An Ape's View of Human Evolution

Our closest living relatives are the chimpanzee and bonobo. We share many characteristics with them, but our lineages diverged millions of years ago. Who in fact was our last common ancestor?

Bringing together ecology, evolution, genetics, anatomy and geology, this book provides a new perspective on human evolution. What can fossil apes tell us about the origins of human evolution? Did the last common ancestor of apes and humans live in trees or on the ground? What did it eat, and how did it survive in a world full of large predators? Did it look anything like living apes or was it more like the fossil apes?

Andrews addresses these questions and more to reconstruct the common ancestor and its habitat. Synthesizing 35 years of work on both ancient environments and fossil and modern ape anatomy, this book provides unique new insights into the evolutionary processes that led to the origins of the human lineage.

Peter Andrews has always had a keen interest in fossils, and an encounter with Dr L.S.B. Leakey while working in the Kenya Forestry Department encouraged him to make the move to anthropology. He has spent much of his career at the Natural History Museum, London, where he was Head of Human Origins until his retirement in 2000. Since then he has been curator of Blandford Museum while retaining an Emeritus Research Associate position at the Natural History Museum, along with honorary professorships at University College London and the University of York. He has published ten books, two with Chris Stringer, and nearly 200 articles in the scientific and popular press.

An Ape's View of Human Evolution

PETER ANDREWS
The Natural History Museum, London

CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE
UNIVERSITY PRESS

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/9781107100671

First published 2015

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 Cataloging-in-Publication Data
Andrews, Peter, 1940–
An ape's view of human evolution / Peter Andrews.
pages cm
Summary: "Our closest living relatives are the chimpanzee and bonobo. We share many characteristics with them, but our lineages diverged millions of years ago. Who in fact was our last common ancestor? Bringing together ecology, evolution, genetics, anatomy and geology, this book provides a new perspective on human evolution. What can fossil apes tell us about the origins of human evolution? Did the last common ancestor of apes and humans live in trees or on the ground? What did it eat, and how did it survive in a world full of large predators? Did it look anything like living apes? Andrews addresses these questions and more to reconstruct the common ancestor and its habitat. Synthesizing 35 years of work on both ancient environments and fossil and modern ape anatomy, this book provides unique new insights into the evolutionary processes that led to the origins of the human lineage"– Provided by publisher.
ISBN 978-1-107-10067-1 (Hardback)
1. Human evolution. 2. Primates–Evolution. 3. Fossil hominids. 4. Paleontology–Miocene. 5. Physical anthropology. I. Title.
GN281.A54 2015
599.93′8–dc23 2015013762

ISBN 978-1-107-10067-1 Hardback

Contents

Preface

It is common knowledge that our human ancestors descended from apes. It is also commonly thought that in the course of this transition, some ape men left the forests, in which their ancestors were living, and entered a life in the African savanna. In the course of this transition, so the story goes, our ancestors started walking upright on two legs, started making tools, and gradually became what we are today. I will be examining the evidence for these assertions, and in particular I will be looking at the evidence for what our ancestors were like and where we came from. In doing so I will try and dispel some of the confusion many people are in because of the long history and great variety of fossil apes, the group from which we arose. In particular, I will be looking at the evidence for our last common ancestor with the apes to try and discover when and where we came from. This will entail over 20 million years of human evolution dating back to the time when apes first appeared in the fossil record.

Many recent surveys of early human evolution take chimpanzees as a model for our ape ancestry. Living apes, and particularly chimpanzees, which are our closest living relatives, are one of the major sources of information about our last common ancestor, in particular identifying characters and behaviour shared in common, and these have been described in some detail in Chapters 2 and 16 based in part on work by Bill McGrew. It would be a mistake, however, to imagine that the last common ancestor looked anything like a chimpanzee, for it, like humans, has evolved from this ancestor by 'descent with modification' in the words of Charles Darwin. It was no surprise that when fossil remains of *Australopithecus anamensis* were found a few years ago, this 4 million-year-old human ancestor looked nothing like chimpanzees; however, it had similarities in its jaws and teeth to the Miocene apes that I was studying at the time. Since it also had human attributes such as adaptations for bipedalism, which is a uniquely human trait, it was completely different from the chimpanzee-like common ancestor that was (and still is for some people) the accepted interpretation of the human/ape common ancestor. I coined the phrase 'ecological apes' for such hominins (early human ancestors) to emphasize its ecological similarities with Miocene apes while recognizing at the same time its place in human ancestry.

