Axial Character Seriation in Mammals:

An Historical and Morphological Exploration of the Origin, Development, Use, and Current Collapse of the Homology Paradigm

by

Aaron G. Filler

PhD Thesis

Department of Anthropology, Harvard University

Cambridge, Massachusetts

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Aaron G. Filler, MD, PhD, FRCS (SN)

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Abstract

The immediate impact of Darwinian theory for nineteenth century morphologists was to assert that the explanatory key to organismal biology lay in common ancestry rather than in repetition of axial structures. This revolution lent the appearance of biological validity to special homology between organisms, but demoted serial homology from its central theoretical position to a place as an unwanted and discarded relict of pre-Darwinian thought. In consequence, not only was this category of homology neglected, but the study of axial structures themselves was effectively abandoned.

Discovery of a serial relation in the mammalian axial skeleton by Goethe in 1790 launched much of the morphological program which continues to this day. A return to the study of mammalian axial anatomy 196 years after that seminal event and 127 years after the Darwinian devastation of this field now reveals a wealth of specific and generalizable morphologic and theoretical information.

Principal morphologic findings are: 1) Much of the unique vertebral anatomy of various mammals groups is due to serial modification of a previously unrecognized neomorph, the laminapophysis, which first appears in some therapsids and defines a clade including all mammals. 2) The serial homology of the lumbar transverse process varies, and in some hominoids it is with a derivative of the laminapophysis, not the rib. The consequences of this morphology includes impressive evidence that the common ancestor of chimpanzees and humans was an upright biped. 3) "Resegmentation" appears to occur variably. 4) Several mammalian groups display structures that may be equivalent with the homeotic mutants used in the genetic dissection of *Drosophila* morphogenesis.

At a theoretical level, the data confirm an old example of contradiction between serial and special homology and identify numerous additional examples. "Field homology" by hierarchical dominance of morphogenetic influence is proposed to account for some of these. However, the collective import of the data show that the homology paradigm in general is based on a misconceived expectation of Platonic typology. Homology is a practical formalism, not a biological phenomenon.

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Preface to the 2007 BrownWalker Edition

Despite the elapse of twenty years since the original version of this work was completed, it remains an extremely useful source for understanding the comparative anatomy of mammalian vertebrae. In addition, for many specialists who have written about the evolution of vertebrae since that time it has served as an important reference. The entire work, kept together as a unified document rather than a series of separated articles, provides a thorough exploration of a much needed revision of spinal nomenclature as well. The Brown Walker edition is being published to make the work more widely available. In particular, the 108 illustrations including 34 striking stereo pairs have been mostly illegible on the microfiche versions of the original edition.

In a variety of ways this work predicted and predated a vast expansion of interest in axial anatomy among biologists. In 1986, studies of vertebrae and serially repeating anatomical features seemed to be arcane and archaic. In 2007, this area has moved to the very center of biology and is the subject of hundreds of recent publications. The recognition that terminal addition of segments (Jacobs et al 2005) is the crucial common feature of the Bilateria (including insects, crustaceans, and vertebrates) has made this among the most elemental of areas of zoology. Other studies have confirmed the odd phenomena of field homology that can transform the serial homology of structures like the lumbar transverse process (Sanchez-Villagra et al 2000). Homeotics and the entire field of “Evo-Devo” is increasingly beginning to focus on the mammalian vertebral system (Burke et al 1995, Narita & Kuratani 2005, Kuratani 2005). Advances in morphologic genetics are bringing together the fields of homeotics with the study of mouse axial mutants (Mansouri et al 2000).

In the primate literature, a series of discoveries of fossil vertebrae, together with an appreciation of some of the points outlined in this thesis, have made the lumbar vertebra a key point of many recent analyses of human evolution (Ward et al 1993, Filler 1993, Sanders & Brodenbender 1994, Shapiro 1995, Köhler and Moya-Sola 1997, Shapiro and Simons 2002, Begun 2003, Haeusler et al 2003, MacLatchy 2004, Moya-Sola et al 2004, Nakatsukasa et al 2004, Pilbeam 2004, Lovejoy 2005, Gommery 2006).

Upon completion of the thesis, I sought a method to clarify the homology of the spinal muscles. My plan was to find an effective way to track the complex, unmapped nerves of the spinal musculature. This led to a wonderful spin-off that has consumed a significant portion of my research effort in the subsequent years - the discovery of a method to image nerves in the intact living human body at an incredible level of detail - MR Neurography (Filler et al 1993, Filler et al 2004). Recently this has led to the establishment of new diagnoses and treatment methods that are relieving previously unreatable pain in many thousands of patients every year (Filler et al 2005). A significant portion of my clinical work has pertained to evaluation and treatment of variants of the brachial plexus & lumbosacral plexus as well as spinal abnormalities and degenerative disorders. (Filler 2004).

This unabridged edition of the 1986 work also provides a snapshot in time of the state of knowledge in this field 150 years after the Great Academy debate that spelled the beginning of the end for vertebral theories of evolution. The project was started in 1977, one year before the initial discovery of the homeobox by Lewis (1978).

Aside from the historical context, the advance of digital technology now also makes it possible to provide downloads of the full set of images (available online at www.axialcharacter.com as either stereo pairs or red-blue anagrams). These images help convey the fascinating quality of seriation of characters that our modern genetic tools are even now just starting to explore.

