WILEY-BLACKWELL ENCYCLOPEDIA OF HUMAN EVOLUTION

Edited by Bernard Wood

WILEY Blackwell

Contents

This encyclopedia is dedicated to the life and work of Clark Howell,
Glynn Isaac, Charlie Lockwood, and Elizabeth Harmon.

COMPANION WEBSITE

This book has a website containing material to accompany the Wiley-Blackwell Encyclopedia of Human Evolution:
www.woodhumanevolution.com

Wiley-Blackwell Encyclopedia of Human Evolution

Edited by

Bernard Wood

Executive Editor

Amanda Henry

WILEY-BLACKWELL

A John Wiley & Sons, Ltd., Publication

This paperback edition first published 2013 © 2011, 2013 by Blackwell Publishing Ltd

Edition History: Blackwell Publishing Ltd (hardback, 2011)

Registered Office
John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Offices
9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

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Library of Congress Cataloguing-in-Publication data has been applied for

ISBN: 978-1-1186-5099-8 (paperback)

A catalogue record for this book is available from the British Library.

Cover design by Design Deluxe

Contributors

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Wood, Bernard
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Harvard University

Strait, David
University at Albany-SUNY

Subiaul, Francys
The George Washington University

Verna, Christine
CNRS, Dynamique de l'Evolution Humaine, UPR2147, Paris

Viola, Bence
Max Planck Institute for Evolutionary Anthropology

Wang, Steve
The City University of New York

Contributors

Adams, Justin
Grand Valley State University

Ashley, Gail
Rutgers University

Auerbach, Benjamin
The University of Tennessee, Knoxville

Bogart, Stephanie
Agnes Scott College, Atlanta

Brooks, Alison
The George Washington University

Claxton, Alex
University of Indianapolis

Constantino, Paul
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Despriée, Jackie
National Museum of Natural History of Paris

de Vos, John
Netherlands Centre for Biodiversity Naturalis

Dizon, Eusebio
National Museum of the Philippines

Domínguez-Rodrigo, Manuel
Complutense University

Drapeau, Michelle
Université de Montréal

Du, Andrew
The George Washington University

Dunsworth, Holly
University of Rhode Island

Farrell, Milly
The Royal College of Surgeons of England

Friedlaender, Jonathan
Temple University

Garcia Garriga, Joan
Rovira i Virgili University-The Human Paleoecology and Social Evolution Institute

Green, David
The George Washington University

Grosse, Ian
University of Massachusetts, Amherst

Gunz, Philipp
Max Planck Institute for Evolutionary Anthropology

Higham, Tom
Oxford Radiocarbon Accelerator Unit University of Oxford

Johanson, Donald
Arizona State University

Joordens, Josephine
Human Origins Group, Faculty of Archaeology, Leiden University

Kelly, Robert
University of Wyoming

Kupczik, Kornelius
Max Planck Institute for Evolutionary Anthropology

Lestrel, Pete
7327 de Celis Place, Van Nuys, California 91406-2853

Louchart, Antoine
CNRS, ENS de Lyon

McNulty, Kieran
University of Minnesota

McPherron, Shannon
Max Planck Institute for Evolutionary Anthropology

MartÚnez Molina, Kenneth
Rovira i Virgili University-The Human Paleoecology and Social Evolution Institute

Martínez-Navarro, Bienvenido
Institut Català de Paleoecología Humana i Evolució Social (IPHES) Universitat Rovira i Virgili, Tarragona

Monge, Janet
University of Pennsylvania

Nelson, Emma
University of Liverpool

Patterson, David
The George Washington University

Quam, Rolf
Binghamton University (SUNY)

Pickering, Travis
University of Wisconsin-Madison

Potts, Richard
National Museum of Natural History, The Smithsonian Institution

Reynolds, Sally
Liverpool John Moores University

Ritzman, Terry
Arizona State University

Roebroeks, Wil
Faculty of Archaeology Leiden University

Ross, Callum
The University of Chicago

Schroer, Kes
The George Washington University

Sémah, Francois
Muséum national d’histoire naturelle

Sept, Jeanne
Indiana University

Setchell, Jo
Durham University

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University College London
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University of Michigan
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University of Michigan
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Canadian Museum of Nature
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University of South Florida
Yellen, John
National Science Foundation
Zawidzki, Tadeusz
The George Washington University

Zipkin, Andrew
The George Washington University
Zonneveld, Frans
Oranjestraat 35, Middelbeers, The Netherlands

Foreword

There is at present a consensus that the 21st century will be the century of biology, just as the 20th century was the century of physics. Biology now has larger budgets and a larger workforce than physics, and it faces problems of great significance and relevance to the understanding of human nature and the conduct of human life. The core of all biological research and understanding is the theory of evolution; evolution by natural selection is the central unifying concept of biology. As the great 20th century evolutionist Theodosius Dobzhansky asserted in 1973, “Nothing in biology makes sense except in the light of evolution.”

