

Reconstructing Human Origins A Modern Synthesis

Second Edition

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Washington University
St. Louis



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*To all creatures still wild and free,
I dedicate this book.
The success of human evolution has not been kind to you.*

Brueghel's Two Monkeys

This is what I see in my dreams
about final exams:
two monkeys, chained to the
floor, sit on the window sill,
the sky behind them flutters,
the sea is taking its bath.

The exam is History of Mankind.
I stammer and hedge.

One monkey stares and listens
with mocking disdain,
the other seems to be dreaming
away—
but when it's clear I don't know
what to say
he prompts me with a gentle
clinking of his chain.

—Wisława Szymborska

Preface

A waggish commentator once observed that the sciences could be conveniently lumped into three categories: the soft sciences, like political science and sociology; the hard sciences, like physics and chemistry; and then the really difficult sciences; like paleoanthropology. What makes paleoanthropology so “difficult” is the realization that human evolution is a unique evolutionary experiment—one that cannot be repeated. For this reason it is not unusual (or unreasonable) to encounter honest disagreements among knowledgeable paleoanthropologists about the nature, *but not the fact*, of human evolution. As in my previous book, *Primate Evolution* (Conroy, 1990), I have tried to convey this state of dynamic tension fairly and honestly without promoting my views to the exclusion of others. While I am certain that my own biases percolate through on occasion, I have made every effort to present the reader with what I take to be a balanced view of the major events and issues in human evolution. My hope is that by the time readers have reached the end of the book, they will have come away with a reasonable grasp of the fossil evidence for human evolution and how that evidence is interpreted in modern paleoanthropological research. I am less concerned, and I hope students agree, if my interpretation or emphasis differs somewhat from that of their own professors. After all, that is what teachers and books are for.

While this book is written mainly with anthropology undergraduate and graduate students in mind, anyone interested in the natural sciences can easily follow the major episodes of human evolution as outlined here by simply starting at the beginning and reading through to the end. Bearing in mind that the fossils themselves are the main “stars” of the book, I have tried to integrate the impact that recent advances in such areas as radiometric dating, functional morphology, molecular biology, and archaeological inference have had on modern interpretations of how hominins

goal

fossils - stars!
dating
functional
morphology
molecular
biology
archaeology
xvii

lived and dispersed across the globe during the Pliocene and Pleistocene epochs (Plio-Pleistocene) of the last 5 million years or so.

ORGANIZATION OF THIS TEXT

Were the changes in human behavior that distinguish us from other primates causally related to the changes in morphology seen in the human fossil record? Can the emergence of humans be considered an evolutionary “revolution” or was it simply a gradual continuation of previously existing evolutionary change both in terms of morphology and culture? What were the selective advantages of the biocultural changes seen in the human fossil record that ultimately allowed us to become dominant in such a relatively short geological time span? These are the kinds of questions we will explore as we follow the course of human evolution through the Plio-Pleistocene.

We begin in Chapters 1 and 2 by putting human evolution into its proper anatomical, temporal, and paleoenvironmental contexts, first by considering the anatomical evidence uniting humans and other primates and then by reconstructing the geologic and paleoenvironmental history of the past 5 million years.

Chapter 3 begins with a general discussion of what an appropriate fossil site looks like and how paleoanthropologists go about their work. It is followed by an extensive review of the various dating methods used in paleoanthropological research, many of which prove critical to modern interpretations of the human fossil (and archeological) record discussed in later chapters.

Chapter 4 introduces three important topics in modern paleoanthropological research: (1) phylogeny reconstruction, (2) classification, and (3) the tempo and mode of evolution. We consider how failure to appreciate the distinction between phylogeny and classification can lead to confusion and misunderstanding in studies of human evolution. The underlying methods, principles, and assumptions of the two major schools of biological classification predominant in paleoanthropology today—evolutionary systematics and phylogenetic systematics (popularly known as cladistics)—are compared and contrasted.

If, as all modern biology suggests, humankind is part of a long evolutionary continuum, we need to know who, or what, preceded us in the evolutionary line. That is the question addressed in Chapter 5. If we seek humankind's antecedents we must search among the fossil hominoids, or primitive “apes,” of the Miocene, the epoch preceding the Pliocene.

As the Miocene drew to a close, a major new episode in primate evolution unfolded as one of these Miocene “apes” began its adaptive radiation throughout Africa—and later the entire world. This unusual “ape” would begin to shape its world in ways no other organism had ever done before it. The story of this last major adaptive radiation in hominoid evolution, the evolution of the human lineage, begins in Chapters 6 to 8 with the appearance of the earliest undoubted hominins in the fossil record, the australopiths of southern and eastern Africa. Here we encounter for the first time evidence of hominization: the emergence of an animal who walked on two legs rather than four, used tools rather than teeth for tearing and cutting, had a relatively large brain, and had evolved behavioral and social mechanisms enabling it to survive the harsh environs of the African savanna. We discuss these trends in detail in Chapter 8.

