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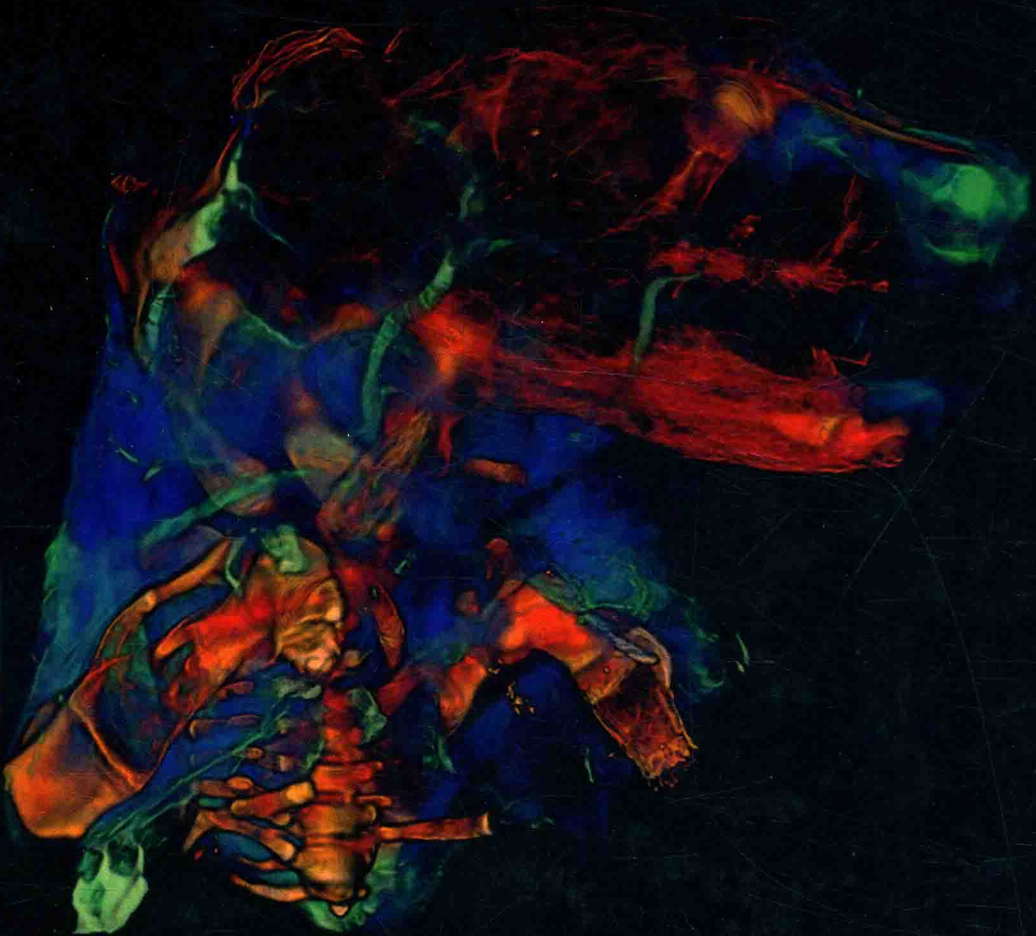
Building Bones

Bone Formation and Development in Anthropology

Edited by
CHRISTOPHER J. PERCIVAL
AND JOAN T. RICHTSMEIER



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CAMBRIDGE
UNIVERSITY PRESS

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University Printing House, Cambridge CB2 8BS, United Kingdom

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org
Information on this title: www.cambridge.org/9781107122789

