

## CORRESPONDENCE

# Why vascular siphons with sub-atmospheric pressures are physiologically impossible in sauropod dinosaurs

Roger S. Seymour<sup>1,\*</sup> and Harvey B. Lillywhite<sup>2</sup>

<sup>1</sup>School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia.

<sup>2</sup>Department of Biology, The University of Florida, Gainesville, FL 32611, USA.

\*Author for correspondence (roger.seymour@adelaide.edu.au)

A recent article in the *Journal of Experimental Biology* revisits the siphon principle to explain how sauropods might have browsed with the head held high in trees (Hughes et al., 2016). Hughes et al. state that the principal objection to a vascular siphon is the creation of sub-atmospheric pressures that would collapse cranial veins and thus prevent flow of blood. Their physical models involve flow of water in rigid ‘arteries’ and deformable, but not collapsible, ‘veins’, or completely collapsible ‘veins’ inside of a rigid tube. These models demonstrate that sub-atmospheric pressures could exist at the top of an inverted U-shaped tube if all of the tubing were rigid or protected from collapse by external rigid structures. Cavitation from ‘boiling’ occurs if the siphon is high enough and the sub-atmospheric pressure is below the water vapour pressure. They postulate that the water would boil at a lesser height at higher altitudes, because the atmospheric pressure is lower. All of these demonstrations are true, because they are simply physics of water flow in single tubes that are essentially rigid or protected from collapse. However, there are at least three separate problems that make the siphon physiologically impossible in the upright neck of a tall sauropod dinosaur.

First, every single blood vessel in the neck and head must be prevented from collapse if the blood pressure at each location is sub-atmospheric. This includes not only the veins, but also the arteries and capillaries at every level. Conceivably, the vessels in the cranium and spinal column could be held open by balancing vascular pressure with sub-atmospheric pressure in the cerebral spinal fluid, as demonstrated in humans (Dilenge et al., 1975; Rushmer et al., 1948), or shunting of flow into a vertebral venous plexus (Zippel et al., 2001). However, there are many blood vessels in the neck and head that cannot be protected. Several arteries proceed up the neck of birds (Glenny, 1951), and it is reasonable to assume that the dinosaurs, which gave rise to birds, also had similar unprotected main arteries in the neck. Very simply, these arteries will collapse if the intravascular pressure falls below atmospheric (Lillywhite and Donald, 1994). Moreover, there must have been small vessels of the microcirculation associated with the sense organs (especially the eyes), mouth, oesophagus, etc., which could not be protected from collapse. If even a single blood vessel in the head and neck were unprotected, it would receive no blood flow if connected to an artery having sub-atmospheric pressure.

Second, if the blood went from the lungs at atmospheric pressure up to the head, oxygen in the blood would be progressively exposed to sub-atmospheric total pressure and would dissociate from the haemoglobin, coming out of solution to form bubbles, long before the blood would boil with water vapour. If the oxygen carrying capacity were similar to that of humans, every litre of blood would hold approximately 200 ml of

oxygen. Thus, if this oxygen came out of 1 litre of blood at 760 mmHg (1 atm), the bubbles would equal 200 ml, but if exposed to a pressure of 260 mmHg (=–500 mmHg sub-atmospheric pressure) in the head, the volume of bubbles would be 585 ml, or over half of the volume of blood. Hughes et al. (2016) assume that the blood gets to the head quickly enough to avoid oxygen bubbles before the oxygen is consumed by the tissues. However, degassing of dissolved nitrogen in the blood is an unavoidable problem, because nitrogen is not consumed. Aviators can get the bends (nitrogen bubbles in the blood) at absolute pressures of approximately 510 mmHg (Hills, 1977), and goats flown to a barometric pressure of 440 mmHg also produce bubbles in the blood (Hill et al., 1994). These hypobaric experiments involved relatively slow aircraft ascents when some loss of nitrogen could occur through the lungs during the ascent. However, the speed of blood flow up the sauropod neck would have been quicker, and no loss of nitrogen is possible. Super-saturated dissolved nitrogen would be delivered continuously to the head, and bubbles would be inevitable at much lower head height than the limit suggested by Hughes et al. (2016).

Third, sub-atmospheric blood pressures would have several problems associated with capillary function and vascular damage. These include lack of ultrafiltration of fluid into tissues, dehydration of tissues including the eyes, lack of lymph flow, lack of a blood clotting mechanism in wounds that do not bleed, and aspiration of air into any wounds larger than the size of arterioles (Seymour and Lillywhite, 2000).

The proposition that sauropods had extravascular hydrostatic gradients throughout the interstitial fluids of the body, thus creating a ‘G-suit’ like those protecting aviators from the effects of high g-forces, has been shown to be impossible, because the high extravascular pressures would bear on the pulmonary vessels, raising pulmonary blood pressures greatly and certainly causing pulmonary oedema (Seymour and Lillywhite, 2000).

