Body Trunk Flexibility

Though beavers and otters are only very distantly related, they lead similar semi-aquatic lifestyles, spending much time both ambulating on land as well as swimming in rivers and ponds. Thus it is of interest to contrast the adaptations both groups have accrued to accomplish such similar locomotory tasks. Based on personal observation, beavers tend to keep their trunks rigid while swimming, while otters (both North American river otters and Asian small clawed otters) demonstrate much more flexibility in their trunks. What phenotypic adaptations and developmental programs underlie such differences?

SKELETON OF A CAT

Skeleton of a cat, serving as a generalized mammalian skeleton. Note particularly the groups of vertebrae in the spine.

The trunk of all vertebrates is organized around the spine, or vertebral column, which serves two main functions: to protect the spinal cord and to support the organism’s soft organs (NMNH Exhibit). Spinal stiffness would seem to enhance both of these functions. Thus, stiffness is probably the “ancestral” version of this trait, and it seems to be adaptive in all vertebrates, including beavers, in the absence of any need for flexibility. Furthermore, beavers swim by paddling their broad tails (Pfeiffer and Culik, 1998), meaning that their locomotory abilities may actually be enhanced by spinal stiffness. Rigidity in the precaudal vertebrae (all vertebrae anterior to the tail – particularly sacral, lumbar, and thoracic) allows a tail to be used more efficiently for locomotion in water (Reidenberg 2007). Therefore, it seems likely that beavers benefit from their rigid vertebral columns.

In contrast, when underwater, otters swim by undulating the lower halves of their bodies (Williams 1989). This is termed carangiform motion. Spinal flexibility accounts for this maneuverability (Gambaryan 1974). In fact, the trunk of an otter is flexible enough to rotate the sacrum a full 90 degrees, and most of this flexibility originates from the lumbar portion of the spine (Taylor 1989). This spinal range of motion is adaptive for two main reasons: in otters, carangiform swimming minimizes drag and incurs a much lower energetic cost than using the paws for paddling, and it allows for increased swimming velocity, quick acceleration, and complex maneuvers (Williams 1989). Beavers are herbivorous and need not hunt, while river otters are piscivorous and rely on agility and speed when hunting (Zoo Exhibit). Thus, it is reasonable to believe that faster and more maneuverable swimming is far more adaptive in otters than beavers, perhaps resulting in this phenotypic difference. Spinal flexibility has arisen in multiple lineages of aquatic carnivores, including also sea lions and seals; this convergent evolution strongly suggests that spinal flexibility is a true adaptation rather than an exaptation or a randomly arisen trait (Estes 1989).
An otter demonstrates its spinal flexibility while hunting.

Based on morphological and developmental studies of otters and other mammals, we hypothesize that three factors have contributed to the evolution of exaggerated spinal flexibility in otters: 1) meristic changes in the vertebrae of carnivores, 2) loss of supportive ligaments in the lumbar region of the spine, and 3) an increased ratio of elastin to collagen in the tendons and ligaments that do exist in the lumbar region of the spine.

Meristic Changes in Vertebrae

Based on a large survey of amniote fossils, Müller et al. found it most likely that the common ancestor of mammals had 19 thoraco-lumbar vertebrae (2010). While the beavers of today also have 19 thoraco-lumbar vertebrae, most carnivores, including otters, have 20 or 21 (Reynolds 1897). Since the joints between vertebrae are responsible for bending of the vertebral column (NMNH Exhibit), an increase in the number of vertebrae, which consequently increases the number of intervertebral joints, should allow for an increase in spinal flexibility.

The number of vertebrae an amniote has is determined by a developmental process called somitogenesis (Müller et al. 2010). Vertebrae develop from embryonic tissue called the presomitic mesoderm (PSM), budding off one at a time at regular time intervals, which are determined by a “segmentation clock” (Dequéant and Pourquié 2008). In a search for the molecular basis of this “segmentation clock,” Dequéant and Pourquié found that in mice embryos, certain cyclic genes are expressed in waves exactly coinciding with the budding of each vertebrae from the PSM – these genes, including Hes1 (hairy enhancer of split 1) and others of this gene family, Dll1 (delta-like 1), and Lfng (lunatic fringe), are all part of the Notch pathway. In particular, the period of oscillation of expression of these genes seems to depend on the half-life of the Hes family RNA and protein products (2008). Thus, we hypothesize that, in otters, a slight modification to the Hes family of RNA products, such as a reduction in the poly-A tail, may allow these RNAs to be degraded faster. This would slightly speed up the cycle of expression of these genes, which would lead to slightly faster ticking of this “segmentation clock” and eventually a slight increase in the number of vertebrae.

However, it is important to note that alterations to somitogenesis are probably not the sole cause of meristic changes in the number of thoraco-lumbar vertebrae in otters. Somitogenesis controls only the total number of vertebrae in an organism – Hox genes are responsible for determining the apportioning of these vertebrae into different functional regions of the spine (Müller et al. 2010). Since an increase in the number
of just thoraco-lumbar vertebrae inherently changes the ratio of thoraco-lumbar vertebrae to cervical vertebrae, slight alterations in regulation by Hox genes were also probably necessary to achieve this adaptation in carnivores.