In Chapter 9 we review the fossil evidence pertaining to the origins of our own genus, *Homo*. The genus *Homo* first appears in Africa about 2.4–2.0 million years ago (mya). This new genus reveals several important evolutionary distinctions from earlier (and contemporary) australopiths, including changes in the cranial and postcranial skeleton, more sophisticated stone-tool-making technology, and most important, new levels of cerebral organization in terms of both absolute size and complexity. These trends continue throughout the Plio-Pleistocene in the various *Homo* lineages, culminating in early members of our own species, *Homo sapiens*, over 100 thousand years ago (kya).

Over the past several decades an increasing number of fossils ascribed to early *Homo* have been discovered in both Africa and Eurasia; but as the pace of discovery has quickened, so have the inevitable questions such discoveries raise: How can early *Homo* be distinguished from australopiths? Is the range of morphological variation subsumed under the name *Homo habilis* too great for a single species? If all these specimens represent more than one species, what *other* taxa are represented in this heterogeneous sample? Does the definition of *Homo* need modification, and if so, how? Is *Homo habilis* really ancestral to *Homo erectus*? We explore these, and other, questions in this chapter.

In Chapter 10 we encounter a larger and more formidable hominin species, and certainly the first to spread out of Africa to populate much of the Old World, *Homo erectus* (or *H. ergaster* as some African specimens are now sometimes called). Prompted mainly by new, rigorous applications of cladistic techniques, some paleoanthropologists have recently begun to challenge some time-honored opinions about *H. erectus*. For example, is *H. erectus* simply an arbitrarily defined stage, or grade, of human evolution, temporally and morphologically sandwiched between Plio-Pleistocene *H. habilis* on the one hand and upper Middle Pleistocene hominins on the other? Or is it a “real” species with definable boundaries in time and space? Did *H. erectus* exist only in the Far East, where it was first discovered,

or can it also be identified in Africa or Europe (e.g., *H. ergaster*)? Was Asian *H. erectus* simply an evolutionary dead end, contributing little to modern human evolution? In this chapter we consider these questions as we examine the fossil evidence for *H. erectus* and related forms.

By some 800–300 kya these populations were gradually being supplanted by, or evolving into, a highly varied group of hominins living throughout much of the Old World. These rather ill-defined or “transitional” fossil hominins of the Middle Pleistocene were often lumped together under the informal and unflattering designation of “archaic *H. sapiens*” because they had not yet evolved morphological features that could be considered typical of later anatomically modern *H. sapiens*. There has been a recent tendency among (most) paleoanthropologists to subdivide this rather motley assortment of hominins into a number of different species, including *H. antecessor*, *H. heidelbergensis*, *H. rhodesiensis*, and *H. neanderthalensis*—and even others. Throughout the Old World these hominins are usually associated with some form of the Developed Oldowan/Acheulean (chopper/handaxe) and/or prepared core (e.g., Levallois) tool complexes. The fossil record of this group is discussed in Chapter 11.

The issue of the biological and behavioral origins of “modern” humans remains one of the most contentious, and exciting, subjects for debate in contemporary paleoanthropology, and the last several decades have seen a virtual revolution in our thinking about modern human origins. This is the topic we fully explore in Chapters 12 and 13. Virtually all anthropologists agree that sometime during the Middle/Upper Pleistocene transition, important biological and cultural changes were taking place in human evolution between populations of (what are best called) “late early hominins” and “early modern humans.” What is not uniformly agreed upon is exactly where, when, and how these “modern” humans first arose. In these last chapters we will discuss the molecular (Chapter 12) and fossil and archeological evidence (Chapter 13) that bears on a number of vexing questions about this important transitional period in human evolution. For instance, was the biocultural transition from late early hominins to early modern humans restricted in time and space, occurring first in Africa, then radiating outward, as the Out of Africa Model predicts, or did it develop independently in several different places across the continents, as the Multiregional Continuity Model predicts?

CHANGES IN THE SECOND EDITION

For those readers familiar with the first edition of *Reconstructing Human Origins*, this second edition embodies extensive updates and reorganizations, as well as numerous new illustrations. These updates and revisions,

along with many new references, bring students up to date with the “state of the art” of paleoanthropology through the spring of 2004. First of all, it will be noted that whereas the first edition had 10 chapters, this second edition has now been expanded to 13 chapters. This increase results from both an abundance of new material and, just as important, a reorganization of chapter topics that I hope will create a more seamless and comfortable fit within the framework of a lecture course on human origins.

