

RESEARCH ARTICLE

Neck length and mean arterial pressure in the sauropod dinosaurs

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ABSTRACT

How blood was able to reach the heads of the long-necked sauropod dinosaurs has long been a matter of debate and several hypotheses have been presented. For example, it has been proposed that sauropods had exceptionally large hearts, multiple 'normal' sized hearts spaced at regular intervals up the neck or held their necks horizontal, or that the siphon effect was in operation. By means of an experimental model, we demonstrate that the siphon principle is able to explain how blood was able to adequately perfuse the sauropod brain. The return venous circulation may have been protected from complete collapse by a structure akin to the vertebral venous plexus. We derive an equation relating neck height and mean arterial pressure, which indicates that with a mean arterial pressure similar to that of the giraffe, the maximum safe vertical distance between heart and head would have been about 12 m. A hypothesis is presented that the maximum neck length in the fossil record is due to the siphon height limit. The equation indicates that to migrate over high ground, sauropods would have had to either significantly increase their mean arterial pressure or keep their necks below a certain height dependent on altitude.

KEY WORDS: Heart, Siphon, Circulation, Internal jugular vein, Vertebral venous plexus

INTRODUCTION

The fossil record indicates that some sauropod dinosaurs had neck lengths of the order of 9–12 m (Choy and Altman, 1992). One of the largest sauropods ever discovered is *Sauroposeidon* (Wedel and Cifelli, 2005), which, based on the remains of fossilised vertebrae, had a neck length of 11.25–12 m. A titanosaur fossil with a neck length of 11.3 m has been discovered in Argentina (Lacovara et al., 2014).

A key question is how sauropod brains were perfused at such a large vertical distance from the heart (Hicks and Badeer, 1992; Hohnke, 1973). If the long-necked sauropods held their heads high, very large hearts would be required to generate sufficient pressure to pump blood to the head.

Seymour and Lillywhite (2000) have calculated that in order to overcome orthostatic or gravitational pressure, sauropod hearts would need to develop a mean arterial pressure of the order of 700 mmHg, requiring a left ventricular (LV) mass of about 2 tonnes. According to Seymour and Lillywhite, this is about 15 times greater

than the LV mass of the whale (135 kg), quite out of proportion to the heart/body mass ratio of extant animals; and if the sauropods were warm blooded (endothermic), a 2 ton LV would consume 64% of basal metabolic rate (BMR), about 2.4 times greater than that of the whale.

To overcome the problems cited above, Seymour (1976) suggested that the sauropods may have favoured aquatic habitats so that the surrounding hydrostatic pressure assisted the circulation. In the same paper, Seymour (1976) also suggests that sauropods may have kept their necks low or had hypertrophied hearts or an unusually strong myocardium. Choy and Altman (1992) suggested that sauropods may have had a chain of hearts up the neck, operating as a relay system, with one heart pumping blood up to the next. Later, Choy and Ellis (1998) defended this view and pointed out that some extant animals, for example the squid, have auxiliary hearts.

Another proposed scenario is that the neutral position of the sauropod neck was horizontal (Stevens and Parrish, 1999; Seymour, 2009), so that a high systolic pressure would be unnecessary to pump blood to the head. It has been argued that a horizontal neck would have enabled the sauropods to feed more efficiently – the idea is that sweeping the head from side to side takes less energy than moving the whole body forward in readiness for the next bite (Sander et al., 2011; Sander, 2013).

Although the horizontal neck hypothesis solves the huge heart problem, it raises other issues. For example, in tropical regions, most of the food mass exists high in the canopy and, if sauropods had horizontal necks, they could easily get into a situation where they were unable to raise their head from one side of a tree to another. Even if the sauropods trampled trees to gain access to the leaves above, it is difficult to see how they could do so without significantly raising their heads for at least some of the time.

Allometric studies of fossilised vertebrae have resulted in different points of view about the natural neck pose of the sauropods. The work of Christian (2010), Christian et al. (2013) and Stevens (2013) suggests that the natural neck pose of the sauropods was horizontal. Taylor and colleagues (Taylor et al., 2009; Taylor and Wedel, 2013) have proposed sauropods held their neck in an erect 'S' shape – like a swan, for example.

Badeer and Hicks (1996) suggested that the siphon principle may have been in operation in the sauropod circulation, so that blood flowing down the neck assisted blood flowing up and therefore the heart would only need to overcome vascular friction and not gravity. However, this hypothesis has been criticised on the basis that negative pressures in the head would cause venous collapse. Experiments have been performed that demonstrate that a siphon cannot operate with completely collapsible tubing (Seymour and Johansen, 1987; Seymour et al., 1994; Pedley et al., 1996; Seymour, 2000).

In view of the uncertainty about the pose of the sauropod necks, we think it worth reopening the debate about whether the siphon principle was involved in the sauropod circulation. The main objection to the siphon hypothesis has been that negative pressure would cause complete collapse of cranial veins, thus preventing flow.

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Badeer and Hicks (1996) suggested that a surrounding column of cerebrospinal fluid or a combination of connective tissue and viscous flow pressure could prevent collapse of intracranial venous vessels. As the sauropods were far larger than extant land animals, it would hardly be surprising if they had adaptations to cope with the low intracranial pressures due to extreme neck length. A modern day example of a large animal adaptation is the aorta of the fin whale for diving (Shadwick and Gosline, 1994).

