

# On the spinal venous sinus of *Alligator mississippiensis*

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## Abstract

The epidural space of the American alligator (*Alligator mississippiensis*) is largely filled by a continuous venous sinus. This venous sinus extends throughout the trunk and tail of the alligator, and is continuous with the dural sinuses surrounding the brain. Segmental spinal veins (sl) link the spinal venous sinus (vs) to the somatic and visceral venous drainage. Some of these sl, like the caudal head vein along the occipital plate of the skull, are enlarged, suggesting more functional linkage. No evidence of venous valves or external venous sphincters was found associated with the vs; the relative scarcity of smooth muscle in the venous wall of the sinus suggests limited physiological regulation. The proatlas (pr), which develops between the occipital plate and C1 in crocodylians, is shaped like a neural arch and is fused to the dorsal surface of the vs. The present study suggests that the pr may function to propel venous blood around the brain and spinal cord. The vs effectively encloses the spinal dura, creating a tube-within-a-tube system with the (smaller volume) spinal cerebrospinal fluid (CSF). Changes in venous blood pressure, as are likely during locomotion, would impact dural compliance and CSF pressure waves propagating along the spinal cord.

## KEYWORDS

epidural space, proatlas, venous sinus

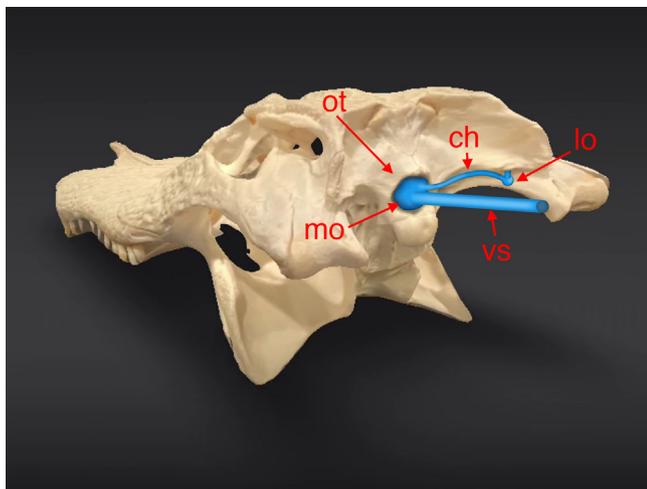
## 1 | INTRODUCTION

In crocodylians, including the American alligator (*Alligator mississippiensis*), the brain and the caudal portion of the skull have both a lateral and median venous drainage (Porter et al., 2016). The lateral venous drainage is by way of the stapedia vein (sv), which exits the skull through the cranioquadrate canal. The median venous drainage is by way of the median occipital sinus (mo) which exits the foramen magnum (fm). Along the caudal surface of the skull, these two venous pathways are linked by the caudal

head vein (ch; Figure 1). A similar venous drainage pattern, with central and lateral venous pathways linked by a ch, has been described in a number of other reptiles (e.g., O'Donoghue, 1921; Oelrich, 1956; Porter & Witmer, 2015). Bruner (1898, 1907) posited that the linked drainage pathways allowed reptiles to perform localized vasodilation and/or localized increases in venous pressure which could facilitate such activities as skin shedding in snakes or thermoregulation. Subsequent studies have confirmed that cephalic shunting of venous blood plays a diverse role in the behavioral ecology of reptiles, such as

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**FIGURE 1** The 3D scan of the skull of a sub-adult *Alligator mississippiensis* with a simple schematic of the linked medial and lateral venous drainage systems. The stapelial vein forms most of the lateral drainage and extends only a short distance beyond the cranioquadrate canal before it merges with the lateral occipital sinus (lo). The median occipital sinus (mo) extends through the foramen magnum and continues along the spinal cord as the spinal venous sinus (vs). The medial and lateral occipital sinuses are link along the caudal surface of the skull by the caudal head vein (ch). ot, otoccipital.

contributing to blood ejection in *Phrynosoma* (Heath, 1966) and the ability to maintain a temperature difference between the head and body (e.g., Johnson, 1975; Webb et al., 1972).

Though the functional or ecological significance of localized cephalic venous shunts have been demonstrated multiple times, aspects of the underlying venous anatomy are not as clear. There has been debate concerning whether some of these venous vessels are veins or sinuses (e.g., Wilhite & Nevarez, 2022; Zippel et al., 2003). This is more than a semantic point, as the lack of smooth muscle in the latter class of vessels (e.g., Balo, 1950; Dagain et al., 2008) limits active physiological regulation. Bruner (1907) described “sphincters” around the cephalic veins of a variety of reptiles; little subsequent work has been done on these sphincters and their histological structure is unknown.

One consequence of shifts in cephalic or spinal venous blood pressure, is alteration of cerebrospinal fluid (CSF) pressure. There is a distinctive pattern of interaction between venous blood pressure and CSF pressure both intracranially and along the spinal cord. Changes in intrathoracic pressure which occur during the ventilatory cycle (Jha et al., 2022) are transmitted to central and spinal venous pressure (e.g., Bloomfield et al., 1997) which, in turn, drives changes in CSF pressure (e.g., Marmarou et al., 1975). The relationship between spinal venous blood

pressure and CSF pressure is particularly complex in the American alligator (*A. mississippiensis*) where the spinal venous sinus (vs), a continuation of the mo (Figure 1), extends along the length of the spinal cord, which means the length of the animal. This continuous vs (Pothiwong et al., 2000; Zippel et al., 2003) is markedly different from the (relatively) smaller and more dispersed venous plexus which characterizes mammals (e.g., Fyeface-Ogan, 2012). The large volume of spinal venous blood in *Alligator*, means that changes in venous blood pressure alter dural compliance, create ventilatory pulsations within the CSF, and can even transmit body movements (English et al., 2023; Taylor et al., 2023). Still, the anatomical relationship between the vs and the spinal dura of *A. mississippiensis* remains poorly known. The goal of the present study was to document the morphology of the vs of *A. mississippiensis*, particularly in relation to intrinsic mechanisms that could influence spinal venous and/or CSF fluid dynamics.

## 2 | MATERIALS AND METHODS

### 2.1 | Specimens examined

This study involved the examination of 13 specimens of the American alligator, *A. mississippiensis*: nine hatchlings/yearlings (total lengths of 24–34 cm), three sub-adults (total lengths 158–164 cm), and one adult (total length of 296 cm). These animals were obtained either from the Louisiana Department of Wildlife and Fisheries, or from commercial vendors. The use and care of these animals followed all applicable national guidelines and was approved by the IACUC of the Kirksville College of Osteopathic Medicine.

### 2.2 | Histological analysis

A bone saw was used to excise the occipital and neck region from four hatchling/yearling specimens that had been previously perfused and preserved using neutral-buffered formalin (nbf). Portions of the vertebral column, extending at least three vertebrae rostral and caudal to the pelvis, were isolated from three of these specimens. Excised tissue blocks were decalcified (RDO rapid decalcifier, Apex Engineering Products), skinned, dehydrated through an ethanol series, cleared in xylene, and embedded in paraplast.