Over and beyond such issues are questions about where our ancestors lived, what they ate and how they got their food. Were our remote ape-like ancestors living in trees or on the ground, and were they eating meat? Did they make or use tools, and if so what kind? How did they manage to survive in a world full of large predators? Most of this book will be about trying to answer these

questions, but answering them is not always straightforward as the fossil record is notoriously patchy. We are unlikely to find the first organisms in a lineage, firstly because they would have been extremely rare, secondly because they may not look anything like what we predicted for them, and thirdly because they may be hard to distinguish from the organisms immediately preceding them: thus the earliest human ancestors would have been almost indistinguishable from the ancestral fossil apes.

A fourth human attribute, intelligence, is even harder to identify in fossils. There is a spectrum of intelligence from rudimentary life forms, such as reactions of unicellular animals to light or heat, to our conscious thought processes by which we anticipate problems and try to solve them. Even beyond that, we solve problems not by individual efforts but by working with other people: we may anticipate the need for communicating by telephone, but we have no idea, as individuals, how to make a telephone; what we anticipate is the process of going to the shops to buy a telephone that has been made by others. This issue will be taken up in Chapter 2.

Many of our questions about human evolution were formalized by two American anthropologists who between them changed the way we look at human evolution. In 1951, Sherwood Washburn proposed in his 'New physical anthropology' that the way to understand human origins required a multidisciplinary approach, with geneticists, anatomists, palaeontologists and social scientists all focusing on the question: where did we come from? This initiative was taken up by F. Clark Howell, who applied this multidisciplinary approach to field studies, emphasizing the need for understanding the context in which fossil humans were found, the nature of the geological deposits representing past environments and the need for good dating techniques. This book follows in their generalist tradition, relating the anatomy, behaviour and genetics of our human ancestors to the context in which they are found in the fossil record, and in particular relating these aspects to the environment in which our ancestors lived.

In these days of overspecialization, entire careers are built upon single fossil taxa, or even single parts of their skeletons, and it is easy to lose sight of the evolutionary picture in so doing. So much effort is placed on these narrow constraints that hypotheses can be built up without finding the need to go out into the field to identify background or underlying context. Many years ago, the Yale scientist Elwyn Simons commented on how few anthropologists visited his laboratory to work on his collection of fossil apes, and I can repeat his sad affirmation that in my 25 years curating the fossil ape collection at the Natural History Museum, with six type specimens, few visitors came to examine them even while writing articles about them. Even more is this true of anthropologists writing about ecological interpretations of fossil apes

and hominins: few anthropologists have carried out ecological analyses of modern habitats before generating sweeping interpretations about past environments. The outcome has been many myths about the past, not least that of the origins of African grasslands and their significance in human evolution. I am no ecologist, but I have participated in ecological surveys ranging from forest (Kakamega) to grassland (Serengeti) and from river flood plains (Tana River) to disturbed habitats (Laetoli). All these, plus my forestry background, have provided insights into the extent we can and cannot delve into past environments.

Living species of ape, chimpanzees, gorillas, orang utans and gibbons are few in number, and there is only a single living human species. However, there is a great range of variation in fossil ape species, and indeed the time preceding the emergence of humans could be called 'the age of the apes', for they were the common primate species living in many places across Africa, Europe and Asia. A few years ago, Terry Harrison and I attempted to look at human ancestry from the bottom up, what we called the worm's eye view of human evolution. We approached human evolution from the point of view of the ape, looking not at the end products of human evolution, ourselves and our immediate ancestors, but at its beginnings from the fossil apes. This was the issue I raised when I coined the phrase 'ecological apes', for these ape-like early hominins should be compared ecologically with the Miocene apes rather than with later hominins. The problem with this is that there are many species of fossil apes extending back at least 20 million years, and the question then arises as to which ape.

