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Why Is Vertebral Pneumaticity in Sauropod Dinosaurs So Variable?

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The vertebrae of sauropod dinosaurs have distinctive and complex pneumatic features, including fossae and foramina on the sides of their centra. These vary between individuals, serially within individuals, and even between the left and right sides of single vertebrae. This presents a conundrum because bone is usually the least variable material in the vertebrate body. Blood vessels, however, are much more labile, as can be seen in the varied occurrence of vascular foramina in the vertebrae not only of sauropods but also of birds, crocodilians, and mammals. Vascular variation arises in part from the ontogeny of vertebrae, which in their embryonic state are vascularised from within the neural canal: the hand-off from these vessels to others that penetrate from outside is not always completed. In birds, pneumatizing diverticula enter the vertebrae alongside blood vessels, in the vascular foramina that they form, before excavating the surrounding bone into larger pneumatic foramina. We propose that the same was true in sauropods, and that variation in vascularization directly caused variation in pneumatization. In most vertebrae, a single vascular foramen carries both artery and vein, but occasionally these vessels separate, and each forms a separate foramen. This explains why, in rare cases, individual sauropod vertebrae have two pneumatic cavities on a single side: each arises from the vascular foramen formed by either the artery or the vein.

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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[1]. For this reason, sauropod vertebrae are unusually diagnostic and are frequently used in species determination[2]. Pneumatization lightened the vertebrae of sauropods[3][4], and this facilitated the evolution of very long necks, which exceeded 10 meters in multiple sauropod lineages[5]. Lightweight vertebrae and long necks were key innovations that allowed sauropods to grow to gigantic sizes and be diverse and widespread for most of the Mesozoic[6].

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Pneumatization also lightened the skeletons of extinct theropod dinosaurs and pterosaurs[7][8], and pneumatic features in the vertebrae of these animals are often quite similar to those in the vertebrae of sauropods[9][10]. Herein, we focus on sauropods because that is the clade in which specific patterns of vertebral pneumaticity have been best documented (e.g., [1][11][12]), but a similar study on non-avian theropods or pterosaurs would be a welcome advance.

Bone is generally the biological material that varies the least in morphology, both between individuals of a species and serially and bilaterally within an individual. Muscle, nerves, and especially blood vessels are more prone to variation[13][14]. However, while pneumatic features of sauropod vertebrae can be characteristic of a species, genus, or clade, they are also highly variable: not only between individuals but also along the column of an individual (e.g., *Diplodocus carnegii*, [15]), 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[16]; and the sequence of vertebrae in the tail of *Giraffatitan brancai* MB.R.5000[11]. Pneumatic features can also be consistently asymmetric along the vertebral column of a single individual, as in the titanosaurs *Neuquensaurus australis* MCS 5 and *Saltasaurus loricatus* PVL 4017[12]. 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 the pneumatic vertebrae of sauropods so much more variable?