All of the excised tissues were sectioned at 10  $\mu\text{m}$ . In the neck region, serial sections were cut in the frontal and sagittal planes; two of the neck blocks were serially sectioned in the transverse plane. Two of the vertebral blocks were serially sectioned in the frontal and sagittal planes. The third vertebral block was sectioned (non-

serially) in the transverse plane. Mounted sections were stained with hematoxylin and eosin, phosphotungstic acid and hematoxylin, or Masson's trichrome stain (the latter two to better demonstrate the structure of the venous wall). The histological structure was observed using a 4000B microscope (Leica Microsystems, Inc.).

Approximately, 200 serial transverse sections through the neck were scanned with a high-resolution digital scanner (Aperio CS2, Leica). These serial transverse images were then imported into BioVis 3D (BioVis) and used to create a 3D reconstruction of the medial and lateral cephalic drainage pattern of *A. mississippiensis*.

### 2.3 | Micro-CT analysis

The head of one of the yearling specimens was pre-treated in Lugol's solution; then scanned at the University of Texas High-Resolution x-ray Computed Tomography (CT) Facility using a custom-built North Star Imaging scanner in volume mode. The x-ray source was set to 130 kV and 0.14 mA with an aluminum foil pre-filter. A total of 3600 projections were acquired over 360° of rotation, at one frame per second with no frame averaging and no detector binning. A beam-hardening correction of 0.25 was applied; the resulting slices measured 1979 × 1979 pixels and had a voxel resolution of 9.65 μm. The resulting Digital Imaging and Communications and Medicine (DICOM) images were examined using Dragonfly (Object Research Systems).

### 2.4 | Gross dissection

The neck region of two previously frozen sub-adult specimens of *A. mississippiensis* were dissected, as was the pelvic vertebral column from one of the specimens. Two previously preserved yearling specimens were dissected. Isolated vertebrae from the adult specimen, previously fixed in nbf and stored in 70% ethanol, were sectioned transversely using a portable bandsaw (Bauer 1678E-B). The dissections were photographed using a digital camera (Nikon D3100) or a dissecting microscope (Leica M80) using the IC80HD digital camera (Leica).

### 2.5 | Latex casting

Two hatchling/yearling specimens were perfused with saline, euthanized, and the heart incised. Batson's #17 latex (Polyscience, Inc.) was injected into the mo of one specimen, and into the vs of the second. The specimens were placed on ice for 24 h, then eviscerated and placed in 40% potassium hydroxide at 50°C for approximately 2 h. The resulting casts

were photographed under the dissecting scope, and with a scanning electron microscope (TM3000, Hitachi).

## 3 | RESULTS

### 3.1 | Median occipital sinus

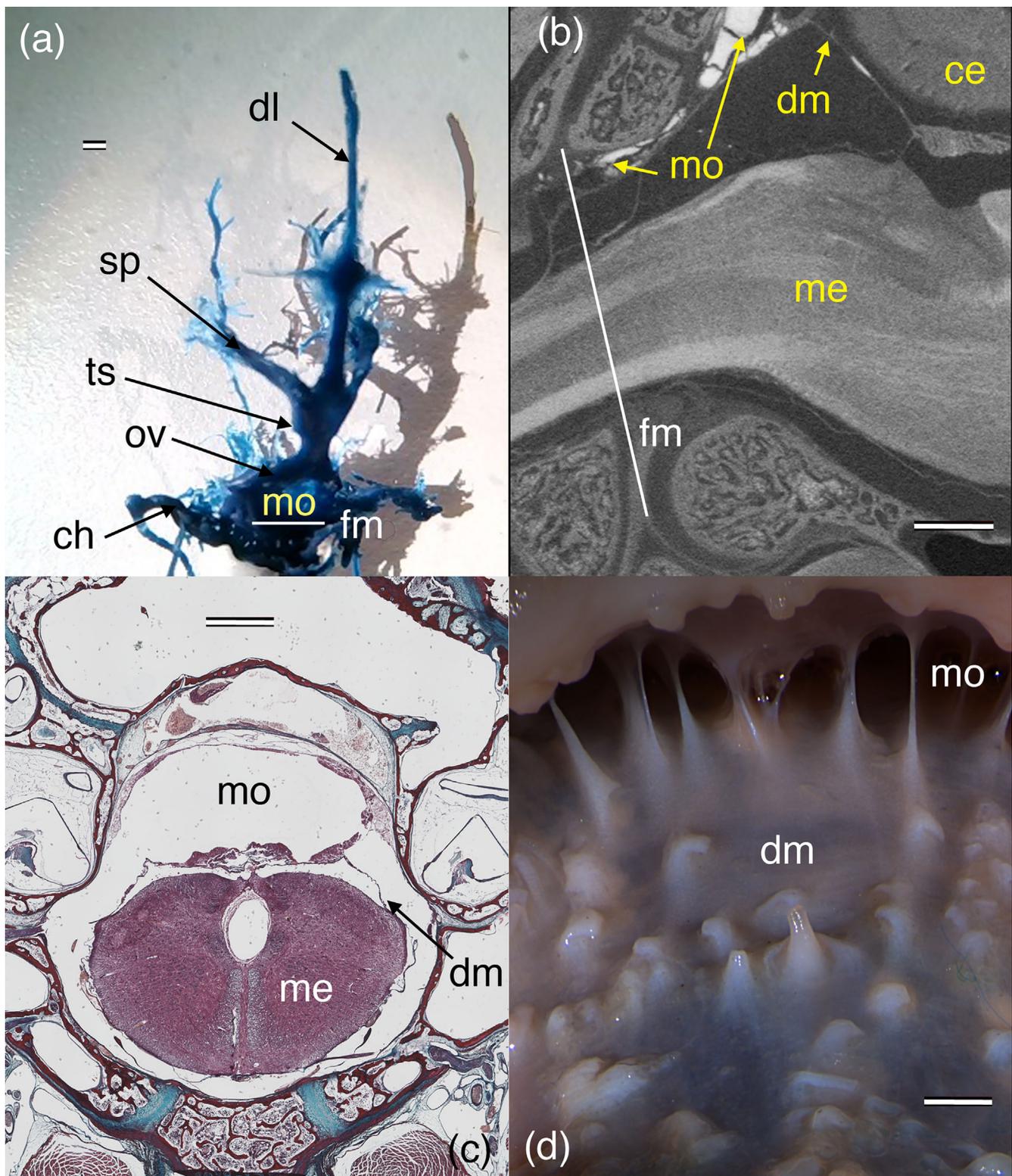
The intracranial dura of *Alligator* includes a dorsal longitudinal sinus (dl) that courses along the dorsal midline of the brain. Between the caudal surface of the cerebral hemisphere and the rostral surface of the midbrain's optic tectum, the sphenoparietal sinus courses dorsally to merge with the dl (Figure 2a). On the caudal surface of the optic tectum, the transverse sinus drains the region rostral to the otic capsule and merges with the dl. The venous sinus system courses around the cerebellum; the occipital venous sinuses are on the rostrolateral surface of the cerebellar hemisphere, while the mo forms on the caudal surface of the cerebellum and extends to the fm (Figure 2). Near the fm, the mo completely encircles the brainstem (Figure 2c). If the mo is drained of blood and opened, a number of connective tissue trabeculae can be seen extending from the superficial surface of the dura (Figure 2d).