Some specific improvements include the following. The taxonomy of fossil hominins used in the text is made very explicit right up front in the preface in order to avoid any nomenclatural confusion in later chapters. Here the student will also find reference to the type specimen of each of the major fossil hominin species as well. The old Chapter 1 is now divided into two chapters. New Chapter 1 provides an introduction to basic primate dental and postcranial anatomy so that students can develop a general working vocabulary of some of the anatomical terms that show up later in the text when describing fossil hominins. New Chapter 2 now focuses on climatic aspects of the Plio-Pleistocene world that had a profound influence on the course of human evolution. I have divided old Chapter 2 into two separate chapters, Chapter 3 (“Finding and Dating Fossil Hominins”) followed by Chapter 4 (“Naming and Classifying Fossil Hominins”) in order to help students better focus on these distinct activities. Old Chapter 3 is now new Chapter 5 (“Before the Biped”), a chapter that has been extensively revised to provide a more synthetic overview of these important Miocene primates that preceeded the earliest hominins.

The discussion of the earliest hominins, the australopiths, is now divided into two chapters. Chapter 6 focuses on the earliest hominins from southern Africa and Chapter 7 focuses on those from eastern Africa. Chapter 6 now offers a gallery of representative hominins at the end, courtesy of J. K. McKee. In both chapters I first lay out the geological and paleoecological settings of the most important hominin sites, and then introduce the fossil hominins themselves. The newest fossil hominin discoveries from each of these regions are presented, including discussions of *Sahelanthropus*, *Orrorin*, *Ardipithecus*, *Kenyanthropus*, and new species of *Australopithecus*, e.g., *A. garhi*. The paleobiology of the earliest hominins follows in Chapter 8 (old chapter 5). In Chapter 9 the “What Is Culture” section joins the discussion on the origins of *Homo* for better continuity.

Later chapters present new information on the oldest hominins from Europe, including those from Dmanisi (Republic of Georgia) and Atapuerca, Spain. Finally, Chapter 12 has been expanded to present a detailed, and I hope balanced, view about what the molecular evidence does, and does not, say about a number of important issues—such as the place of Neandertals in later human evolution and the Multiregional versus the Out of Africa hypotheses. Chapter 13 provides a “reality check” on what the actual fossils say about modern human origins.

I have also added a new section at the end of the book called “Brain-teasers.” This is an essay I wrote for *Evolutionary Anthropology* several years ago on what I thought were some “hot issues” or “nonissues” in human evolution (Conroy, 1998). It is reproduced here as food for student intellects to munch on. I have had fun thinking about the issues they raise; I hope students do too. There is more to them than meets the eye, so tread carefully!

And finally, for ease of reference the extensive bibliography, current through spring 2004, is now presented as a single alphabetically arranged reference list at the end of the book in the style of the *American Journal of Physical Anthropology*.

TAXONOMY USED IN THIS TEXT

Most paleoanthropologists now follow some type of cladistic classification system in which the living great apes (gorillas, chimpanzees, orangutans) and certain fossil taxa (e.g., *Dryopithecus*, *Sivapithecus*, *Gigantopithecus*) are included together with humans in the family Hominidae (see Chapters 4 and 5). The student should be aware that while this is cladistically correct, it may lead to some potential confusion as to what is actually meant by the terms *hominid* and *hominin*. Since one of the most important attributes of any classification system should be ease of communication, the classification of higher primates used in this text is given below (Wood and Richard, 2000).

When referring solely to “humans” and their immediate fossil relatives, I will use the cladistically correct term *hominin*, a member of the tribe Hominini, rather than the term *hominid*, a member of the family Hominidae, which includes the great apes. The names applied to some of these higher categories follow certain established rules.

For each of the hominin species listed below, its type specimen (i.e., the particular specimen to which the species name was first properly applied) is given.¹

Superfamily: Hominoidea (hominoids)

Family: Hylobatidae

Genus: *Hylobates*

Family: Hominidae (hominids)

Subfamily: Ponginae

Genus: *Pongo* (pongines)

¹Note that some of these taxa are not universally accepted, but are included here for completeness (e.g., *A. crassidens*, *A. praegens*, *A. bahrelghazali*, and *H. neanderthalensis*). Also, the placement of late Miocene (about 6 mya) *Orrorin* and *Sahelanthropus* in the tribe Hominini is still debatable, and thus are considered here incertae sedis. Note also that in this text *Paranthropus* is considered a subgenus of *Australopithecus*.

Subfamily: Gorillinae

Genus: *Gorilla* (gorillines)

Subfamily: Homininae (hominines)

Tribe: Panini

Genus: *Pan* (panins)

Tribe: Hominini (hominins)

Subtribe: Australopithecina (australopiths)

Genus: *Ardipithecus*

Ar. ramidus (ARA-VP-6/1; associated set of teeth)

Ar. kadabba (ALA-VP-2/10; right mandible with M₃)

Genus: *Australopithecus*

A. anamensis (KNM-KP 29281; adult mandible)

A. afarensis (L.H.-4; adult mandible)

A. africanus (Taung; juvenile skull)

A. garhi (BOU-VP-12/130; cranial fragments and maxilla)

A. (Paranthropus) robustus (TM 1517; Adult partial cranium and mandible)

A. (Paranthropus) boisei (OH 5; adult cranium)

A. (Paranthropus) aethiopicus (Omo 18; adult mandible)

A. (Paranthropus) crassidens (SK 6; adolescent mandible)

A. bahrelghazali (KT 12/H1; adult mandible)

A. praegens (KNM-T1 13150; adult mandible)

Genus: *Kenyanthropus*

K. platyops (KNM-WT 4000; adult partial cranium)

Subtribe: Hominina (hominans)