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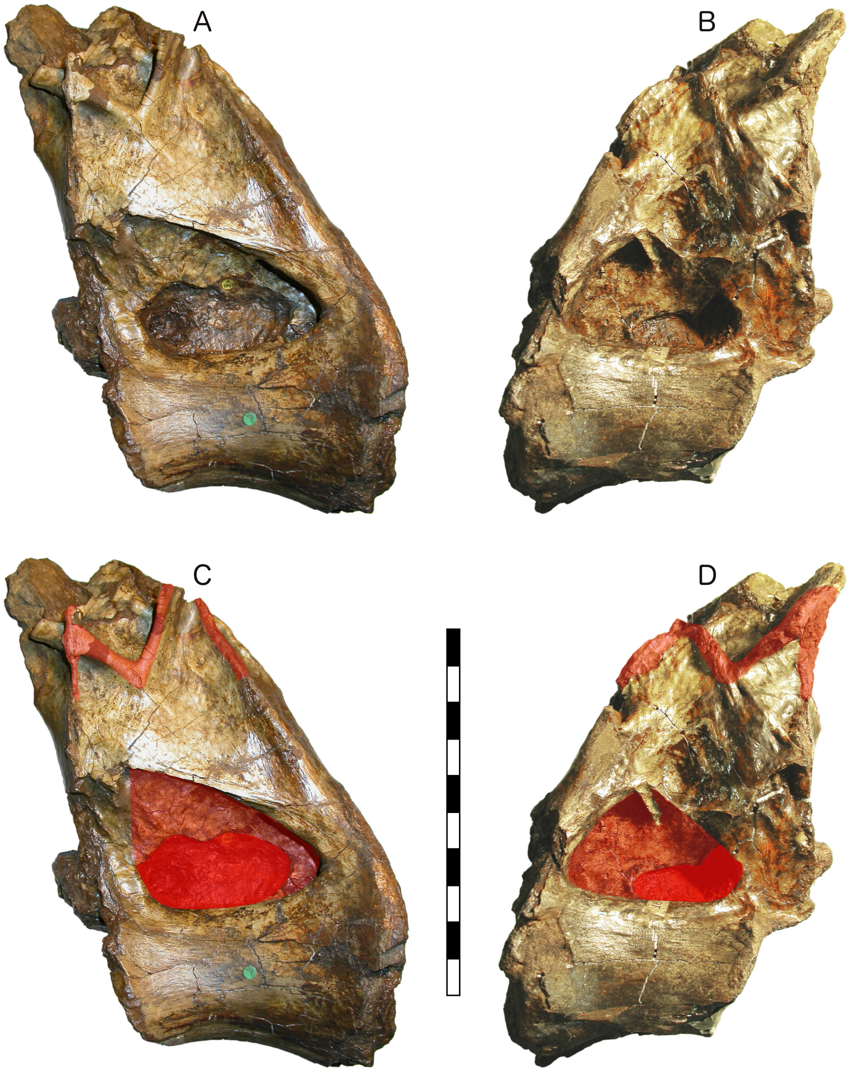

Figure 1. NHMUK PV R2095, the holotype and only known vertebra of the rebbachisaurid sauropod *Xenoposeidon proneneukos*. A: left lateral view. B: right lateral view. C: left lateral view with pneumatic features highlighted. D: right lateral view with pneumatic features highlighted. The pneumatic fossae and "M"-shaped complexes of laminae are highlighted in pale red; the pneumatic foramina within the fossae are highlighted in deep red. Note that, while the general outline of the pneumatic features is the same on both sides, there are numerous differences in detail: the fossae and their contained foramina are different shapes, the fossa on the right contains an accessory lamina, the "M" is better defined on the left, etc. Scale bar = 20 cm. After Taylor[17].

Analysis

It has been generally assumed that variation in pneumatic features is essentially random: as Witmer[18] 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[19] 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[9] 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 vertebrae with and without external vascular foramina to be random. For example, in the tail of a juvenile specimen of the crocodilian *Tomistoma* (Figure 2), only about half of the first 13 caudal vertebrae have vascular foramina on each side, and the vertebrae that have these foramina on the right are not consistently the same ones that have them on the left.