### 3.2 | Proatlas

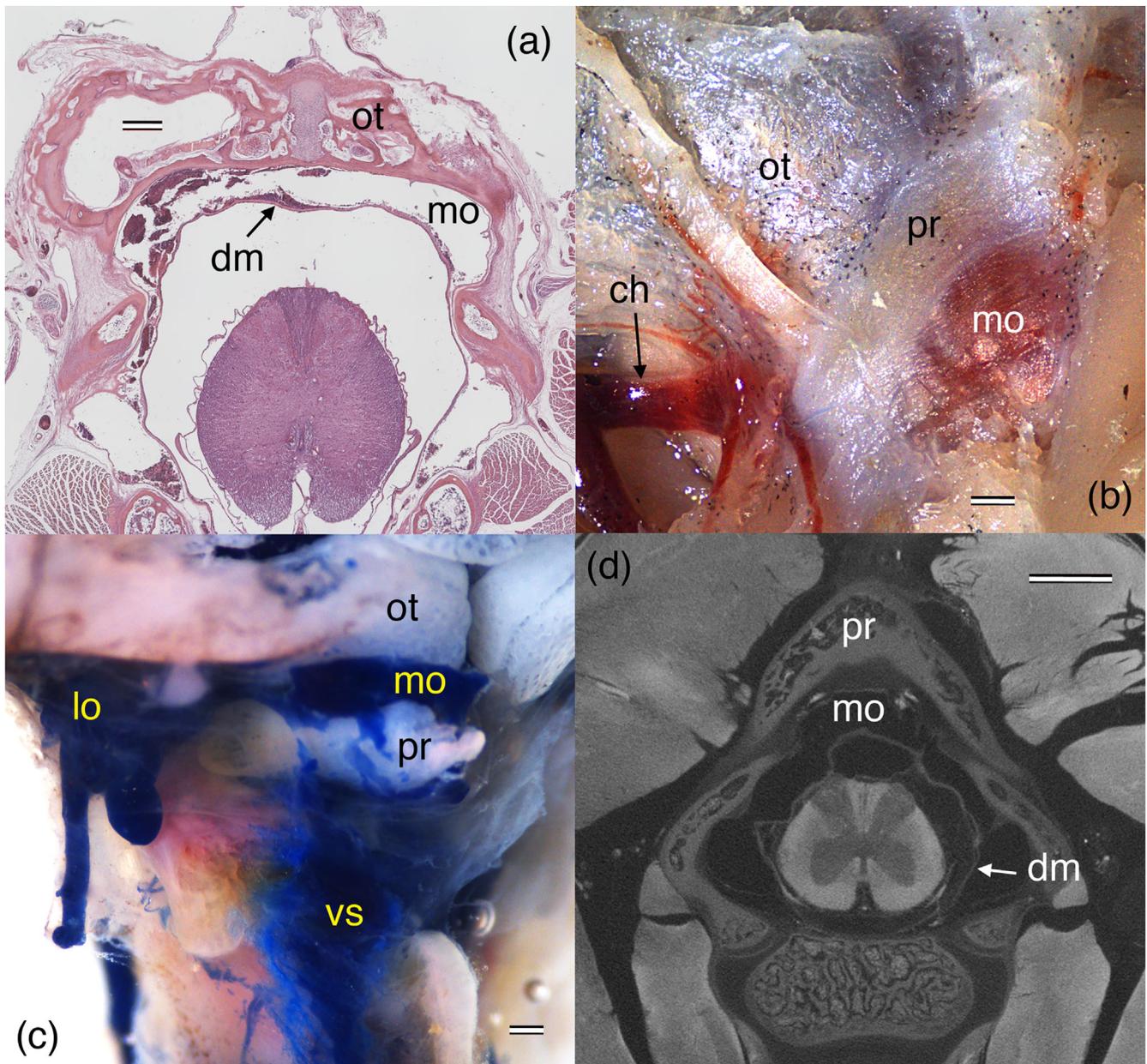
The dorsal surface of the fm is formed by the paired otoccipital bones, which, in younger specimens, are separated by a midline plate of hyaline cartilage (Figure 3a). As the mo extends through the fm, its dorsal and dorsolateral surfaces are covered by the proatlas (pr) (Figure 3b). The pr forms no true articulation with the skull or vertebrae; however, the deep surface of the pr is fused to the superficial surface of the mo (Figure 3c,d).

### 3.3 | Lateral occipital sinus

The sv courses through the cranioquadrate canal then merges with the more lateral temporalmandibular vein (tm) (Figure 4). The junction between the tm and sv is an expanded body herein termed the lateral occipital sinus (lo) (Figure 4). The median and lateral occipital sinuses are linked by the nearly horizontal ch, which merges with the mo near the ventral tip of the pr (Figure 4). There are several small veins that drain into the ch, the most prominent is the cerebral carotid vein which courses parallel to the vertebral column and forms additional (sequential) links to the vs particularly between C1 and C2, as well as C2 and C3 (Figure 4). The lo is drained by the jugular vein (jv).



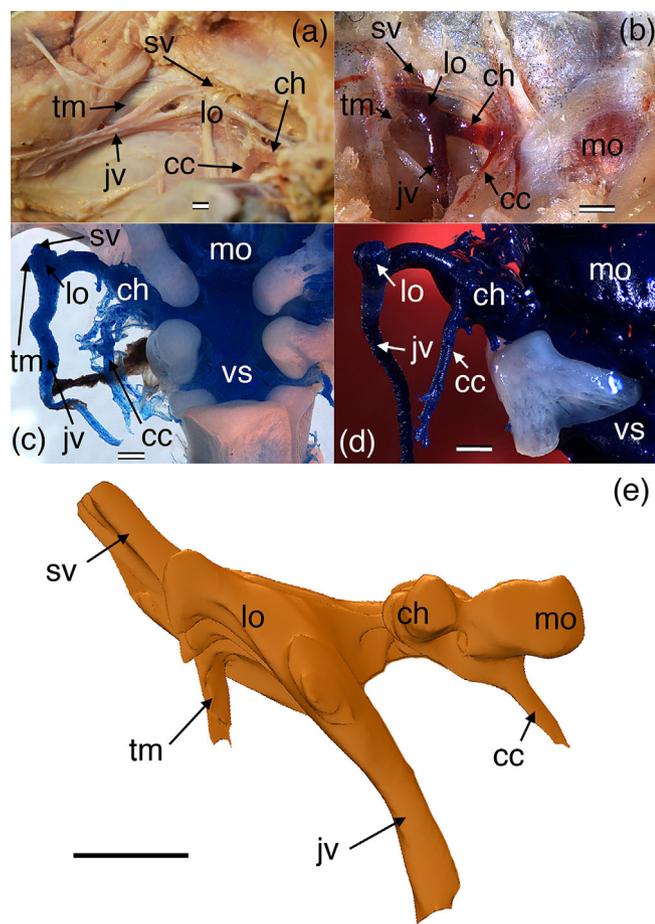
**FIGURE 2** Morphology of the median occipital sinus (mo) in *Alligator mississippiensis*. (a) Latex corrosion cast showing the intracranial sinuses connecting to the mo. (b) Parasagittal micro-CT image; within the skull, the mo expands between the caudal surface of the cerebellum (ce) and the dorsal surface of the medulla oblongata (me). (c) Masson's trichrome stained transverse section through the brainstem just rostral to the foramen magnum; note that the mo completely encircles the cranial dura. (d) Interior view of the mo. The dura of *Alligator* has a blue coloration which is evident through the fused wall of the sinus; there are numerous fine trabeculae within the sinus. ch, caudal head vein; dl, dorsal longitudinal sinus; dm, dura mater; fm (white line), foramen magnum; ov, occipital venous sinus; sp, sphenoparietal sinus; ts, transverse sinus. Scale bars = 1 mm.