First published 2017

Printed in the United Kingdom by TJ International Ltd. Padstow Cornwall

A catalogue record for this publication is available from the British Library

Library of Congress Cataloguing in Publication data
Names: Percival, Christopher J., editor. | Richtsmeier, Joan T., editor.
Title: Building Bones: Bone Formation and Development in Anthropology / edited by Christopher J. Percival and Joan T. Richtsmeier.
Other titles: Cambridge studies in biological and evolutionary anthropology.
Description: Cambridge; New York : Cambridge University Press, 2016. | Series: Cambridge studies in biological and evolutionary anthropology | Includes bibliographical references and index.
Identifiers: LCCN 2016049379 | ISBN 9781107122789 (hardback : alk. paper)
Subjects: | MESH: Bone Development | Anthropology, Physical | Biological Evolution | Anthropometry
Classification: LCC GN70 | NLM GN 70 | DDC 599.9/47–dc23
LC record available at https://lccn.loc.gov/2016049379

ISBN 978-1-107-12278-9 Hardback

Building Bones

Bone Formation and Development in Anthropology

Bone is the tissue most frequently recovered archaeologically and is the material most commonly studied by biological anthropologists, who are interested in how skeletons change shape during growth and across evolutionary time. This volume brings together a range of contemporary studies of bone growth and development to highlight how cross-disciplinary research and new methods can enhance our anthropological understanding of skeletal variation. The novel use of imaging techniques from developmental biology, advanced sequencing methods from genetics, and perspectives from evolutionary developmental biology improve our ability to understand the bases of modern human and primate variation. Animal models can also be used to provide a broad biological perspective to the systematic study of humans. This volume is a testament to the drive of anthropologists to understand biological and evolutionary processes that underlie changes in bone morphology and illustrates the continued value of incorporating multiple perspectives within anthropological inquiry.

Christopher J. Percival is a postdoctoral researcher at the University of Calgary. His research focusses on the basis for variation in skull form.

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Contents

Contributors *page ix*

Introduction **1**
Christopher J. Percival and Joan T. Richtsmeier

1 **What Is a Biological 'Trait'?** **13**
Kenneth Weiss

2 **The Contribution of Angiogenesis to Variation in Bone Development and Evolution** **26**
Christopher J. Percival, Kazuhiko Kawasaki, Yuan Huang, Kenneth Weiss, Ethylin Wang Jabs, Runze Li and Joan T. Richtsmeier

3 **Association of the Chondrocranium and Dermatocranium in Early Skull Formation** **52**
Kazuhiko Kawasaki and Joan T. Richtsmeier

4 **Unique Ontogenetic Patterns of Postorbital Septation in Tarsiers and the Issue of Trait Homology** **79**
Valerie B. DeLeon, Alfred L. Rosenberger and Timothy D. Smith

5 **Exploring Modern Human Facial Growth at the Micro- and Macroscopic Levels** **104**
Sarah E. Freidline, Cayetana Martinez-Maza, Philipp Gunz and Jean-Jacques Hublin

6 **Changes in Mandibular Cortical Bone Density and Elastic Properties during Growth** **128**
Paul C. Dechow

7 **Postcranial Skeletal Development and Its Evolutionary Implications** **148**
David B. Burr and Jason M. Organ

8 **Combining Genetic and Developmental Methods to Study Musculoskeletal Evolution in Primates** **175**
Terence D. Capellini and Heather Dingwall

9 Using Comparisons between Species and Anatomical Locations to Discover Mechanisms of Growth Plate Patterning and Differential Growth **205**
Kelsey M. Kjosness and Philip L. Reno

10 Ontogenetic and Genetic Influences on Bone's Responsiveness to Mechanical Signals **233**
Ian J. Wallace, Brigitte Demes and Stefan Judex

11 The Havers–Halberg Oscillation and Bone Metabolism **254**
Russell T. Hogg, Timothy G. Bromage, Haviva M. Goldman, Julia A. Katris and John G. Clement

12 Structural and Mechanical Changes in Trabecular Bone during Early Development in the Human Femur and Humerus **281**
Timothy M. Ryan, David A. Raichlen and James H. Gosman

Appendix to Chapter 3: Detailed Anatomical Description of Developing Chondrocranium and Dermatocranium in the Mouse **303**
Kazuhiko Kawasaki and Joan T. Richtsmeier

Index 316

The color plates are between pages 180 and 181.