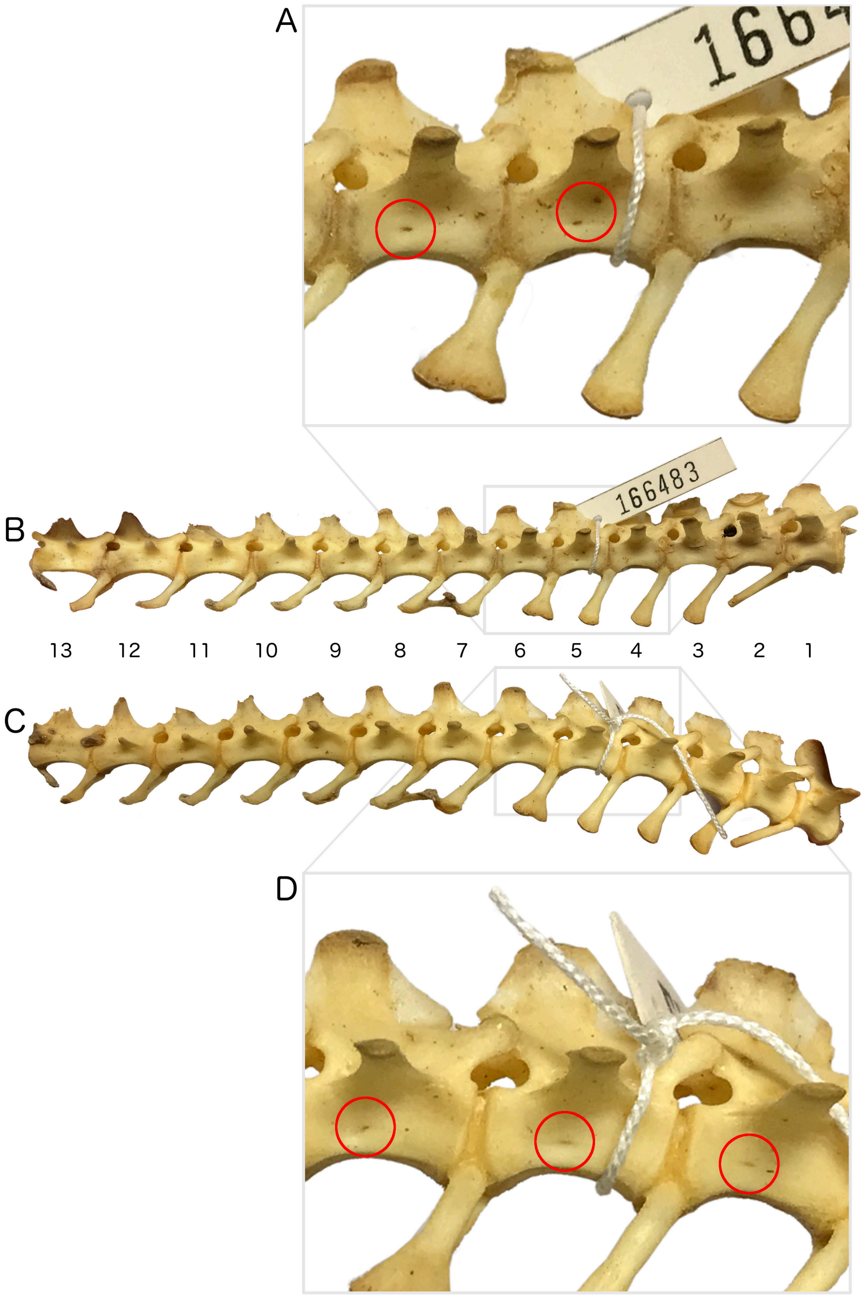

Figure 2. Proximal tail skeleton (first 13 caudal vertebrae) of LACM Herpetology 166483, a juvenile specimen of the false gharial *Tomistoma schlegelii*. A: close-up of caudal vertebrae 4–6 in right lateral view, red circles highlighting vascular foramina: none in Ca4, two in Ca5, and one in Ca6. B: right lateral view. C: left lateral view (reversed). D: close-up of caudal vertebrae 4–6 in left lateral view (reversed), red circles highlighting vascular foramina: one each in Ca4, Ca5, and Ca6. In right lateral view, vascular foramina are apparent in the centra of caudal vertebrae 5–7 and 9–11; they are absent or too small to make out in vertebrae 1–4, 8, and 12–13. In left lateral view (reversed), vascular foramina are apparent in the centra of caudal vertebrae 4–7 and 9; they are absent or too small to make out in vertebrae 1–3, 8, and 10–13. Caudal centra 5–7 and 9 are therefore vascularised from both sides; 4 and 10–11 from one side only; and 1–3, 8, and 12–13 not at all.

In sauropods, too, vascularization is variable along the vertebral sequence (Figure 3) and between sides of an individual vertebra.

Figure 3. *Brontosaurus excelsus* holotype YPM 1980, caudal vertebrae 7 and 8 in right lateral view. Lines indicate the location of foramina. 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.

Why is vascularization so variable?

The ontogenetic development of vertebral vasculature is a complex process. Early in embryonic development, the spinal cord is much larger than the vertebrae. Arteries serve the cord first; then, as the notochord segments are replaced by the cartilaginous anlagen of the vertebrae, branches of the medullary arteries tunnel into the cartilage and support the growth of the vertebrae[20]. All the blood supply to developing vertebrae, therefore, comes from inside the neural canal. Branches of the segmental arteries subsequently penetrate the vertebrae from the outside, and anastomotic connections develop inside the vertebra, connecting the internal and external systems (see example in [21]).