**FIGURE 3** Relation of the proatlas to the median occipital sinus. (a) Hematoxylin and eosin stained transverse section just rostral to the foramen magnum (fm). The median occipital sinus completely encircles the dura, expanding slightly laterally where the caudal head vein (ch) will merge. Dorsal to the median occipital sinus are the paired otoccipital bones (ot) with a plate of hyaline cartilage between them. Pushing into the dorsolateral surface of the sinus is the ventral tip of the proatlas. (b) Gross dissection of a hatchling/yearling from a caudo-dorsal perspective. The proatlas can be seen immediately caudal to the otoccipital coursing over the median occipital sinus and covering the confluence between the sinus and the ch. (c) Dorsolateral view of a corrosion cast of a latex-injected specimen. The median occipital sinus passes through the fm (here demarcated by the otooccipital bones), before passing deep to the proatlas. The latex corrosion cast clearly demonstrates the continuity between the median occipital sinus and both the ch (laterally) and the spinal venous sinus (vs) (caudally). (d) Transverse micro-CT image; this image is at a plane slightly caudal to the histological slice in (a) and represents the caudal margin of the proatlas. The venous sinus extends all around the spinal dura, and is directly deep to the proatlas. ce, cerebellum; dm, dura mater; lo, lateral occipital sinus; mo, median occipital sinus; pr, proatlas bone. Scale bars = 500  $\mu$ m.

The confluence of the lateral end of the ch, the sv, the tm vein, and the jv produces an expansion in cross-sectional area (Figure 5a). It is this expanded venous segment that is herein termed the lo. There is

a transition in venous structure between these four veins and the lo (Figure 5b). In each case, the vein has a distinctive tunica media with a high density of collagenous fibers and smooth muscle cells. In the lo,



**FIGURE 4** Morphology of the occipital venous drainage in *Alligator mississippiensis*. (a) Superficial dissection of the lateral occipital sinus (lo) and the veins that merge with it in a sub-adult specimen. (b) Gross dissection of the lo and the veins that merge with it in a hatchling/yearling specimen. (c) Dorsal view of a corrosion cast of a latex-injected specimen; note that the proatlas has been removed from this specimen. (d) Dorsal view of a corrosion cast of a second latex-injected specimen; note that the proatlas and otoccipital bones have been removed from this specimen. (e) The 3D reconstruction of serial transverse histological sections. cc, cerebral carotid vein; ch, caudal head vein; jv, jugular vein; mo, median occipital sinus; sv, stapedial vein; tm, temporalmandibular vein; vs, spinal venous sinus. Scale bars = 1.0 mm.

the wall is thicker (Figure 5c), but there was a lower density of collagenous fibers which showed little organization. There were few (if any) smooth muscle cells present. No evidence of a smooth or skeletal muscle sphincter was found on any of the vessels examined.

### 3.4 | Spinal venous sinus

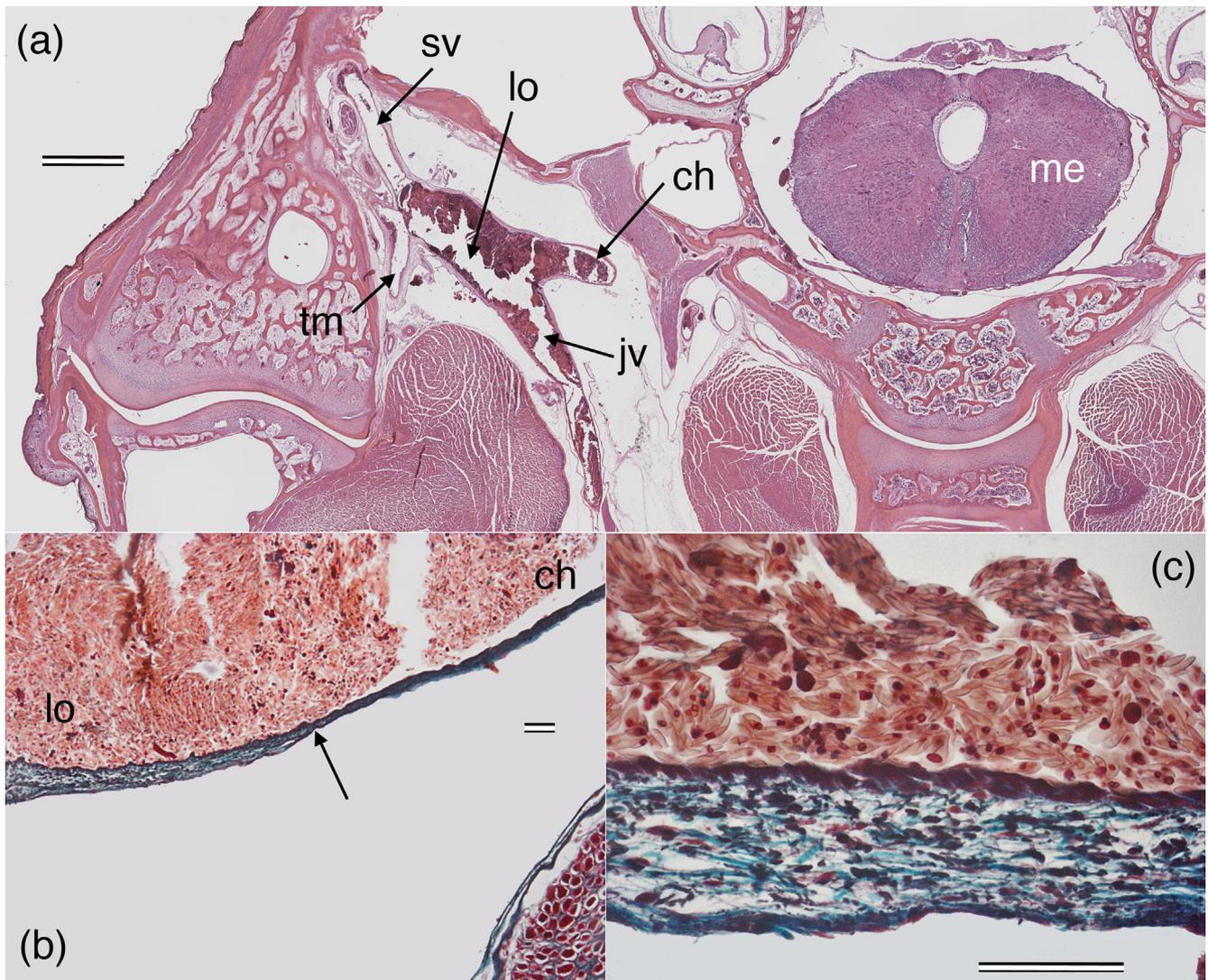
The vs extends caudally from the mo to near the caudal end of the spinal cord. As the spinal cord extends to the terminal caudal vertebra of the tail in *Alligator* (Greer

