



Crossing the frontier: a hypothesis for the origins of meristic constraint in mammalian axial patterning[☆]

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ABSTRACT

Serially homologous systems with high internal differentiation frequently exhibit meristic constraints, although the developmental basis for constraint is unknown. Constraints in the counts of the cervical and lumbosacral vertebral series are unique to mammals, and appeared in the Triassic, early in their history. Concurrent adaptive modifications of the mammalian respiratory and locomotor systems involved a novel source of cells for muscularization of the diaphragm from cervical somites, and the loss of ribs from lumbar vertebrae. Each of these innovations increased the modularity of the somitic mesoderm, and altered somitic and lateral plate mesodermal interactions across the lateral somitic frontier. These developmental innovations are hypothesized here to constrain the anteroposterior transposition of the limbs along the column, and thus also cervical and thoracolumbar count. Meristic constraints are therefore regarded here as the nonadaptive, secondary consequences of adaptive respiratory and locomotor traits.

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1. Introduction

The evolution of adaptive morphology by natural selection is the major theme and guiding principle of comparative morphology. But a strict correlation of structure and function is complicated by structures that appear to be resistant to natural selection, even over long evolutionary time periods and under extremely different selection regimes. The existence of static or poorly adaptive structures is commonly attributed to the origin of evolutionary novelties by the modification of already existing structures, a process that François Jacob (1977) memorably compared to “tinkering”. In this tinkering, ancestral developmental programs and morphology are incompletely and imperfectly re-engineered for new functions. They can therefore exert a bias in the production of the phenotypes on which natural selection acts (Brakefield, 2006). Here, a rich fossil record documenting the synapsid–mammal transition, adaptively diverse living mammalian taxa, and a large body of recent developmental work on axial patterning are integrated to propose a synthetic hypothesis for the origin of a well-known example of evolutionary stasis, vertebral count in mammals.

Structures composed of multiple serially homologous subunits can provide accessible and discrete systems for addressing the imposition of evolutionary stasis. In many but not all cases, the elements of ancestral series are “primordially similar”, while the

elements of descendant series have been adapted “to the most diverse purposes” (Darwin, 1859). In *Materials for the Study of Variation*, William Bateson (1894) noted that, “on the whole, series containing large numbers of undifferentiated parts more often show meristic variation than series made up of a few parts much differentiated”. An example of the evolutionary transition from undifferentiated segments with high and variable counts to differentiated segments with lower and more constrained counts has been elegantly traced in arthropods using the 250 million year fossil record of trilobites (Hughes, 2007).

The developmental link between morphological differentiation and count constraint is only poorly understood. A general hypothesis suggests that the same developmental program generates each serially homologous subunit ancestrally, identifying the entire composite structure as a single morphological and developmental module. As evolution proceeds, downstream developmental steps are added in isolated areas of the series, producing regionally unique morphology that is selectively adaptive. After multiple generations of differentiation, each developmentally and morphologically differentiated region of the series becomes an internally integrated submodule that is resistant to incorporation or expansion into adjacent, differently specialized submodules without significant adaptive cost. This developmental entrenchment leads to stasis of count.

Vertebrates vary in the extent of their column regionalization. Minimal morphological regionalization and high count variability are found in the columns of ancestral vertebrates and many living teleosts (e.g., Ward and Brainerd, 2007). The columns of tetrapods are regionalized by their integration with limb girdles into cervical, dorsal, sacral, and caudal series, but series counts in many taxa are

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variable (Müller et al., 2010). In contrast, the axial skeleton of mammals exhibits both high morphological differentiation and minimal meristic variation. Five specialized series (cervical, thoracic, lumbar, sacral, caudal), several with intra-regional differentiation, are usually recognized. Cervical count is effectively fixed at 7, total thoracolumbar count is more loosely constrained at 19 or 20, and sacral count is typically 3 or 4. Only the caudal series varies widely in count. The adaptation of mammalian axial anatomy to a wide diversity of lifestyles over a long geologic history (Buchholtz, 2012) has thus been limited primarily to changes in vertebral shape and caudal count.

The historically remote and subcellular origins of the developmental innovations responsible for vertebral constraint complicate its analysis. The reappearance of ancestral structures following experimental expansion of *hox* gene expression domains led Pollock et al. (1995) to hypothesize that morphological differentiation of the vertebral column reflects the progressive restriction of expression domains that were originally expressed over much, or all, of the column. Although this pattern is not universally observed (e.g., Mallo et al., 2010), an evolutionary increase in developmental modularity is clear. On a morphological level, the adaptive clues typically provided by the structure–function paradigm are absent, as count is fixed in mammals with widely different adaptations. Additionally, variable counts in non-mammalian taxa argue against the adaptive superiority of any particular count. However, if regionalization was the product of a developmental program that generated a trait with high adaptive value, and secondarily also limited changes in vertebral count, stasis could be imposed without any inherent adaptive advantage. This scenario demands a developmental tie between the adaptive trait and meristic constraint, as well as their synchronous origin.