Genus: *Homo*²

H. habilis (OH 7; partial calotte and hand bones)

H. rudolfensis (KNM-ER 1470; adult cranium)

H. ergaster (KNM-ER 992; adult mandible)

H. erectus (Trinil 2; adult calotte)

H. heidelbergensis (Mauer 1; adult mandible)

H. neanderthalensis (Neanderthal 1; adult calotte and partial skeleton)

H. antecessor (ATD6-5; partial mandible with teeth)

H. sapiens (none)

Tribe: Incertae Sedis

Genus: *Orrorin*

Orrorin tugenensis (BAR 1000'00, 1000a'00, 1000b'00
(fragmentary mandibles)

Genus: *Sahelanthropus*

Sahelanthropus tchadensis (TM 266-01-060-1 (partial cranium)

²It has recently been suggested that *H. habilis* and *H. rudolfensis* should be transferred to the genus *Australopithecus* (Wood and Collard, 1999b), a view that I tend to be sympathetic to and that will be explored further in Chapter 9.

For comparison, an alternative classification based solely on DNA data and following strict cladistic rules classifies the genus *Homo* as follows (Goodman et al., 2001; Wildman et al., 2003):³

Tribe: Hominini

Subtribe: Hominina

Genus: *Gorilla*

Genus: *Homo*

Subgenus: *H. (Pan)*

H. (Pan) paniscus

H. (Pan) troglodytes

Subgenus: *H. (Homo)*

H. (Homo) ramidus (Ardipithecus ramidus)

H. (Homo) anamensis (Australopithecus anamensis)

H. (Homo) afarensis (Australopithecus afarensis)

H. (Homo) africanus (Australopithecus africanus)

H. (Homo) boisei (Australopithecus boisei)

H. (Homo) robustus (Australopithecus robustus)

H. (Homo) habilis (Homo habilis)

H. (Homo) erectus (Homo erectus)

H. (Homo) sapiens neanderthalensis (Homo neanderthalensis)

H. (Homo) sapiens sapiens (Homo sapiens)

Note that in this strictly cladistic molecular classification, both common and pygmy chimpanzees, plus all members of the human lineage, are classified within the genus *Homo* (but within separate subgenera, *Pan* and *Homo*, respectively). In addition, this classification scheme also places gorillas, chimpanzees, and humans all within the tribe Hominini (i.e., they would all be considered “hominins”). This is a legitimate, although still not widely adopted, alternative to the terminology used in this book. Indeed, some advocates of such strict molecular perspectives to hominin taxonomy suggest that there may have been only around 4 species, *in toto*, on the direct line to modern humans since the last common ancestor of chimpanzees and humans, and that only one species of human, *H. sapiens*, was in existence for most of the last 2 million years (Curnoe and Thorne, 2003).

Two other colloquial terms, *gracile* and *robust*, have often been used in the literature as a convenient shorthand label to refer to *Australopithecus africanus* and *A. afarensis* (*gracile*) on the one hand and *A. robustus* and *A. boisei* (*robust*) on the other. However, as we shall see in later chapters,

³The traditional taxonomic names for each taxon are given in parentheses. Approximately 95–99% of DNA base pairs are shared between chimpanzee and human DNA (Britten, 2002; Goodman et al., 2001; Wildman et al., 2003). Human-chimp DNA sequence divergence is roughly 10 times that between random pairs of humans. Initial studies suggest that genes relating to both olfaction and hearing have undergone distinct, rapid changes over the course of human evolution compared to chimpanzees (Clark et al., 2004).

Writing a textbook can sometimes be a forbidding and lonely task. “Like fly-fishing, writing is an elaborate conspiracy to make lyrical an activity that is inherently a business of barbs and worms” (Fields, 1990). However, the process was made so much more pleasant by the congenial atmosphere provided by friends and colleagues within the anthropological community of Washington University, St. Louis (James Cheverud, Jane Phillips-Conroy, D. Tab Rasmussen, Richard Smith, Robert Sussman, Erik Trinkaus). I am grateful to them for sharing with me over the years their considerable and diverse insights into many of the topics discussed in this book.

The first edition of this book was completed while I was a Weatherhead Foundation Resident Scholar at the School of American Research (SAR) in Sante Fe, New Mexico. To the foundation and its then president, Douglas Schwartz, I am most grateful for the time spent under the pinyons. To all those who graciously gave of their time to review and improve various portions of the manuscript—David Begun, Robert Blumenschine, Russell Ciochon, Robert Eckhardt, David Frayer, Michael Little, Jim Moore, Jane Phillips-Conroy, D. Tab Rasmussen, John Relethford, Betsy Schumann, Jeffrey Schwartz, Richard Smith, Frank Spencer, Mark Teaford, Alan Templeton, Erik Trinkaus, and Tim White—I thank you for your strong words of encouragement and your gentle words of criticism.