In this paper, we adapt the standard siphon equation and apply it to the sauropod circulation and demonstrate that if the sauropod heart was able to generate pressures similar to those of a giraffe heart, and venous collapse was prevented, the maximum height before cavitation occurred would be about 12 m. This is commensurate with the maximum sauropod neck length found in the fossil record. An interesting question is whether this is coincidence or indirect evidence that sauropods had some means of preventing venous collapse.

MATERIALS AND METHODS

Circulation with 30 m ‘artery-like’ tubing

An experiment to test the sauropod siphon hypothesis was performed in the Gardens Theatre of Queensland University of Technology (QUT). The theatre ceiling is 15 m above the stage floor and has a fly bar system for suspending scenery backdrops. A simplified model of a sauropod circulation was constructed using a submersible electric pool pump (Pondmax PP5000, nominal head of 3.5 m) placed in a bucket of tap water, a 30 m length of 13 mm inner diameter (i.d.) transparent Boston PVC pressure hose, and a paddle flow meter.

Fig. 1A shows a schematic diagram of the experimental setup and Fig. 1B shows the corresponding circulation in a sauropod. The middle of the hose was attached to a fly bar using cable ties. A section of 0.5 m PVC tubing was sliced in half and one half used to undergird the 13 mm hose where it attached to the fly bar to prevent kinking. Red food colouring was added to the water to aid visibility. A flexible tape measure was attached to the fly bar to measure the height above the stage.

A paddle flow meter (Flow Stat ES/Economy series/pulse output, Lake Monitors Inc., Milwaukee, WI, USA) was inserted into the circulation near the exit. The output of the flow meter was connected to an Agilent 1253A logging multimeter set to frequency mode. The hose was primed by switching on the pump when the bar was 1 m above the stage floor. During the experiment, atmospheric pressure was 767 mmHg (101.49 kPa) and the water temperature was 20°C.

The multimeter display was videoed as the fly bar was manually raised towards the roof of the theatre, simulating a sauropod raising its neck. As the bar rose, a member of the team read out the height of the bar in 1 m increments (Fig. 2). Height measurements were accurate to ± 0.1 m. Frequency values were converted to flow in litres per minute (1 min^{-1}) using calibration data supplied by the flow meter manufacturer. A Druck PTX1400 pressure transducer was used to measure pressure at the positions shown in Fig. 1A.

Circulation with 15 m artery-like tubing and 15 m vein-like tubing

A second experiment was conducted in which 15 m of the tubing used in the first experiment was connected to 15 m of collapsible silicone tubing with an i.d. of 12 mm and outer diameter (o.d.) of 17 mm. The pressure hose modelled an artery and the silicone tubing a vein. The two types of tubing were connected using a 13 mm barb connector with Teflon tape wrapped around the barbs to

prevent the ingress of air when the tubing was under negative pressure above the theatre floor.

Flow was recorded as the circulation was raised 1, 5, 10, 11 and 12 m above the pump. As in the first experiment, the multimeter was videoed during the ascent to obtain flow readings. For each height, 10 multimeter readings were averaged and the standard deviation calculated (except for 12 m, where only seven values were available). During this part of the experiment, the water temperature was 21.5°C and atmospheric pressure was 768 mmHg (102.4 kPa).