Thirty-six species of Miocene apes are currently known, but this is only a fraction of the fossil apes that actually lived during this period. The number of Old World higher primates living today has been documented by Colin Groves as 141 species, and it is reasonable to suppose that in the past there may have been at least as many fossil species living at any one time. Multiply that number by 20 million years and it is a safe assumption that fossil ape diversity over the 15 million years preceding the split between humans and apes was many times greater than 36. It is unlikely, therefore, that the fossil apes known at present give a full picture of the morphological diversity present in the Miocene, but what I will be doing is to describe what we do know at present to illustrate the range of morphology from which both humans and chimpanzees were derived.

For those who are put off by the large numbers of fossil apes now in the literature, it may be a relief to know that I am not going to be looking at this 'multitude' in its entirety but shall concentrate on just three groups of fossil apes that seem to me to be particularly relevant to human evolution. I have selected those groups because I believe they can tell us about ape and human

ancestry, and they come from sites ranging from the early Miocene to the Pliocene. In making these choices, I may cause offence to some scientists who feel that 'their' fossil ape has been neglected, but my choice has been dictated to a large extent by degrees of completeness of the fossil apes and by my first hand knowledge of the specimens. In cases where less well-represented fossil apes add information to the ape/human common ancestor they will be briefly mentioned. As far as possible, I will be avoiding taxonomic issues: two comprehensive books have been published recently with full descriptions of all presently known fossil apes and humans. These are *The Primate Fossil Record* edited by Walter Hartwig and *Cenozoic Mammals of Africa* edited by Lars Werdelin and Bill Sanders, and for the most part I have used the classifications currently in place in these two works. This has not always been easy, for names are changing all the time, particularly for the dryopithecines, but the names themselves are a peripheral issue in terms of the morphology and environment of the last common ancestor between apes and humans. Writing this book has given me a number of insights into the present state of fossil ape taxonomy, some of which may inadvertently emerge in discussion, but I have done my best to keep my opinions on ape taxonomy under wraps.

Chapter 1 of this book looks at the background to the study of common ancestry of apes and humans. The study of all forms of life rests ultimately on how we classify them, and this in turn rests on the assumption that life is structured. Although evolution has followed a random trajectory, the fact that life has evolved, one species giving rise to another, has led to the structure that we recognize when we classify birds as birds or fish as fish. If species had been created without this structure, each one would consist of a random set of characters: there might be cold-blooded birds, fish with legs, or for that matter fish and birds with shells. There would be no expectation of underlying shared structure, but biology has shown that all plants and animals have shared common ancestors with related species at some time in the past, and they have inherited characters from that ancestor, although we might not recognize them as belonging to that group. For example, all birds have feathers and wings, and an early bird fossil would be recognized as a bird if it had feathers and wings, but since these characters are exclusive to birds it cannot be the common ancestor that birds shared with dinosaurs since it is already a bird. This is the conundrum facing those who attempt to decipher evolutionary history. The common ancestor of apes and humans would be expected to share characters with both but not to have characters exclusive to one or the other or itself to be unique.

Part I provides the background to the study of apes, their anatomy and behaviour (Chapter 2), their genetics (Chapter 3), and a brief review of their taxonomy (Chapter 4). I will explain the taxonomic terminology used in

this book in Chapter 3, but suffice it to say for now that I am using the term Hominidae, and its vernacular, hominid, as the family encompassing the great apes and humans. Together with the Hylobatidae (gibbons and siamangs) they are grouped in the superfamily Hominoidea. Some fossil hominids are recognized as apes, while those placed on the human lineage are designated hominins. Some late Miocene and Pliocene hominids are claimed to be human ancestors, but there is some doubt whether these fossil hominids precede the split between apes and humans or if they are early human ancestors. For the purposes of this inquiry, this is not an important distinction, for I will be looking at their morphology, not their taxonomic status. In another sense, however, knowing the time and place of the ape-human divergence can only be depicted by taxonomic decisions, however arbitrary.

Part II reviews the present and past environments of apes (Chapter 5). This both provides a classification of vegetation types and short introductions into the environments occupied by apes. Chapter 6 describes the methods by which the environments of living and fossil apes and humans are analysed and reconstructed. Throughout this book I will be emphasizing the environments to which fossil apes and humans were adapted, for only by this way can we build up a picture of what these fossil species looked like and how they behaved. I will therefore be relating the morphology of the fossil species to their associated environments in order to show how they inter-relate and how the changes giving rise to chimpanzees and humans are affected, or not, by changes in the environment. The numerous environmental indicators will be briefly described, with examples from the fossil record. They include: geological and isotope evidence; evidence from plants; environmental reconstruction from the functional anatomy of mammals (ecomorphology); and evidence from species richness, ecological diversity and community ecology.