Below I present a hypothesis for the origin of cervical and thoracolumbar constraints in mammalian axial patterning as secondary consequences of developmental innovations tied to the highly adaptive mammalian respiratory/locomotor complex. Each innovation is associated with increased modularity of the column, has a developmental link to limb placement, and first appeared roughly synchronously with constraint imposition.

2. Mammalian respiration and locomotion

Living mammals possess a unique suite of integrated characters that enhance respiratory and locomotor performance. This character complex includes elevated body temperature, a high resting metabolic rate, the capacity for sustained activity, parasagittal excursion of the limbs, and dorsoventral movement of the vertebral column (Carrier, 1987; Ruben et al., 1987). A muscularized diaphragm located posterior to the lungs is a key soft-tissue character that integrates components of the complex. On contraction of the diaphragm, thoracic cavity volume increases, reducing intrathoracic pressure and enhancing inspiration and gas exchange. The diaphragm also limits anterior movement of the viscera into the thorax (Klein and Owerkowicz, 2006). Instead, abdominal viscera are displaced outwardly in the rib-free abdominal/lumbar region during inspiration (Perry et al., 2010). In contrast to non-mammalian amniotes, whose lateral column flexion during locomotion limits costal-based aspiration, the sagittal locomotor movements of the mammalian column allow continuous ventilation, supporting the elevated body temperature and aerobic demands of the sustained activity so characteristic of mammals (Carrier, 1987; Ruben et al., 1987; Perry et al., 2010).

The sequence and antiquity of mammalian respiratory/locomotor traits can be estimated by mapping those with osteological correlates onto a consensus phylogeny. Respiratory turbinates, heat and moisture conserving structures present only

in living endotherms, were present in the Middle Triassic cynodont *Massetognathus* (Hillenius and Ruben, 2004). The Middle Triassic dicynodont *Wadiasaurus* (Bandyopadhyay, 1988) possessed femoral and acetabular morphology interpreted as indicating upright hind limb posture; the co-occurrence of elongate vertebral transverse processes that allow the separation of respiratory and locomotor muscle groups (Carrier, 1987) supports this interpretation. The differentiation of an anticlinal vertebral region typical of dorsoventral column movement was present in the Late Triassic morganucodonts *Eozostrodon* and *Megazostrodon* (Sues and Jenkins, 2006). The Early Triassic cynodont *Thrinaxodon* exhibited incipient differentiation of a lumbar vertebral series with shortened, movable ribs (Jenkins, 1970). The loss of lumbar ribs and the stabilization of lumbar count at 19–20 are somewhat later and more variable in occurrence, and likely homoplastic in origin (Luo et al., 2007). Multiple authors (e.g., Brink, 1956; Perry et al., 2010) have argued that shortened or absent lumbar ribs are indicators of mammalian style locomotion and/or the presence of diaphragm-assisted inspiration, and that the transition from thoracic to lumbar morphology is associated with the location of the diaphragm in almost all living mammals (Buchholtz et al., 2012). What evidence is available therefore indicates that the mammalian respiratory/locomotor complex, including a muscularized diaphragm, was assembled very early in mammalian history, during the Triassic period. This transition is roughly coincident with the origin of fixed cervical count, seen in *Thrinaxodon* and all more derived synapsids and mammaliomorphs. In contrast, the reduction and loss of free ribs on cervical vertebrae are restricted to monotremes and more derived mammalian taxa, and significantly postdate the onset of cervical count stasis (Fig. 1).

3. Patterning of somitic and lateral plate mesodermal structures

The vertebrate postcranial musculoskeletal system is composed of mesodermal tissues that have two different developmental origins, the somites and the lateral plate mesoderm. The somitic mesoderm forms as paraxial bands lateral to the neural tube. These bands are later subdivided into segments in the process of somitogenesis. Segment number is controlled by the speed of a molecular “segmentation clock” (e.g., Dequeant and Pourquie, 2008), while somite differentiation is controlled by *hox* and other transcription factors (e.g., Wellik, 2009). Expression domains of the *hox* genes overlap anteroposteriorly along the body axis, and are colinear with respect to their locations on the chromosome. In contrast, the laterally located lateral plate mesoderm (LPM) is not segmented. Like the somites, it is patterned by *hox* genes during development, but LPM patterning is independent of that of the somites and is not colinear (McIntyre et al., 2007).

The tissues that comprise the postcranial musculoskeletal system can be placed into three categories based on their developmental histories. (i) The axial musculature, vertebrae, proximal ribs, and intermediate ribs are somitic in origin, and are patterned in a somitic or primaxial environment (Burke and Nowicki, 2003). (ii) The limb bones, sternum and the pelvis have their developmental origin in the lateral plate mesoderm, and are patterned in a lateral plate or abaxial environment. (iii) A third group of tissues are of somitic origin, but enter the abaxial environment during early development and are patterned there with tissues of lateral plate origin (Burke and Nowicki, 2003). These tissues include the distal portions of the ribs (origin in the sclerotome of the somites) and the migrating muscle precursor cells (MMPs, origin in the dermomyotome of the somites) that enter and differentiate within their destinations as the musculature of the tongue, limbs, and diaphragm (Birchmeier and Brohmann, 2000). A reporter expressed

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