Introduction

Christopher J. Percival and Joan T. Richtsmeier

There is little doubt that much of what we know in biological anthropology is based on the experimentation with and excavation, measurement, and analysis of mineralized tissues. From the earliest excavation and recovery of fossil primate specimens, anthropologists have routinely used comparative skeletal materials and particular features on those materials to classify human and nonhuman primate species and to infer evolutionary relationships. Although early studies of skeletal biomechanics were primarily done by anatomists and orthopedists, anthropologists adopted biomechanical principles to infer activity from the shape of bones and to make inferences about life histories and habitual behaviors in the early part of the twentieth century (Washburn, 1951; Ruff, 2008). Our current interpretation of human and nonhuman primate origins and evolutionary history is still based primarily on osseous traits, although genetic and genomic data are being effectively used to resolve phylogenetic relationships that have resisted consensus based solely on skeletal traits (e.g., Perelman *et al.*, 2011; Meyer *et al.*, 2016). Currently, anthropologists explicitly recognize that the development and evolution of mineralized tissues are intertwined, with changes in developmental processes serving as a basis for phenotypic change (e.g., Lovejoy *et al.*, 1999; Chiu and Hamrick, 2002; Hlusko *et al.*, 2004). Consequently, anthropologists have been early adopters of technologies and approaches from other disciplines (e.g., genome-wide association study (GWAS), quantitative trail locus (QTL) analysis, quantitative imaging, breeding experiments), and have contributed to the design of new methods to acquire and measure data pertaining to changing biomechanical properties and to ontogenetic change of mineralized tissues (e.g., Cheverud *et al.*, 1983; Ruff and Hayes, 1983; Richtsmeier *et al.*, 1992; Richtsmeier and Lele, 1993; Smith and Tompkins, 1995; Strait *et al.*, 2005, 2007; Slice, 2007; Raichlen *et al.*, 2015). The adoption of a developmental focus has helped to shift emphasis away from the anatomy and classification of particular skeletal traits towards questions pertaining to developmental processes that underlie the production of those traits and their variation (Hallgrímsson & Lieberman, 2008; Reno *et al.*, 2008; Hallgrímsson *et al.*, 2009; Young *et al.*, 2010; Serrat, 2013; Kjosness *et al.*, 2014; Reno, 2014; Rolian, 2014). In this way, anthropological analyses of skeletal remains have expanded from comparisons based on external features and metrics that are used to build phylogenies to the advance of approaches aimed at uncovering the developmental basis for variation in skeletal morphology and evolution. This book includes research conducted by a broad sample of anthropological researchers who are using their expertise to dissect the ways in which development of both the cranial and postcranial skeleton can be used to further our understanding of the basis of novel variation and the role that changes in developmental processes play in the evolution of skeletal morphology.

Because biological anthropological data sets have historically been principally skeletal in nature, anthropologists have always been favorable toward developing or adopting new technology and novel approaches to the analysis of skeletal tissues. During the twentieth century, investigators began to interrogate bone in new ways. Engineering principals as applied to bony architecture were codified by Wolff's law and anthropologists applied this law in the study of skeletal samples under the paradigm that bone is a living tissue that responds mechanically to stress and/or strain in ways that insure tissue strength and resistance to loads where it is needed. The patterns visualized in bone were interpreted as forming in response to mechanical loading. Wolff's law, and predictions stemming from it, were routinely used to check the relationship between lifestyle and bone architecture in living primate species and to propose the locomotory mode of recovered fossil species. However, further laboratory work showed that bone can have highly variable responses to similarly applied forces and that variations in the skeleton can derive from a complex mix of genetic and epigenetic influences (Pearson and Lieberman, 2004; Ryan and Shaw, 2014). Genetic history, sex, nutrition, diet, hormonal influences, life history, phylogenetic history, maturity, microstructural properties of a particular bone region, and body size comprise some of the additional factors that are found to contribute to the osseous response to applied forces. Mineralized tissues may be those most accessible to anthropologists, but the information they contain relating to life history, function and evolution might be harder to tease from inert and sometimes fossilized samples than once thought. Such realizations provided an impetus for the use of experimental animals by anthropologists where certain of these variables can be experimentally controlled and the influence of the others can be tested.