Part III provides the detailed descriptions of the three groups of fossil ape. Chapters 7 to 15 give accounts of the fossil apes interspersed with chapters describing their environments. These chapters show where and when fossil apes were living, what they were eating and how they moved around on the ground and in the trees. In all these respects, the environments they were living in are critical to understanding their position in hominid evolution: I will show, for example, that the majority of known fossil apes were not forest dwellers but lived in woodland savanna of varying degrees of openness, and many of them were terrestrial as well as living in trees.

The distinction between woodland and forest in tropical environments should be explained, for it is an important one, and very few animal species are found today living in or adapted to both. (It is perhaps no coincidence that chimpanzees are one of the few mammal species able to exist in both forest and woodland savanna.) Tropical forest is generally multi-canopied, so that

even quite large tree-living animals can follow aerial pathways through the different layers of the canopies, moving from one canopy level to another to pass from tree to tree. Tropical woodlands, however, have single tree canopies, and even when the crowns of the trees are in contact, the branches at the extremities of the canopies are too slender to support the weight of animals bigger than large squirrels (examples of woodland are illustrated in Chapter 2, Figure 2.3, and Chapter 5, Figure 5.3). Most fossil and living primates are too large to be fully arboreal in tropical and subtropical woodland habitats, and they must come to the ground when moving from tree to tree. This applies equally to subtropical and temperate forests, which in general have single canopies and structurally are more akin to tropical woodlands than to tropical forest. Getting back to fossil ape environments, as woodland dwellers there was no 'departure from forest to savanna', for the primary adaptation of most fossil apes was not to forest in the first place; there was no abrupt 'down from the trees' in the transition from ape to human, for as woodland dwellers the fossil apes living in the time preceding the transition must have had some degree of ground-living activity in their behaviour. The key human morphologies – upright bipedal locomotion, early increases in brain size and changes in the teeth – arose in woodland habitats with no major change of ecology, and they evolved from apes that were already partly dependent on moving about on the ground.

In Part IV, Chapters 16 and 17 provides an overview of the evidence for the acquisition of human characters and the environments in which this occurred. This is a personal inquiry bringing together the results of field and laboratory work that I have been involved in at many of the fossil localities mentioned here. I will therefore be citing my own work extensively in addition to that of many others throughout this book. I have been fortunate in being able to collaborate with many friends and colleagues in the course of my work, and my collaboration with Terry Harrison, for example, goes back more than 30 years, from the time when he was my first postgraduate student. I was very lucky in having three brilliant students during my early years at the Natural History Museum: Terry of course, Lawrence Martin and Stephen Dreyer, all of whom I co-supervised with Leslie Aiello (figure). Between them they have contributed much to my research, and if I have not always expressed my debt of gratitude to them, this is now an opportunity to do so.

I also benefited greatly, if indirectly, from my PhD supervisor, Dr L.S.B. Leakey, whose inspirational approach to research and life in general turned research into an adventure. I spent most of my time working on my doctorate while I was living in Nairobi, and there I was also helped greatly by Alan Walker, who showed me the value (and hazards) of asking questions. The Van Couvering family enlivened my time at Cambridge, and Judy in particular (now Judith Harris) introduced me to taphonomy and good

The author with Leslie Aiello, Terry Harrison and Lawrence Martin at the conference Human and Primate Evolution in Context held in London on 21 September, 2009. Photo by Terri Harrison.

