

Winfried Henke  
Ian Tattersall  
*Editors*

# Handbook of Paleoanthropology

Winfried Henke  
Ian Tattersall  
*Editors*

# Handbook of Paleoanthropology

# Handbook of Paleoanthropology

Winfried Henke · Ian Tattersall (Eds.)

# **Handbook of Paleoanthropology**

## **Volume I Principles, Methods and Approaches**

In collaboration with Thorolf Hardt

With 102 Figures and 33 Tables

Winfried Henke · Ian Tattersall (Eds.)

# **Handbook of Paleoanthropology**

## **Volume II Primate Evolution and Human Origins**

In collaboration with Thorolf Hardt

With 49 Figures and 8 Tables

Winfried Henke · Ian Tattersall (Eds.)

# **Handbook of Paleoanthropology**

## **Volume III Phylogeny of Hominids**

In collaboration with Thorolf Hardt

With 113 Figures and 26 Tables

**Prof. Dr. Dr. h. c. Winfried Henke**  
Institut für Anthropologie (1050)  
Fachbereich 10 - Biologie  
Johannes Gutenberg-Universität Mainz  
D-55099 Mainz  
Germany  
email: henkew@uni-mainz.de

**Dipl. Biol. Thorolf Hardt**  
Institut für Anthropologie (1050)  
Fachbereich 10 - Biologie  
Johannes Gutenberg-Universität Mainz  
D-55099 Mainz  
Germany  
email: thormuel@students.uni-mainz.de

**Prof. Dr. Ian Tattersall**  
Division of Anthropology  
American Museum of Natural History  
New York, NY 10024-5192  
USA  
email: iant@amnh.org

**ISBN-13: 978-3-540-32474-4**

This publication is available also as:  
Electronic publication under ISBN 978-3-540-33761-4 and  
Print and electronic bundle under ISBN 978-3-540-33858-1

**Library of Congress Control Number: 2006936414**

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in other ways, and storage in data banks. Duplication of this publication or parts thereof is only permitted under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer-Verlag. Violations are liable for prosecution under the German Copyright Law.

**Springer is part of Springer Science+Business Media**

springer.com

© Springer-Verlag Berlin Heidelberg New York 2007

The use of registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Product liability: The publishers cannot guarantee the accuracy of any information about the application of operative techniques and medications contained in this book. In every individual case the user must check such information by consulting the relevant literature.

Editor: Dieter Czeschlik, Heidelberg/Sandra Fabiani, Heidelberg  
Development Editor: Susanne Friedrichsen, Heidelberg  
Production Editor: Frank Krabbes, Heidelberg  
Cover Design: Frido Steinen-Broo, Spain

Printed on acid-free paper

SPIN: 2109 - 5 4 3 2 1 0

We dedicate these volumes to our long-time colleagues  
**Hartmut Rothe** and **Theodoros Pitsios**  
in appreciation of their friendship and unique contributions to  
primatology and paleoanthropology.



# Preface to the Series

Palaeoanthropology is perhaps the most multidisciplinary of all the sciences. Any complete account of the evolution and of the cultural and biological contexts of *Homo sapiens* must combine information from geology, paleoecology, primatology, evolutionary biology and a host of other fields. Above all, historical information garnered from the fossil record needs to be combined with, and interpreted in the light of, what we know of the living world. In these volumes we have brought together contributions by a variety of leading specialists that reflect the broad spectrum of modern paleoanthropology, in an attempt to provide a resource that we hope will be useful to professionals and students alike.

Volume I of this three-volume Handbook deals with principles, methods, and approaches. In recent years enormous advances have been made in such areas as phylogenetic analysis, evolutionary theory and philosophy, paleoecology, and dating methods. The contributions aim to present the state of the art in these and other relevant fields, as well as to furnish succinct introductions to them and to reflect the many ways in which they interact. Human beings are primates, and Volume II is devoted to primate origins, evolution, behavior, and adaptive variety. In this compilation the emphasis is on the integration of fossil data with the vast amount that is now known of the behavior and ecology of living primates in natural environments. The third and final volume deals directly with the fossil and molecular evidence for the evolution of *Homo sapiens* and its fossil relatives (the family Hominidae or subfamily Homininae, according to taste, a matter that we have left to each individual contributor). Paleoanthropology is a pluralistic and actively developing field in which much remains to be settled, and we have not tried to impose any uniformity of viewpoint on our authors. Instead, while maintaining an emphasis on the data, we have encouraged them to express their individual interpretations rather than to cover all possible points of view. This has inevitably led to a certain degree of heterogeneity of opinion between the covers of this Handbook; but we believe that this is the best way of reflecting the excitement and momentum of the field and that it is best for the reader to be left to reach his or her own conclusions. Science is, after all, a process rather than a static product, and one of our primary aims here is to reflect the ongoing dynamism of that process in paleoanthropology.