Hughes et al. (2016) acknowledge previous discussion of the siphon principle in regard to sauropod necks and assert that the subject is ‘controversial’. However, a scientific controversy should have valid arguments or at least recognition of the arguments on both sides. Proponents of the siphon principle have never responded to critical facts. Surprisingly, Hughes et al. (2016) cite papers with other models of cephalic circulation (Seymour, 2000) and arguments as to why sub-atmospheric pressures in sauropod heads are unsustainable (Seymour and Lillywhite, 2000), yet they do not criticise, or even mention, the relevant points made there. Unfortunately, the siphon principle continues to attract speculation related to postural behaviour of long-necked dinosaurs, despite the facts that make its relevance physiologically untenable.

## References

- Dilenge, D., Perey, B., Geraud, G. and Nutik, S. (1975). Angiographic demonstration of the cervical vertebral venous plexus in man. *J. Can. Assoc. Radiol.* **26**, 77–81.
- Glenny, F. H. (1951). A systematic study of the main arteries in the region of the heart – Aves XII. Galliformes, Part 1. *Ohio J. Sci.* **51**, 47–54.
- Hill, R. C., Miller, C. W. and Tucker, A. (1994). Influence of carbon dioxide on venous gas emboli production during altitude decompression in goats. *Aviat. Space Environ. Med.* **65**, 139–143.
- Hills, B. A. (1977). *Decompression Sickness*. New York: Wiley.
- Hughes, S., Barry, J., Russell, J., Bell, R. and Gurung, S. (2016). Neck length and mean arterial pressure in the sauropod dinosaurs. *J. Exp. Biol.* **219**, 1154–1161.
- Lillywhite, H. B. and Donald, J. A. (1994). Neural regulation of arterial blood pressure in snakes. *Physiol. Zool.* **67**, 1260–1283.
- Rushmer, R. F., Beckman, R. L. and Lee, D. (1948). Protection of the cerebral circulation by the cerebrospinal fluid under the influence of radial acceleration. *Am. J. Physiol.* **151**, 355–365.
- Seymour, R. S. (2000). Model analogues in the study of cephalic circulation. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **125**, 517–524.
- Seymour, R. S. and Lillywhite, H. B. (2000). Hearts, neck posture and metabolic intensity of sauropod dinosaurs. *Proc. R. Soc. B Biol. Sci.* **267**, 1883–1887.
- Zippel, K. C., Lillywhite, H. B. and Mladinich, R. J. (2001). New vascular system in reptiles: anatomy and postural hemodynamics of the vertebral venous plexus in snakes. *J. Morphol.* **250**, 173–184.

10.1242/jeb.140988

## Can giraffes be supersized? Response to ‘Why vascular siphons with sub-atmospheric pressures are physiologically impossible in sauropod dinosaurs’

S. Hughes<sup>1,\*</sup>, J. Barry<sup>1</sup>, J. Russell<sup>2</sup>, R. Bell<sup>3</sup> and S. Gurung<sup>4</sup>

<sup>1</sup>Queensland University of Technology, Gardens Point Campus, 2 George Street, Brisbane, QLD 4000, Australia.

<sup>2</sup>Royal Brisbane and Women’s Hospital, Herston, Brisbane, QLD 4029, Australia.

<sup>3</sup>CSIRO Education, EcoSciences Precinct, 41 Boggo Road, Dutton Park, QLD 4102, Australia.

<sup>4</sup>Paro College of Education, Royal University of Bhutan, Paro, Bhutan.

\*Author for correspondence (sw.hughes@qut.edu.au)

In their correspondence ‘*Why vascular siphons with sub-atmospheric pressures are physiologically impossible in sauropod dinosaurs*’, Seymour and Lillywhite discuss a number of physiological problems with a siphon operating in sauropods. They cite three main objections: (1) collapse of blood vessels in the head and neck outside the protection of the cerebral spinal fluid; (2) outgassing of oxygen and nitrogen bubbles due to low hydrostatic pressure; and (3) several problems associated with capillary function and vascular damage if interstitial fluid created a protective head-to-claw hydrostatic gradient.

If these issues are insurmountable, then it would be reasonable to conclude that the natural pose of the sauropod neck was horizontal. However, the purpose of our paper (Hughes et al., 2016) is to stimulate discussion about whether vertical necks really are impossible or whether there is a solution. Our paper postulates that a parallel pathway in the neck, i.e. veins and vertebral venous plexus, would provide a continuous fluid stream back to the heart so that a siphon could operate. If this was the case, the left ventricle of the sauropod heart would not need to generate pressures of the order 760 mmHg to overcome gravity. Another important consideration is energy. If a siphon were in operation, the sauropod heart would only need to supply sufficient energy to overcome vascular friction and not gravity.