I must add to this list my gratitude to my editors at W. W. Norton & Company over the years, particularly Jim Jordan for starting me down this path many years ago, and John Byram and Leo Wiegman, who saw the first and second editions, respectively, through to the end.

Finally, and most important, is the loving support provided on the home front. Sox the wonder dog was always waiting at the door when I came home late at night. And to my wife and colleague, Jane Phillips-Conroy—as Elton John wrote, “*How wonderful life is, while you’re in the world.*”

Reconstructing Human Origins

Second Edition

CHAPTER I

Humans as Primates

INTRODUCTION

WHAT DISTINGUISHES HUMANS
FROM OTHER PRIMATES?

BASIC PRIMATE MORPHOLOGY

Cranial Morphology

Dental Morphology

Postcranial Morphology

INTRODUCTION

The question of human origins and the immensity of time through which we have evolved has provoked humankind's collective imagination for as long as recorded history. Henry David Thoreau, in one of his musings at Walden Pond, expressed it quite beautifully (1854): "Time is but the stream I go a-fishing in. I drink at it; but while I drink I see the sandy bottom and detect how shallow it is. Its thin current slides away, but eternity remains." Indeed, interest in the subject is as pervasive today as it was in earlier times.

The modern study of human evolution encompasses many fields and is based on a large body of empirical research. Paleoanthropology is a subject that appeals to a remarkably wide range of people. There are a number of reasons why this is so. To some, much of its colorful history conjures up images of romance and adventure in far away and exotic places, a tale of dramatic discoveries and heated controversies amid the sound and fury of clashing egos. In others it evokes sublime reflections about our place in nature, about our collective past and future. And then there are those who simply believe in George Santayana's (1905) aphorism: "Those who cannot remember the past are condemned to repeat it."

The major emphasis in this book is on the discovery and interpretation of the fossil evidence for human evolution. To many dedicated students of human evolution, fossil discovery is the very heart and soul of paleoanthropology because fossils are the most *direct* and *unequivocal* evidence documenting the course of our evolutionary history. Fossil discoveries connect us to eternity, giving us the privilege of glimpsing, if ever so briefly and imperfectly, the blurred image of those who walked the earth hundreds of thousands, or even millions of years before us. We may not always be certain about their proper taxonomic label, or their exact place on the human evolutionary tree, but that does not diminish the wonder. We still recognize them as being a part of us, and us as being a part of them.

Even though it is fossil discovery that usually stokes the fire of public imagination, intellectual adrenaline flows into paleoanthropology from a number of other interrelated disciplines as well. Such diverse fields as geochronology, archeology, phylogenetic reconstruction, functional morphology, paleoecology, behavioral ecology, and molecular biology all play critical roles in modern paleoanthropological research. For this reason, one of the aims of this book is to integrate information from these, and other, fields into our ever expanding knowledge of, and appreciation for, the human fossil record.

Human evolution should not be considered to have a definite beginning or (barring a nuclear holocaust, “hot” virus disaster, or asteroid impact) a definite end. Humankind is part of an evolutionary continuum of primates stretching back to the origins of the order some 70–90 million years ago (mya). What we think of as “human” evolution has occupied only the last 5–7% of that time, approximately the last 5 million years or so, and that story is the subject matter of this book.

WHAT DISTINGUISHES HUMANS FROM OTHER PRIMATES?

Before launching into the story of human evolution, perhaps it is best to start with a more basic consideration. What distinguishes primates from other mammals and what distinguishes humans from other primates? Carolus Linnaeus, the originator of the modern scientific system of classifying and naming organisms, first put forward the definition of the mammalian order **Primates** in the 10th edition of his great work *Systema Naturae* (1758). He characterized primates as possessing several distinctive anatomical features, including (1) four cutting teeth, or **incisors**, at the front of the jaw; (2) two collarbones, or **clavicles**; (3) two mammary glands, or **mammae**, on the chest; and (4) at least two grasping, or **prehensile**, extremities that function as hands in the sense of being able to grasp objects by means of an opposable first digit. He divided the order into four genera, to which he gave the Latin names *Homo*, *Simia*, *Lemur*, and *Vespertilio*. Within *Homo* he distinguished between *Homo diurnus* (which included European, Native American, Asian, and African humans) and *Homo nocturnus* (the orangutan) (Cela-Conde and Ayala, 2003). *Simia* included monkeys and the rest of the apes, *Lemur* included lemurs and other “lower,” less human-like forms, and *Vespertilio* included various species of bats.