Bone is a living tissue whose characteristics, even within species, are highly variable in time and space. In the 1970s and 1980s, bioarcheologists began to take advantage of this variation to pose population-level questions of skeletal series. Skeletal remains came to be used as the primary data set of problem-oriented research aimed at the investigation of mortuary practice (e.g., Buikstra, 1981), disease vectors in paleopathology (e.g., Armelagos *et al.*, 2005; Wolfe *et al.*, 2007), population dynamics and paleodemography (e.g., Wood *et al.*, 1992), fracture healing (e.g., Boldsen *et al.*, 2015), and biological (genetic) relationships among populations (e.g., Buikstra *et al.*, 1990). In these applications, skeletal variation became the criterion upon which hypotheses pertaining to the sociocultural context of associated populations represented by the skeletal remains were tested. These approaches are the foundation of modern bioarcheology that recognizes the necessity of large sample sizes for understanding processes at the population level.

In addition to these important research directions that remain valid and currently in use, anthropologists have always shown an interest in the changing shapes of bones during growth and in the differences observed between immature and mature skeletons. Anthropologists have led the way in developing methods that tease more information from the bones than would seem evident at first glance. In the simplest examples, knowledge of the sequence of developmental events and how bone grows (e.g., the order and timing of closure of epiphyses and of cranial sutures, the changing morphology of bones throughout life) have enabled the aging of single skeletons and the analysis of population dynamics and demography when these data are available from samples of known provenience. More complex analyses of growth patterns using varied types of morphological data from varied skeletal tissues and multiple methods of analysis have been used to estimate the age of fossil specimens (e.g., Holly, 1992; Smith and Tompkins, 1995), to compare growth between species (e.g., Ackermann and Grovitz, 2002; Bastir and Rosas, 2004; Berge and Penin, 2004; Bulygina *et al.*, 2006; Bastir *et al.*, 2007; Boughner and Dean, 2008), to determine the influence of particular patterns of growth on known morphologies (e.g., Richtsmeier *et al.*, 1993), and to predict the morphology of "hypothetical forms" by mathematically applying estimated growth trajectories to given morphologies (e.g., Richtsmeier and Lele, 1993; McNulty *et al.*, 2006). These approaches have largely been based on what could be coaxed from measured morphological changes associated with bone growth, namely change in size and shape. More recently, anthropologists have been able to use advanced imaging technologies to study important morphological indicators of growth at much smaller scales, develop novel methodologies for their use in the study of populations, and derive new knowledge from these observations. The field of genetics has also become increasingly relevant to the anthropological study of phenotypes and their growth. Not only does knowledge of the genetics of bone development inform us of how bone is formed (e.g., Long, 2012), but correlations between specific genetic variants and variation in quantitative skeletal traits over developmental time point to the contribution of genetic variation to variation in skeletal phenotypes. For example, Hager and colleagues (2009) conducted a series of quantitative trait loci experiments to identify genomic regions that affect body size growth processes revealing that distinct genomic regions affect early postnatal growth (1–3 weeks) while others affect later growth (4–10 weeks) (Hager *et al.*, 2009).