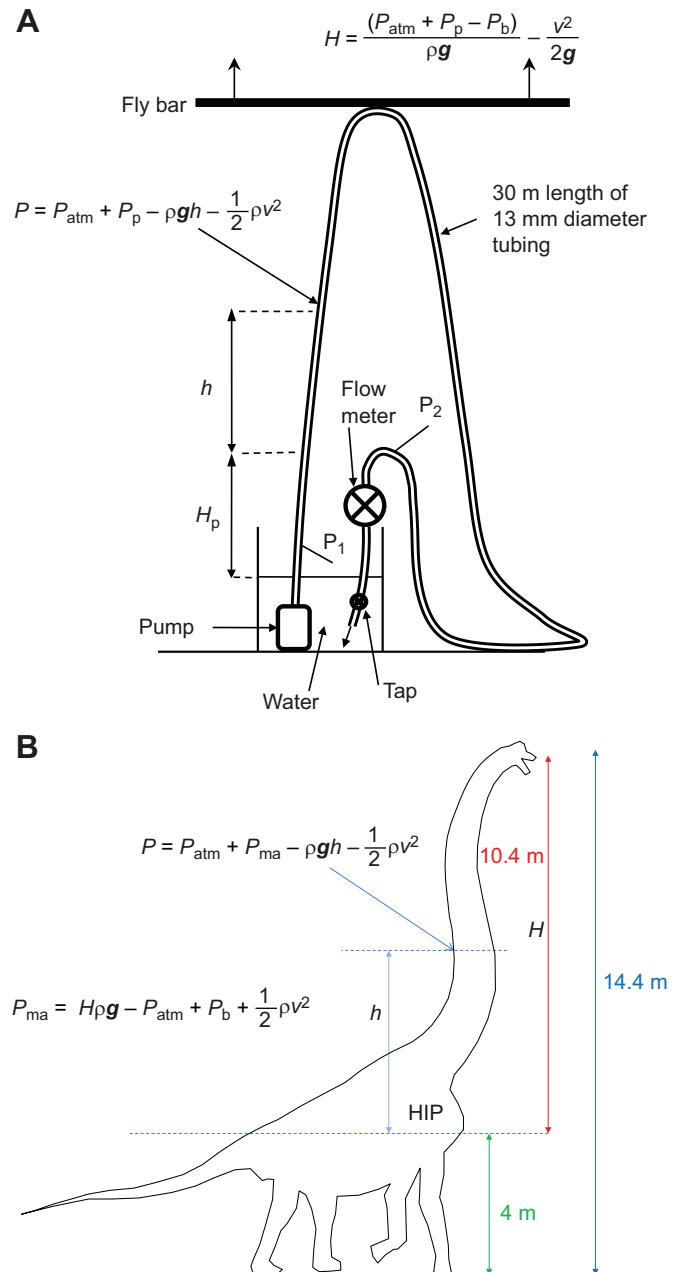


Fig. 1. Simplified model of sauropod circulation. (A) Simulation of head circulation. P₁ and P₂ are the locations where pressure measurements were made. H_p is the head height of the pump (3.5 m). (B) Schematic diagram of a sauropod dinosaur showing an estimate of the position of the hydrostatic indifferent point (HIP) in the thorax. For definitions of variables, see Eqns 3, 4 and 7 (Discussion).

Circulation with 15 m artery-like tubing and 15 m dialysis tubing

A third experiment was performed with a 15 m length of completely collapsible 25 mm-wide dialysis tubing replacing the silicone tubing. Flow values were monitored as the circulation was raised. This experiment failed, although there was some flow up to about 8 m, when the tubing snapped under its own weight; therefore, a fourth, smaller scale experiment was conducted.

Collapsible dialysis tubing

In view of the failure of the circulation with the dialysis tubing, additional experiments were performed to see whether a column of fluid surrounding the dialysis tubing could protect against collapse. Initially, a fourth experiment was performed in which a water pump (AQUAPRO AP200) with nominal head of 60 cm was stuck to the bottom of a stainless steel laboratory sink. A vertical length of 6 mm i.d. PVC tubing was attached to the pump outlet and the head was measured as 60 ± 0.5 cm. A length of 25 mm i.d. dialysis tubing was attached to the end of the 6 mm i.d. PVC tubing. When filled with water, the nominal diameter was $50 \text{ mm}/\pi \approx 16$ mm. This was raised above the surface of the water to demonstrate tube collapse to act as a 'control' for the experiment described below.

Dialysis tubing surrounded by water

A fifth experiment was performed in which the 6 mm i.d. PVC tubing, with the attached length of 25 mm i.d. dialysis tubing was inserted into a 25 mm i.d. PVC tube filled with water, as shown in Fig. 3. For this experiment, the pump was placed in a large glass beaker of water and red food colouring was added. The pump was switched on and the red water observed flowing through the dialysis tubing.

Microsoft Excel for Mac 2011 was used to analyse the data and generate Figs 4 and 5. Fig. 4 (both parts) shows all the data points collected.

RESULTS

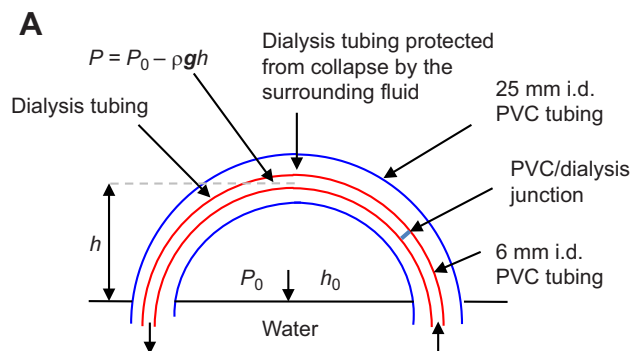
Flow independent of height in a siphon

In the first experiment, as the circulation was raised, flow remained constant at $9.80 \pm 0.07 \text{ l min}^{-1}$ (mean \pm s.d.) to a height of 13 m, but then reduced and stopped at 14.2 m (Fig. 4A). At

13.4 m, the water was seen to boil at the top of the circulation. The pump pressure was $242.5 \pm 1.6 \text{ mmHg}$ ($3.3 \pm 0.2 \text{ m H}_2\text{O}$) and the pressure at the flow meter was $12 \pm 0.6 \text{ mmHg}$ ($0.16 \pm 0.08 \text{ m H}_2\text{O}$). The equation of a straight line fitted to the flow (Q) versus height (h) data was $Q = -0.0062 h + 9.8494$, with a correlation coefficient of 0.135, indicating a high degree of uncorrelation. For a flow of 9.8 l min^{-1} , the mean velocity (v) of the water in the tube was 1.2 m s^{-1} , obtained from $v = Q/A$, where A is the cross-sectional area of the tube. Some bubbles were seen in the water, but these never became large enough to break the circulation.

Siphon flow maintained with partially collapsed tubing

In the second experiment, with the artery+vein, the flow was $9.83 \pm 0.05 \text{ l min}^{-1}$ at 1 m, almost identical to the flow recorded in the first experiment, and then reduced with height, as shown in



B



Fig. 3. Prevention of the collapse of dialysis tubing by a surrounding column of water. (A) PVC and dialysis tubing surrounded by a column of water, which protects the dialysis tubing from collapse. (B) Photograph of dyed water flowing through the dialysis tubing surrounded by a column of water in a 25 mm inner diameter (i.d.) PVC tube. The dialysis tubing was connected to 6 mm i.d. PVC tubing – the three cable ties can be seen about half-way up the right-hand side of the tube.