Linnaeus’s taxonomic lumping together of humans and apes did not meet with universal approval and a succession of eighteenth- and nineteenth-century comparative anatomists devoted much effort and ingenuity to devising anatomical and behavioral criteria that could convincingly distinguish the two groups. They pointed not only to measurable anatomical characters,

such as bone structure and dentition, but also to such qualitative traits as the human capacity for speech, reason, and what were called other “higher” brain functions (McCown and Kennedy, 1972; Owen, 1858). None of their alternative classification schemes made much headway, however, and the Linnaean formulation stood more or less unchanged for more than a century.

The true evolutionary link between apes and humans finally received scientific validity in the mid-nineteenth century through the writings of Charles Darwin and Thomas Huxley, among others. Having established the general principles of his theory of natural selection in *The Origin of Species* (1859), Darwin went on to apply them specifically to the question of human evolution in *The Descent of Man* (1871). He wrote:

It is notorious that man is constructed on the same generalized type or model with the other mammals. All the bones in his skeleton can be compared with the corresponding bones in a monkey, bat or seal. So it is with his muscles, nerves, blood vessels and internal viscera. The brain, the most important of all the organs, follows the same law. . . . It is, in short, scarcely possible to exaggerate the close correspondence in general structure, in the minute structure of tissues, in chemical composition and in constitution, between man and the higher animals, especially the anthropomorphous apes.

Darwin even speculated on the likely geographic region where the human species most likely emerged. He noted that

in each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's closest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.

The first significant post-Darwinian modification of the Linnaean system of primate classification was proposed in 1873 by the English anatomist St. George Mivart. Removing bats and colugos (“flying lemurs”) from the order, he reorganized the remaining members into two suborders: the primitive **Prosimii**, or “premonkeys” (lemurs, lorises, and the like), and the more advanced **Anthropoidea** (monkeys, apes, and humans). He also proposed an expanded list of traits to further distinguish primates from other mammals. Primates, he wrote, were

unguiculate [having nails or claws], clavicate [having clavicles], placental mammals, with orbits [eye sockets] encircled by bone, three kinds of teeth [incisors, canines, and molars], at least at one time of life; brain always with a posterior lobe and a calcarine fissure [a transverse groove along the medial surface of that lobe]; the innermost digit of at least one pair of extremities opposable; hallux [big toe] with a flat nail or none; a well-developed caecum [a pouchlike part of the large intestine]; penis pendulous; testes scrotal; always two pectoral mammae.

Although none of these characters, it turns out, are peculiar to primates, their *combination* has long been accepted as diagnostic of the order.

Evolutionary trends

An alternative approach to the problem of defining the primates, advocated chiefly by the English anatomist Sir Wilfred Le Gros Clark (1959) nearly a half century ago, sought to characterize the order in terms of a complex of evolutionary *trends* rather than a simple listing of morphological traits. According to this view, the distinctive evolutionary trends that set the early primates apart from other placental mammals included progressive enlargement of the brain, convergence of the axes of vision, shortening of the snout, atrophy of the olfactory sense, prolongation of the postnatal growth period, and specializations of the extremities for grasping. Most of these trends, it was thought, were related to a tree-living, or **arboreal**, way of life.

Habitat

More recently, a much more elaborate definition of the living primates has been proposed that takes into account such diverse factors as geographic distribution, habitat, means of locomotion, influence of major sense organs on the shape of the **cranium**, relative brain size, reproductive biology, and dental patterns (Martin, 1986). For example, living primates are typically arboreal animals living mainly in tropical and subtropical ecosystems (there are some obvious exceptions, such as the more savanna-dwelling baboons of Africa and the temperate forest-dwelling macaques of Asia). Anatomical features of the hands and feet, the **manus** and **pes**, respectively, are adapted for prehension (grasping). This is clearly evidenced in the foot by the widely divergent big toe, or **hallux**, in all primates except humans. In addition, the digits have nails instead of claws, which serve as supportive structures for the tactile cutaneous ridges on the fingertips that reduce slippage on arboreal supports.

Anatomy

In all modern primates the visual sense is emphasized over the olfactory sense. For this reason the eyes are usually relatively large and are protected either by a **postorbital bar** (typical of lemurs and lorises) or by a complete bony cup, a condition referred to as **postorbital closure** (typical of monkeys, apes, and humans). The emphasis on vision has other anatomical consequences. For example, the orbits have become enlarged and have moved from a more lateral-facing to a more forward-facing position in the cranium. This feature is associated with **binocular vision**, by which both eyes focus on the target object and thereby allow it to be perceived with greater depth perception (Fig. 1.1).

Life history

Compared with most other mammals the primate brain is enlarged relative to body size. Indeed, primates are unique among living mammals in that the brain constitutes a significantly larger proportion of body weight at all stages of gestation. Modern primates have long gestation periods relative to maternal body size, and both fetal and postnatal growth is characteristically slow in relation to maternal size. Consequently, sexual maturation is attained late, and life spans are correspondingly long relative to body size. In sum, it takes longer for modern primate populations to reproduce themselves than is the case for populations of most other mammals (Martin, 1986).

