

Primate Craniofacial Function and Biology

DEVELOPMENTS IN PRIMATOLOGY: PROGRESS AND PROSPECTS

Series Editor: Russell H. Tuttle, University of Chicago, Chicago, Illinois

This peer-reviewed book series melds the facts of organic diversity with the continuity of the evolutionary process. The volumes in this series exemplify the diversity of theoretical perspectives and methodological approaches currently employed by primatologists and physical anthropologists. Specific coverage includes: primate behavior in natural habitats and captive settings; primate ecology and conservation; functional morphology and developmental biology of primates; primate systematics; genetic and phenotypic differences among living primates; and paleoprimatology.

PRIMATE BIOGEOGRAPHY

Edited by Shawn M. Lehman and John Fleagle

REPRODUCTION AND FITNESS IN BABOONS: BEHAVIORAL, ECOLOGICAL, AND LIFE HISTORY PERSPECTIVES

Edited By Larissa Swedell and Steven R. Leigh

RINGTAILED LEMUR BIOLOGY: LEMUR CATTALINA IN MADAGASCAR

Edited by Alison Jolly, Robert W. Sussman, Naoki Koyama, and Hantanirina Rasamimanana

PRIMATES OF WESTERN UGANDA

Edited by Nicholas E. Newton-Fisher, Hugh Notman, James D. Paterson, and Vernon Reynolds

PRIMATE ORIGINS: ADAPTATIONS AND EVOLUTION

Edited by Matthew J. Ravosa and Marian Dagosto

LEMURS: ECOLOGY AND ADAPTATION

Edited by Lisa Gould and Michelle L. Sauter

PRIMATE ANTI-PREDATOR STRATEGIES

Edited by Sharon L. Gursky and K.A.I. Nekaris

CONSERVATION IN THE 21ST CENTURY: GORILLAS AS A CASE STUDY

Edited by T.S. Stoinski, H.D. Steklis, and P.T. Mehlman

ELWYN SIMONS: A SEARCH FOR ORIGINS

Edited by John G. Fleagle and Christopher C. Gilbert

THE BONOBO: BEHAVIOR, ECOLOGY, AND CONSERVATION

Edited by Takeshi Furuichi and Jo Thompson

PRIMATE CRANIOFACIAL FUNCTION AND BIOLOGY

Edited by Chris Vinyard, Matthew J. Ravosa, and Christine E. Wall

Chris Vinyard · Matthew J. Ravosa ·
Christine Wall
Editors

Primate Craniofacial Function and Biology

 Springer

Editors

Chris Vinyard
Department of Anatomy
Northeastern Ohio University
College of Medicine
4209 Cpy Route 44
Rootstown, OH 44272-0095
USA
cvinyard@neoucom.edu

Matthew J. Ravosa
University of Missouri School of Medicine
Columbia, MO 65212
USA
ravosam@health.missouri.edu

Christine Wall
Department of Biological
Anthropology and Anatomy
Duke University
Box 90383
Durham, NC 27708
USA
christine_wall@baa.mc.duke.edu

ISBN: 978-0-387-76584-6

e-ISBN: 978-0-387-76585-3

DOI: 10.1007/978-0-387-76585-3

Library of Congress Control Number: 2008931523

© 2008 Springer Science+Business Media, LLC

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Springer Science+Business Media, LLC, 233 Spring Street, New York, NY 10013, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in this publication of trade names, trademarks, service marks, and similar terms, even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

Printed on acid-free paper

springer.com

Preface

William Hylander is synonymous with primate craniofacial function. For the first three-quarters of the 20th century, studies of the primate masticatory apparatus typically inferred function by examining form. William Hylander revolutionized studies of the primate masticatory apparatus through his use of *in vivo* techniques to quantify bone strain, jaw-muscle activity, and jaw movements in living primates while they chewed. His direct measures of jaw, tooth, and jaw-muscle function during chewing are the empirical cornerstone that many biological anthropologists build upon today. We dedicate this volume surveying recent developments in primate craniofacial function and biology to William Hylander and his lifelong contribution to biological anthropology.

Today, the amount of craniofacial research on primates is immense. Functional studies alone range from *in vivo* analyses of living animals to morphological and finite element explorations of extinct primate cranial remains. The results of these research efforts have been fundamental in developing our understanding of primate biology and evolution. The sheer magnitude of craniofacial studies affirm that furthering our knowledge of primate craniofacial biology is one of the most important research agendas in modern biological anthropology.

Outside of primatology, many mammalian biologists have provided key insights into primate form and function through their comparative analyses of mammalian clades. Some biological anthropologists have continued a tradition of studying non-primate mammals as model taxa, as alternative functional designs, or as comparative radiations for exploring form–function associations observed in primates. We make a concerted effort to include this broader mammalian perspective to build on its fundamental contribution to our understanding of primate craniofacial biology.

It is impossible to adequately incorporate current research on primate craniofacial function and biology into a single volume. Our strategy was to put together a volume in honor of William Hylander, which will give readers an overview of what is current in a number of different research areas. Because several of the contributors worked closely with Hylander throughout his career, we have the deepest coverage in topics focusing on craniofacial function during feeding. This having been said, we attempted to provide a wide range of current research. We hope that readers will be able to capitalize on this approach to integrate otherwise disparate ideas and methodologies for their own work. The cost of our approach is that good scientists

and good science were left out. If by bringing together this wide range of researchers we can help catalyze future work on primate craniofacial biology and function, then we feel this cost will have been worth it.

Several of the chapters in this volume were initially presented at a 2005 symposium entitled: “Primate Craniofacial Function and Biology: A Symposium in Honor of William L. Hylander” during the American Association of Physical Anthropology Meetings in Milwaukee, WI. Building from this initial group of presentations, we had the good fortune of adding several chapters to the current volume. In the end, we were able to include twenty chapters in five sections that broadly explore different approaches to studying the skulls of primates and other mammals.

This volume would not have been possible without the advice and assistance of numerous individuals. Specifically, thanks to Andrea Macaluso, Tom Brazda, Lisa Tenaglia, Krista Zimmer, Melanie Wilichinsky, and Russell Tuttle for guiding us through the editorial process. Diana Dillon and Marie Dockery provided invaluable administrative assistance. Several external reviewers provided insightful comments that advanced the scholarship of these contributions. We thank the American Association of Physical Anthropologists for hosting and supporting the 2005 symposium in honor of William Hylander, which was the catalyst for this volume. Kirk Johnson has made one of the biggest contributions to the studies of primate feeding. Throughout his more than 25 years of work in the field, each of us became indebted to Kirk for his guidance and friendship – thank you.

