Variation in pneumatic features in vertebrae of sauropod dinosaurs

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# Introduction

The vertebrae of sauropod dinosaurs have complex pneumatic features such as 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, these 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?

XXX Figure B Xeno left and right: <https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-B--Xenoposeidon-bilateral-variation.jpeg>

# 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.

XXX Figure D Matt’s Tomistoma tail: <https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-D--Tomistoma-caudals-1-13.jpeg>

XXX variable vascular foramina in YPM Bronto tail: Figure A at <https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-A--variable-formamina-in-brontosaurus-tail.jpeg>

# Discussion

Vascular foramina are rarely if ever seen in sauropod vertebrae that feature 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?

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 similarly 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).

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 diverticula and each developed into a pneumatic fossa.

XXX Giraffatitan caudal 25 at <https://raw.githubusercontent.com/MikeTaylor/palaeo-pv/master/figures/export/figure-C--Giraffatitan-caudals-24-26.jpeg>

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