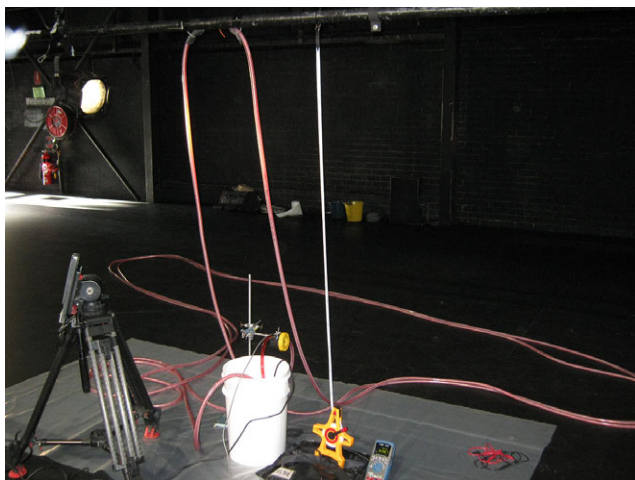


Fig. 2. Photo of the model circulation. The paddle flow meter is seen at the top of the bucket, which is connected to the blue multimeter to the right of the yellow 15 m tape measure.

Fig. 4B. When the top of the circulation was at 13 m, inspection of the tubing revealed that it was flattened within a few metres of the top, although with side channels still open. The flow meter stopped rotating when the tubing was at 13 m, although water still flowed.

Failure of siphon with dialysis tubing

In the third experiment, the flow was much less because of the collapsed dialysis tubing but the tubing snapped at 8 m as the tubing was unable to support its own weight.

Dialysis tubing collapses under slight negative pressure

In the fourth experiment, when the end of the tubing was below the surface of the water, the dialysis tubing was full of water and rounded. However, when the end of the PVC tubing was raised a few centimetres above the water, the dialysis tubing collapsed, although some flow continued out of the sides of the collapsed tubing up to 60 cm, i.e. the pump head. Above this height, flow stopped. When the height was less than the head height, there was a small amount of pressure to push the water through the channels at the side of the collapsed tubing.

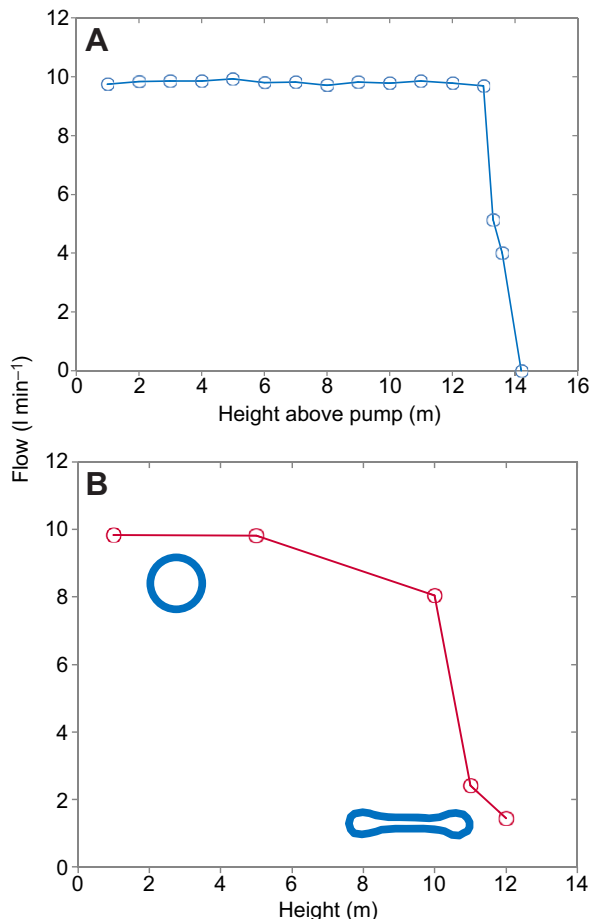


Fig. 4. Circulation flow versus the height of the circulation apex above the pump. (A) First experiment, using the artery-like tubing. Vertical error bars are less than half the diameter of the circles. (B) Second experiment, where half the circulation was replaced with collapsible vein-like silicone tubing. For 1, 5 and 10 m, the vertical error bars are much less than half the diameter of the circles; for 11 and 12 m, the vertical error bars are $\sim \pm 0.5$ l min⁻¹. The insets show the approximate cross-section of the venous section of the tube below 10 m (top left) and above 10 m (bottom right).