The theory of evolution has transformed our understanding of life on planet Earth. Evolution provides a scientific explanation for why there are so many different kinds of organisms and why they all share the same chemical components in similar proportions, and why all organisms share DNA as their hereditary material, and why enzymes and other proteins, which are the fundamental constituents and engines of cell processes, are all made up of the same 20 amino acids, despite hundreds of amino acids existing in organisms. Evolution demonstrates why some organisms that look quite different are in fact related, while other organisms that may look similar are only distantly related. It accounts for the origins of humans on Earth and reveals our species’ biological connections with other living things in varying degrees. Evolution explains the similarities and differences among modern human groups and modern human individuals. It enables the development of effective new ways to protect ourselves against constantly evolving bacteria and viruses, and to improve the quality of our agricultural products and domestic animals.

We owe the concept of evolution by natural selection to Charles Darwin. Natural selection was proposed by Darwin primarily to account for the adaptive organization, or design, of living beings; it is a process that preserves and promotes adaptation. Evolutionary change through time and evolutionary diversification (multiplication of species) often ensue as byproducts of natural selection fostering the adaptation of organisms to their milieu. Evolutionary change is not directly promoted by natural selection and, therefore, it is not its necessary consequence. Indeed, some species remain unchanged for long periods of time, as Darwin noted. Nautilus, *Lingula*, and other so-called living fossils were used by Darwin as examples of organisms that have remained unchanged in their appearance for millions of years.

Evolution affects all aspects of an organism's life: morphology (form and structure), physiology (function), behavior, and ecology (interaction with the environment). Underlying these changes are changes in the hereditary materials. Hence, in genetic terms, evolution consists of changes in an organism's hereditary makeup and can be seen as a two-step process. First, hereditary variation arises by mutation; second, selection occurs by which useful variations increase in frequency and those that are less useful or injurious are eliminated over the generations. As Darwin (*The Origin of Species*, 1859) saw it, individuals having useful variations "would have the best chance of surviving and procreating their kind" (p. 81). As a consequence, useful variations increase in frequency over the generations, at the expense of those that are less useful or are injurious.

Natural selection is much more than a "purifying" process, for it is able to generate novelty by increasing the probability of otherwise extremely improbable genetic combinations. Natural selection in combination with mutation becomes, in this respect, a creative process. Moreover, it is a process that has been occurring for many millions of years, in many different evolutionary lineages, and in a multitude of species, each consisting of a large number of individuals. Evolution by mutation and natural selection has produced the enormous diversity of the living world with its wondrous adaptations and it accounts for our presence, *Homo sapiens*, on planet Earth.

There is a version of the history of ideas that sees a parallel between two scientific revolutions, the Copernican and the Darwinian. In this view, the Copernican Revolution consisted of displacing the Earth from its previously accepted locus as the center of the universe, moving it to a subordinate place as just one more planet revolving around the sun. Similarly, in a congruous manner, the Darwinian Revolution is viewed as consisting of the displacement of modern humans from their exalted position as the center of life on Earth, with all other species created for the service of humankind. According to this version of intellectual history, Copernicus had accomplished his revolution with the heliocentric theory of the solar system. Darwin's achievement emerged from his theory of organic evolution. (Sigmund Freud refers to these two revolutions as "outrages" inflicted upon humankind's self-image and adds a third one, his own. He sees psychoanalysis as the "third and most bitter blow upon man's craving for grandiosity," revealing that man's *ego* "is not even master in his own house.")

What the standard versions of the Copernican and Darwinian revolutions say is correct but inadequate. It misses what is most important about these two intellectual revolutions, namely that they ushered in the beginning of science in the modern sense. These two revolutions may jointly be seen as the one Scientific Revolution, with two stages, the Copernican and the Darwinian.

The Copernican Revolution was launched with the publication in 1543, the year of Nicolaus Copernicus' death, of his *De revolutionibus orbium celestium* (*On the Revolutions of the Celestial Spheres*), and it bloomed in 1687 with the publication of Isaac Newton's *Philosophiae naturalis principia mathematica* (*The Mathematical Principles of Natural Philosophy*). The discoveries by Copernicus, Kepler, Galileo, Newton, and others, in the 16th and 17th centuries, had shown that Earth is not the center of the universe, but is a small planet rotating around an average star; that the universe is immense in space and in time; and that the motions of the planets around the sun can be explained by the same simple laws that account for the motion of physical objects on our planet. These include laws such as $f = m \times a$ (force = mass×acceleration) or the inverse-square law of attraction, $f = g(m_1 m_2)/r^2$ (the force of attraction between two bodies is directly proportional to their masses, but inversely related to the square of the distance between them).

