstein et al., 1970; Dilenge and Perey, 1973; Dilenge et al., 1975; Kornienko and Shubin, 1978). Although it is primarily the jugular veins that drain the head in horizontal subjects, direct observations reveal that gravity causes the jugulars to collapse, at least partially, in upright humans (Brecher, 1956; Knebel and Ockenga, 1960; Duomarco and Rimini, 1962; Gauer and Thron, 1965; Eckenhoff, 1966; Blomqvist and Stone, 1983; Pedley, 1987; Ganong, 1995), giraffes (Goetz and Keen, 1957; Pedley, 1987), and dogs (Franklin, 1937; Holt, 1941; Brecher, 1956; Alexander, 1963). The radiographic studies cited above support these observations; little if any jugular activity is observed during upright posture. Venous return in upright primates occurs primarily through the encased plexus, which remains patent due to the structural support of the surrounding bone (Epstein et al., 1970; Dilenge and Perey, 1973). Considering that humans spend most of their time in vertical sitting or standing postures, the vertebral plexus must be considered the primary avenue of venous return from the head (Dilenge and Perey, 1973).

Rat snakes and juvenile Burmese pythons are semiarboreal and frequently adopt a vertical posture while climbing trees, thereby subjecting the blood in their vessels to gravitational stress. As has been observed in many mammals, jugular collapse is evident in some vertically tilted snakes (Seymour and Lillywhite, 1976; Lillywhite and Pough, 1983; Lillywhite, 1993). We have demonstrated that, as in primates, jugular collapse in upright snakes is associated with passage of venous blood into the vertebral plexus. Bruner (1907), based on anatomical observations, estimated that the internal jugular vein in reptiles would carry 90% of the blood from the head, the rest passing through the external jugulars, spinal veins, and other "small" vessels. At least in snakes, this supposition is incorrect for animals in vertical postures.

The system functions in reverse during head-down posture in primates, with blood from the posterior extremities being shunted into the plexus, then into the superior vena cava prior to being returned to the heart (Dilenge and Perey, 1973). The distended dural sac occludes the plexus at the dependent end, so that usually only one end of the plexus is thought to be functional at any given time. Our observations of snakes tilted head-up and head-down support this view.

Although some critics have questioned the ability of the plexus to function as a collateral route of venous flow (see comments of Dean in Falk, 1990), the fact that radiologic studies have verified this repeatedly (see above) and that the plexus can immediately accommodate the venous return after bilateral jugular ligation or ligation of the azygous vein and the anterior vena cava (Batson, 1944; Worthman, 1956b; Barnett et al., 1958, and references therein) is irrefutable.

The Venous Plexus and the Siphon Controversy

Background. There has been considerable debate in the literature regarding venous return and energy expenditure in vertical blood circuits. One group claims that a siphon-like mechanism is in effect whereby the descent of blood in the jugular veins facilitates the ascent of blood in the carotid arteries (e.g., Badeer and Hicks, 1997, and references therein). Others liken venous return through collapsible jugulars to a vascular waterfall where gravitational energy is not reclaimed but rather is lost as frictional heat to the walls of the collapsed vessels (e.g., Pedley et al., 1996, and references therein). In light of the preceding discussion, we wish to help resolve the siphon controversy by drawing attention away from the role of the jugular veins.

A siphon is simply a fluid-filled tube used to drain a reservoir. The high end of the siphon tube is immersed in the reservoir and the low end is either open to the atmosphere at any point lower than the fluid surface or it is immersed in a second reservoir in which the fluid surface is lower than that of the first reservoir. The fluid moves from a point of higher gravitational potential energy in the upper reservoir to one of lower gravitational potential energy nearer the ground. The distinction between a siphon and a drain is that some portion of the siphon tube passes above the fluid surface in the upper reservoir; the fluid first moves up (against gravity) before it moves down. The only energy required to begin the process is to bring the fluid over the summit and to the point where the fluid level in the descending tube is just below that in the higher reservoir. From that point on, fluid draining down the longer descending arm of the siphon draws fluid up the shorter ascending arm and siphoning continues without the input of additional energy.