Aaron Filler, MD, PhD, FRCS (SN) November 2006
Santa Monica, CA

Preface Bibliography

Begun, D. R. (2003) – The planet of the apes. Sci. Am. 289:74-83.

Burke, A. C., C. E. Nelson, B. A. Morgan, and C. Tabin (1995) – *Hox* genes and the evolution of vertebrate axial morphology. Development 121:333-346.

Filler A.G. (1993) - Evolution of the sacrum in hominoids. In: Surgical Disorders of the Sacrum, JR Doty and SS Rengachary eds. 13-20, Thieme, New York.

Filler A. G., F. A. Howe, C. E. Hayes, M. Kliot, H. R. Winn, B. A. Bell, J. R. Griffiths, and J. S. Tsuruda (1993) - Magnetic resonance neurography. Lancet 341:659-661.

Filler A. G. (2004) - Do You Really Need Back Surgery: A Surgeon's Guide to Neck and Back Pain and How to Choose Your Treatment. Oxford University Press. New York.

Filler A. G., K. R. Maravilla, J. S. Tsuruda (2004) - MR Neurography and muscle MR imaging for image diagnosis of disorders affecting the peripheral nerves and musculature. Neurologic Clinics 22:643-682.

Filler A. G., J. Haynes, S. Jordan, J. Prager, J. P. Villablanca, K. Farahani, D. Q. McBride, J. S. Tsuruda, B. Morisoli, U. Batzdorf, and J. P. Johnson (2005) - Sciatica of Non-Disk Origin & Piriformis Syndrome: Diagnosis by MR Neurography and Interventional MRI with Outcome Study of Resulting Treatment. Journal of Neurosurgery – Spine 2:99-115.

Gommery, D. (2006) – Evolution of the vertebral column in Miocene Hominoids and Plio-Pleistocene Hominids. In: H. Ishida, R. Tuttle, M. Pickford, N. Ogihara, and M. Nakatsukasa (eds.): Human Origins and Environmental Backgrounds – Developments in Primatology: Progress and Prospects – R. Tuttle (series editor). 31-43, Springer, New York, N.Y.

Haeusler, M., S. A. Martelli, and T. Boeni (2003) – Vertebrae numbers of the early hominid lumbar spine. J. Hum. Evol. 43:621-643.

Jacobs, D. K., N. C. Hughes, S. T. Fitz-Gibbon, and C. J. Winchell (2005) Terminal addition, the Cambrian radiation and the Phanerozoic evolution of bilaterian form. Evol. Dev. 7:498-514.

Köhler, M., and S. Moya-Sola (1997) – Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. PNAS 94:11747-11750.

Kuratani, S. (2005) – Craniofacial development and the evolution of the Vertebrates: the old problems on a new background. Zool. Sci. 22:1-19.

Lewis, E. B. (1978) – A gene complex controlling segmentation in *Drosophila*. Nature 276:565-570.

Lovejoy, C. O. (2005) – The natural history of human gait and posture. Part 1. Spine and pelvis. Gait Posture 21:95-112.

MacLatchy, L. (2004) – The oldest ape. Evol. Anthropol. 13:90-103.

Mansouri, A., A. K. Voss, T. Thomas, Y. Yokota, and P. Gruss (2000) – *Uncx4.1* is required for the formation of the pedicles and proximal ribs and acts upstream of *Pax9*. Development 127:2251-2258.

Moya-Sola, S., M. Köhler, D. M. Alba, I. Casanovas-Vilar, and J. Galindo (2004) – *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 306:1339-1344.

Nakatsukasa M., C. V. Ward, A. Walker, M. F. Teaford, Y. Kunimatsu and N. Ogihara (2004) – Tail loss in *Proconsul heseloni*. J. Hum. Evol. 46:777-784.

Narita Y, and S. Kuratani (2005) - Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. (Mol. Dev. Evol.) 304:91-106.

Pilbeam, D. (2004) – The anthropoid postcranial axial skeleton: Comments on development, variation, and evolution. J. Exp. Zool. (Mol. Dev. Evol.) 302B:241-267.

Sanchez-Villagra, M. R., R. J. Burnham, D. C. Campbell, R. M. Feldmann, E. S. Gaffney, R. F. Kay, R. Lozsan, R. Purdy, and J. G. M. Thewissen (2000) – A new near-shore marine fauna and flora from the early Neogene of Northwest Venezuela. J. Paleontol. 74:957-968.

Sanders, W. J., and B. E. Bodenbender (1994) – Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto hominoid. J. Hum. Evol. 26:203-237.

Shapiro, L. (1995) – Functional morphology of Indrid lumbar vertebrae. Am. J. Phys. Anthropol. 98:323-342.

Shapiro, L. J., and V. M. Simons. (2002) – Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes. J. Hum. Evol. 42:53-783.

Ward C. V., A. Walker, M. F. Teaford, and I. Odhiambo (1993) – Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. Am. J. Phys. Anthropol. 90:77-111.

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David Pilbeam continued to press me to struggle with these issues in order to produce a generally useful and comprehensive written summary of the work. As my ideas began to gel early this year, crucial conversations with Stephen Gould and George Lauder were extremely helpful.

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whose presence is greatly missed.

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