Skeletal Function and Form

Mechanobiology of Skeletal Development, Aging, and Regeneration

The intimate relationship between form and function inherent in the design of animals is perhaps nowhere more evident than in the musculoskeletal system. In the bones, cartilage, tendons, ligaments, and muscles of all vertebrates there is a graceful and efficient physical order.

This book is about how function determines form. It addresses the role of mechanical factors in the development, adaptation, maintenance, aging, and repair of skeletal tissues. The authors refer to this process as mechanobiology and develop their theme within an evolutionary framework. They show how the normal development of skeletal tissues is influenced by mechanical stimulation beginning in the embryo and continuing throughout life into old age. They also show how degenerative disorders such as arthritis and osteoporosis are regulated by the same mechanical processes that influence development and growth. *Skeletal Function and Form* bridges important gaps among disciplines, providing a common ground for understanding, and will appeal to a wide audience of bioengineers, zoologists, anthropologists, paleontologists, and orthopedists.

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To my wife Alice who has been a constant source of encouragement and ideas and to my children Mandy, Todd, and Robert who continue to inspire my work and life.

– D.R.C.

To Mom, Dad, and Steve who have provided a lifetime of encouragement and support and to my wife Sally in appreciation of her companionship, spirit, and compassion.

– G.S.B.

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Preface

This book is about how function determines form. Our objective is to present a consistent approach for understanding the role of mechanical factors in skeletal development, growth, maintenance, functional adaptation, and aging. A conceptual framework for understanding how mechanically mediated events may influence the evolution of the vertebrate skeleton is also provided. The text is a synopsis of the scientific perspective that has been developed by our research group at Stanford University and the VA Palo Alto Health Care System. Our intention is to provide a single source in which these ideas are summarized for anatomists, anthropologists, bioengineers, biologists, biophysicists, molecular geneticists, paleontologists, physicians, surgeons, and students in the physical and life sciences.

A phylogenetic framework is introduced in which chronological stages of skeletal ontogeny are followed in successive chapters. The first chapter provides a historical background on the study of musculoskeletal form and function, touching on developmental and evolutionary questions. The second chapter presents basic information on the histomorphology of skeletal tissues and a brief introduction to mechanical principles that are used throughout the book. Chapters 3 through 8 then follow human skeletal ontogeny from the initial formation of joints and bone in the embryo through the destruction of articular cartilage in the aged. Chapter 9 then returns to the phylogenetic level to consider the implications of developmental mechanics for the skeletal features in extinct and extant taxa. Chapter 10 offers some closing thoughts on the physical nature of living things.

We aspire to bridge important gaps between disciplines in a manner that will provide common ground for understanding and future investigation. The interdisciplinary nature of the topics covered and the varied backgrounds of those in our audience require that both the authors and readers of this book make some compromises. Depending on the background and training of the reader, some sections may seem too elementary and others too obscure. One decision that we have made in this regard is to remove most of the details of engineering analyses and justifications from the main chapters of the text. Readers who would prefer more presentation and justification of engineering concepts are referred to the Appendixes and the references that are provided.

We sincerely thank and acknowledge our students and former students. Without their contributions, this book could not have been written. These individuals include Patricia Blenman-Fyhrie, Mary Bouxsein, Ken Fischer, David Fyhrie, Virginia Giddings, Nicholas Giori, Chris Hernandez, Chris Jacobs, Amanda LeNay, Marc Levenston, Elizabeth Loboa, Jay Mandell, Borjana Mikić, Terri Nauenberg, Tracy Orr, Cheryl Pattin, Daniel Rapperport, Vineet Sarin, Sandra Shefelbine, Sheila Stevens, Kim Thomas, Marjolein van der Meulen, Robert Whalen, Marcy Wong, and Tishya Wren. We would also like to thank our close professional colleagues William Caler, Greg Erickson, Stuart Goodman, Jean Heegaard, David Kingsley, Kevin Padian, Armand de Ricqlès, David Schurman, R. Lane Smith, and Ramiah Vasu. Their work and advice have been crucial in generating the results and ideas presented in this book. We thank Wilson C. Hayes who introduced both of us to research on mechanical regulation of the skeleton over two decades ago. Finally, a special thanks to Paul Green whose teaching and discussions with faculty and students have been a source of support and encouragement to many of us. His research on the role of mechanics in pattern development and growth in plants serves as a continual reminder of the ubiquitous nature of physical influences in biology.

Over the last 150 years, Charles Darwin, Wilhelm Roux, Karl Culman, G. Hermann von Meyer, Julius Wolff, W. Gebhardt, D'Arcy Thompson, Friedrich Pauwels, and Harold Frost have recognized the importance of mechanical stresses in skeletal development and evolution. In many ways this book is a logical extension of their ideas and research. We hope that our efforts will contribute to the further appreciation and assimilation of physical science within the province of modern biology. The relationship between physical forces and the morphology of living things has piqued the curiosity of every artist, scientist, or philosopher who has contemplated a tree or drawn the human figure. Its importance was a concern of Galileo and later of Thompson whose writings remind us that physical causation plays an inescapable role in the development of biological form:

> It would, I dare say, be an exaggeration to see in every bone nothing more than a resultant of immediate and direct physical or mechanical conditions; for to do so would be to deny the existence, in this connection, of a principle of heredity. … But I maintain that it is no less an exaggeration if we tend to neglect these direct physical and mechanical modes of causation altogether, and to see in the characters of a bone merely the results of variation and heredity.

D'Arcy Wentworth Thompson
On Growth and Form, 1917