As the growth of the vertebrae outpaces that of the cord, there is a handoff of arterial supply from the original medullary arteries that serve the cord to the secondary, external arteries: foramina inside the neural canal shrink with age, while those on the external surface of the vertebra enlarge[22]. However, this handoff is not always completed, and asymmetric arterial supply is common[22]. Consequently, centra frequently lack an external vascular foramen on one or both sides. This is not a problem, as the medullary arteries can provide the necessary blood supply, but in sauropods, the absence of such external foramina means there is no point of entry for a diverticulum that otherwise would subsequently produce pneumatic cavities in the side of the bone.

In summary, since external pneumatic cavities follow the vascularization of the outer wall, and the latter is variable, it follows that pneumatization is also variable, reflecting the variation in the soft tissues that guide its development.

The fossil record provides additional evidence that pneumatic diverticula follow vascular pathways when pneumatizing the postcranial skeleton. Three observations are of particular relevance: 1. In non-avian theropods, the evolution of pneumaticity in dorsal and sacral vertebrae follows a “neural arch first” pattern[8]; 2. In basal sauropodomorphs (and possibly other archosaurs), deep, complex fossae ventral to the diapophyses and zygapophyses are among the earliest-evolving correlates of pneumatization[23][24]; 3. In juvenile sauropods, well-developed laminae and fossae are present in the neural arches of dorsal vertebrae before all the centra are pneumatized[25][26]. Pneumatization favored the neural arches over the centra in these cases because developing diverticula followed the large segmental arteries that serve the spinal cord. It is therefore not surprising that the earliest signs of pneumaticity, both ontogenetically and phylogenetically, should be near the neural canal, low on the neural arch.

The morphogenetic rules governing cervical and caudal pneumatization are less clear than in the torso. In the cervical column, the arteries that supply the spinal cord branch from the paired vertebral arteries, which lie alongside the vertebral centra, and this may explain the “centrum first” pattern of pneumatization in the cervical vertebrae of non-avian theropods[8]. The caudal vertebrae of juvenile diplodocids are less pneumatic than those of adults[25][26], and in *Giraffatitan*, extensive caudal pneumaticity is present only in large individuals[11]. These observations suggest that caudal pneumatization in sauropods continued for several years after the vascular handoff from neural canal arteries to arteries on the external surface of the centrum, possibly explaining the mix of “centrum first” and “arch first” pneumatization observed in sauropod caudal vertebrae. Among extant large animals, including humans, remodeling of arterial supply to the vertebrae continues for years or decades[22][27]. If both the blood vessels and the pneumatic diverticula of sauropods were remodeled over years or decades, the interplay between those changing systems probably contributed to the very high level of variation in vertebral pneumaticity, especially in the caudal series, where the process of pneumatization may have been particularly drawn-out[11].

It is also notable that paired pneumatic fossae or foramina occur lateral or dorsolateral to the neural canal in every archosaurian clade with postcranial pneumaticity (Figure 4). These fossae and foramina occur in taxa with and without lateral cavities in the centra, and with and without laminated neural arches, so they are probably the most consistent osteological correlates of pneumaticity across non-avian ornithodirans. The consistent appearance of vertebral pneumaticity in areas adjacent to the neural canal corroborates the hypothesis that segmental spinal arteries were crucial in “piloting” pneumatic diverticula as they developed.

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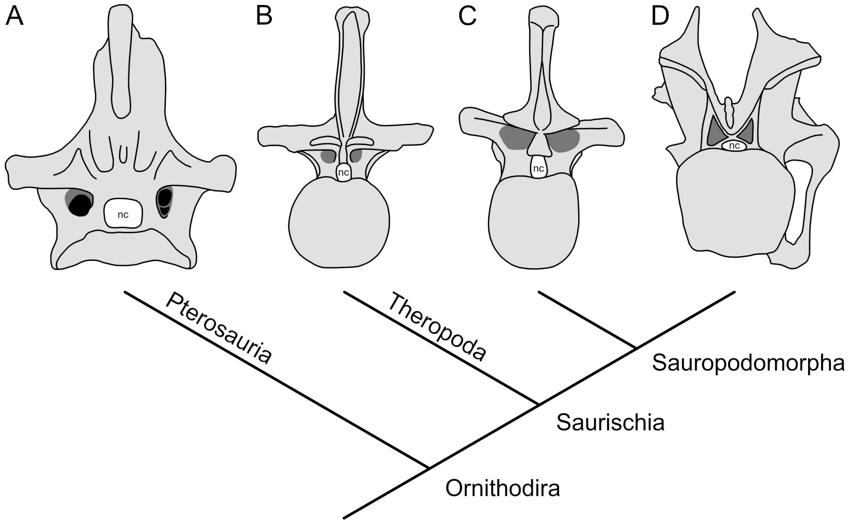