et al., 2023), there is a continuous venous sinus coursing nearly the entire body length of the animal. The vs fills the dorsal portion of vertebral canal (Figure 6a). The wall of the vs is little more than endothelial tissue; the wall is thinner than what was found in the lo (Figure 5), and does not appear to include a tunica media. The dorsal and dorsolateral surfaces of the vs form localized focal adherences with the inner surface of the neural arches and ligamentum flavum. In contrast, the ventral surface of the vs is fused to the dorsal surface of the spinal dura (Figure 6a).

The vs can be divided into three regions: sinus proper, trabeculate region (tr), and anastomotic region (ar). The sinus proper is what is described above, the large continuous sinus coursing along the dorsal surface of the spinal dura (Figure 6a,b). The tr is located on the dorsolateral and lateral surfaces of the spinal dura; it is continuous with the sinus proper superiorly (Figure 6a,b). The tr is defined by the presence of large connective tissue trabeculae, or septa, which subdivide the branches of the sinus proper into a series of (typically three to four) smaller, roughly parallel, sinuses all extending rostral-caudal. The ar is located on the ventrolateral and ventral surfaces of the spinal dura (Figure 6a,b). The ar is composed of small branches off of the most inferior sinus in the tr; these smaller sinus branches run in a variety of directions and will anastomose in the ventral midline. The small sinus branches within the ar are surrounded by loose connective tissue. The combination of the numerous venous sinuses and surrounding connective tissue gives the ar the appearance of erectile tissue (Figure 6b), more so at the level of gross dissection than histology.

A spinal vein (sl) passes through each intervertebral foramen (Figure 6c). While it is lateral to the foramen, the venous wall has the histological characteristics of a vein, but the tunica media is lost in the foramen as the sl fuses with the sinus branches of the tr. In addition to the sl, and the trabeculate branches, there is a segmental pattern of small supraspinous veins (draining dorsal to ligamentum flavum). Zippel et al. (2003) detailed the sl of *Alligator*. Some of these sl are more specialized. Along the tail, the sl link the vs to the caudal vein which parallels the vs, but courses on the ventral surface of the centrum. At the level of the two sacral vertebrae of *Alligator*, three successive sl (Figure 6d) merge to form the large pelvic vein. The ch may represent a specialized rostral sl.

The unusual structure of the vs in *Alligator*, makes the epidural space in this species distinctive. The majority of the epidural space is located dorsal to the spinal cord, and is occupied almost exclusively by the vs proper (Figure 7a). The parallel sinus branches of the tr occupy the majority of the epidural space deep to the spinal lamina, expanding in each intervertebral space (Figure 7b).



**FIGURE 5** Structure of the lateral occipital sinus (lo) of *Alligator mississippiensis*. (a) Hematoxylin and eosin stained transverse section through the lo. Due to the curvature of the caudal surface of the skull of *Alligator* (Figure 1), the jaw joint (left) and occipital condyle (right) extend further caudally than the rest of the skull. Note the increase in cross-sectional area/volume associated with the lo, compared to any of the associated veins. (b) Masson's trichrome stain showing the merger of the caudal head vein (ch) (right) and the lo (left); note the marked transition (arrow) in the size and structure of the vascular wall. (c) Masson's trichrome stain of the lateral occipital sinus, the thickness of the vascular wall is due to the relatively low density of the collagen fibers. Note the lack of a distinct tunica media. jv, jugular vein; me, medulla oblongata; sv, stapedial vein; tm, temporalmandibular vein. Scale bar in (a) = 1.0 mm; Scale bars in (b and c) = 50  $\mu$ m.

The ventral portion of the epidural space is the smallest, and is primarily filled by the anastomotic branches of the vs (Figure 7c). When the latex cast is viewed from a rostral or caudal perspective (Figure 7d), it is clear that the vs forms an essentially continuous vascular ring around the spinal dura.