An important recent development of relevance to the head high/low discussion is a paper by Smerup et al. (2016), referenced in our paper, who hypothesise that giraffe hearts have a small intraventricular cavity and a relatively thick ventricular wall to generate high arterial pressures, albeit with normal left ventricular wall tension.

This at least raises the possibility that sauropod hearts were actually able to generate higher pressures than previously thought without a huge heart out of proportion to extant animals. The paper by Smerup et al. (2016) raises the question of whether the giraffe heart could be extrapolated to generate the pressure and flow required for a high head. If not, are giraffe necks at the maximum height allowed by physiology?

Many extant organisms are adapted to extreme environments, for example, extreme cold (Duman, 2015) or extremely low barometric pressure (Scott, 2011). High-altitude birds are particularly relevant to the current discussion. Rüppell’s vulture purportedly holds the height record at 11,278 m. The bar-headed goose flies over the Himalayas as it migrates between Tibet and India, and has been seen flying over Everest at 9000 m.

At 10,000 m, the barometric pressure is 25% of the pressure at sea level, equivalent to the hydrostatic pressure inside a siphon 7.5 m above the upper reservoir. High-altitude birds have to cope with two main challenges – flapping their wings more vigorously to stay aloft in the rarefied air and extracting oxygen from air with only one-quarter the amount per volume at sea level.

Suppose there were no extant high-altitude birds, the bar-headed goose was extinct and only fossilised remains of the bar-headed goose had been found on the top of Everest. It might be reasonable to conclude that because no extant birds fly over Everest, the bar-headed geese had been blown on top of the mountain by a storm. However, the bar-headed goose exists and studies have revealed various high-altitude flying ‘survival features’, such as haemoglobin with an increased affinity for oxygen. Did the sauropods have ‘survival’ features allowing a high-altitude head?

In the case of high-altitude birds, because the barometric pressure can be as low as 0.25 bar, the absolute partial pressure of oxygen in the tissues will also be 75% lower. The relative partial pressure of oxygen between the red blood cells and the tissues will be similar to that at low altitude, and so oxygen detaches from the haemoglobin and diffuses across to the tissues. Could sauropods have had a similar type of haemoglobin to high-altitude birds?

The following is a hypothesis that could resolve all three of Seymour and Lillywhite’s objections to a sauropod siphon. The hypothesis is that the interstitial fluid above the heart of the sauropods had the same or similar pressure reference as the hydrostatic indifferent point (HIP). If this were the case, the interstitial pressure would reduce at the same rate as in the

circulation. Because the relative partial pressure of oxygen between the blood and tissues would be similar at different levels, oxygen would not leave the haemoglobin 'early' as blood ascended to the head. The same goes for dissolved nitrogen. This resolves issue 1 in the list above.

Another advantage of this schema is that all of the small blood vessels out to the surface of the skin would be protected from collapse by the interstitial fluid. This resolves issue 2. Also, because of the negative hydrostatic pressure of the interstitial fluid above the HIP, the fluid would not bear down on the vasculature below the HIP. Effectively, the neck of the sauropod would be like a barometer. In a barometer, the column of water is supported by the difference in pressure between the atmosphere and low pressure (vapour pressure of water) at the top. The hydrostatic pressure in the column is negative above the level of the water in contact with the atmosphere, which means the pressure directly beneath the barometer column is the same as at any other point at the same depth.

If this were the case in the sauropod neck, it would mean that weight of the interstitial fluid would be supported by the ambient atmospheric pressure (via the lungs) and so would not increase the hydrostatic pressure in the limbs. In the case of the sauropods there

would also be some support from hydrogen bond attraction, which would ultimately be supported by the skeleton. As a result, pressures below the HIP for a sauropod with a raised head would be the same as for a horizontal neck. This resolves issue 3.

Of course, it could be countered that there is no evidence for the above hypothesis. However, in the presumed absence of Jurassic Park-style cloning, at some point in the future it might be possible to generate a physiologically realistic computer simulation to test the viability of this hypothesis.

#### References

- Duman, J. G.** (2015). Animal ice-binding (antifreeze) proteins and glycolipids: an overview with emphasis on physiological function. *J. Exp. Biol.* **218**, 1846-1855.
- Hughes, S., Barry, J., Russell, J., Bell, R. and Gurung, S.** (2016). Neck length and mean arterial pressure in the sauropod dinosaurs. *J. Exp. Biol.* **219**, 1154-1161.
- Scott, G. R.** (2011). Elevated performance: the unique physiology of birds that fly at high altitudes. *J. Exp. Biol.* **214**, 2455-2462.
- Smerup, M., Damkjaer, M., Brondum, E., Baandrup, U. T., Kristiansen, S. B., Nygaard, H., Funder, J., Aalkjaer, C., Sauer, C., Buchanan, R. et al.** (2016). The thick left ventricular wall of the giraffe heart normalises wall tension, but limits stroke volume and cardiac output. *J. Exp. Biol.* **219**, 457-463.

10.1242/jeb.141879