Figure 4. Fossae and foramina adjacent to the neural canal in ornithodiran archosaurs. Fossae are shown in dark grey, foramina in black. Neural canals are labelled "nc". A: Pterosauria, represented by cervical vertebra 9 of *Pteranodon* sp. YPM 2767 in anterior view (traced from [28]). B: Theropoda, represented by dorsal vertebra 14 of *Allosaurus fragilis* UUVP 6000 in anterior view (traced from [29]). C: Basal Sauropodomorpha, represented by a posterior dorsal vertebrae of *Aardonyx celestae* BP/1/6566 in posterior view (traced from [24]). D: Neosauropoda, represented by cervical vertebra 5 of *Diplodocus carnegii* CM 84 in posterior view (traced from [15]).

Discussion

As noted by O'Connor[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.[30] show that in the cervical vertebrae of humans, the transverse foramen, through which the vertebral artery and vein pass, 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; [30].) 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 3).

If our hypothesis that pneumatization follows vascularization is correct, then this could explain why there are sometimes two pneumatic fossae on one side of a centrum, for example, the left side of caudal 25 of the *Giraffatitan brancai* tail MB.R.5000 (Figure 5): the two vascular foramina carrying an artery and a vein were each followed by a pneumatic diverticulum, and each developed into a pneumatic fossa.

Figure 5. *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 24 is more shallowly excavated than 25, but may also exhibit two separate fossae.

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

When a blood vessel enters a bone through a vascular foramen, it is still detectable in CT scans as a tunnel through the trabeculae[23], but the vessels usually arborize into arterioles and capillaries quickly once they're inside. So before a bone becomes pneumatized by a fossa, the artery has already branched into many small vessels. When the diverticulum subsequently enlarges the vascular foramen into a pneumatic fossa, pneumatization likely excavates the bone around the already-branched arterial tree that existed inside the bone. There should, therefore, be multiple vascular foramina inside the fossa, representing the multiple branches of the artery — as can be observed in at least some vertebrae of ducks (Figure 6).

Figure 6. Domestic duck *Anas platyrhynchos*, dorsal vertebrae 2–7 in left lateral view. Note that the two anteriormost vertebrae (D2 and D3) each have a shallow pneumatic fossa penetrated by numerous small foramina.

However, these foramina will be much smaller than those that remain at the surface of apneumatic vertebrae. They may not be well preserved by fossilization, and even when preserved, they will be difficult to spot during fossil preparation — especially as pneumatic cavities in large, delicate bones are already difficult to prepare. We recommend that sauropod workers carefully check pneumatic fossae and foramina for evidence of contained vascular foramina.

Conclusion

In general, bones are the least variable part of a body, followed by muscles, nerves, and finally blood vessels, which are very 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.

Museum Abbreviations

- BP — Bernard Price Institute (Palaeontology), University of the Witwatersrand, Johannesburg, South Africa.
- CM — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
- LACM — Natural History Museum of Los Angeles County, Los Angeles, California, USA.
- MB.R. — Museum für Naturkunde Berlin, Berlin, Germany (fossil reptile collection).
- MCS – Museo de Cinco Saltos, Río Negro, Argentina.
- NHMUK — Natural History Museum, London, United Kingdom.
- PVL – Instituto Miguel Lillo, Collection of Vertebrate Paleontology, Tucumán, Argentina.
- UUVP — Natural History Museum of Utah, Salt Lake City, Utah, USA.
- YPM — Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

Statements and Declarations

Data Availability

The datasets analyzed for this study comprise observations of fossil and extant vertebrate specimens housed in publicly accessible museum collections, as listed in the Museum Abbreviations section, and information derived from published literature cited in the References section. Further inquiries can be directed to the corresponding author.

Author Contributions

Conceptualization, M.T. and M.W.; methodology, M.T. and M.W.; investigation, M.T. and M.W.; writing—original draft preparation, M.T. and M.W.; writing—review and editing, M.T. and M.W.; visualization, M.T. and M.W.

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