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Osteological correlates for quadrupedality in ornithischian dinosaurs

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The evolution of quadrupedality from bipedal ancestors is an exceptionally rare transition in tetrapod evolution, but it has occurred several times within the herbivorous dinosaur clade Ornithischia. Stegosauria, Ankylosauria, and Ceratopsidae are all uncontroversially quadrupedal, while basal ornithischians and basal ornithopods are uncontroversially bipedal. However, stance in iguanodontian ornithopods, including the hadrosaurs, and in non-ceratopsid ceratopsians is debated because robust osteological correlates of quadrupedality have not been identified. We examine a suite of characteristics that have been previously proposed as osteological correlates for bipedality or quadrupedality in dinosaurs. These include both discrete anatomical features, which we assess as correlates for quadrupedality using character optimization onto a composite cladogram, and proportional ratios, which we assess as correlates by reconstructing nodal ancestral states using squared-change parsimony, followed by optimization. We also examine the correlation of these features with body size. An anterolateral process on the proximal ulna, hoof-shaped manual unguals, a transversely broadened ilium, a reduced fourth trochanter and a femur longer than the tibia are found to be robust correlates of quadrupedality in ornithischian dinosaurs. Along the ceratopsid "stem" lineage, quadrupedal characters were acquired in a stepwise fashion, with forelimb characters developing prior to changes in the hind limb. In contrast, iguanodontid ornithopods display a mosaic of character states, indicating varying degrees of facultative quadrupedality that probably arose for a variety of different reasons. Hadrosaurs are found to possess all character states associated with quadrupedality and were probably predominantly quadrupedal. In general, quadrupedal ornithischians do not appear to have been constrained by their bipedal ancestry to a particular order of character acquisition.

Key words: Dinosauria, Ornithischia, osteological correlate, quadrupedality.

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