Finally, we wanted to express our utmost thanks to Bill Hylander. There is no end to our appreciation of your friendship, advice, and commitment to biological anthropology and experimental biology.

Rootstown, OH, USA
Columbus, MO, USA
Durham, NC, USA

Christopher J. Vinyard
Matthew J. Ravosa
Christine E. Wall

Contents

Part I Historical Perspective on Experimental Research in Biological Anthropology

- 1 Experimental Comparative Anatomy in Physical Anthropology: The Contributions of Dr. William L. Hylander to Studies of Skull Form and Function** 3
Daniel Schmitt, Christine E. Wall, and Pierre Lemelin

Part II In Vivo Research into Masticatory Function

- 2 A Nonprimate Model for the Fused Symphysis: In Vivo Studies in the Pig** 19
Susan W. Herring, Katherine L. Rafferty, Zi Jun Liu, and Zongyang Sun
- 3 Symphyseal Fusion in Selenodont Artiodactyls: New Insights from In Vivo and Comparative Data** 39
Susan H. Williams, Christine E. Wall, Christopher J. Vinyard, and William L. Hylander
- 4 Does the Primate Face Torque?** 63
Callum F. Ross
- 5 Motor Control of Masticatory Movements in the Southern Hairy-Nosed Wombat (*Lasiiorhinus latifrons*)** 83
Alfred W. Crompton, Daniel E. Lieberman, Tomasz Owerkowicz, Russell V. Baudinette*, and Jayne Skinner
- 6 Specialization of the Superficial Anterior Temporalis in Baboons for Mastication of Hard Foods** 113
Christine E. Wall, Christopher J. Vinyard, Susan H. Williams, Kirk R. Johnson, William L. Hylander

Part III Modeling Masticatory Apparatus Function

- 7 Effects of Dental Alveoli on the Biomechanical Behavior of the Mandibular Corpus** 127
David J. Daegling, Jennifer L. Hotzman, and Andrew J. Rapoff

- 8 Surface Strain on Bone and Sutures in a Monkey Facial Skeleton: An In Vitro Approach and its Relevance to Finite Element Analysis** . 149
Qian Wang, Paul C. Dechow, Barth W. Wright, Callum F. Ross, David S. Strait, Brian G. Richmond, Mark A. Spencer, and Craig D. Byron

- 9 Craniofacial Strain Patterns During Premolar Loading: Implications for Human Evolution** 173
David S. Strait, Barth W. Wright, Brian G. Richmond, Callum F. Ross, Paul C. Dechow, Mark A. Spencer, and Qian Wang

Part IV Jaw-Muscle Architecture

- 10 Scaling of Reduced Physiologic Cross-Sectional Area in Primate Muscles of Mastication** 201
Fred Anapol, Nazima Shahnoor, and Callum F. Ross

- 11 Scaling of the Chewing Muscles in Prosimians** 217
Jonathan M.G. Perry and Christine E. Wall

- 12 The Relationship Between Jaw-Muscle Architecture and Feeding Behavior in Primates: Tree-Gouging and Nongouging Gummivorous Callitrichids as a Natural Experiment** 241
Andrea B. Taylor and Christopher J. Vinyard

Part V Bone and Dental Morphology

- 13 Relationship Between Three-Dimensional Microstructure and Elastic Properties of Cortical Bone in the Human Mandible and Femur** 265
Paul C. Dechow, Dong Hwa Chung, and Mitra Bolouri

- 14 Adaptive Plasticity in the Mammalian Masticatory Complex: You Are What, and How, You Eat** 293
Matthew J. Ravosa, Elisabeth K. Lopez, Rachel A. Menegaz, Stuart R. Stock, M. Sharon Stack, and Mark W. Hamrick

**15 Mandibular Corpus Form and Its Functional Significance:
Evidence from Marsupials 329**
Aaron S. Hogue

**16 Putting Shape to Work: Making Functional Interpretations
of Masticatory Apparatus Shapes in Primates 357**
Christopher J. Vinyard

**17 Food Physical Properties and Their Relationship to Morphology:
The Curious Case of *kily* 387**
Nayuta Yamashita

18 Convergence and Frontation in Fayum Anthropoid Orbits 407
Elwyn L. Simons

**19 What Else Is the Tall Mandibular Ramus of the Robust
Australopiths Good For? 431**
Yoel Rak and William L. Hylander

20 Framing the Question: Diet and Evolution in Early *Homo* 443
Susan C. Antón

Index 483

Contributors

Fred Anapol

Department of Anthropology, University of Wisconsin-Milwaukee, Milwaukee, WI 53211, fred@uwm.edu

Susan C. Antón

Center for the Study of Human Origins, Department of Anthropology, New York University, New York, NY 10003, susan.anton@nyu.edu

Russell V. Baudinette

School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia

Mitra Bolouri

Department of Biomedical Sciences, Baylor College of Dentistry, Texas A&M Health Science Center, Dallas, TX 75254

Craig D. Byron

Department of Biology, Mercer University, Macon, GA 31207

Dong Hwa Chung

Department of Orthodontics, School of Dentistry, Dankook University, Chung Nam, South Korea

Alfred W. Crompton

Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, acrompton@oeb.harvard.edu

David J. Daegling

Department of Anthropology, University of Florida, Gainesville, FL 32611-7305, daegling@anthro.ufl.edu

Paul C. Dechow

Department of Biomedical Sciences, Baylor College of Dentistry, Texas A&M Health Science Center, Dallas, TX 75254, pdechow@bcd.tamhsc.edu

Mark W. Hamrick

Department of Cellular Biology and Anatomy, Medical College of Georgia, Augusta, GA 30912

Susan W. Herring

Department of Orthodontics, University of Washington, Seattle, WA 98195–7446,
herring@u.washington.edu

Aaron S. Hogue

Department of Biological Sciences, Salisbury University, Salisbury, MD 21801,
ashogue@salisbury.edu

Jennifer L. Hotzman

Department of Anthropology, University of Florida, Gainesville, FL 32611–7305

William L. Hylander

Department of Biological Anthropology and Anatomy, Duke University Lemur
Center, Duke University, Durham, NC 27710

Kirk R. Johnson

Department of Biological Anthropology and Anatomy, Duke University, Durham,
NC 27710, USA

Pierre Lemelin

Division of Anatomy, Faculty of Medicine and Dentistry, University of Alberta,
Edmonton, Alberta, Canada T6G 2H7

Daniel E. Lieberman

Peabody Museum, Harvard University, Cambridge, MA 02138

Zi Jun Liu

Department of Orthodontics, University of Washington, Seattle, WA 98195–7446

Elisabeth K. Lopez

Department of Cell and Molecular Biology, Northwestern University Feinberg
School of Medicine, Chicago, IL 60611–3008