excavation processes, and I was also lucky enough to coincide with both David Pilbeam and Colin Groves during their short tenures in the Anthropology Department at Cambridge University. They were an inspiration that is still having its effects today. My time at the Natural History Museum brought me into contact with a variety of experiences, as anyone who has worked in such monolithic institutions will know all about, but my determined avoidance of the administration and office politics kept much at bay, while I was lucky enough to come in contact with some brilliant minds. Chris Stringer and I have worked in harmony for nearly 40 years and we have published several books together, to say nothing of the first publication of the fossil evidence for the 'Out of Africa' hypothesis that we published together in 1988. I am grateful to my many students, for some of whom I shared supervision duties with Leslie Aiello, and who have all contributed much to my research programme. I am also grateful to my many friends and collaborators, who each in their separate ways have also contributed much to my work: Jorge Agusti, Leslie Aiello, Rosa Maria Albert, Berna Alpagut, Songül Alpaslan, Libby Andrews, Miranda Armour-Chelu, Margaret Avery, Catherine Badgley, Marion Bamford, Peter Banham, Larry Barham, David Begun, Kay Behrensmeyer,

Lynne Bell, Ray Bernor, Alan Bilsborough, Bill Bishop, Rob Blumenschine, Louis de Bonis, Basak Boz, Douglas Brandon-Jones, Tim Bromage, David Cameron, Thure Cerling, David Chivers, Desmond Clark, Ron Clark, Juliet Clutton-Brock, Margaret Collinson, Sam Cobb, Jill Cook, Shirley Coryndon, Jack Cronin, John Damuth, Yannick Dauphin, Chris Dean, Eric Delson, Arzu Demeril, Christiane Denys, Peter Ditchfield, Patricio Dominguez-Alonso, Stephen Dreyer, Sarah Elton, Ayhan Ersoy, Yolanda Fernàndez-Jalvo, Mikael Fortelius, Eva-Maria Geigl, Insaf Gençtürk, Barbara Ghaleb, Phil Gingerich, Mireille Giovanola, Colin Groves, Judith Harris, Terry Harrison, Robin Harvey, Sylvia Hixson, Kathy Homewood, Jerry Hooker, Jenny Horne, Clark Howell, Louise Humphrey, Hugh Iltis, Emma Jenkins, Jay Kelley, Rick Johnson, Bill Kimbel, Tania King, Jonathan Kingdon, Richard Klein, Meike Köhler, George Koufos, Kristin Kovarovic, Robert Kruszynski, Michael Le Bas, Roger Lewin, Helen Liversidge, Jayne Lord, Orie Loucks, Josep Marmí, Henry McHenry, Bill McGrew, Lawrence Martin, Theya Molleson, Norah Moloney, Georgia Mortzou, Salvador Moyà-Solà, John Murray, Fred Njau, Kenneth Oakley, Eileen O'Brien, Paul O'Higgins, Colin Patterson, Charles Peters, Martin Pickford, David Pilbeam, Ana Pinto, Rosemary Powers, Jay Quade, Denne Reed, Lorenzo Rook, Antonio Rosas, Brian Rosen, Fred Rögl, Phil Rye, Bill Sanders, Freidemann Schrenk, Jeff Schwartz, Louis Scott, Elwyn Simons, Christophe Soligo, Ian Stannistreet, Chris Stringer, Anthony Sutcliffe, Mark Teaford, Ibrahim Tekkaya, Heinz Tobien, Alan Turner, Dick Vane-Wright, Suvi Viranta, Alan Walker, Lars Werdelin, Eleanor Weston, Tim White, Peter Whybrow, Jim Williams, Terry Williams, Bernard Wood and Levon Yepiskoposyan.

I wish to acknowledge the kindness of the following for allowing me to use illustrations from their work: Mikael Fortelius, Jay Kelley, Tania King, Salvador Moyà-Solà, Josep Marmí, Fred Rögl, Phil Rye, Gen Suwa and Tim White.

I would like to acknowledge the help of the following from Cambridge University Press: Megan Waddington, who helped steer me through the preparation of figures and text, Beata Mako, the production editor, and Penny Lyons who copy-edited the text. I am very grateful for all their help.

Finally, I wish to give special thanks to Terry Harrison, Sylvia Hixson and Kristin Kovarovic for reading drafts of this manuscript and providing many valuable comments and suggestions for its improvement.

Note added in proof

As this book was going to the printers, an article by McNulty et al. (*Journal of Human Evolution* 84, 42–61) attributed two species of *Proconsul* to a new genus: *Ekembo nyanzae* and *Ekembo heseloni*: see Chapter 7. This changes could not be made to the text.