

Axial Character Seriation in Mammals:

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

by

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PhD Thesis

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Axial Character Seriation in Mammals: An Historical and Morphological Exploration
of the Origin, Development, Use, and Current Collapse of the Homology Paradigm

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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

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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

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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.

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November 2006

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This work is the product of many influences and is not at all what I anticipated at the outset. Leonard Radinsky introduced me to comparative anatomy as an undergraduate and inspired me to undertake the study of brain evolution. I chose to work on primates in the setting of human evolution under the guidance of Russell Tuttle, and it was his suggestion that I first do a master's thesis concerned with axial anatomy. After completing that work I left the University of Chicago for Harvard University in anticipation of beginning work on brain evolution. In my first year there however, the results of my master's thesis received attention from Sherwood Washburn and Farish Jenkins and they, together with Irven DeVore encouraged me to continue work in axial anatomy. The academic environment at the Peabody Museum and the Museum of Comparative Zoology provided an incredibly stimulating opportunity for the development of my ideas and data.

Farish Jenkins invited me to move to the MCZ and provided facilities for dissection and experimental work as well as access to a wide variety of research material. Irven DeVore and Erik Trinkaus provided a firm base of continuing support and enthusiasm throughout this period.

A. W. Crompton and Stephen Gould provided counterposed intellectual models which left me in continuing turmoil about how to approach the subject. Experimental reductionism in a physiological context is clearly a mandatory program for isolating reliable information about anatomic diversity. However, Gould has forced the issue of the relevance of function to morphologic change at higher taxonomic levels.

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.

Throughout the years at Harvard and after my return to the University of Chicago, I've had the excellent good fortune of close association with Terry Deacon as a colleague and a friend. He played a major role in the formation of my ideas, both as a critic and as an in-

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Most of the photographs were taken by Ron Testa at the Field Museum of Natural History or by Al Coleman at the Museum of Comparative Zoology respectively as indicated by the specimen numbers in the figure captions. Material for dissection was made available by the Peabody Museum at Harvard, by the MCZ, the USNM, and the New England Primate Research Center. Osteological material was made available by the MCZ, FMNH, USNM, Cleveland Museum of Natural History, and by the Peabody at Harvard. Embryological material at the Carnegie Collection was kindly made available by Dr. Ronan O'Rahilly. This work was supported in part by NIH PHS musculoskeletal biology training grant #5 T32 GM07117-09 0011.

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a wonderfully inspiring teacher and scholar
whose presence is greatly missed.

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