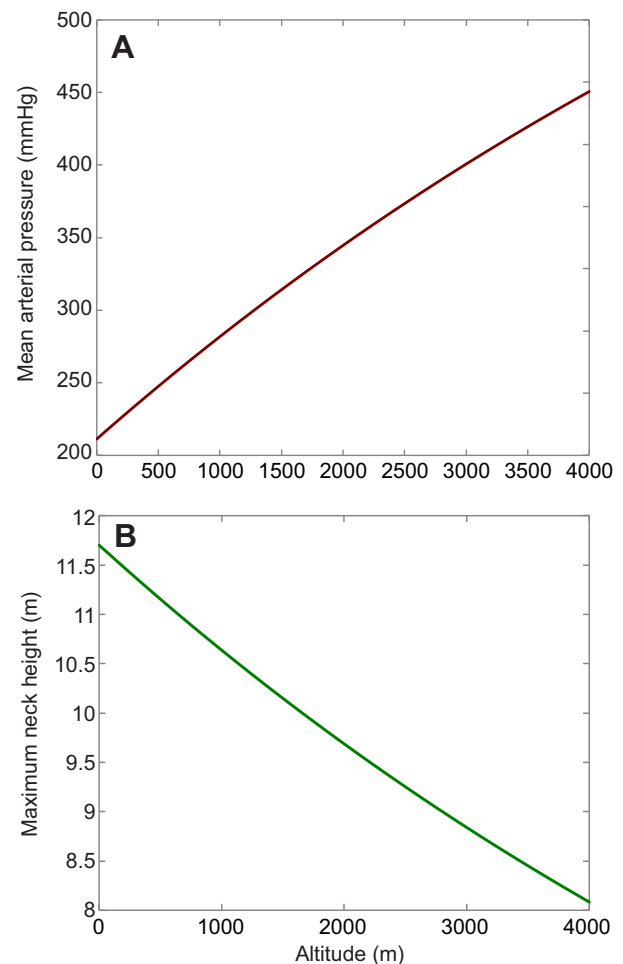


Fig. 5. Variation of mean arterial pressure and neck height with altitude. (A) Plot of the variation of mean arterial pressure with altitude, assuming a fixed vertical neck length of 12 m, with an initial mean arterial pressure similar to that of the giraffe at sea level. (B) Variation of maximum vertical neck height with altitude, assuming a constant mean arterial pressure similar to that of the giraffe.

Dialysis surrounded by a water column is protected from collapse

When the PVC tubing with the dialysis tubing connected was inside the 25 mm i.d. PVC tubing surrounded by water, the dialysis tubing did not collapse. The height of the arch was several times greater than the height that caused collapse when the dialysis tubing was above the surface of the water.

DISCUSSION

Our experiments demonstrate that in a model of the sauropod circulation, flow can be maintained to a height of 13 m with a pump pressure similar to the mean arterial pressure of the giraffe. The constancy of flow indicates that the pressure gradient across the circulation was constant up to 13 m. This demonstrates that the siphon effect was in operation. The water in the ascending column was counterbalancing the water in the descending column; therefore, the pump only needed to provide energy to push water through the 'vascular' resistance.

In the artery+vein experiment, although the flow was less than in the first experiment, flow continued to 13 m because the partially collapsed tubing had channels remaining open at the sides, as shown in the inset in Fig. 4B. This observation corroborates the experimental work of Badeer and Hicks (1996). However, flow

ceased when completely collapsible tubing was used. Our fifth experiment demonstrates that a surrounding column of fluid can prevent collapse of the dialysis tubing. The result of this particular experiment is independent of scale. An analogy is performing an experiment demonstrating the increase of hydrostatic pressure with depth in a fish tank and applying the result to a glass of water and the ocean.

Giraffe circulation

Of relevance to the discussion in this paper is whether a siphon operates in the giraffe circulation. For example, Mitchell et al. (2006) suggest that the high mean arterial pressure of the giraffe is to overcome gravity and that complete venous collapse prevents a siphon from operating. In contrast, experiments performed by Goetz et al. (1960) have shown that when giraffes raise their head, the increase in systolic pressure is not enough to compensate for the change in orthostatic pressure. Badeer (1988, 1997) has shown that the high aortic pressure of the giraffe is required not to overcome gravitational pressure but rather to ‘push’ against the high peripheral resistance of the systemic circulation. This effect largely cancels the gravitational reduction in venous pressure so that the venous pressure stays close to atmospheric pressure without collapse of the veins (Badeer, 1986).

Whether or not veins completely collapse in the giraffe is not strictly relevant to whether or not a siphon operates in the giraffe circulation. Even if giraffe jugular veins completely collapse when vertical, venous return continues as giraffes can stand for long periods of time without fainting. If there is a continuous fluid column, a siphon can operate.

A recent finding relevant to this discussion is that the left ventricle of giraffe hearts is able to develop high pressure with normal wall tension at the expense of a reduced stroke volume and cardiac output (Smerup et al., 2016). An interesting question is whether the sauropod heart was an ‘extrapolation’ of the giraffe heart. If this was the case, then this may explain how blood was able to reach the high head of the sauropods. A siphon would still be in operation as this occurs whenever there is a continuous fluid column. This would reduce the energy requirements of the heart.

Human circulation

There is evidence that a siphon operates in the human cranial circulation. The venous system above the heart is at negative pressure (Chapman et al., 1990) and there is little change in cranial blood flow when pilots undergo training in high-*g* centrifuges (Howard, 1977). Negative cranial pressures are of particular concern in cranial neurosurgery where venous air emboli are a well-known phenomenon when operations are performed with the head above the heart (Gale and Leslie, 2004; Munis and Lozada, 2000). The human venous system has various features that protect against collapse; for example, the major cerebral veins (or venous sinuses) are rigid structures permanently held open as a result of splitting of the fibrous dura mater, despite transient pressure changes (Greenberg, 2006). It is possible that sauropods also had similar features to cope with extreme negative cranial pressures.