Physiologists studying the cardiovascular system have taken a keen interest in the "inverted U" portion of the siphon, which superficially resembles the circulation above the heart in an upright tetrapod. The idea that fluid descent in one arm of a vertical circuit could influence fluid ascent in the other is appealing in terms of optimization and energy conservation. The common model of the superior circulation has the inverted U portion of the siphon with both arms of equal length and immersed in a common reservoir (e.g., Seymour and Johansen, 1987). Fluid is recirculated and does not achieve a lower energetic state, so some energy is required to perfuse the loop, but no more than if the loop were horizontal. It is thus not truly a siphon, but if such a *siphon-like mechanism* were operating in the anterior vessels of an upright animal, gravity would have no effect on cephalic blood flow and no addi-

tional energy would be required to perfuse an elevated brain. The only requirement for a siphon-like system is that the gravitational pressure gradients in ascending and descending arms are equal and parallel (Seymour et al., 1993).

In an inverted-U system without flow, the conduits must be rigid to support negative intraluminal pressure without collapsing. However, negative pressures are not required for a siphon-like system to exist. In a system with flow, the ascending conduit can be collapsible if the output of the pump is sufficient to maintain positive pressure in that conduit, i.e., the standing head of the pump is higher than the summit. In the circulation of vertebrates adapted to upright posture, the standing head is always above the summit of the circuit: the heart is capable of pumping blood to the head without any assistance from venous return. This must be so, for even if blood supply to and from the structurally supported cranium occurred through rigid conduits and formed a siphon-like system, the blood vessels of the extracranial tissues are not so protected and cannot support negative intraluminal pressure. To perfuse the sensory organs and other facial tissues, arterial blood pressure must be positive to the top of the head (Seymour et al., 1993).

The descending conduit, on the other hand, must be rigid for a siphon-like effect to occur. This concept was perspicuously conveyed by a series of models in an article by Seymour and Johansen (1987). A rigid descending conduit allows the development of negative pressure downstream from the summit. This negative pressure drives up the perfusion pressure across the summit, thereby facilitating perfusion and compensating for a gravity-induced drop in pressure in the ascending conduit. If the rigid descending conduit of the vertical circuit is removed or replaced by a compliant conduit, negative pressures cannot be sustained downstream from the summit. The pressure there must be atmospheric or greater, and the perfusion pressure gradient and flow are proportionally reduced. Fluid simply falls through the partially collapsed conduit at a fraction of its original rate and "waterfall" dynamics apply. Clearly, the return conduit must be rigid for fluid descent to facilitate fluid ascent (see Seymour and Johansen, 1987, for further discussion).

Jugular vs. spinal veins. Although the jugulars are typically thought of as the primary veins of the anterior circuit, it is now apparent that many vertebrates have prominent spinal veins of one form or another encased within the bony vertebral column (see above). While they surely evolved for reasons unrelated to circulation in vertical circuits, spinal veins have adopted this role in some terrestrial vertebrates. In those animals that have been examined radiographically (humans, rhesus monkeys, rat snakes, and hatchling Burmese pythons), the vertebral plexus is the primary route of venous return from the head during upright posture. The jugulars

receive little flow and are presumed (and sometimes observed) to be at least partially collapsed. The spinal veins, however, are protected from gravity. They always remain patent by way of extensive periosteal adhesion to the bones of the cranium and vertebral column, thus providing a noncollapsible conduit for venous return that is capable of supporting a gravitational pressure gradient parallel to that of the arteries. As blood passes through the cerebral capillary bed, it moves into the open system of cranial venous sinuses and descends through rigid spinal veins. Although the jugulars do receive some efflux from extracranial tissues, the majority of arterial flow to the head is intracranial and passes from the cranial sinuses into the vertebral plexus. The role of the jugulars in vertical circuits therefore seems relatively unimportant.