In many respects, what distinguishes humans from other primates is simply an extension of what distinguishes primates from other mammals.

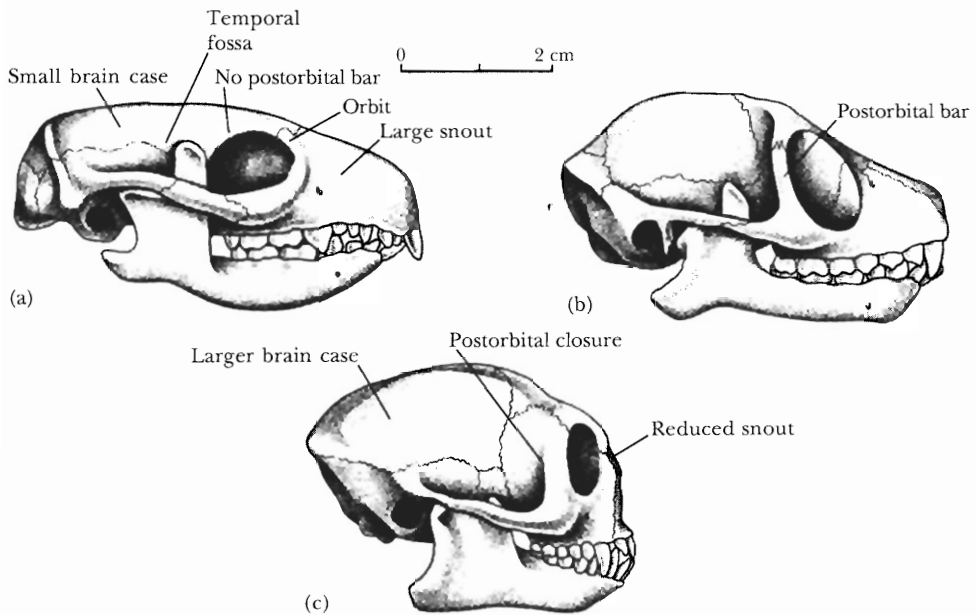


Fig.1.1. Several morphological features distinguishing modern primate and non-primate skulls. (a) Insectivoran (hedgehog); (b) prosimian (*Lepilemur*); (c) New World monkey (*Callithrix*). Note the relative sizes of the brain and snout, development of the postorbital bar and postorbital closure, and position of the eye sockets. (Conroy, 1990.)

For example, the trends noted above toward increased brain size, delayed maturational periods, and specializations of the hand for object manipulation reach their most extreme development in modern humans.

Harvard anthropologist David Pilbeam (1992) nicely summarized some of the features that distinguish humans from other primates, in other words, some of the things that “make us human.” For example, he notes that in terms of population size and distribution and genetic structure modern human populations are found in virtually every environment on the planet, far exceeding the tropical and subtropical ranges characteristic of most nonhuman primate populations. Humans can accomplish this enormous range extension only because we, in a sense, provide our own microenvironments wherever we go (e.g., clothes, shelters, and climate-control contraptions like furnaces and air-conditioners).

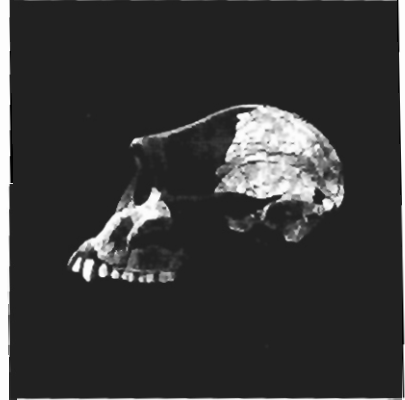
Compared to other primates, humans are a genetically uniform species, with most of our genetic variation occurring within single populations (so-called within-group diversity as opposed to between-group diversity), so much so that even if all human populations were to disappear except one, about three quarters of the world’s total human genetic diversity would still be preserved (Lewontin, 1972).

It has been calculated that an average human population sampled from anywhere in the world would include 85% of all human variation at autosomal (i.e., nonsex) loci and 81% of all human variation in mtDNA sequences. Differences among populations from the same continent contribute another 6% variation; only 9–13% of genetic variation differentiates populations from different continents. As far as variation in the Y chromosome is concerned, an average population includes only 36% of the world's Y chromosome variation; most Y chromosome variation (53%) occurs in populations from different continents. Since mtDNA is maternally inherited and the Y chromosome paternally inherited, these differences between mtDNA and Y chromosome patterns are best explained by higher migration rates among females than among males (Owens and King, 1999).