We thank all of the contributors to these volumes for their participation. Some initially responded enthusiastically while others needed convincing about the basic strategy of the Handbook, but all responded marvellously to the

particular needs of a corporate effort such as this one. We are particularly grateful to those authors who responded at short notice to needs that became apparent only as the project progressed. This series was conceived in collaboration with Prof. Hartmut Rothe of the University of Göttingen, who was later forced to withdraw for reasons beyond his control. We thank him most warmly for his creativity in the conceptual stages and for his subsequent moral support. The laborious process of putting together the volumes could not have been accomplished without the cheerful help of Thorolf Hardt, whose active involvement was indispensable throughout.

This project could never have come to fruition without the enthusiastic support of Dr. Dieter Czeschlik, editor life sciences at Springer Publishing, and the efficient assistance of Mrs. Ursula Gramm. We express our deep gratitude to Mrs. Susanne Friedrichsen and Mrs. Caroline Simpson, who showed both care and commitment during the phases of copyediting and product development. The continuous cooperation and dialogue with them and their professionalism gave us the courage to see the project through. Further thanks go to Mrs. Sandra Fabiani and her colleagues at Springer Publishing, who prepared the eReference. Ms. Nitya Swaruba, compositor at SPi Technologies, deserves warm thanks for her efficient help, and finally our gratitude goes in addition to Britta Hardt, Peter Menke and Monika Sandführ, who also rendered much valuable assistance.

Winfried Henke and Ian Tattersall  
Mainz and New York City  
November, 2006

# Table of Contents

## Volume 1

<b>1 Historical Overview of Paleoanthropological Research</b> . . . . .	<b>1</b>
<i>Winfried Henke</i>	
<b>2 Evolutionary Theory in Philosophical Focus</b> . . . . .	<b>57</b>
<i>Philippe Huneman</i>	
<b>3 The Ontogeny–Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology</b> . . . . .	<b>103</b>
<i>Peter R. Menke</i>	
<b>4 Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms</b> . . . . .	<b>141</b>
<i>Michael Ohl</i>	
<b>5 Quantitative Approaches to Phylogenetics</b> . . . . .	<b>167</b>
<i>Kaila E. Folinsbee · David C. Evans · Jörg Fröbisch · Linda A. Tsuji · Daniel R. Brooks</i>	
<b>6 Homology: A Philosophical and Biological Perspective</b> . . . . .	<b>217</b>
<i>Olivier Rieppel</i>	
<b>7 Taphonomic and Diagenetic Processes</b> . . . . .	<b>241</b>
<i>Gisela Grupe</i>	
<b>8 Archeology</b> . . . . .	<b>261</b>
<i>Miriam N. Haidle</i>	
<b>9 Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction</b> . . . . .	<b>289</b>
<i>Julia Lee-Thorp · Matt Sponheimer</i>	
<b>10 Chronometric Methods in Paleoanthropology</b> . . . . .	<b>311</b>
<i>Günther A. Wagner</i>	

**11 Geological Background of Early Hominid Sites in Africa ..... 339**  
*Ottmar Kullmer*

**12 Paleoclimate ..... 357**  
*Keith Alverson*

**13 Paleosols ..... 383**  
*Gregory Retallack*

**14 Quaternary Deposits and Paleosites ..... 409**  
*Klaus-Dieter Jäger*

**15 Zoogeography: Primate and Early Hominin Distribution and Migration Patterns ..... 421**  
*Alan Turner · Hannah O'Regan*

**16 Patterns of Diversification and Extinction ..... 441**  
*Walter Etter*

**17 Paleoecology: An Adequate Window on the Past? ..... 503**  
*Thorolf Hardt · Britta Hardt · Peter R. Menke*

**18 Hominin Paleodiets: The Contribution of Stable Isotopes ..... 555**  
*Matt Sponheimer · Julia Lee-Thorp*

**19 Estimation of Basic Life History Data of Fossil Hominoids ..... 587**  
*Helmut Hemmer*

**20 Population Genetics and Paleoanthropology ..... 621**  
*John H. Relethford*

**21 Ancient DNA ..... 643**  
*Susanne Hummel*

**22 Paleodemography of Extinct Hominin Populations ..... 673**  
*Janet Monge · Alan Mann*

**23 Modeling the Past: The Primatological Approach ..... 701**  
*R. W. Sussman · Donna Hart*

**24 Modeling the Past: The Paleoethnological Evidence ..... 723**  
*Paolo Biagi*

<b>25 Modeling the Past: The Linguistic Approach</b> .....	<b>747</b>
<i>Bernard Comrie</i>	
<b>26 General Principles of Evolutionary Morphology</b> .....	<b>769</b>
<i>Gabriele A. Macho</i>	
<b>27 Computer-Based Reconstruction: Technical Aspects and Applications</b> .....	<b>787</b>
<i>Lilian Ulhaas</i>	
<b>28 Prospects and Pitfalls</b> .....	<b>815</b>
<i>Jean-Jacques Hublin</i>	