Passage of cerebral efflux into the spinal veins has great bearing on the siphon controversy. By allowing the development of a gravitational pressure gradient parallel to that developed in the arteries, the encased spinal veins facilitate cerebral perfusion during upright posture in what can be considered a *partial siphon-like mechanism*. Gravitational pressure gradients develop in the anterior arteries and cranial arterial pressure can be reduced by as much as 75% without loss of consciousness (Henry et al., 1951) because a similar gradient develops in the anterior veins. Negative pressure in the cranial venous sinuses has been calculated (Burton, 1972; Badeer and Rietz, 1979) and directly observed (Dilenge et al., 1975; Guyton and Hall, 1996), and clearly obtains during radial acceleration (Rushmer et al., 1947; Henry et al., 1951). These sinuses feed both the jugular and vertebral plexus veins. However, the jugulars are incapable of supporting negative intraluminal pressures and tend to collapse in upright animals. The vertebral venous plexus, on the other hand, is maintained patent by adhesion to the surrounding bone and a negative pressure is maintained within. A collapsing jugular is still capable of receiving flow; however, the plexus offers a patent route of greater pressure drop relative to the jugulars, thereby driving up the perfusion pressure across the brain. As in the models (Seymour and Johansen, 1987), the nature of the return conduit determines the driving pressure and therefore flow. This is only a *partial siphon-like effect* because a small portion of the cephalic blood is descending in the jugulars and in portions of the plexus outside the vertebral column. The potential energy of this blood is not reclaimed.

The effect of negative pressure is directly demonstrable. Lambert (1945) showed that during radial G_z acceleration to simulate hypergravity, perfusion of the unprotected (collapsible) cephalic tissues failed before intracranial circulation, as evidenced by loss of vision but not consciousness. He could restore vision (the unprotected circulation) in one or

both eyes with the application of light suction in a sealed mask over one or both eyes, respectively.

Role of cerebrospinal fluid. The role of the spinal veins in facilitating cerebral perfusion is augmented by interactions with the cerebrospinal fluid (CSF). Vertical posture also induces a gravitational pressure gradient in the CSF and a negative pressure is generated in the cranial dura (Rushmer et al., 1947; Bradley, 1970; Rushmer, 1970; Eckenhoff, 1971). As cranial blood pressures fall, so too do pressures in the CSF that surrounds the blood vessels. As a result, transmural pressure differences similar to those seen in the supine posture are maintained and cerebral blood flow continues uninterrupted (Rushmer et al., 1947). Laboratory models in which "CSF" pressure can be manipulated demonstrate that this parallel change is vital: if "CSF" pressure in the rigid "cranium" is above atmospheric, the compliant vessels representing the cerebral capillaries begin to collapse and perfusion of the "brain" ceases (Seymour, 2000). A similar result obtains in bluefish and rabbits, where artificial increases in intracranial (CSF) pressure cause a decrease in cerebral blood flow that is only partially compensated by a subsequent increase in mean systemic arterial pressure (Beiner et al., 1997).

The second contribution of CSF is only understood when one considers the interaction between CSF and venous blood in the vertebral column. The tissues of the central nervous system and the CSF that bathes them are contained within the rigid bones of the cranium and vertebral column. The volume of this bony compartment is relatively unchanging (Monro-Kellie doctrine) and somewhat larger than that of the nerve tissues and CSF. Much of the remaining space is filled by blood in the venous sinuses of the skull and in the spinal veins of the vertebral column. The amount of each fluid in the craniovertebral system cannot change, but their distributions can. In the horizontal posture, pressures in the CSF and craniovertebral venous systems are approximately equal and fluids in each system are evenly distributed throughout the vertebral column, within their respective conduits (Eckenhoff, 1970, 1971; Nystrom et al., 1998). During upright posture, CSF and blood are both pulled posteriorly in the column. Blood can and does exit the lumbar spinal veins through connections with the abdominal caval veins, but CSF has no such vent: it pools in the lumbar dural sac, further driving the efflux of blood from the lumbar plexus (Reitan, 1941; O'Connell, 1943; Eckenhoff, 1970, 1971; Dilenge and Perey, 1973). Furthermore, approximately 1–2 ml of CSF exit the cranium during upright posture (Reitan, 1941; Eckenhoff, 1971). As CSF is redistributed from the cranium and cervical and upper thoracic regions of the column to the lumbar region, a similar volume of blood, drawn primarily from the cranial sinuses, replaces it. Blood is simultaneously aspirated through the cerebral capillary bed into the cranial sinuses to maintain constant volume of the whole compartment. Note that this role of CSF in facilitating cerebral perfusion is transient and ends when a volume of blood equal to that which left the lumbar plexus is aspirated through the capillary bed; the effect is not sustained throughout the duration of upright posture. This brief augmentation of cerebral blood flow may be an important factor in the maintenance of consciousness at the initiation of vertical stance before other compensatory mechanisms are activated (Henry et al., 1951).

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