## EXPANDED NEUROCENTRAL JOINTS IN THE VERTEBRAE OF SAUROPOD DINOSAURS

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In most vertebrates, the paired neural arch elements attach to the centrum at cartilaginous joints (synchondroses), which usually co-ossify and fuse during ontogeny. Typically, the neural elements enclose the spinal cord dorsally and laterally, hence the term 'neural arch'. But in some cases the neurocentral joints may be shifted ventrally or dorsally relative to the neural canal by varying the relative contributions to the pedicles from the neural and central elements. As a result, the canal may end up mostly or entirely enclosed by either the neural arch or the centrum. Shifts in both directions happened in sauropod dinosaurs, sometimes in the same individual (Figure 1).

In all cases, the neural canal remains immediately dorsal to the articular surfaces of the centrum, so it makes more sense to talk about the neurocentral joint shifting relative to the neural canal, rather than the canal shifting relative to the joint. Ventral shifts in the neurocentral joints appear to be phylogenetically more common. In the embryos and young of many vertebrates, including mammals, each unfused neural arch pedicle is ventrally expanded to form a 'bouton' (French for "button"), which creates a broad contact surface for the neurocentral joint

(Schaefer et al., 2009). An unfused neural arch of a juvenile Alamosaurus, BIBE 45885, has enlarged boutons that almost meet at the midline, but are still separated by a very narrow ( $\sim$ 1 mm) gap. Caudal vertebrae 3-7 of a subadult Haplocanthosaurus, CM 879, illustrate an even more extreme condition, in which the paired boutons are so large that they meet on the midline, ventrally enclosing the neural canal in a complete ring of bone. The neural arch in such a vertebra is really a tunnel rather than an arch, and the centrum does not contribute to the neural canal at all.

Dorsal shifts in the neurocentral joints occurred in the dorsal vertebrae of some sauropods. In Haplocanthosaurus, CM 879, and Giraffatitan, MB.R. 3823, dorsals have pedicles that extend from the dorsal surface of the centrum to the top of the neural canal but do not meet at the midline, leaving a tiny gap. In Camarasaurus, YPM 1901, the centrum pedicles project dorsally in a similar manner, and meet to form the roof of the neural canal (Ostrom & McIntosh, 1966: plates 23-25). As in the Haplocanthosaurus caudals discussed above, the neural canal is entirely enclosed in a ring of bone, but in the Camarasaurus dorsals the neural canal lies in what is developmentally the centrum rather than the arch. In such vertebrae, the neural arch doesn't contribute to the neural canal, so technically it is neither neural nor an arch. Both ventral and dorsal shifts in the position of the neurocentral joints can be present in a single individual, as illustrated by Haplocanthosaurus. In CM 879, the neurocentral joints lie entirely below the neural canals in the proximal caudal vertebrae, but the joints are almost entirely above the neural canals in the dorsal vertebrae, and the vertebrae exhibiting these different conditions are only separated by the five sacral vertebrae.

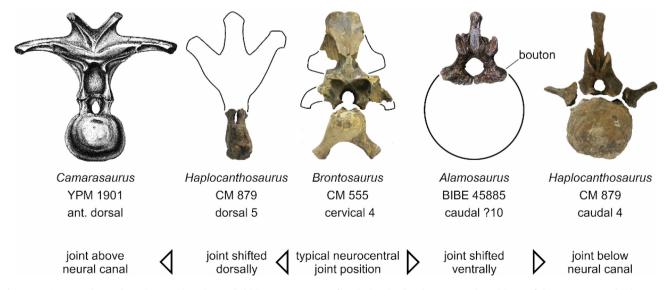


Figure 1. Sauropod vertebrae in anterior view exhibiting a spectrum of variation in the dorsoventral positions of the neurocentral joints.

Fronimos and Wilson (2017) suggested that the complex interdigitations of the neurocentral joints in sauropods were an adaptation for resisting biomechanical stresses associated with large body size and long necks. Shifting the position of the neurocentral joint dorsal or ventral to the neural canal may have served a similar function, by essentially merging the left and right halves of each joint into one and thereby increasing the surface area of the joint. Even if some other adaptive or developmental cause provided the impetus for such change, these shifts would at least have had the exaptive effect of increasing the surface area available for the joints.

Sauropods therefore increased the surface area of the neurocentral joints in all available directions: craniocaudally and dorso-ventrally by increasing the height and complexity of the interdigitations, and medio-laterally by shifting the joints dorsally or ventrally to eliminate the gap created by the neural canal.

This leaves the question of why neurocentral joints are shifted dorsally in some vertebrae and ventrally in others. To date, all examples we have found of dorsally-shifted neurocentral joints occur in dorsal vertebrae, and all ventrally-shifted joints occur in caudal vertebrae. The dorsal centra of most sauropods are deeply excavated by lateral pneumatic fossae or foramina, even in very young individuals (Wedel et al., 2000: Figure 14), and shifting the joint ventrally might have either reduced the surface area available for the joint, or interfered with the process of pneumatization. In sauropod caudal vertebrae, the neural arches become narrower dorsally, so shifting the neurocentral joint dorsally would have expanded the surface area of the joint little, if at all. Shifting the joint ventrally not only widened the contact between the neural arch and the centrum, but also allowed the arch to be partially morticed between the caudal ribs, which probably strengthened the joint even further.

Alternatively, the direction of the shift in the position of the joint may have been influenced more by a need to protect the spinal cord from trauma. Perhaps the caudal centra of sauropods were more susceptible to injury than the neural arches, although this is neither obvious a priori nor backed up by data. A global survey of vertebral pathologies in sauropods is outside the scope of this work, but it could provide useful insights. Furthermore, as we have only described herein a handful of examples of shifted neurocentral joints, a more comprehensive survey in other sauropods, in basal sauropodomorphs, and indeed in other dinosaurs would also be most welcome. In conclusion, dorsal and ventral shifts in the positions of the neurocentral joints in many sauropods could plausibly have strengthened the vertebrae, improved protection

for the spinal cord, or both. These hypotheses await

testing by further paleontological discoveries, and by biomechanical modeling.

Institutional Abbreviations: BIBE, Big Bend National Park, Texas; CM, Carnegie Museum, Pittsburgh, Pennsylvania; MB.R., Museum für Naturkunde Berlin, Berlin, Germany; YPM, Yale Peabody Museum, New Haven, Connecticut. We thank Matt Lamanna and Amy Henrici at the Carnegie Museum of Natural History and Ron Tykoski of the Perot Museum of Nature and Science for access to specimens in their care.

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Technical Session 3: Terrestrial Ecosystems - Late Jurassic (Friday, June 9, 2023, 2:15 PM)

MICROVERTEBRATE EXPANSION OF KNOWN FAUNA OF THE MORRISON FORMATION OF OKLAHOMA WILL ENABLE MORE MEANINGFUL COMPARISONS WITH OTHER REGIONS

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The vertebrate fauna of the Jurassic Morrison Formation as it crops out in the valley of the Cimarron River near Kenton, Oklahoma, USA was discovered in 1931 and worked 1935 - 1942 under the direction of Dr. Willis Stovall. The fossil-bearing exposures lie near the eastern edge of the Upper Jurassic Morrison Basin, where the formation is about 60m thick and thins to the East (Richmond et al., 2020). Analysis of pedogenic calcite