Rachel A. Menegaz

Department of Pathology and Anatomical Sciences, University of Missouri School
of Medicine, Columbia, MO 65212

Tomasz Owerkowicz

School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA
5005, Australia

Jonathan M.G. Perry

Department of Biological Anthropology and Anatomy, Duke University Medical
Center, Durham, NC 27710, jmp20@duke.edu

Katherine L. Rafferty

Department of Orthodontics, University of Washington, Seattle, WA 98195–7446

Yoel Rak

Department of Anatomy and Anthropology, Sackler Faculty of Medicine, Tel Aviv
University, Tel Aviv 69978, Israel, yoelrak@post.tau.ac.il

Andrew J. Rapoff
Department of Mechanical Engineering, Union College, Schenectady, NY
12308-3107

Matthew J. Ravosa
Department of Pathology and Anatomical Sciences, University of Missouri School
of Medicine, Columbia, MO 65212, ravosam@missouri.edu

Brian G. Richmond
Center for the Advanced Study of Hominid Paleobiology, Department
of Anthropology, The George Washington University, Washington DC 20052

Callum F. Ross
Department of Organismal Biology & Anatomy, University of Chicago, Chicago,
IL 60637, rossc@uchicago.edu

Daniel Schmitt
Department of Evolutionary Anthropology, Duke University Box 90383, Durham,
NC 27708, USA, Daniel.Schmitt@duke.edu

Nazima Shahnoor
Department of Anthropology, University of Wisconsin-Milwaukee, Milwaukee, WI
53211

Elwyn L. Simons
Duke Primate Center, Division of Fossil Primates, Department
of Biological Anthropology and Anatomy, Duke University, Durham, NC
27705, esimons@duke.edu

Jayne Skinner
School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA
5005, Australia

Mark A. Spencer
School of Human Evolution and Social Change, Institute of Human Origins,
Arizona State University, Tempe, AZ 85287

M. Sharon Stack
Department of Pathology and Anatomical Sciences, University of Missouri School
of Medicine, Columbia, MO 65212

Stuart R. Stock
Department of Molecular Pharmacology and Biological Chemistry, Northwestern
University Feinberg School of Medicine, Chicago, IL 60611-3008

David S. Strait
Department of Anthropology, University at Albany, Albany, NY 12222,
dstrait@albany.edu

Zongyang Sun

Department of Orthodontics, University of Washington, Seattle, WA 98195–7446

Andrea B. Taylor

Doctor of Physical Therapy Division, Department of Community and Family Medicine, Duke University School of Medicine and Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, andrea.taylor@duke.edu

Christopher J. Vinyard

Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, OH 44272, cvinyard@neoucom.edu

Christine E. Wall

Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA, christine_wall@baa.mc.duke.edu

Qian Wang

Division of Basic Medical Sciences, Mercer University School of Medicine, Macon, GA 31207, WANG_Q2@Mercer.edu.

Susan H. Williams

Department of Biomedical Sciences, Ohio University, Athens, OH 45701, willias7@ohio.edu

Barth W. Wright

Department of Anatomy, Kansas City University of Medicine and Biosciences, Kansas City, MO 64106–1453

Nayuta Yamashita

Department of Anthropology, University of Southern California, Los Angeles, CA 90089–1692, nayutaya@usc.edu

List of Figures

2.1	Theoretical patterns of deformation of the pig symphysis	22
2.2	Pig mandibles, showing methodology used	25
2.3	Examples of raw recordings of mastication	27
3.1	Summary data of peak masseter activity in primates and selenodont artiodactyls	42
3.2	Summary data of in vitro symphyseal strains along the labial (<i>left</i>) and lingual surfaces of the alpaca symphysis during simulating lateral transverse bending, or wishboning	43
3.3	Drawing of an alpaca mandible sectioned in the sagittal plane through the symphysis	46
3.4	Principal strains and the direction of maximum principal tension recorded from the symphyses of anesthetized alpacas during simulated manual reverse wishboning	47
3.5	Expected patterns of strain during reverse wishboning and wishboning of the alpaca symphysis	47
3.6	Raw and transformed symphyseal strains during mastication by Alpaca 4	48
3.7	Summary strain data from the symphysis of alpacas during left and right chews	50
3.8	Theoretical stresses and their expected patterns of strain during dorsoventral shear, anteroposterior shear, and transverse twisting of the symphysis	53
3.9	Graphs showing the relationship between the principal strains, direction of $\epsilon_1(\alpha)$ and integrated masseter EMG from a single power stroke during chewing by an alpaca	56
3.10	Symphyses of four species of unfused selenodont artiodactyls	57
3.11	The symphyseal region in South American camelids	58
4.1	Diagram of rostral and lateral views of <i>Eulemur fulvus</i> skull illustrating the principal external forces hypothesized to impose twisting moments (torques) on the facial skeleton	65
4.2	Diagrams of cylinders fixed at one end and subjected to opposite torques at the free end	67

4.3	Lateral view of skull of <i>Eulemur fulvus</i> showing position of strain gage in experiment 72, and the orientation of the A-element of the gage	69
4.4	Lateral views of skull of <i>Eulemur fulvus</i> showing position of strain gages in experiment 74, and the orientation of the A-elements of the gages	70
4.5	Dorsal views of skull of <i>Eulemur fulvus</i> showing position of strain gages in experiment 76, and the orientation of the A-elements of the gages	71
4.6	Dorsal views of skull of <i>Eulemur fulvus</i> showing position of strain gages in experiment 78, and the orientation of the A-elements of the gages	72
4.7	Dorsal views of skull of <i>Eulemur fulvus</i> showing position of strain gages in experiment 79, and the orientation of the A-elements of the gages	73
4.8	Anterior and lateral views of skull of <i>Eulemur fulvus</i> illustrating loading regimes hypothesized for the skull of <i>Eulemur fulvus</i> during unilateral biting or mastication	78
5.1	Control of jaw movements in an opossum, goat, and macaque	86
5.2	<i>Lasiorhinus latifrons</i>	88
5.3	<i>Lasiorhinus latifrons</i> . Occlusal function	89
5.4	<i>Lasiorhinus latifrons</i> . Lateral and posterior views of the adductor musculature	91
5.5	<i>Lasiorhinus latifrons</i> . Average orientation of muscle fibers within the principal adductor muscles in lateral, ventral, anterior, and posterior views	92
5.6	<i>Lasiorhinus latifrons</i> . EMGs of a selection of adductor muscles during shifts in the chewing side in nine different wombat experiments	99
5.7	<i>Lasiorhinus latifrons</i> . EMGs of adductor muscles during rhythmic chewing on lucerne, with synchronous strain on the ventral surface of the mandibular symphysis	101
5.8	<i>Lasiorhinus latifrons</i> . Synchronous EMGs of four adductors and strain on the ventral surface of the mandible on both sides of the symphyseal suture and ventral surface of the right mandibular ramus	102
5.9	<i>Lasiorhinus latifrons</i> . Synchronous EMGs and strain of three chewing cycles on the right, followed by three on the left	103
5.10	<i>Lasiorhinus latifrons</i> . Synchronous EMGs and strain during three chewing cycles on the right, followed by three on the left	104
5.11	Ventral view of the skulls of the red kangaroo and Southern hairy-nosed wombat, comparing the areas of origin of the superficial masseter and the medial pterygoid muscles	108
6.1	Coronal section through the cranium of an adult male <i>Papio anubis</i>	114
6.2	Lateral view of the temporalis muscle in an adult male <i>Papio anubis</i>	115
6.3	Digitized raw-EMGs and the corresponding root-mean-square (rms-) EMGs	118