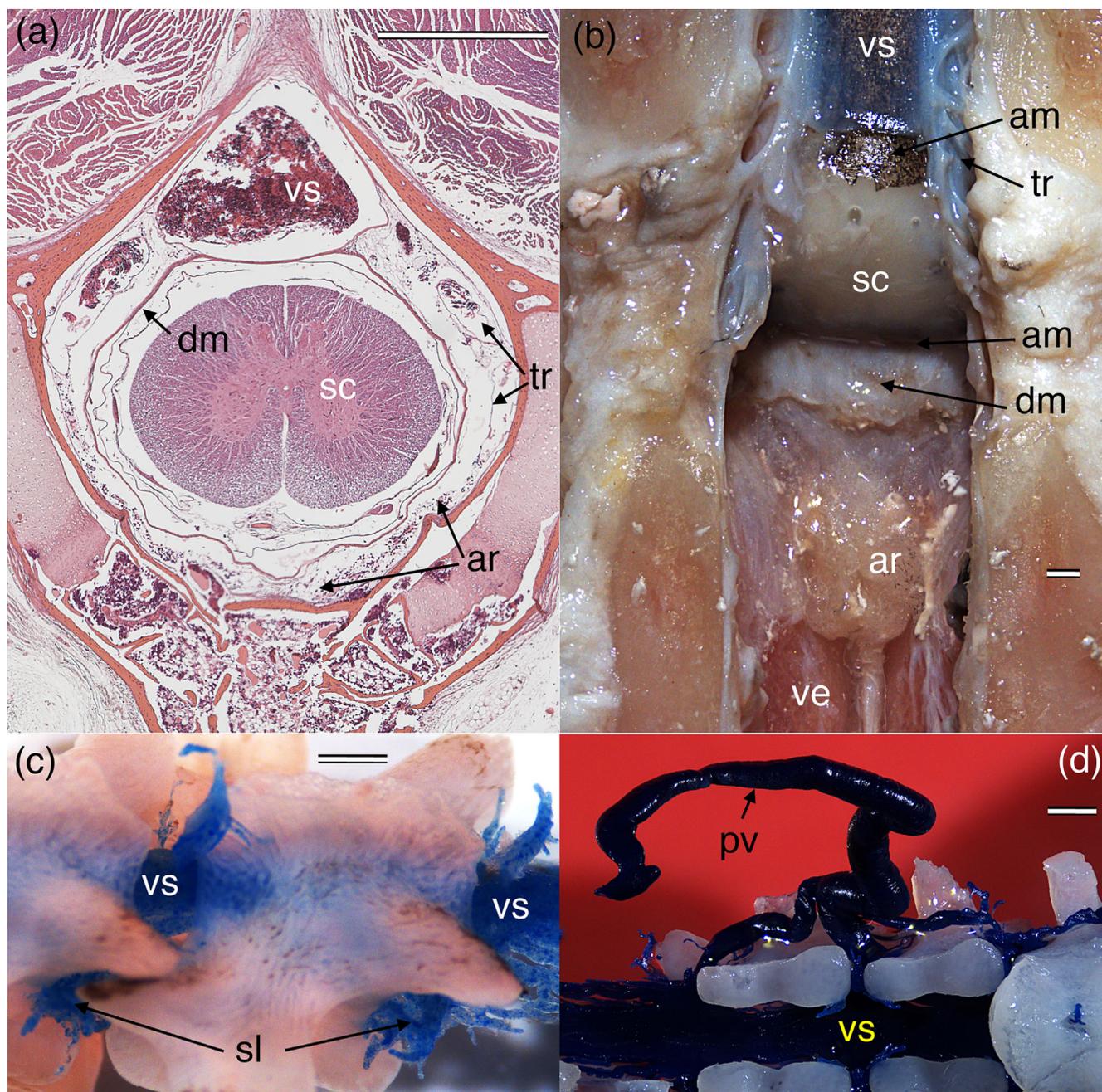
### 3.5 | Luminal morphology

The serial sections cut through the vs showed no evidence of a venous valve (Figure 8a). The sl can be traced through the intervertebral foramen (Figure 8b) and into the vs without encountering any luminal features

suggestive of a valve. The serial sections through the medial and lateral occipital sinuses did not reveal any valves (Figure 8c). The latex injected into the venous system never filled much of the stapedial or tm; this could be due to the presence of venous valves or it may be that the lateral venous drainage was inadequate so simple pressure impeded the flow of the latex.

## 4 | DISCUSSION

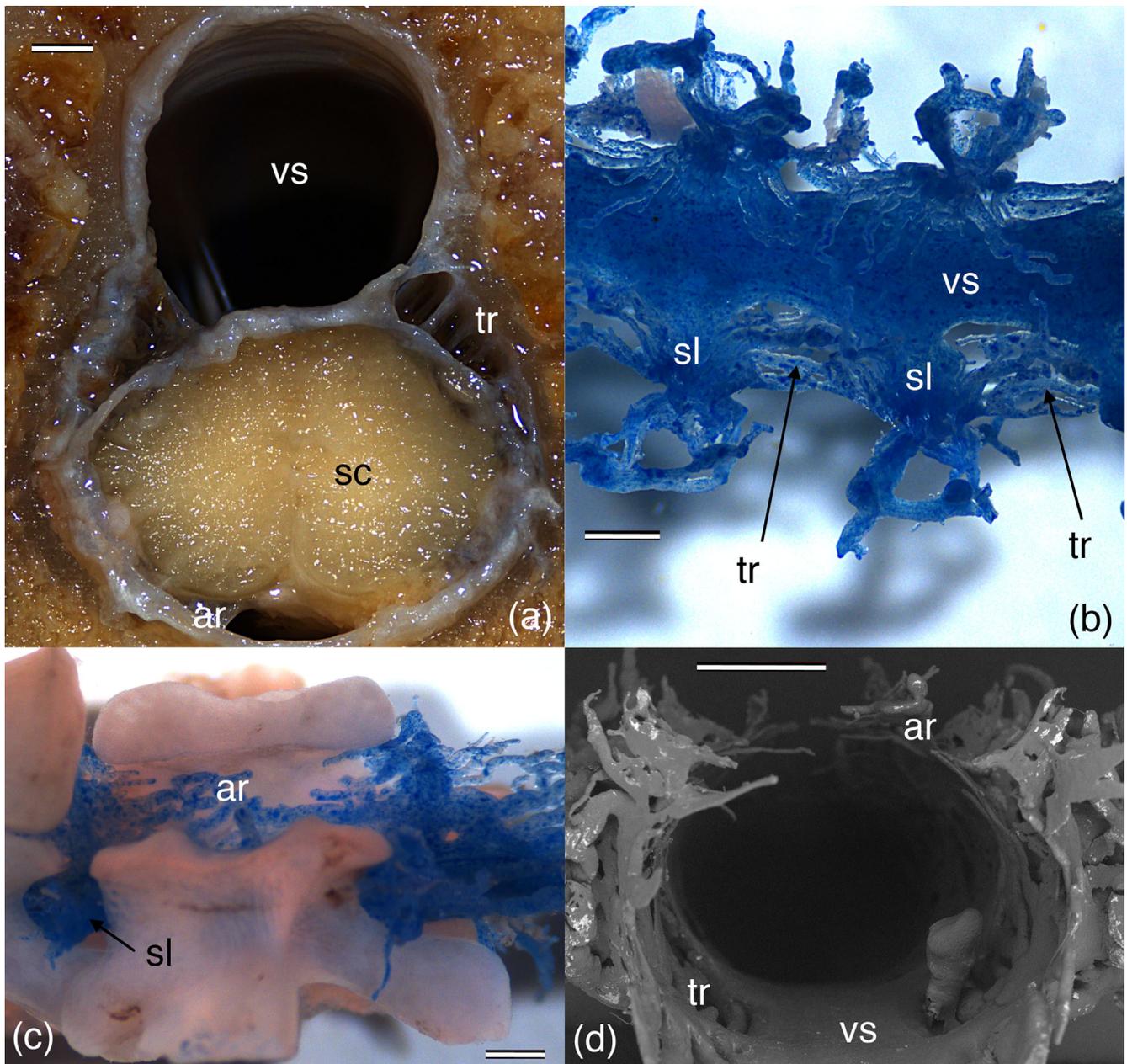
The present study was intended as an extension and merger, of two previous studies; Porter et al. (2016) detailed the venous drainage of the brain and skull, while



**FIGURE 6** Morphology of the spinal venous sinus (vs) of *Alligator mississippiensis*. (a) Hematoxylin and eosin stained transverse section through a vertebra of a hatchling/yearling alligator. The vs encircles the spinal dura and can be divided into three regions: sinus proper, trabeculate region, anastomotic region. (b) Sequential dissection (superficial to deep, top to bottom); fused ventral surface of the vs and the dorsal surface of the spinal dura; trabeculae of the vs; pigmented arachnoid of the spinal meninges; spinal cord (sc); pigmented arachnoid of the spinal meninges; spinal dura; anastomotic region of the vs; dorsal surface of the vertebral centrum. (c) Dorsolateral view of a corrosion cast of a latex-injected specimen; note the spinal vein passing through the intervertebral foramen. (d) Dorsal view of a corrosion cast of a latex-injected specimen. The pelvic vein merges with the vs through three sequential spinal veins. am, arachnoid mater; ar, anastomotic region of the spinal venous sinus; dm, dura mater; pv, pelvic vein; sl, spinal vein; tr, trabeculate region of the spinal venous sinus; ve, vertebra. Scale bars = 1 mm.

