Variation in pneumatic features in vertebrae of sauropod dinosaurs

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# Introduction

The vertebrae of sauropod dinosaurs are distinctive not only because of their size but also because they have complex pneumatic features. These include fossae and foramina, in both the centrum and neural arch; and laminae connecting landmarks such as the zygapophyses, diapophyses and parapophyses (Wedel 2003). For this reason, sauropod vertebrae are unusually diagnostic and are frequently used in species determination (McIntosh 1990).

While these features can be characteristic of a species, genus or clade, they are also highly variable: not only between individuals, but also invariably along the column of an individual (e.g. *Diplodocus carnegii*, Hatcher 1901:plates 3 and 7), and even sometimes between the sides of a single vertebra. Examples of the latter include the single vertebra that is the *Xenoposeidon proneneukos* holotype: Taylor and Naish (2007:1552, Figure B); and the sequence of vertebrae in the tail of *Giraffatitan brancai* MB.R.5000 (Wedel and Taylor 2013:5–7 and figures 4 and 5). In contrast, the vertebrae of mammals, non-dinosaurian reptiles and even other dinosaurs are much more uniform, exhibiting less individual, serial and bilateral variation. Why are sauropod vertebrae so much more variable?

[**Figure B.**](https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-B--Xenoposeidon-bilateral-variation.jpeg) NHMUK PV R2095, the holotype and only known vertebra of the rebbachisaurid sauropod *Xenoposeidon proneneukos*. A: left lateral view. B: right lateral view. Note that, while the general outline of the pneumatic features is the same on both side (large fossa on the centrum, “M”-shaped complex of laminae at the dorsalmost preserved extent), there are numerous differences in detail: the fossae are different shapes, it contains an accessory lamina on the right side, the “M” is clearer on the left, etc. Scale bar = 20 cm. Modified from Taylor (2018:figure 1).

# Analysis

It has been generally assumed that variation in pneumatic features is essentially random: as Witmer (1997:64) wrote of the antorbital paranasal sinus in archosaurs, “pneumatic diverticula are viewed simply as opportunistic pneumatizing machines, resorbing as much bone as possible within the constraints imposed by local biomechanical loading regimes”. However, here we will develop another explanation.

Bremer (1940:200) demonstrated that in extant birds, developing diverticula follow blood vessels as they radiate through the body: “Into this loose tissue, along the vein, the air sac [i.e. diverticulum in modern usage] finally grows in the form of a long tube … The actual entrance of the air sac into the main marrow cavity is effected at first at the internal opening of the vein”. O’Connor (2006:10) confirmed that “vascular injection studies on birds with pneumatic postcrania reveal that nutrient vessels share (i.e., co-occupy) foramina with pneumatic diverticula to gain access to the medullary space”. It is parsimonious to assume the same was true in sauropods.

But vascularization of vertebrae is itself highly variable, and it is common for the pattern of which vertebrae have external vascular foramina to be random. For example, in a juvenile specimen of the crocodilian *Tomistoma*, only about half of the first 13 caudal vertebrae have foramina on their right side (Figure D).

[**Figure D.**](https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-D--Tomistoma-caudals-1-13.jpeg) Proximal tail skeleton (first 13 caudal vertebrate) of the tail of LACM Herpetology 166483, a juvenile specimen of the false gharial *Tomistoma schlegelii*, in right lateral view. Vascular foramina are apparent on the centra of caudal vertebrae 5, 6, 7, 9, 10, 11 and maybe 8 and 13; they are absent in vertebrae 1, 2, 3, 4 and 12.

In sauropods, too, vascularization is variable along the vertebral sequence and between sides of an individual vertebra (Figure A).

XXX Insert Matt’s section on vascularization of neural canal from the spinal cord.

# Discussion

As noted by O’Connor (2006:9), “Whereas arteries and veins often utilize a single nutrient foramen within a given vertebra, occasionally there are separate foramina for each”. Similarly, Travan et al. (2015) show that in the cervical vertebrae of humans the transverse foramen, which the vertebral artery and vein pass through, is sometimes double, with the two vessels each passing through its own opening rather than the usual shared opening. (In rare cases, a triple transverse foramen occurs, with the sympathetic nerve plexus passing through a third opening rather than sharing the opening used by one or both blood vessels.) A similar phenomenon can be observed in the tail of the *Brontosaurus excelsus* holotype YPM 1980, in which the right side of the centrum of caudal 7 has the usual single vascular foramen but that of caudal 8 has two (Figure A).

[**Figure A.**](https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-A--variable-formamina-in-brontosaurus-tail.jpeg) *Brontosaurus excelsus* holotype YPM 1980, caudal vertebrae 7 and 8 in right lateral view. Caudal 7, like most of the sequence, has a single vascular foramen on the right side of its centrum, but caudal 8 has two; others, including caudal 1, have none.

If our hypothesis that pneumatization follows vascularization is correct, then then this could explain why there is sometimes a pair of pneumatic fossae on one side of a centrum, e.g. the left side of caudal 25 of the *Giraffatitan brancai* tail MB.R.5000 (Figure C): the two vascular foramina carrying artery and vein were each followed by a pneumatic diverticulum and each developed into a pneumatic fossa.

[**Figure C.**](https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-C--Giraffatitan-caudals-24-26.jpeg) *Giraffatitan brancai* tail MB.R.5000, part of the mounted skeleton at the Museum für Naturkunde Berlin. Caudal vertebrae 24–26. in left lateral view While caudal 26 has no pneumatic features, caudal 25 has two distinct pneumatic fossae, likely excavated around two distinct vascular foramina carrying an artery and a vein. Caudal 25 is more shallowly excavated than 26, but may also exhibit two separate fossae.

Vascular foramina are rarely if ever seen in sauropod vertebrae that feature pneumatic fossae or foramina. They do not appear alongside these features, as the features were excavated around the blood vessels, but why do foramina not appear within pneumatic fossae or foramina?

We considered the possibility that this is because the nerve was accompanied by the diverticulum that then excavated the pneumatic fossa or foramen, but in these cases the blood vessels did not terminate within the pneumatic space but still needed to get into the bone. So we would expect to see a vascular foramen within each pneumatic fossa or foramen. We do not know why this is not observed: perhaps the foramina are rarely prepared out? XXX integrate Matt’s text on this.

# Conclusion

In general, bones are the least variable part of a body, followed by muscles, nerves, and finally blood vessels ,which are vary variable in all vertebrates. Pneumatic fossae and foramina are skeletal features, so they might be expected to fall at the least variable end of the spectrum. But since diverticula follow blood vessels as they develop, the variability of pneumatic features in bones is not a coincidence: the variability of blood vessels causes the variability of diverticula, and of their skeletal traces.

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