6.4	The hard/soft ratio in the deep anterior temporalis and superficial anterior temporalis on both the working side and the balancing side in the male and female baboons	120
7.1	An infinite plate with a hole of diameter d is subjected to a uniaxial load	129
7.2	Theoretical stress concentration factors for four different “virtual mandibles,”	132
7.3	Alternative models of corpus sections as open or closed	135
7.4	Mandibular sections from the left anterior corpus of <i>Macaca fascicularis</i>	140
7.5	Relationship of elastic modulus of cortical bone with proximity to alveolar margins as determined through microindentation	143
7.6	MicroCT image of a transverse section through alveolar process of the anterior corpus of an adult male <i>Procolobus badius</i>	145
8.1	Experiment setup	152
8.2	Twenty-six gage sites	155
8.3	Real-time strain records at a bone surface site	157
8.4	Shear strain during 130 N load on central incisor	165
8.5	Shear strain during 195 N load on fourth premolar	165
8.6	Shear strain during 260 N load on third molar	166
9.1	Solid model of <i>M. fascicularis</i> skull	176
9.2	Finite element mesh consisting of 311,057 polyhedral elements	177
9.3	Maximum principal strain in the finite element model as induced by a left-side chew	185
9.4	Minimum principal strain in the finite element model as induced by a left-side chew	187
9.5	Nodes in the anterior rostrum corresponding to high strain concentrations during premolar loading	190
10.1	Bivariate plot of \log_e of the square root of the sum of all muscle’s RPCA cm^2 against \log_e cube root of body mass (g)	209
10.2	Bivariate plot of \log_e of the square root of the sum of all muscle’s RPCA cm^2 against \log_e of craniobasal length (CBL)	209
11.1	Method of calculating pinnation	220
11.2	Log of the sum of the PCSA values for all seven adductor muscles plotted against the log of body mass	230
11.3	Log of the sum of the muscle mass values for all seven adductor muscles plotted against the log of body mass	230
11.4	Log of the mean of the fiber length values for all seven adductor muscles plotted against the log of body mass	231
12.1	Schematic representation of the upper and lower jaws in lateral view depicting the distance from the condyle to both the masseter origin and insertion (<i>solid lines</i>)	247
12.2	Schematic of a left masseter muscle and temporalis muscle of <i>Callithrix jacchus</i>	248

12.3 Superior view of the internal architecture of marmoset masseter and temporalis 249

12.4 Schematic of a bipinnate muscle depicting the measurements taken in this study 251

12.5 Box plots comparing masseter and temporalis muscle fiber lengths . . . 252

12.6 Box plots comparing relative masseter and temporalis muscle fiber lengths 253

12.7 Box plots comparing relative masseter and temporalis PCSAs 253

12.8 Box plots comparing the ratio of total tendon length to fasciculus + tendon length 254

12.9 Bivariate plot demonstrating the architectural trade-off between muscle force and muscle excursion for masseter and temporalis muscles 255

12.10 The PCSA of the masseter and temporalis, expressed as a percentage of the combined PCSA for both muscles 257

13.1 Region of bone sampling for human mandibular bone specimens 268

13.2 Graphical explanation of material anisotropy 268

13.3 Hypothetical Haversian canal segment within a box oriented to the orthogonal material axes of the cortical bone specimen 272

13.4 Ultrasonic longitudinal velocities (10 MHz) versus wave direction in the femoral and mandibular specimens used in the μ CT portion of the study 273

13.5 Images of mandibular cortical bone reconstructed from confocal microscope scans 274

13.6 Compilations of collapsed confocal images to show entire cross-sections of the bone specimen in the 2-3 plane or perpendicular to the 3 or longitudinal axis 276

13.7 The number of nodes correlates with the longitudinal length of the osteonal segments 277

13.8 Example of a splitting pattern in a complex osteonal segment 277

13.9 Rosette histograms of angles of all osteonal segments in all 95 reconstructed confocal volumes 278

13.10 Reconstructions of cortical bone volumes from μ CT scans 279

13.11 Rosette histograms of the orientations of all osteonal segments per micron length relative to the plane of projection 280