Zippel et al. (2003) described the venous system surrounding the spinal cord. There are few detailed descriptions of the cephalic vasculature of crocodylians prior to Porter et al. (2016); the work of Hochstetter (1906) being

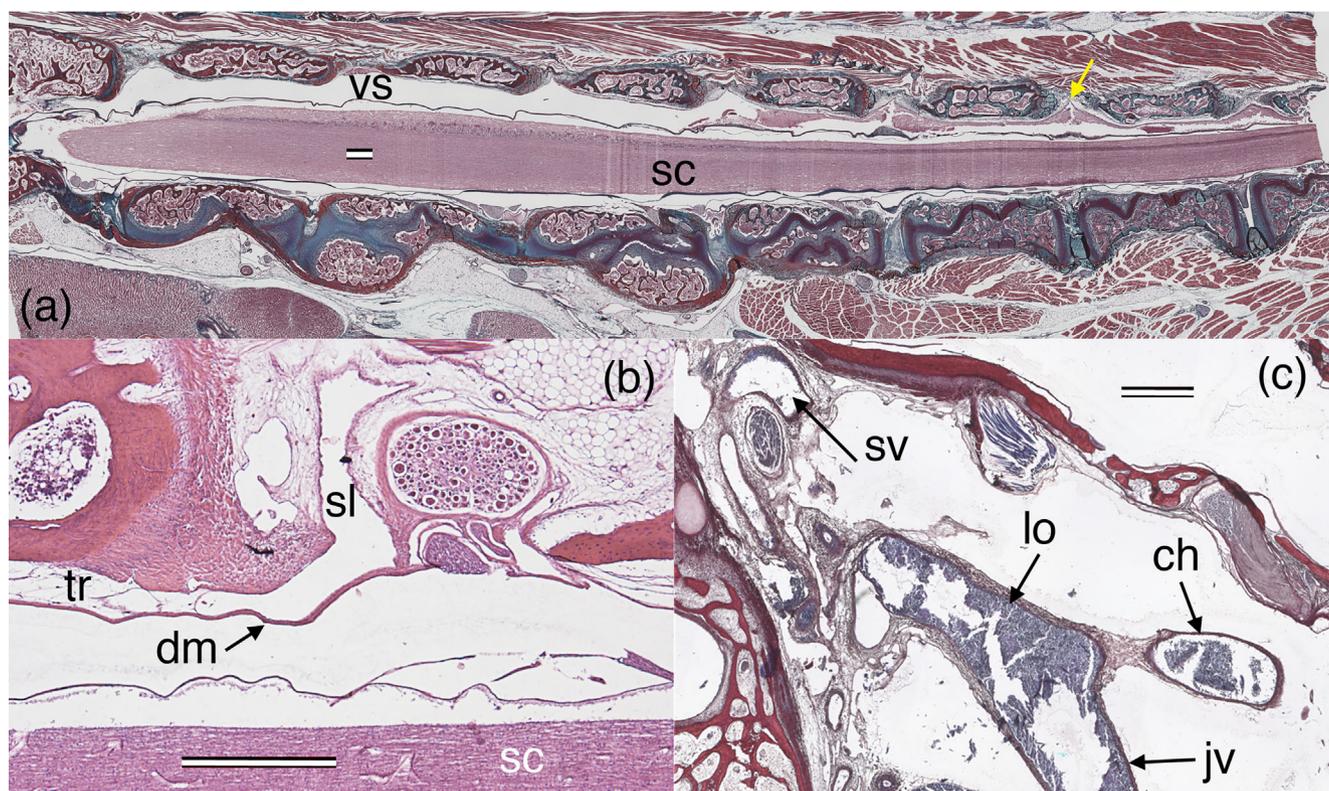
a particular exception. There are only minor discrepancies between the present findings and the work of Porter et al. (2016), most of these are likely due to the combination of anatomical variation, and the fact that the large



**FIGURE 7** The epidural space and spinal venous sinus (vs) of *Alligator mississippiensis*. (a) Gross dissection of an adult *Alligator*, note the relative size of the vs and the prominent trabeculate region. (b) Dorsal view of a corrosion cast of a latex-injected specimen; the nearly parallel sinus branches of the trabeculate region merge with the spinal veins. (c) Ventrolateral view of a corrosion casts of a latex-injected specimen; the fine sinus branches of the anastomotic region course in a variety of directions and anastomose along the ventral midline. (d) Scanning electron micrograph of a corrosion cast of a latex-injected specimen; the sinus proper is on the bottom of the image, while the anastomotic region is on the top of the image. Note that the opening in this corrosion cast would be filled by the spinal dura and spinal cord (sc). ar, anastamotic region of the spinal venous sinus; sl, spinal vein; tr, trabeculate region of the spinal venous sinus. Scale bars = 1 mm.

scope of the Porter et al. (2016) study necessitated that they omit some small vessels. Wilhite and Nevarez (2022) refined one aspect of the Porter et al. (2016) study by describing the lo; the findings of the present study agree with those of Wilhite and Nevarez (2022) and include histological confirmation that this vascular region is a true venous sinus.

The findings of the present study are in general agreement with the description of the spinal venous system provided by Pothiwong et al. (2000) and Zippel et al. (2003). The nature of the arborization region of the vs was not clear in the work of Zippel et al. (2003). This discrepancy may be a purely technical issue as the distribution of the injected latex is dependent on a lack of



**FIGURE 8** Luminal morphology of selected venous elements in *Alligator mississippiensis*. (a) Phosphotungstic acid and hematoxylin (PTAH) stained sagittal section through the pelvic region. The spinal venous sinus (vs) proper is above the spinal cord (sc) while the anastomotic region is below; supraspinous veins can be seen merging with the vs (arrow). No venous valves are present in this section. (b) Hematoxylin and eosin stained frontal section showing a spinal vein passing through the intervertebral foramen (note the dorsal root ganglion) and merging with the vs. No venous valves are present in this section. (c) PTAH stained transverse section through the lateral occipital sinus (lo) and merging veins. None of the luminal walls support valves. ch, caudal head vein; dm, dura mater; jv, jugular vein; sl, spinal vein; sv, stapedial vein; tr, trabeculate region of the spinal venous sinus. Scale bars = 500  $\mu$ m.

resistance in the venous system; as noted above, the presence of retained fluid in the lateral portion of the skull may have impeded the latex filling of the stapedial and tm in the present study. The main distinction between Zippel et al. (2003) and the present study, is that they refer to the venous system surrounding the spinal cord as a vein, while the histological results of the present study indicate it is a sinus. A similar conclusion was reached by Myburgh et al. (2014), whose work was restricted to the region of the fm. While there can be variation in the relative wall thickness of dural and venous sinuses (e.g., Balik, 2019), the relative lack of a tunica media and organized smooth muscle in the walls of sinuses render them less responsive to physiological control.