These and other discoveries greatly expanded modern human knowledge. The conceptual revolution they brought about was more fundamental yet: a commitment to the postulate that the universe obeys immanent laws that account for natural phenomena. The workings of the universe were brought into the realm of science: explanation through natural laws. Potentially, all physical phenomena could be accounted for, as long as the causes were adequately known.

The advances of physical science brought about by the Copernican Revolution had driven humankind's conception of the universe to a split-personality state of affairs, a condition that persisted well into the mid-19th century. Scientific explanations, derived from natural laws, dominated the world of nonliving matter, on the Earth as well as in the heavens. Supernatural explanations, which depended on the unfathomable deeds of the creator, were accepted as explanations of the origin and configuration of living creatures. Authors, such as William Paley in his *Natural Theology* (1802), had developed the “argument from design,” the notion that the complex design of organisms could not have come about by chance, or by the mechanical laws of physics, chemistry, and astronomy, but was rather accomplished by an omnipotent deity, just as the complexity of a watch, designed to tell time, was accomplished by an intelligent watchmaker.

Darwin completed the Copernican Revolution by drawing out for biology the notion of nature as a lawful system of matter in motion that modern human reason can explain without recourse to supernatural agencies. Darwin’s greatest accomplishment was to show that the complex organization and functionality of living beings can be explained as the result of a natural process: natural selection. The origin and adaptations of organisms in their profusion and wondrous variations were thus brought into the realm of science.

Darwin’s theory of evolution by natural selection disposed of Paley’s arguments: the adaptations of organisms are not outcomes of chance, but of a process that, over time, causes the gradual accumulation of features beneficial to organisms. There is “design” in the living world: eyes are designed for seeing, wings for flying, and kidneys for regulating the composition of the blood. But the design of organisms is not intelligent, as would be expected from an engineer, but imperfect and worse: defects, dysfunctions, oddities, waste, and cruelty pervade the living world. Darwin’s focus in *The Origin of Species* (1859) was the explanation of design, with evolution playing the subsidiary role of supporting evidence.

It follows from Darwin's explanation of adaptation that evolution must necessarily occur as a consequence of organisms becoming adapted to different environments in different localities, and to the ever-changing conditions of the environment over time, and as hereditary variations become available at a particular time that improve, in that place and at that time, the organisms' chances of survival and reproduction. *Origin*'s evidence for biological evolution is central to Darwin's explanation of design, because this explanation implies that biological evolution occurs, which Darwin therefore seeks to demonstrate in the second half of the book.

Darwin and other 19th century biologists found compelling evidence for biological evolution in the comparative study of living organisms, in their geographic distribution, and in the fossil remains of extinct organisms. Since Darwin's time, the evidence from these sources has become stronger and more comprehensive, while biological disciplines that have emerged recently – genetics, biochemistry, ecology, animal behavior (ethology), neurobiology, and especially molecular biology – have supplied powerful additional evidence and detailed confirmation. Accordingly, evolutionists are no longer concerned with obtaining evidence to support the fact of evolution, but rather are concerned with finding out additional information of the historical process in cases of particular interest. Moreover and most importantly, evolutionists nowadays are interested in understanding further and further how the process of evolution occurs.

Nevertheless, important discoveries continue, even in traditional disciplines, such as paleontology. Skeptical contemporaries of Darwin asked about the "missing links," particularly between the extant apes and modern humans, but also between major groups of organisms, such as between fish and terrestrial tetrapods or between reptiles and birds. Evolutionists can now affirm that these missing links are no longer missing. The known fossil record has made great strides over the last century and a half. Many fossils intermediate between diverse organisms have been discovered over the years. Two examples are *Archaeopteryx*, an animal intermediate between reptiles and birds, and *Tiktaalik*, intermediate between fishes and tetrapods.

The missing link between apes and humans is not, either, missing any longer. Not one, but hundreds of fossil remains from hundreds of individual hominins have been discovered since Darwin's time and continue to be discovered at an accelerated rate. The history of hominin discoveries is narrated in this encyclopedia, as well as the anatomical and other changes that occur through time.

Darwin wrote two books dedicated to human evolution: *The Descent of Man, and Selection in Relation to Sex* (2 vols, 1871) and *The Expression of the Emotions in Man and Animals* (1872). What we now know about human evolution is immensely more than what Darwin knew. But, even concerning hominin fossil history, much remains to be discovered. Indeed, the sequence that goes from the most primitive hominins to *Homo sapiens*, our species, is not resolved. That is, in many cases we do not know whether a particular hominin fossil belongs to the line of descent that goes to our species, or whether it belongs to a lateral branch.

