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 and figure 4 parts 1 and 2); 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 illustrate Xeno left and right

XXX re-use Giraffatitan tail illustration

# 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 variable vascular foramina in YBM Bronto tail

XXX Matt’s croc specimen

# Discussion

Vascular foramina are rarely seen in sauropod vertebrae that feature pneumatic fossae or foramina. This XXX is because the blood vessels were wrapped in diverticula, see O’Connor on perivascular plexus.

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”. XXX cite Travon on this, too. If our hypothesis that pneumatization follows vascularization is correct, then then this could explain why there are 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 (Wedel and Taylor 2013:figure 5): the two vascular foramina representing artery and vein are both followed by a pneumatic diverticular and each develops into a pneumatic fossa.

# Acknowledgements

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