The internal jugular veins and vertebral venous plexus

Recent studies of the human circulation have looked at the interplay between venous flow via the internal jugular veins (IJVs) and vertebral venous plexus (VVP). The experimental evidence suggests that the IJVs may be either completely or partially collapsed when vertical (Gisolf et al., 2004; Ciuti et al., 2013) and open when horizontal. When the IJVs are vertical and collapsed,

venous flow is diverted through the VVP. In reality, the two pathways probably experience constant flow; however, their flow distributions vary depending on the height of the brain relative to the heart. Clearly, the vessels of the VVP must be protected from collapse. This could be by the surrounding interstitial fluid and the cerebrospinal fluid – as suggested by our fifth experiment. Whatever the situation, venous flow is equal to arterial flow when the circulation above the heart is vertical, otherwise venous hypertension would result in loss of consciousness.

Even if venous return were split between the IJVs, VVP and other vessels, a siphon would still be in operation because a continuous fluid column exists. It would seem reasonable that the sauropods also had two alternative pathways for venous return from the head: IJVs for the head-down position when drinking (otherwise they would have to reside close to a tall waterfall) and a VVP system for holding their head high.

The Bernoulli equation applied to a circulation with pump and siphon

The siphon form of Bernoulli’s equation can be modified and applied to the sauropod circulation. The basic ‘text book’ form of Bernoulli’s equation is:

$$P + \rho gh + \rho v^2/2 = \text{constant}, \quad (1)$$

where *P* is the pressure along a streamline in the siphon, ρ is the density of the liquid, *g* is the acceleration due to gravity (9.8 m s^{-2}), *h* is the height above the upper reservoir level and *v* is the velocity of the liquid at a point in the streamline. The term ρgh gives the pressure due to gravity, and $\rho v^2/2$ the pressure due to kinetic energy.

The constant in Eqn 1 can be evaluated by calculating the pressure at the surface of the water in the reservoir (*h*=0) at zero flow (*v*=0). In this case, the constant is atmospheric pressure (P_{atm}). After some rearranging, Eqn 1 becomes:

$$P = P_{\text{atm}} - \rho gh - \frac{1}{2} \rho v^2. \quad (2)$$

In our experimental arrangement, the pump pressure (P_p) augments atmospheric pressure and so Eqn 2 becomes:

$$P = P_{\text{atm}} + P_p - \rho gh - \frac{1}{2} \rho v^2. \quad (3)$$

If *P* in Eqn 3 is made equal to the vapour pressure of water at a given temperature, i.e. the pressure at which water begins to boil at a given temperature ($P=P_b$), Eqn 3 can be rearranged to give the maximum height (*H*) of the circulation before the water column breaks due to cavitation, i.e. the height at which water boils:

$$H = \frac{(P_{\text{atm}} + P_p - P_b)}{\rho g} - \frac{v^2}{2g}. \quad (4)$$

The last term ($v^2/2g$) only has a small effect on the maximum height. For example, if the average water velocity is 1.2 m s^{-1} the negative pressure is $0.72 \text{ m H}_2\text{O}$. Therefore, when dealing with a circulation several metres high with a flow velocity of the order of a few m s^{-1} , the kinetic energy term can reasonably be neglected.

Inserting the values for the first experiment into Eqn 4, i.e. an atmospheric pressure (P_{atm}) of 767 mmHg (101.49 kPa), pump pressure (P_p) of 242 mmHg (21.8 kPa) and water vapour pressure of 16.5 mmHg (2.18 kPa) at 20°C, produces a maximum height of 13.4 m.

Boiling and bubbles

In the first experiment, water was seen to boil at 13.4 m, although flow continued up to 14.2 m. This is probably because bubbles were quickly swept from the top of the siphon and condensed in the higher pressure region downstream before expanding sufficiently to break the circulation. There is good agreement between the experiment and the theoretical maximum circulation height H given by Eqn 4.

The rate of bubble formation is relevant to the maintenance of flow above 13.4 m. The water/gas interface of bubbles has a surface energy, which is often referred to as surface tension. The surface energy of the water/gas interface is 0.0272 J m^{-2} . For a bubble to be stable it must be supported by the internal pressure of the gas. The pressure in a bubble is given by the approximate formula (the formula is accurate for an ideal gas; Fréchet et al., 2009) $P \approx 2\gamma/r$, where γ is the surface energy (J m^{-2} or N m^{-1}) and r (m) is the bubble radius. A good benchmark pressure is the atmospheric pressure, which is $1.013 \times 10^5 \text{ Pa}$ (N m^{-2}). An internal pressure of 1 atm could support a bubble of radius r where:

$$r = \frac{2\gamma}{P} = \frac{2 \times 7.2 \times 10^{-3}}{1.013 \times 10^5} = 1.421 \times 10^{-6} \text{ m} = 1.42 \text{ } \mu\text{m}. \quad (5)$$

That is, an internal pressure of 1 atm is generated by a bubble of $1.42 \text{ } \mu\text{m}$ radius. Put another way, in the absence of a mechanism to create an internal gas pressure, a negative (tensile) pressure of 1 atm is required to maintain a bubble radius of $1.42 \text{ } \mu\text{m}$. Therefore, sub-micrometre diameter bubbles in water will tolerate a high tensile stress.

In our siphon experiment, the water retains tensile strength equivalent to at least a 0.8 m water column (7.8 kPa). The tap water used in the siphon experiment contained dissolved gases such as carbon dioxide, oxygen and nitrogen. The dissolved gases tend to evolve when water is placed under reduced pressure. It is the evolution of dissolved gases that can cause a siphon to fail when water is under tension. The evolution of dissolved gas can be reduced by boiling the water before using it in a siphon.