14.1 MicroCT of symphysis proportions and biomineralization 300

14.2 MicroCT of TMJ biomineralization 301

14.3 Symphyseal cortical bone thickness 304

14.4 Symphyseal proteoglycan content 305

14.5 TMJ proteoglycan content 306

14.6 Symphyseal type II collagen 306

14.7 TMJ type II collagen 307

14.8 Symphyseal apoptosis 307

14.9 TMJ apoptosis 308

14.10 TMJ anatomy and proportions 310

14.11	TMJ proteoglycan content	312
14.12	TMJ type II collagen	312
14.13	Symphyseal proteoglycan content	314
14.14	TMJ proteoglycan content	315
14.15	Symphyseal type II collagen	316
14.16	TMJ type II collagen	317
14.17	Symphyseal apoptosis	317
14.18	TMJ apoptosis	318
15.1	Schematic depiction of the principle loading regimes experienced by the mandibular corpus	333
15.2	Phylogeny of the 65 marsupial species in this sample	343
15.3	Plot of ACA $\ln M_2/M_3$ corpus I_x versus ACA \ln mandibular length	345
15.4	Plot of ACA M_2/M_3 corpus I_x LS residuals versus the proportion of foliage or hard, strong, or tough foods in the diet	346
15.5	Plot of standardized contrasts of M_2/M_3 corpus I_x LS residuals versus standardized contrasts of the proportion of foliage or hard, strong, or tough foods in the diet	347
15.6	Plot of ACA $\ln M_2/M_3$ corpus K versus ACA \ln mandibular length	347
15.7	Plot of ACA M_2/M_3 corpus K LS residuals versus the proportion of foliage, vertebrates, or products of tree gouging in the diet.	348
15.8	Plot of standardized contrasts of M_2/M_3 corpus K LS residuals versus standardized contrasts of the proportion of foliage, vertebrates, or products of gouging in the diet.	349
16.1	A diagrammatic representation of the mechanical advantage of the jaw-closing muscles for producing vertical bite force at the incisors	362
16.2	Examination of the functional consequences and scaling of mechanical advantage for the jaw-closing muscles across 45 haplorhine primates	363
16.3	A cartoon example of changing jaw shapes with similar functional consequences	365
16.4	Box plots comparing corporal depth of the mandible at M_1 in papionins and colobines relative to body mass ^{1/3} and jaw length	369
16.5	Box Plots of relative jaw length among galagids created using five different shape ratios	376
17.1	Unripe kily fruit and seeds dropped by sifakas	391
17.2	Force–displacement graph of scissors cutting test of ripe kily fruit shell and unripe kily fruit	392
17.3	Time spent feeding on kily parts throughout year compared to total annual feeding time on same food parts	395
17.4	Logged toughness (R) values of phenophases of <i>Tamarindus indica</i>	396
17.5	Toughness (R) comparisons of entire <i>kily</i> diet of two lemur species	396
17.6	Toughness (R) comparisons of individual <i>kily</i> plant parts between the two lemur species	397
17.7	Comparisons of total crest lengths between ringtailed lemurs and sifakas using within-family residuals	398

17.8	Comparisons of protocone/talonid radii between ringtailed lemurs and sifakas using raw data values	399
17.9	Comparisons of talonid basin area between ringtailed lemurs and sifakas using within-family residuals	399
17.10	Average cusp radius and height between ringtailed lemurs and sifakas using within-family residuals. Comparisons are not significant ($P = 0.062$ and 0.846 , respectively). See Fig. 17.5 caption for explanation of symbols	400
18.1	<i>Parapithecus grangeri</i> and <i>Aegyptopithecus zeuxis</i> crania	412
18.2	<i>Proteopithecus sylviae</i> CGM 42214 and <i>Catopithecus browni</i> DPC 11594 show convergence angles measured from the degree symbols in individuals of these two species	415
18.3	Crania of <i>Aegyptopithecus zeuxis</i> showing age-related changes in convergence angles	416
18.4	Convergence angles for <i>Apidium boweni</i> DPC 5264, <i>Arsinoea kallimos</i> DPC 11434, and <i>Proteopithecus sylviae</i> DPC 14095	417
19.1	Occlusal topography of <i>Australopithecus africanus</i> (left) and <i>A. robustus</i>	436
19.2	A comparison of the effect of a short mandibular ramus and a tall mandibular ramus on the movement of the lower teeth relative to the upper teeth in the final stages of occlusion	438
19.3	A schematic representation of the effect of anterior condylar translation on the height of the axis of rotation and the magnitude of the anterior movement of the lower teeth	438
19.4	The glenoid fossa and articular eminence in a chimpanzee and <i>A. boisei</i> specimen KNM-ER 23000.	439
20.1	Relationship between body size (femur length and stature) and brain size	455
20.2	Dentognathic summary statistics by species group	457
20.3	Dentognathic summary statistics for <i>H. habilis s.l.</i> , African <i>H. erectus</i> (including Dmanisi), Sangiran, Ternifine, and Zhoukoudian <i>H. erectus</i>	458
20.4	Bivariate plots among molar dimensions, corpus size, and symphyseal size	460
20.5	Molar dimensions, symphysis, and corpus size	461
20.6	Bivariate relationship between molar dimensions and body size (femur length and stature)	463
20.7	Bivariate relationship between jaw dimensions and body size (femur length and stature)	465
20.8	Molar and jaw dimensions relative to cranial capacity	466
20.9	Molar and jaw dimensions through geological time	468

List of Tables

2.1	Subjects and instrumentation	24
2.2	Mandibular distortion in the transverse direction during chewing	28
2.3	Magnitude ($\mu\epsilon \pm$ s.d.) and orientation of principal strains during mastication	29
2.4	Condition of the symphyseal suture in 115 pig mandibles as a function of age	31
3.1	Summary data of symphyseal strains at 25% loading, peak, and 25% unloading of the power stroke of mastication	49
4.1	Descriptive statistics for maximum principal strain magnitudes and directions recorded from the postorbital bars during experiments 72, 73, and 74	74
4.2	Descriptive statistics for maximum principal strain magnitudes and directions recorded from the dorsal orbital and dorsal interorbital regions during experiments 76, 78, and 79	75
5.1	Weight and percentage of the total weight of the adductor muscles, in <i>Lasiorhinus latifrons</i>	93
5.2	Data collected on nine hairy-nosed wombats	95
5.3	Summary of cycle length and percentage of cycle with active adductors in six wombats feeding on different foods	99
5.4	Working-to-balancing side ratios of adductor activity during the power stroke in different adductors of <i>Lasiorhinus latifrons</i>	100
5.5	Descriptive statistics for peak principal strains and angle of peak tensile strain on the ventral margin of the right hemi-mandible and ventral surface of the mandibular symphysis	105
6.1	Fiber type proportions in the deep and superficial anterior temporalis based on myosin ATPase reactivity.	116
6.2	EMG amplitude during hard- and soft-object feeding in the deep anterior temporalis and the superficial anterior temporalis in adult male and adult female <i>Papio</i>	119
6.3	Hard/soft ratio in the working- and balancing-side deep anterior temporalis and superficial anterior temporalis in adult male and female <i>Papio</i>	120
7.1	Effects of tooth removal on mandibular bone strain	137