There are many other important issues concerning the evolutionary origin of modern human traits – anatomical, physiological, behavioral, and cultural – that remain largely unknown. I will briefly point out three great research frontiers that seem to me particularly significant: ontogenic decoding, the brain/mind puzzle, and the ape-to-human transformation. By ontogenetic decoding I refer to the problem of how the unidimensional genetic information encoded in the DNA of a single cell becomes transformed into a four-dimensional being, the individual that develops, grows, matures, and dies. Cancer, disease, and aging are epiphenomena of ontogenetic decoding. By the brain/mind puzzle I refer to the interdependent questions of (a) how the physicochemical signals that reach our sense organs become transformed into perceptions, feelings, ideas, critical arguments, aesthetic emotions, and ethical values; and (b) how, out of this diversity of experiences, there emerges a unitary reality, the mind or self. Free will and language, social and political institutions, technology, and art are all epiphenomena of the modern human mind. By the ape-to-human transformation I refer to the mystery of how a particular ape lineage became a hominin lineage, from which emerged, after only a few million years, modern humans able to think and love, who have developed complex societies and uphold ethical, aesthetic, and religious values. But the modern human genome differs little from the chimp genome.

I will refer to these three issues as the egg-to-adult transformation, the brain-to-mind transformation, and the ape-to-human transformation. The egg-to-adult transformation is essentially similar, and similarly mysterious, in modern humans and other mammals, but it has distinctive human features. The brain-to-mind transformation and the ape-to-human transformation are distinctively human. These three transformations define the *humanum*, that which makes us specifically modern human. Few other issues in human evolution are of greater consequence for understanding ourselves and our place in nature.

The instructions that guide the ontogenetic process, or the egg-to-adult transformation, are carried in the hereditary material. The theory of biological heredity was formulated by the Augustinian monk Gregor Mendel in 1866, but it became generally known by biologists only in 1900: genetic information is contained in discrete factors, or genes, which exist in pairs, one received from each parent. The next step toward understanding the nature of genes was completed during the first quarter of the twentieth century. It was established that genes are parts of the chromosomes, filamentous bodies present in the nucleus of the cell, and that they are linearly arranged along the chromosomes. It took another quarter century to determine the chemical composition of genes: deoxyribonucleic acid (DNA). DNA consists of four kinds of nucleotides organized in long, double-helical structures. The genetic information is contained in the linear sequence of the nucleotides, very much in the same way as the semantic information of an English sentence is conveyed by the particular sequence of the 26 letters of the alphabet.

The first important step toward understanding how the genetic information is decoded came in 1941 when George W. Beadle and Edward L. Tatum demonstrated that genes determine the synthesis of enzymes; enzymes are the catalysts that control all chemical reactions in living beings. Later it became known that amino acids (the components that make up enzymes and other proteins) are encoded, each by a set of three consecutive nucleotides. This relationship accounts for the linear correspondence between a particular sequence of coding nucleotides and the sequence of the amino acids that make up the encoded enzyme.

Chemical reactions in organisms must occur in an orderly manner; organisms must have ways of switching genes on and off since different sets of genes are active in different cells. The first control system was discovered in 1961 by François Jacob and Jacques Monod for a gene that encodes an enzyme that digests sugar in the bacterium *Escherichia coli*. The gene is turned on and off by a system of several switches consisting of short DNA sequences adjacent to the coding part of the gene. (The coding sequence of a gene is the part that determines the sequence of amino acids in the encoded enzyme or protein.) The switches acting on a given gene are activated or deactivated by feedback loops that involve molecules synthesized by other genes. A variety of gene control mechanisms were soon discovered, in bacteria and other micro-organisms. Two elements are typically present: feedback loops and short DNA sequences acting as switches. The feedback loops ensure that the presence of a substance in the cell induces the synthesis of the enzyme required to digest it, and that an excess of the enzyme in the cell represses its own synthesis. (For example, the gene encoding a sugar-digesting enzyme in *E. coli* is turned on or off by the presence or absence of the sugar to be digested.)

The investigation of gene-control mechanisms in mammals (and other complex organisms) became possible in the mid-1970s with the development of recombinant DNA techniques. This technology made it feasible to isolate single genes (and other DNA sequences) and to multiply them, or "clone" them, to obtain the quantities necessary for ascertaining their nucleotide sequence. One unanticipated discovery was that most genes come in pieces: the coding sequence of a gene is divided into several fragments separated one from the next by noncoding DNA segments. In addition to the alternating succession of coding and noncoding segments, mammalian genes contain short control sequences, like those in bacteria but typically more numerous and complex, that act as control switches and signal where the coding sequence begins.

Much remains to be discovered about the control mechanisms of mammalian genes. The daunting speed at which molecular biology is advancing has led to the discovery of some prototypes of mammalian gene control systems, but much remains to be unraveled. Moreover,