Application of the Bernoulli equation to the sauropod circulation

Eqn 4 can be applied to the sauropod circulation, or any animal circulation, by making the pump pressure (P_p) equal to the mean arterial pressure (P_{ma}), the vapour pressure equal to the pressure at which blood boils (P_b), and H the maximum allowed vertical distance between the heart and head. The height could also be taken as the vertical distance between the head and the hydrostatic indifferent point (HIP), which is the point in the neck, or thorax, where the pressure is equal to the atmospheric pressure:

$$H = \frac{(P_{atm} + P_{ma} - P_b)}{\rho g} - v^2/2g. \quad (6)$$

An important point to note is that the pressure at the highest point in the circulation depends on the vertical distance between the heart and head and not the length of the neck. If the length of a sauropod neck is L , then the height (H) is $H = L \times \sin(\theta)$, where θ is the angle between the central axis of the neck and the horizontal. When $\theta = 0^\circ$ the neck is horizontal and when $\theta = 90^\circ$ the neck is vertical. Eqn 6 can be rearranged to obtain the mean arterial pressure in terms of the vertical distance between the heart and head:

$$P_{ma} = H\rho g - P_{atm} + P_b + \frac{1}{2}\rho v^2. \quad (7)$$

For convenience, we will call this adaptation of the Bernoulli equation (Eqn 7) the sauropod siphon equation (SSE). To apply this equation to the sauropod circulation, a plausible value for P_b , the vapour pressure of water in blood at body temperature, needs to be chosen.

Ambient atmospheric pressure has an influence on the internal circulation of the body. Blood pressure is referenced to the ambient pressure, so for example the blood pressure of a person climbing up a mountain will be about the same relative to ambient pressure as at sea level although the absolute pressure will be less. At the other end of the scale, the internal fluid pressure of a diver increases as they descend, increasing the amount of dissolved gases, especially nitrogen, which leads to the problem of the bends. So, in other words, the hydrostatic fluid pressure in the body varies with ambient pressure, whereas the hydrodynamic pressure is relatively invariant.

The point in the circulation at the same pressure as ambient pressure is known as the hydrostatic indifferent point (HIP). In humans, it is in the vicinity of the diaphragm. The pressure (P) at a height h above the HIP is negative ($P = -\rho gh$) and it is positive below ($P = +\rho gh$). The absolute HIP pressure is the same as the ambient atmospheric pressure. Blood pressure-measuring instruments are referenced to the ambient pressure so can be used at varying altitude – although there is some error in the instruments as a result of altitude (Kametas et al., 2006).

In the first experiment described in this paper, water boiled at 13.4 m because at the apex of the siphon the pressure had dropped to the vapour pressure of water at room temperature. If the experiment had been conducted at high altitude – for example at 4 km, where atmospheric pressure is 60% of sea level pressure – the water would have boiled when the top of the circulation reached about $13.4 - 4 = 9.4 \text{ m}$. An experiment demonstrating the effect of low ambient pressure on a siphon is described by Hughes and Gurung (2014).

Animal studies have shown that bubbles begin to appear in blood at an ambient pressure of 70 mmHg (0.95 m H_2O), and blood begins to boil when the ambient pressure falls below 47 mmHg (6.3 kPa, 0.63 m H_2O) (Howard, 1977). The altitude at which exposed body fluids begin to boil is known as the Armstrong limit, which occurs at an altitude of about 63,000 feet (19.2 km).

The boiling point of normal saline (0.9% NaCl concentration) is taken as 100°C ; therefore, the boiling point of blood even with extra solutes would be expected to be about the same. When a P_b of 70 mm and P_{ma} of 242 mmHg are inserted into the SSE, the maximum neck height is 12 m. In other words, below 12 m bubbles will not form in the blood and a sauropod would be safe from embolisation. A sauropod could lift its head above the 12 m limit for a brief period, provided that the release of dissolved gas from the blood was slow and the blood flow rate sufficiently rapid to avoid embolisation in the head.

Some extra embolisation protection would be afforded by blood velocity. Any water vapour bubbles that formed in the extreme low-pressure region in the brain would be quickly swept into the lower, higher pressure region and condense. A sauropod would probably have been able to raise its head for a few seconds above the ‘bubble line’, for example to reach a succulent leaf, with no ill effects, as any bubbles would quickly condense when the head was lowered.

It could be argued that it might be more appropriate to use the diastolic pressure rather than the mean arterial pressure in the SSE. However, it is probably valid to use the mean arterial pressure because the sauropod brain was remote from the heart and therefore the muscular walls of the carotid arteries would smooth out beat-to-

beat variations in arterial pressure. In any case, the arterial pressure would be above the mean pressure for over half the cardiac cycle and therefore any bubbles formed during diastole would condense during systole.

The sauropod circulation, and indeed any circulation, can be split into two independent compartments: hydrostatic and hydrodynamic. (This is analogous to a combined DC and AC signal in electronics.) The hydrostatic component is the foundation for the hydrodynamic component and is independent of vascular resistance, which is a function of vessel radius, length and fluid viscosity. The model presented here is a hydrostatic model of the sauropod circulation. In principle, the experiments described in this paper could have been performed with a wide range of tube diameters and liquid densities and still been an accurate hydrostatic model of the sauropod circulation.