7.2	Effect of indenter orientation on hardness	141
8.1	Strain gage sites, orientations, and descriptions	154
8.2	In vitro strain measurements when a load of 130 N was placed on right and left central incisors	158
8.3	In vitro strains measurements when a load of 195 N was placed on right and left fourth premolars	161
8.4	vitro strains measurements when a load of 260 N was placed on right and left third molars	163
9.1	Muscle forces applied to finite element model	177
9.2	Elastic properties employed in finite element analysis	180
9.3	Validation of FE model	182
9.4	Comparisons of maximum shear strains between experiments	189
9.5	Strains in the anterior rostrum	191
10.1	Mean variables of species used in the regressions	205
10.2	Pearson's product-moment correlation coefficients between body weight ^{1/3} (M) \times craniobasal length (CBL), $RPCA^{1/2} \times$ body weight ^{1/3} , and $RPCA^{1/2} \times$ craniobasal length	206
10.3	Regression statistics for linear regressions of craniobasal length on body weight ^{1/3} , $RPCA^{1/2}$ on body weight ^{1/3} , and $RPCA^{1/2}$ on craniobasal length	207
10.4	Review of previous published scaling studies relevant to the data presented in this paper	212
11.1	Specimens included in this study	219
11.2	Synonyms for masticatory muscle terminology used here	222
11.3	Values of physiological cross-sectional area for sixteen species of prosimians	226
11.4	Values of reduced physiological cross-sectional area for twelve species of prosimians	227
11.5	Muscle mass for sixteen species of prosimians	228
11.6	Fiber length for sixteen species of prosimians	229
11.7	Pinnation values, PCSA values relative to body mass, and RPCSA values relative to body mass	229
11.8	Results of reduced major axis regressions of muscle dimensions on body mass	231
12.1	Muscle fiber architecture variables and predicted differences between tree-gouging marmosets and a nongouging tamarin	250
12.2	Comparison of masseter and temporalis fiber architecture between tree-gouging marmosets and a non-gouging tamarin	252
14.1	Dietary properties of rabbit experimental foods	298
14.2	Comparison of size-adjusted means for load-resisting and force-generating elements between cohorts of 10 subjects each	303
14.3	Comparison of rabbit symphyseal mean biomineralization levels between cohorts of seven subjects each	303

14.4 Comparison of rabbit TMJ mean biomineralization levels between cohorts of eight subjects each 304

14.5 Comparison of size-adjusted means of load-resisting and force-generating structures between loading cohorts 309

14.6 DFA comparison of mouse TMJ biomineralization levels 310

14.7 DFA of mouse symphysis bone-density levels that are similar to patterns for the TMJ 311

14.8 Comparison of rabbit symphyseal mean mineral density levels between cohorts of three subjects each 313

14.9 Comparison of rabbit TMJ mean biomineralization levels between cohorts of three subjects each 314

15.1 Marsupial sample, body mass, dietary classification, and number of specimens 337

15.2 Regression equations for ACA ln corpus I_x and K versus ACA ln mandibular length 344

15.3 Correlation of ACA corpus I_x and K residuals with ACA diet proportions 345

15.4 Kruskal-Wallis One-Way ANOVA results contrasting ACA corpus I_x and K residuals between diet categories 346

15.5 Slopes of LS regression lines and correlation coefficients for standardized contrasts of corpus I_x and K residuals versus standardized contrasts of diet proportions 346

16.1 The six denominators used in shape variable comparisons 371

16.2 Morphological predictions used to examine how shape variable denominators influence functional hypothesis tests 373

16.3 The five-level ranking scale for assessing similarity among hypothesis test results 373

16.4 Percentage similarity of ranks based on statistical outcomes from hypothesis tests using various shape variable denominators. 374

17.1 Lemur species included in regressions 393

17.2 Comparisons between lemur species of toughness of kily parts eaten . . 397

17.3 Comparisons of tooth features between the two lemur species^a 398

18.1 Convergence angles calculated for Fayum primates who belong in diverse taxonomic groups 414

18.2 Frontation angles for Fayum primates 414

20.1 Body size by geographic region in *H. habilis* and *H. erectus* 446

20.2 Dentognathic summary statistics for *H. habilis* and *H. erectus* (worldwide) and for *H. erectus* by region/locality 451

20.3 Individuals and chimera-used in body size-brain size scaling relationships 452

20.4 Regression results for the relationship between body size and cranial capacity 455

20.5 Results of ordinary least-squares regression of dentognathic height and breadth dimensions in fossil *Homo* 459

20.6 Results of ordinary least-squares regression of dental variables
versus jaw size 462

20.7 Results of ordinary least-squares regression of dentognathic variables
versus body size estimates 464

20.8 Results of ordinary least-squares regression of dentognathic size
versus cranial capacity 467

20.9 Results of ordinary least-squares regression of dentognathic size and
time (in Ma) 469

20.10 Samples and chimeras used in analyses. 474

Part I

Historical Perspective on Experimental Research in Biological Anthropology

Anthropologists have committed countless hours to understanding how the skull works. These endeavors have been fundamental in shaping biological anthropology over the generations. For the past 35 years, William Hylander has been a leader in this effort by furthering our understanding of primate skull function. The core of Hylander's contribution focuses on his rigorous attempts to document how muscles are recruited and how bones respond when alert primates chew and bite. These *in vivo*, experimental data provide the empirical baseline for numerous studies examining skull form, feeding behaviors, and craniofacial adaptations in living and fossil primates.

Schmitt, Lemelin, and Wall begin the volume with a historical review of William Hylander's contribution to experimental research in biological anthropology. They initially place Hylander's work in the broader context of the "new physical anthropology" championed by Washburn in the 1950s, which advocated an experimental comparative approach. Schmitt et al. proceed by discussing three of Hylander's key contributions and noting how each paper has fundamentally advanced biological anthropology. They conclude by discussing how Hylander's collective work will benefit the future of primate craniofacial research.

Chapter 1

Experimental Comparative Anatomy in Physical Anthropology: The Contributions of Dr. William L. Hylander to Studies of Skull Form and Function

Daniel Schmitt, Christine E. Wall, and Pierre Lemelin

Contents

1.1 Introduction	3
1.2 Experimental Comparative Anatomy in Physical Anthropology	4
1.3 The Experimental Approach and Contributions of Bill Hylander	7
1.3.1 Bone Mechanical Properties	8
1.3.2 Scaling in Craniofacial Structures	10
1.3.3 EMG of Mastication	10
1.4 Conclusion	11
References	12

1.1 Introduction

Two important events occurred during the 74th Annual Meeting of the American Association of Physical Anthropology (AAPA) held in Milwaukee, WI (USA), in the spring of 2005. On the one hand, it was the 75th anniversary of the AAPA and a special symposium was held discussing the scientific impact of its founders and early contributors. On the other hand, colleagues and friends of Professor William Hylander gathered to present their most recent work and pay tribute to Dr. Hylander's lifetime contribution to studies of skull functional morphology in primates. Although these two important events were coincidental, they both reminded us of a critical event in the history of physical anthropology: that is, the rise of what Washburn defined as the "New Physical Anthropology" (Washburn, 1951a, b), which advocated for the use of an experimental approach in physical anthropology.