With the advent of evolutionary developmental biology, additional experimental tools, laboratory methods, and genetic approaches became available to anthropologists interested in determining the developmental basis for evolutionary change within the fossil record and phylogenetic differences between living species. Approaches developed within the emerging field of evolutionary developmental biology (evo-devo) enabled the characterization how change occurring within developmental programs is fundamental to evolutionary processes (Carrol *et al.*, 2001). Evo-devo encompasses research on how variation in development relates to the evolutionary changes that occur between generations. Early traces of the evo-devo perspective can be found in the work of, for example, Bonner (1982), Gould (1977), Waddington (1942), and De Beer (1940), but the molecular revolution that occurred in the last decade of the twentieth century made a new set of tools and resources (e.g., increasingly accessible sequencing technology; increasing computational power; novel immunohistochemistry assays; increased understanding of the complexity of the genome) potentially available to anyone with an interesting question pertaining to the mechanisms that link the genotype with the phenotype and how change measured within a single generation relates to change across many generations.

Although first developed and widely used in other disciplines, resources including specific reagents, transgenic technologies, techniques for gene editing (e.g., CRISPR), genomic sequencing, and genotyping and biological imaging technologies, have become increasingly available at diminishing cost. The traditional training offered in anthropology graduate programs meant that, at their introduction, few anthropologists were appropriately trained to adopt and apply these tools. Thankfully, there were investigators from other disciplines with the appropriate expertise who were eager to work on anthropological problems and to work collaboratively with anthropologists on subjects pertaining to human evolution. These collaborative beginnings, followed by a rapid increase in the number of biological anthropologists seeking training in these techniques, prompted a maturation of the field that is now evident in many aspects of biological anthropology. For example, while the relevance of experimental studies in mice in studies of human evolution was openly questioned only 20 years ago, it is now commonplace for anthropologists to propose and test hypotheses about human and nonhuman primate growth, development and evolution using data from non-primate animal models. The amazing number of genomes now sequenced, along with emerging knowledge of the evolution of genomes, enables an even more direct connection of human biology with fish, mammal and chick biomedical models, illuminating the relevance of distantly related species to understanding the evolution of human developmental processes and the function of human regulatory sequences (see, for example, Lamason *et al.*, 2005; Braasch *et al.*, 2016).

These new research trends in anthropology have not occurred due to a directed reorganization of the discipline, but instead represent an organic expansion of the field of biological anthropology as scientists observe what is happening in the larger world of biological research and imagine how they might apply those technologies and skill sets to anthropologically inspired research questions. Bridges have always existed across the subfields of anthropology (biological, cultural, and archeology traditionally, and more recently with ecological, forensic, and genetic anthropology), but connections between biological anthropology and other disciplines are creating collaborative links that previously would have seemed incongruent. These relationships serve as the foundation for necessary changes in anthropological training programs and independent research projects that welcome the incorporation of methods, knowledge, and perspectives from outside of anthropology. The push towards collaborative, cross-disciplinary research in many universities is evident in the chapters presented in this book, and we hope that this volume helps to create and inspire additional connections within the field and across disciplines by exposing anthropologists to a variety of new perspectives in the study of bone development.

The diverse training becoming progressively available to students of biological anthropology provides new knowledge for those eager to translate observations of lifeless skeletal remains into hypotheses that concern behavioral, molecular and morphological evolution, mechanisms of osseous development, and the relationship between organisms and their environment. These new opportunities enable anthropologists to expand their work from theory-driven analyses of skeletal features to experimental approaches that are aimed at revealing biological mechanisms that underlie phenotypic changes evidenced in skeletal remains. Developmental biology, evolutionary developmental biology, genetics and genomics are probably the fields that have contributed most to the changing world of biological anthropology research, and our chapters reflect that contribution. However, the influence of other disciplines is also apparent in this volume, and it would be premature to predict which fields will provide important discoveries and collaborative inputs in the future. Because anthropologists are trained broadly to consider problems pertaining to human evolution, they often can make connections that might be missed by people working in other fields. The challenge for current and future generations of anthropologists is to maintain this broad perspective *and* obtain adequate training in their chosen area of specialization including becoming proficient in necessary technological, computational and/or laboratory skills while resisting the impulse of becoming overspecialized.