The final experiment demonstrated that a siphon can be formed with completely collapsible tubing on the downside if the tubing is sheathed in an enclosed column of water communicating with the HIP. If the veins and venules in the cranium of a sauropod were bathed in fluid, this would protect against collapse. The protective fluid column would not necessarily have to be a reservoir like the cerebrospinal fluid sac but could be interstitial fluid. A useful analogy here is a water tank being lifted out of waterlogged ground. The water does not have to be clear of embedded material to provide buoyancy. In the case of waterlogged earth, the water and earth form a tight matrix. In some ways, the hypothesis we propose here is related to the idea suggested by Seymour (1976) that sauropods may have preferred an aquatic environment – except in this case it is an internal aquatic environment.

If collapse was prevented by the surrounding fluid, or the veins were embedded in some kind of matrix that prevented complete collapse, the blood could still boil because the ambient pressure would be below the HIP pressure. Therefore, embolisation is still an issue.

The SSE needs to be used with caution as it only has physical meaning in situations where the combination of neck height and atmospheric pressure produce a hydrostatic pressure close to the bubble limit. At lower neck lengths, the minimum mean arterial pressure required to prevent bubble formation is negative, which means that bubbles will never form – even at zero mean arterial pressure.

In applying the SSE to the sauropod circulation, we need to assume values for atmospheric pressure, the acceleration due to gravity and the density of dinosaur blood. In the age of the dinosaurs, there is no reason to suppose that atmospheric pressure, or the acceleration due to gravity, were different from today's values (101 kPa and 9.8 m s^{-2} , respectively). Atmospheric pressure depends on the acceleration due to gravity, which in turn depends on the mass of the Earth. There is no evidence that the mass of the Earth was significantly different in the distant past compared with today. It also seems reasonable to assume that the density of dinosaur blood was similar to that of extant animals, i.e. $\sim 1.05 \text{ g cm}^{-3}$.

If we insert the estimates of the neck length of *Sauroposeidon* (11.25–12 m) into the SSE, we obtain a mean arterial pressure in the range 178–236 mmHg (23.8–31.5 kPa), similar to the arterial pressure of the giraffe (mean 214 mmHg, diastolic 161 mmHg, systolic 235 mmHg). Of course, sauropod hearts would need a much greater stroke volume than the giraffe heart.

There are other examples of animals with similar mean arterial blood pressure but dissimilar stroke volume. For example, the sheep and whale both have mean arterial pressures of the order of 97 mmHg (13 kPa), although clearly the stroke volume of the whale is much larger than that of the sheep.

A study of extant animals reveals that blood pressure is not necessarily related to neck length. For example, the mean arterial pressure of the UK house sparrow is 180 mmHg, only 20 mmHg less than that of the giraffe, in spite of the house sparrow having a much shorter neck (Hicks, 2005). This is strong evidence that mean arterial blood pressure is a function of vascular resistance and not head height.

It follows from the SSE that if sauropods had a mean arterial pressure similar to that of the giraffe, they would need to live close to sea level to safely raise their heads 12 m above the heart. This has important implications for sauropod migration. Fricke et al. (2011) have presented evidence that sauropods may have migrated to higher altitudes. If this were the case, sauropods with a neck length of 12 m would either have to lower their necks when travelling over high ground or increase their mean arterial pressure.

Scenarios

To assess the ability of sauropods to migrate across high terrain, the SSE was used in two scenarios, one in which the elevation of the head was fixed at 12 m above the heart with variable mean arterial pressure (Fig. 5A), and another in which the mean arterial pressure was constant with variable head height (Fig. 5B). A sauropod with a 12 m neck held erect would require a mean arterial pressure of nearly 500 mmHg to migrate safely across a mountain pass 4 km above sea level. Conversely, for a fixed mean arterial pressure similar to that of a giraffe, a sauropod would need to lower its head to 8 m to safely migrate across a 4 km mountain pass.

Head lowering would appear to be the most likely scenario as neck height is much easier to adjust than mean arterial pressure. However, if the neutral position of the sauropod neck was 45 deg, as for the giraffe, perhaps via the equivalent of the nuchal ligament (ligamentum nuchae) in the giraffe as proposed by Tsuihiji (2004), the head height would be equal to $\sin(45 \text{ deg}) \times 12 = 8.4 \text{ m}$, which would allow global roaming. The head height would also be considerably less than the neck length if sauropods held their necks in a swan-like 'S' pose, in which case the neck height would be about 2/3 of the length, i.e. 8 m in the case of a 12 m long neck. (The 2/3 ratio estimate was obtained by author S.H. using a flex-curve.)

The fossil record shows that sauropod vertebra were of a light bird-like construction, which would make it easier for them to raise and lower their necks. Prasad et al. (2005) examined fossilised dung in the vicinity of titanosaur sauropod fossils and discovered the fossilised remains of grass, conifers and palms – evidence that sauropods were able to bend down to eat grass and raise their heads to eat tree leaves.

Conclusion

In conclusion, we have derived an equation relating sauropod neck length to mean arterial pressure. If the mean arterial pressure in the sauropods was comparable to that of the giraffe, they would be able to raise their heads 11–12 m above the heart, which accords with estimates of maximum neck length based on fossils. This has implications for the geographical distribution of sauropods and their ability to migrate across high ground. This hypothesis could be tested by looking for a correlation between sauropod neck length and the elevation of fossil finds.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

S.H. designed the experiment and wrote paper. J.B. assisted with the experiment and reviewing the paper. J.R. wrote the section of the paper relating to neurosurgery. R.B. and S.G. assisted with the experiment. All authors reviewed the manuscript.

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