D. Schmitt

Department of Evolutionary Anthropology, Duke University Box 90383, Durham, NC 27708, USA
e-mail: Daniel.Schmitt@duke.edu

Our goal in this chapter is to briefly review the historical context that led to Washburn's important, albeit at the time controversial, call for a comparative experimental anatomy and to show how that call was answered by the functional morphologists interested in the evolution of the skull and feeding apparatus of primates and other mammals. In particular, the contribution of Bill Hylander to this important area of research will be reviewed and some directions for the future, which build on Bill's pioneering work, will be discussed.

1.2 Experimental Comparative Anatomy in Physical Anthropology

In 1951, Sherwood Washburn published two seminal essays in which he explicitly urged physical anthropologists to adopt a laboratory-based methodology to address questions of human evolution (Washburn, 1951a, b). The view espoused in these papers is considered a paradigm shift from the typological approach that characterized physical anthropology at the time to a more multidisciplinary approach where experiments played a major role (Stini, 2005). Washburn's (1947; Mednick and Washburn, 1956) approach using laboratory-based data to resolve conflicts in scenarios of human evolution was not always well received by his peers at the time. Indeed, one famous contemporary of Washburn questioned him about the validity of using rats to understand the human phenomenon (Washburn, 1983; Marks, 2000). Moreover, many of his peers saw the experimental method as a major threat because "they thought it was destroying the evidence" (DeVore, 1992:417).

At the time Washburn made the call for a "modern, experimental, comparative anatomy" (Washburn, 1951a:67), there was little activity of that type in the field of physical anthropology. The pioneering studies of Hildebrand (1931) and Elftman and Manter (1935) represent some of the few laboratory-based studies of mastication and locomotion, respectively, completed at the time. Despite the scarcity of such studies in 1951, Washburn foresaw the relevance of these types of data for the evaluation of functional and evolutionary hypotheses in physical anthropology. In addition, he understood the burgeoning technological revolution that would make the experimental approach possible.

The term "experimental comparative anatomy" is cumbersome and on the surface seems too vague to have any meaning. But what Washburn meant is very clear. He meant to expand the available tools for assessing the functional significance of a given morphological trait by controlled, laboratory-based testing of hypotheses derived from comparative anatomy. He wanted anthropologists to go beyond the "opinions," theoretical models, and simple correlations that dominated comparative anatomy at the time.

By the late 1960s and 1970s, there was a rapidly growing trend in the use of laboratory-based methods to study the functional morphology of primates. Much of this was directed toward a better understanding of the primate postcranium and began incorporating the newest techniques available (see Fleagle, 1979; Jouffroy, 1989; Churchill and Schmitt, 2003; Schmitt, 2003; Lemelin and Schmitt, 2007 for

historical accounts). But the focus of this chapter is the parallel development of laboratory-based studies of primate craniofacial biology.

In order to fully explore the ways in which laboratory-based studies have influenced our understanding of primate craniofacial anatomy and evolution, it is worth beginning by discussing the foundations of experimental comparative anatomy. In a seminal paper in 1977, Rich Kay and Matt Cartmill formalized the methodological principles that had guided studies of functional morphology for many decades. They laid out four clear steps for making inferences about behavior in fossil animals. Kay and Cartmill (1977) stressed that any trait which we wished to use as a surrogate for a behavior had to be present in extant animals and its function had to be known. But they did not discuss in detail how to determine the function of a trait.

Treated simply, at least two comparative approaches can be used to assess function based on studying morphological traits: (1) an approach capitalizing on convergence or divergence to relate organismal form with presumed functions (Brooks and McLennan, 1991) and (2) an “argument from design” that applies theoretical principles of engineering and design to interpret organismal function based on form (Rudwick, 1964; Lauder, 1996). Both approaches have their strengths and flaws that have been reviewed elsewhere (Bock and von Walther, 1965; Bock, 1977; Fleagle, 1979; Homberger, 1988; Lauder, 1995, 1996), so we will just briefly touch on them here. The central point here is that conclusions derived from traditional comparative anatomy or engineering-style “argument from design” studies must be viewed not as end-results, but rather as hypotheses to be tested. In many instances, those tests are best accomplished in the laboratory.

Laboratory-based hypothesis testing is exactly what Washburn had in mind and what Hylander and his contemporaries have been pursuing for the past 30 years. But they represent the leaders of a small group within physical anthropology. In spite of the theoretical strengths and observed success of an experimental comparative approach, few physical anthropologists test their functional models with experimental data. There are a lot of reasons for the lack of rigorous testing using laboratory data. Many anthropologists misunderstand how the experimental approach can be used to test functional hypotheses. Too often, criticisms are made about small sample sizes, unnatural laboratory conditions, and the highly technical aspect of the methods used in the laboratory. These concerns inhibit the willingness of physical anthropologists to collect experimental data and the acceptance of such data when they are presented. In the absence of experimental data, confirmation of a functional model can only be achieved via traditional comparative anatomy (e.g., the prediction that long legs are mechanically critical for leaping primates is confirmed by the observation that other leaping animals have long legs). This mode of checking functional models may lead to correct conclusions; but as Bock (1977), Homberger (1988), and others have noted, this is not always the case. Lauder (1996:56) points out that such conclusions are based on untested assumptions and that:

...in our desire to draw conclusions about biological design and to support theoretical views of how organism are built, we have been too willing to make assumptions about the relationship between structure and mechanical function...[and]... we have not often

conducted the mechanical and performance tests needed to assess the average quality of organismal design.

Similarly, Fleagle (1979:316) noted that “Regardless of how mechanically plausible and convincing [functional] explanations may be, they can be rigorously tested only by *in vivo* studies”. The work of Bill Hylander and his colleagues represents an ideal combination of basic design principles (e.g., beam theory to describe the jaw) and experimental analyses. His approach has led to a better understanding of both structure–function relationships and the evolution of primate craniofacial function and is a model for how to proceed in testing morphological hypotheses with laboratory data.

There are three possible outcomes when using an experimental approach to determine structure–function relationships. The first possibility is that a given hypothesis developed from comparative data or engineering principles will be supported. This is a common, although not universal, outcome.