## Volume 2

<b>1 Primate Origins and Supraordinal Relationships: Morphological Evidence</b> .....	<b>831</b>
<i>Mary T. Silcox · Eric J. Sargis · Jonathan I. Bloch · Doug M. Boyer</i>	
<b>2 Molecular Evidence on Primate Origins and Evolution</b> .....	<b>861</b>
<i>Hans Zischler</i>	
<b>3 Fossil Record of the Primates from the Paleocene to the Oligocene</b> .....	<b>889</b>
<i>D. Tab Rasmussen</i>	
<b>4 Fossil Record of Miocene Hominoids</b> .....	<b>921</b>
<i>David R. Begun</i>	
<b>5 The Biotic Environments of the Late Miocene Hominids</b> .....	<b>979</b>
<i>Jordi Agustí</i>	
<b>6 Postcranial and Locomotor Adaptations of Hominoids</b> .....	<b>1011</b>
<i>Carol V. Ward</i>	
<b>7 Hominoid Cranial Diversity and Adaptation</b> .....	<b>1031</b>
<i>Alan Bilsborough · Todd C. Rae</i>	
<b>8 Dental Adaptations of African Apes</b> .....	<b>1107</b>
<i>Mark F. Teaford · Peter S. Ungar</i>	
<b>9 Evolution of the Primate Brain</b> .....	<b>1133</b>
<i>Dean Falk</i>	

**10 Primate Life Histories ..... 1163**  
*Elke Zimmermann · Ute Radespiel*

**11 The Biology and Evolution of Ape and Monkey Feeding ..... 1207**  
*Joanna E. Lambert*

**12 Great Ape Social Systems ..... 1235**  
*Angela Meder*

**13 Primate Intelligence ..... 1273**  
*Richard W. Byrne*

**14 Chimpanzee Hunting Behavior ..... 1295**  
*Nicholas E. Newton-Fisher*

**15 Cooperation, Coalition, and Alliances ..... 1321**  
*Charlotte K. Hemelrijk · Jutta Steinhauser*

**Volume 3**

**1 Potential Hominoid Ancestors for Hominidae ..... 1347**  
*George D. Koufos*

**2 Defining Hominidae ..... 1379**  
*Jeffrey H. Schwartz*

**3 Origins of Homininae and Putative Selection Pressures  
Acting on the Early Hominins ..... 1409**  
*Bogusław Pawłowski*

**4 Role of Environmental Stimuli in Hominid Origins ..... 1441**  
*Elisabeth S. Vrba*

**5 The Origins of Bipedal Locomotion ..... 1483**  
*William E. H. Harcourt-Smith*

**6 The Earliest Putative Hominids ..... 1519**  
*Brigitte Senut*

**7 The Species and Diversity of Australopiths ..... 1539**  
*William H. Kimbel*

<b>8 Defining the Genus <i>Homo</i></b> .....	<b>1575</b>
<i>Mark Collard · Bernard Wood</i>	
<b>9 The Earliest Putative <i>Homo</i> Fossils</b> .....	<b>1611</b>
<i>Friedemann Schrenk · Ottmar Kullmer · Timothy Bromage</i>	
<b>10 <i>Homo ergaster</i> and Its Contemporaries</b> .....	<b>1633</b>
<i>Ian Tattersall</i>	
<b>11 Defining <i>Homo erectus</i>: Size Considered</b> .....	<b>1655</b>
<i>Susan C. Antón · Fred Spoor · Connie D. Fellmann · Carl C. Swisher III</i>	
<b>12 Later Middle Pleistocene <i>Homo</i></b> .....	<b>1695</b>
<i>G. Philip Rightmire</i>	
<b>13 Neanderthals and Their Contemporaries</b> .....	<b>1717</b>
<i>Katerina Harvati</i>	
<b>14 Origin of Modern Humans</b> .....	<b>1749</b>
<i>Günter Bräuer</i>	
<b>15 Analyzing Hominid Phylogeny</b> .....	<b>1781</b>
<i>David Strait · Frederick E. Grine · John G. Fleagle</i>	
<b>16 Phylogenetic Relationships (Biomolecules)</b> .....	<b>1807</b>
<i>Todd R. Disotell</i>	
<b>17 Population Biology and Population Genetics of Pleistocene Hominins</b> .....	<b>1825</b>
<i>Alan R. Templeton</i>	
<b>18 Species Concepts and Speciation: Facts and Fantasies</b> .....	<b>1861</b>
<i>Colin Groves</i>	
<b>19 Human Environmental Impact in the Paleolithic and Neolithic</b> .....	<b>1881</b>
<i>Wolfgang Nentwig</i>	
<b>20 The Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia</b> .....	<b>1901</b>
<i>Christy G. Turner II · G. Richard Scott</i>	