Physiological studies (e.g., Seebacher & Franklin, 2007) have shown the importance of blood distribution in the regulation of head and body temperature in crocodylians. The anatomical understanding of this system has lagged behind the physiological studies. Porter et al. (2016) filled a significant gap by detailing the vascular system of the crocodylian head. This study was intended, in part, as an extension of

the Porter et al. (2016) study. Due to its length, the vs has a larger total volume than the venous system of the head. Despite the large volume of blood it contains, there is no apparent intrinsic control system to the vs. Neither valves nor external sphincters were found associated with the vs. The lack of valves is a common feature of spinal venous plexus, and leads to its role in the spread of pathologies (Griessenauer et al., 2015). Bruner (1898, 1907) only found external sphincters on veins of the lateral cephalic drainage (and certainly not in all reptiles), so the absence of regulatory sphincters is not remarkable. The extensive integration between the vs and both the head (via the mo and the ch) and the body (via the segmental sl) creates multiple potentials for bidirectional influence on venous blood pressure.

The epidural space of *A. mississippiensis* is unusual among vertebrates due to the elaboration of the venous sinus, which effectively encircles the spinal dura (Figure 7). In humans and other mammals, there is a venous plexus in the epidural space (Liguoro & Barreau, 2020), but this plexus fills only a portion of the “reserve space” within the vertebral canal (Vital, 2020).

In *Alligator*, where there is little to no epidural adipose tissue, no prominent epidural arterial network, and little non-venous space, the vertebral canal is effectively filled by the venous sinus and the spinal dura it surrounds. There is a similar vs located in the dorsal portion of the avian vertebral canal (e.g., Hansen-Pruss, 1923), but it does not appear to branch as extensively nor to encircle the spinal dura as was found in *Alligator*. An extensive vs is not a common reptilian feature. Brocklehurst (1979) does not reference or illustrate it in the turtle. Zippel et al. (2001) described the venous plexus in snakes, where there are paired interconnected sinuses on the ventrolateral edges of the vertebral canal; but as the authors note, in snakes this spinal sinus lacks a “dorsal portion.”

In mammals, and many other vertebrates, the spinal venous drainage can be simplistically divided into several discrete functional groups or layers. Spinal veins drain the neural tissue of the spinal cord (Lasjaunias et al., 2001; Santillan et al., 2012), while radiculomedullary and bridging veins link the sl to the venous sinuses (and/or veins) in the spinal dural (Komiyama, 2020; Thron et al., 2015). Shorter bridging veins connect the dural venous system to the epidural venous plexus; ultimately the venous blood within the vertebral canal is drained by vertebral/sl located on the exterior of the vertebral canal (e.g., Stringer et al., 2012). Multiple specializations have been described at the junction of the bridging veins and the dura, including some non-muscular “sphincters” (e.g., Vignes et al., 2007); these have led researchers to propose that the bridging veins may play a key role in stabilizing venous blood flow (e.g., Mortazavi et al., 2013). While the present study found the “typical” vertebral/sl draining the vs, no clear evidence of bridging veins was observed (Figures 6 and 7). The inner (dural) surface of the latex corrosion casts made from the spinal dural sinus were consistently smooth and devoid of any linking veins (Figures 6 and 7). The results of the present study suggest that in *Alligator*, unlike the more common vertebrate pattern, the spinal epidural venous drainage is largely separate from the deeper spinal venous drainage.

The mobility of the pr, coupled with the close proximity of that bone to the vs (Figure 3), suggests that the pr may function to redistribute blood within the cranial and spinal venous systems. In *A. mississippiensis* displacement of the neck or displacement of the head relative to the neck, or even activation of some of the cervical muscles adjacent to the pr, could all cause displacement of the pr relative to the outer surface of the vs and medial occipital sinus. This displacement would likely influence the flow dynamics within the venous sinus complex, and possibly within the spinal CSF. In this way, the pr is proposed as an osseous analog to the better known myodural bridge system (e.g., Zhang et al., 2016). In *Alligator*,

contractile activation of the myodural bridge skeletal muscle fibers results in displacement of the spinal dura, localized changes in the subdural volume, and associated changes in spinal CSF pressure (Young et al., 2020). Herein, it is proposed that the pr may function in a similar way to influence venous blood pressure, and possibly CSF pressure as well.

The spinal venous system of *A. mississippiensis* suggests that this may be an ideal species in which to explore the full locomotor complexity of the CSF. Locomotion in *Alligator* is driven, as in all other vertebrates, by lower motor (spinal) neurons and the associated spinal neuronal circuitry (El Manira, 2014). Body movements in *Alligator* create pressure waves within both the CSF (Young & Cramberg, 2022a, 2022b) and the vs (Taylor et al., 2023). The pressures waves within the vs simultaneously convey physiological pressures (e.g., inspiration) to the CSF, differentially propagate pressures along the length of the spinal cord, and influence existing CSF pressure waves by altering dural compliance (English et al., 2023). The end result is a dynamic pattern of pressure waves within the spinal CSF of *Alligator* (Young et al., 2021). In vertebrates, presumably including *Alligator*, the spinal cord includes sensory neurons which detect pressure changes within the CSF (Wyart et al., 2023) and have been shown to synapse on the spinal locomotor circuitry (e.g., Böhm et al., 2016).

The vs that fills the epidural space of *A. mississippiensis*, appears to be an extreme among vertebrates. The adult specimen examined for this study had a venous sinus over 3 m in length. Exploring the links between locomotor kinematics and the blood within the crocodylian spinal venous system would provide insights not only into the mechanics of venous blood flow, but also the fluid dynamics within the “ensheathed” spinal CSF.

## AUTHOR CONTRIBUTIONS

**Bruce A. Young:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; formal analysis; project administration; data curation; supervision; resources. **Seth Parker:** Investigation; visualization; writing – review and editing; formal analysis. **Michael Cramberg:** Investigation; visualization; writing – review and editing; formal analysis. **Anchal Scott:** Investigation; visualization; writing – review and editing; formal analysis. **Stephanie Sopko:** Investigation; visualization; writing – review and editing; formal analysis. **Annelise Swords:** Investigation; visualization; writing – review and editing; formal analysis. **Ethan Taylor:** Investigation; visualization; writing – review and editing; formal analysis.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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