**Loss of Supportive Ligaments**

Mammals which use their lumbosacral joint primarily for locomotion rather than support often have a truncated supraspinous ligament (Gál 1993a). Extending down the spine of a mammal, the supraspinous ligament is a rigid cord of connective tissue that connects each of the thoracic and lumbar vertebrae to one another and to the sacrum; the loss of this connector between the lumbar vertebrae and sacral vertebrae could allow much greater flexibility of the lower spine (Gál 1993a). Furthermore, in animals which show extreme spinal flexibility, such as seals, other connective tissues that function in spinal support, including the ligamenta flava and the articular capsules, are highly reduced or totally absent (Gál 1993b). The locations of these anatomical structures are diagrammed below.

![Diagrams of lumbar vertebrae and their associated connective tissues](image)

Three diagrams of lumbar vertebrae and their associated connective tissues, which are successively removed in the progression of A to B to C (Gál 1993b).

Thus, it is possible that the loss of the caudal half of the supraspinous ligament as well as drastic reductions in the ligamenta flava and articular capsules have played a major role in allowing an adaptive increase of spinal flexibility in the otter lineage.

The loss of this connective tissue probably results from changes early in development. During mammalian development, the scleraxis gene is expressed exclusively and continually in mesenchymal cells that will later differentiate into tissues that connect muscle and bone – namely, tendons and ligaments (Schweitzer et al. 2001). An unknown signal from the ectoderm also appears to be necessary for cell differentiation into tendons or ligaments, while signaling via bone morphogenetic protein (BMP) inhibits tendon formation (Schweitzer et al. 2001).
Signals affecting the development of cells destined to become tendons or ligaments, here termed “tendon progenitors” (Schweitzer et al. 2001). Since Schweitzer’s study, it has been found that BMP is implicated in processes involving both cell differentiation and apoptosis (Xiao et al. 2007). Thus, it is possible that mutations in the enhancer regions of one or several BMP genes in the otter lineage upregulates BMP expression in the developing precursor to the lumbosacral spinal region. This may cause the death of the scleraxis-transcribing “tendon progenitor” cells, or perhaps alter their differentiation trajectory, resulting in the loss of supporting ligaments in the lower spine. Furthermore, it is known that scleraxis itself is a transcription factor that may regulate genes involved in the differentiation of a progenitor cell into a connective tissue cell, implying that scleraxis expression is not just a marker for connective tissue progenitors but is actually necessary for the development of tendons and ligaments (Cserjesi 1995). Thus, cis-regulatory mutations in the scleraxis gene that prevent its transcription in the lumbosacral spinal region may also be responsible for the lack of the superspinous ligament and other connective tissues in otters.

**Increased Elastin:Collagen Ratio**

Ligaments are composed of networks of protein fibers, within which actual living cells are distributed (NMNH Exhibit). Two very common protein fibers are collagen, which is rigid, and elastin, which is flexible and stretchy. Increasing the relative amount of elastin in the connective tissues that do exist (though possibly quite reduced, as noted above) in the spines of certain mammals would result in much greater intervertebral joint flexibility (Gál 1993b). Furthermore, smaller mammals incorporate higher proportions of elastin in their connective tissues than do larger mammals, while larger mammals incorporate higher proportions of collagen (Gál 1993b). A general decrease in mobility of the lumbar region of the spine with increasing size has also been noted in a variety of animals (Smeathers 1981 as cited in Gál 1993a). In this light, it is informative to consider evidence from the fossil record. The American beaver is one of the largest living rodents, and beavers of the Pleistocene were far larger (NMNH Exhibit), often reaching the size of a black bear (Harington 2007). Meanwhile, remains of some species of adult otters from the early Pleistocene suggest body sizes no larger than today’s otters (Leffler 1964). If the elastin:collagen ratio has varied with body size since the Pleistocene, this may represent an example of constraints due to particular evolutionary histories. Beavers have stiff spines simply because they inherited a genetic program specifying high amounts of collagen in connective tissues from their large ancestors. Meanwhile, otters may have inherited genetic programs specifying high amounts of elastin in connective tissues as a consequence of the small size of their ancestors, contributing to the flexible spines of today’s otters.

**Further Complexities**

Though the evolution of a flexible spine has clearly been adaptive in otters, while the retention of a rigid spine seems to suit beavers just fine, certain other traits also contribute to locomotory abilities. Examples of these traits include fur structure, webbed feet (addressed in this wiki), and relative limb length (NMNH Exhibit, Anderson 2002, Wund 2005). Limb length may be a particularly interesting trait to consider, given that it appears to exhibit the effects of allometric growth: beavers have hind limbs that are much longer than their front limbs, while all four limbs of otters are very short relative to body size (Anderson 2002, Wund 2005). But an in-depth analysis of this trait is another story for another day (and another wiki).