This book presents explicit examples of cross-disciplinary research in biological anthropology with the uniting principle of a focus on early formation and growth of bone, the tissue most often left behind in paleoanthropological and archeological contexts. Although the book is organized according to studies that focus on the appendicular versus axial skeleton, many of the chapters focus on fundamental issues that could apply to either part of the skeleton. Our volume starts with an introductory and historical perspective from **Ken Weiss**. By asking the question "What is a biological trait?" this chapter provides important observations of both theoretical and practical concern by considering the genetic basis for traits like those that have been used by biological anthropologists to assign specimens to a taxon. The development of these traits is complex and this complexity must be acknowledged when attempting to understand the production of these phenotypic traits from genetic information. What besides the genetic information that can be tabulated contributes to the morphology produced? What role do those additional components have? And what, in reality, is a complex trait?

The chapter by **Christopher Percival and Joan Richtsmeier and colleagues** provides a brief review of processes underlying skull formation and development, followed by the description of primary research in a mouse model that helps to illuminate the role that blood vessels play during craniofacial osteogenesis. The results of this work suggest ways in which dysregulation of the relationship between blood vessels and bone might contribute to variation within and between extant primate species, while also illustrating how the quantification of multiple aspects of craniofacial skeletal phenotypes can provide a more complete understanding of how genetic changes modify osteogenesis in the skull. While existing biomedical models can be leveraged to develop a more complete understanding of potential developmental bases for evolutionary change in the skull, anthropologists and evolutionary biologists must take the lead in applying these models to evolutionary questions because researchers interested in disease will not.

Kazuhiko Kawasaki and Joan Richtsmeier present a detailed embryological description of the anatomy of the chondrocranium: that part of the endoskeleton that protects the brain and three principal sense organs but does not include the pharyngeal endoskeleton. After years of studying the genetic basis of bones and teeth (Kawasaki) and the morphology and growth of the mammalian skull (Richtsmeier), these authors provide precise definitions and detail the distinction between the cranial base and the chondrocranium. To provide definitions that are based on the evolution of the endoskeleton and dermal skeleton, these authors combine developmental, evolutionary, and anatomical approaches in the analysis of cranial evolution, and use embryological observations of the laboratory mouse to define the chondrocranium and the dermatocranium and the coordinated development of these structures. Finally, the authors use data relating to the spatiotemporal associations of the chondrocranium and dermatocranium to suggest their dynamic interaction during skull formation and suggest implications for understanding cranial modularity and integration.

Postorbital septation in primates has long been a morphological trait of interest. **Valerie DeLeon, Alfred Rosenberger, and Tim Smith** describe the unique ontogenetic patterns of postorbital septation in tarsiers and apply their findings to the question of trait homology to show how ontogeny of skeletal elements can provide evidence of phylogenetic relationships. Using a comparative ontogenetic approach, the authors show that early postnatal tarsier orbits show ontogenetic adaptations that delay osseous closure of the orbital fossa to allow eye enlargement, followed by the development of an osseous septum that serves to support the overly large eye. The authors conclude that postorbital septation in tarsiers is secondary to eye hypertrophy. Based on this conclusion, they propose possible scenarios for the evolution of septation in tarsier and anthropoid lineages and emphasize the importance of ontogenetic continuity in evaluating hypotheses about trait homology.

In a chapter about facial shape change during growth, **Sarah Freidline, Cayetana Martinez-Maza, Philipp Gunz, and Jean-Jacques Hublin** combine data pertaining to patterns of bone modeling (formation and resorption fields on the face and mandible) and morphometric measures of facial shape and form in an attempt to understand the correspondence between large-scale morphological shape changes and bone modeling patterns at a microstructural level. These investigators characterize the size and shape of a cross-sectional ontogenetic sample of human skulls of various ages whose patterns of facial bone formation and resorption fields were previously mapped to investigate whether or not these two types of data can be combined to create informative growth models. Interesting observations pertaining to the correspondence in patterns of variation at both the microscopic and macroscopic levels of analysis are provided.