A second possible outcome is that a mechanical hypothesis relating a specific structure to a particular function may be found to be in error; however, the underlying correlation between structure and behavior still exists. In this case, experimental studies can yield a better understanding of the underlying causal relationship between a trait and its function, and may lead to novel areas for investigation. One good example of how laboratory studies may clarify or change conclusions based on the measurements of morphology is the debate over adaptations to tree gouging in primates. Prior to any laboratory work, researchers measuring jaws and teeth, especially the highly modified incisors of many gouging primates, argued that tree gouging induced large forces on the masticatory system (e.g., Szalay and Seligsohn, 1977; Rosenberger, 1992; Dumont, 1997; Spencer, 1999). This conclusion seems logical, but *in vivo* work on marmosets has shown that this is not the case and that, in fact, the forces generated during gouging can be seen as being relatively low (Vinyard et al., 2001, *in press*). This does not invalidate the correlation between chisel-like incisors and gouging behavior in callitrichids. But the finding of relatively low bite forces during gouging in callitrichids is unexpected and it opens up new areas of research into structural modifications of the bones and muscles of the skull that may not be related to force production but instead allow for the use of large gapes in primates (Williams et al., 2002; Taylor and Vinyard, 2004; Perry, 2006).

A final potential outcome is that experimental data change our perception of both structure–function correlations and causal relationships. Understanding the mechanics of phase II during the power stroke of mastication, which began with Hiiemae and Kay (1972, 1974a, b) and was further investigated by Hylander and Crompton in the late 1980s (Hylander and Crompton, 1986; Hylander et al., 1987), represents a perfect example. Prior to the work of Hylander and Crompton, it was assumed that powerful grinding occurs during phase II. This is a heavily embedded assumption in comparative studies of the primate molar dentition. For example, certain occlusal facets on the molar teeth are identified as “phase II facets,” and pitting and abrasions observed on the occlusal surfaces have been linked to forceful contact between the

teeth and food during phase II (Kay, 1977, 1987; Grine, 1986). More recently, in a combined video and electromyographic study designed to confirm Hylander's earlier work, Wall et al. (2006) found in baboons that there is negligible force produced by the major jaw adductors during phase II and that mandibular movements were minimal during phase II as compared to phase I. Their results showed that phase II movement is likely trivial for breaking down food. Instead, most food breakdown on the phase II facets probably takes place late in phase I movement, in association with crushing of the food object (see also Hiiemae, 1984; Teaford and Walker, 1984; Teaford, 1985). Additional work to characterize phase II jaw movements in other primate species is underway, but the experimental data clearly suggest the need for an alternative functional explanation for the structure and microwear patterns on the phase II facets of primates.

1.3 The Experimental Approach and Contributions of Bill Hylander

Clearly, the experimental approach is a critical tool for physical anthropologists. Despite the obvious relevance of this approach to the study of primate craniofacial biomechanics, little laboratory-based research was conducted before Bill Hylander began his career. Bill was a graduate student at the University of Chicago in the 1960s. He returned to graduate school after practicing dentistry for several years. His goal was to combine his knowledge of the functional anatomy of the teeth and jaws with the study of the evolution of the primate skull. In the 1970s, he pioneered the experimental approach to understanding the functional anatomy of the skull in primates.

As a graduate student, Bill was interested in developing biomechanical models explaining craniofacial form and function that could ultimately be tested with experimental data. In his thesis, Bill evaluated competing hypotheses to explain the functional anatomy of the Eskimo skull (Hylander, 1972). Specifically, he wanted to know which of the features seen in the cranium and mandible were related to the aspects of tooth use and diet and which could be explained as cold adaptations. This work was eventually published in an edited volume (Hylander, 1977a) in the same year that Bill published his first *in vivo* bone strain paper (Hylander, 1977b). Bill developed a biomechanical model to explain such features as a robust mandible, high temporal lines, and large bicondylar dimensions as structures that aid in the generation and dissipation of high vertical bite forces.

In another study that demonstrates his knack for critically evaluating competing hypotheses, Bill published a seminal analysis of the human mandible as a lever system (Hylander, 1975). A number of workers had claimed that the jaw functioned as a mechanical link, and thus generated no reaction force at the temporomandibular joint (TMJ). Bill showed that the mandible does function as a third-class lever, and that many aspects of mandibular morphology can be explained in this context.

Since then Bill has made an enormous and fundamental contribution to studies of primate skulls and teeth. Bill has published over 75 research articles, including papers in many edited volumes. A Science Citation search indicates that since 1980, Bill's work has been cited more than 933 times in published articles. His research has been continuously funded by the National Science Foundation, National Institutes of Health, and private foundations for more than 30 years.

Although Bill is probably best known for his work documenting and interpreting the functional significance of *in vivo* patterns of bone strain in the primate skull (Hylander, 1977b, 1979a, b, c, 1984; Hylander and Johnson, 1992, 1997a, b; Hylander and Ravosa, 1992; Hylander et al., 1991a, b, 1998; Ravosa et al., 2000; Ross and Hylander, 1996 and many others), he has made seminal contributions in the areas of theoretical jaw mechanics (Hylander, 1975b), jaw kinematics (Hylander, 1978; Hylander and Crompton, 1986; Hylander et al., 1987), bone biology (Bouvier and Hylander, 1981, 1996; Hylander et al., 1991b; Hylander and Johnson, 2002), muscle function (Hylander and Johnson, 1985, 1994; Hylander et al., 2000, 2005), and comparative morphometrics (Hylander, 1972, 1975a, 1977, 1985, 1988; Kay and Hylander, 1978). Along the way, he has trained a number of graduate and post-doctoral students who have published extensively in these areas.

Because of the massive volume of Bill's work, it is impossible to review it entirely in this short contribution. Furthermore, we feel that simply reiterating all that Bill has done cannot do justice to how influential his thinking has been on the field of primate craniofacial function and biology. As an alternative approach, we consider what we think are three key articles and discuss how they have molded thinking on mammalian craniofacial biology and the evolution of the primate masticatory system. Other authors might have chosen different articles, but to our way of thinking the work we describe below exemplifies not only the scope of Bill's career but also raise important issues that will remain at the forefront of research on craniofacial functional anatomy for decades to come. We will discuss the implications of Bill's pioneering studies on understanding bone mechanical properties, the scaling of craniofacial structures in primates, and muscle activity during mastication.

1.3.1 Bone Mechanical Properties

One area that Bill focused on is the mechanical determinants of bone size and shape. In 2002, he published a paper with his long-time associate Kirk Johnson, which summarizes his research on this topic and places these results within the context of the functional adaptation/optimal strain environment model of bone remodeling (Hylander and Johnson, 2002; see also Bassett, 1968; Hylander and Johnson, 1997a, b; Lanyon and Rubin, 1985; Pauwels, 1980; Rubin, 1984). Briefly, the phrase "functional adaptation" describes the supposition that normal, day-to-day loading conditions play an important role in maintaining bone mass and geometry (e.g., Hert et al., 1971; Bouvier and Hylander, 1981; Lanyon and Rubin, 1985;