SHORT COMMUNICATION

THE EVOLUTION OF LATERAL ACCESSORY ARTICULATIONS IN THE LUMBAR REGION OF PERISSODACTYLS

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Citation for this article: Jones, K. E., and L. T. Holbrook. 2016. The evolution of lateral accessory articulations in the lumbar region of perissodactyls. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2016.1224892.

Perissodactyla is a diverse order of ungulate mammals that spans a wide body size range and includes specialized cursorial forms (MacFadden, 1992; Janis, 1998; Prothero, 2009; Janis et al., 2012; Gould, 2013). Whereas adaptations of the perissodactyl appendicular skeleton for cursorial locomotion have been well documented (e.g., particularly for Equidae), the axial skeleton is much less well understood (Hussain, 1975; Thomason, 1986; Hermanson and MacFadden, 1996). Extant equids are known for using dorsostable running gaits and hence have specializations of the lumbar region for stability (Hildebrand, 1959; Townsend and Leach, 1984; Preuschoft et al., 1994; Bertram and Gutmann, 2009). Here, we examine the evolution of an interesting and unusual axial stabilization feature that is unique to perissodactyls: lateral accessory articulations in the lumbar region (lateral joints).

Lateral joints are large synovial articulations that form bilaterally between the transverse processes of adjacent vertebrae in the last one to three lumbar joints (Fig. 1; see also Stecher, 1962; Stubbs et al., 2006). These unusual joints are found in all living perissodactyls, but no other living mammals (to our knowledge). Lateral joints are functionally important in the domestic horse (Equus caballus), reinforcing the lumbosacral articulation laterally, and forming a hinge joint capable of considerable sagittal bending but restricting lateroflexion (Jeffcott and Dalin, 1980; Townsend and Leach, 1984; Denoix, 1999; Jones, 2016). Flexion at the lumbosacral hinge is timed with limb movement during fast, asymmetric gaits, modulating intrathoracic pressure, and producing locomotor-respiratory coupling (Bramble and Carrier, 1983; Carrier, 1987). Simultaneously, the lateral joints stabilize the posterior lumbar region from lateral and torsional forces from the pelvis during unilateral stance phases (Townsend et al., 1983). Lateral joints are one of many features that contribute to the highly stabilized lumbar region of horses (Fig. 1A–C) and are hypothesized to have evolved in response to loading associated with increasing size in the equid lineage (Stecher, 1962; Jeffcott and Dalin, 1980; Zaneb et al., 2013). However, their presence in both rhinos and tapirs (Fig. 1D–F), in spite of significant locomotor differences, suggests that they may have evolved deeper in the evolutionary history of Perissodactyla. Data from fossil perissodactyls are needed to understand the timing and potential influencing factors on lateral joint evolution. Here, we gather together new and existing information on the presence of lateral joints in extant and fossil perissodactyls and discuss the potential role of body size and meristic variations in vertebral count in their evolution.


MATERIALS AND METHODS

Presence of lateral joints was noted, and the findings were compared with vertebral count and body mass in 22 extant and extinct Perissodactyl taxa (Table 1). Extant data were either gathered directly from the collections at the MCZ and USNM or taken from compiled literature sources (Williams, 2011; S. A. Williams, pers. comm.). Data for the 13 fossil taxa were gathered from the primary literature, or by direct observation (Table 1). Thoracic vertebrae were defined as those possessing costal facets, whereas sacral vertebrae were defined as those contributing to the sacral foramina, coincident or posterior to the pelvic articulation, in order to distinguish them from lumbar with lateral joints (Schultz and Straus, 1945). Body mass estimates were taken from the literature, with the exception of Isectolophus latidens, for which the body mass was estimated from lower first molar area (Damuth, 1990; Lucas et al., 2003).

The presence of lateral joints was mapped onto perissodactyl phylogeny using maximum parsimony in Mesquite (Maddison and Maddison, 2010). Multiple alternative topologies were used, and the relationships of the major perissodactyl groups were used as a guide for constructing a composite phylogeny based on each study (Froehlich, 1999:fig. 1; Hooker and Dashzeveg, 2004: fig 7b; Rose et al., 2014:supplementary fig. 3). Arenahippus grangeri is considered a basal equid on those phylogenies that do not include it, following Froehlich (1999, 2002). The phanocodontid condylarth Phenacodus primaevus, and the cambaytheriid Cambaytherium thewissi were used as outgroups.

A nonparametric Spearman’s rank correlation was used to test potential relationships between the presence of lateral joints, body size, and vertebral counts (thoracolumbar, thoracic, lumbar). To take into account shared patterns due to phylogenetic relatedness, the same test was repeated on standardized independent contrasts, generated in the PDAP module for Mesquite,