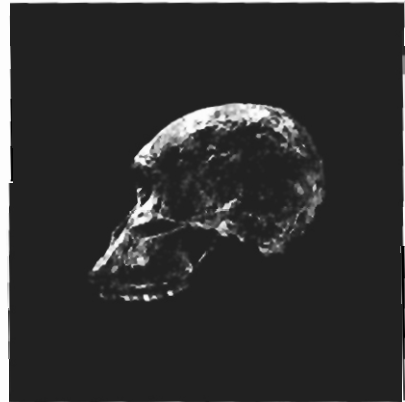
One method commonly used to quantify within-to-among population genetic diversity is through the F_{st} statistic. This statistic ranges from 0 to 1, where 0 indicates that all the genetic diversity within a species is shared equally by all populations and there are no genetic differences among populations and 1 indicates that all genetic diversity within a species is fixed among populations and there is no genetic diversity within populations. This statistic in human populations is about 0.156, indicating that most human genetic diversity exists as differences among individuals within populations. Major human “races” differ genetically by only about 15% (Templeton, 1999).

We are also distinguished from most other primates by our feeding habits. Whereas most nonhuman primates have fairly restricted or specialized dietary preferences (e.g., fruit eating, or frugivory; leaf eating, or folivory; insect eating, or insectivory), human populations are eclectic in their feeding preferences, selecting from almost every type of plant and animal food available. As we shall see in later chapters, the type of foods our ancestors ate, and the way they procured and processed those foods, had a tremendous influence on human evolution. Many features of our ancestor's cranial and dental anatomy directly reflect the types of stresses generated by powerful chewing (masticatory) muscles (Fig. 1.2a). In addition, the development of increasingly sophisticated tool technologies beginning about 2.5 million years ago has clearly been influenced by food procurement strategies throughout much of human evolution. Indeed, probably the most distinctive feature of modern humans compared to other primates is our now complete reliance on material culture (i.e., tools) for survival.

Fig. 1.2. There are many anatomical and behavioral distinctions between humans and other primates. (a) The size and shape of the human cranium have changed dramatically over the past 4 million years. Most of these changes relate to (1) the gradual reduction in the size of the teeth, jaws, and chewing muscles and (2) the threefold increase in brain size. (b) Adaptations of the pelvis and lower limbs for bipedal walking are another one of the major anatomical distinctions between humans and other primates. In this model of *Australopithecus afarensis* (dated to over 3 mya), many of these unique adaptations were already well under way. (Photos courtesy of David Brill. Weaver, 1985.)



Australopithecus afarensis (composite specimen)



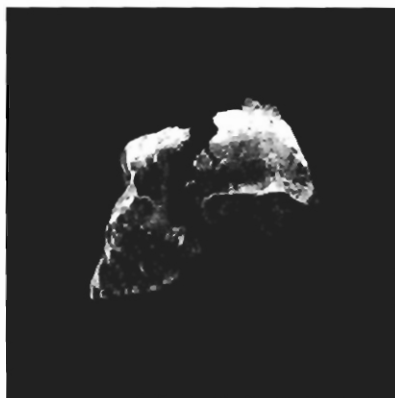
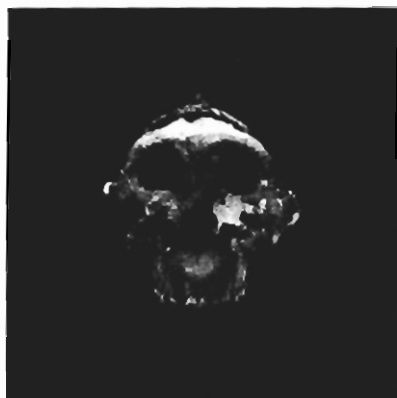
Australopithecus africanus (Sts 71)



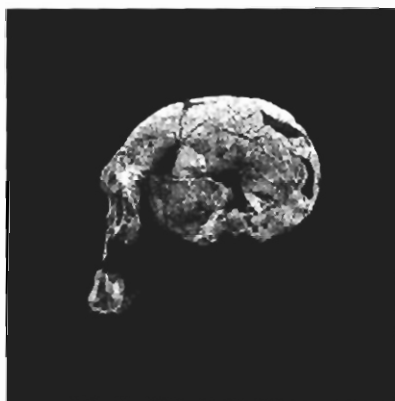
Australopithecus robustus (SK 48)

(a)

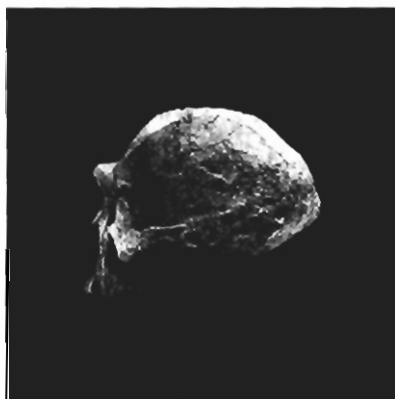
(Continued)



Australopithecus boisei (OH 5)



Homo habilis (KNM-ER 1470)



(a)

Homo erectus (KNM-ER 3733)

Fig. 1.2. (Continued)



"Archaic" *Homo sapiens* (Petalona 1)



Homo sapiens (Ferrassie 1 Neandertal)



Homo sapiens (Cro-Magnon 1)

Fig. 1.2. (Continued)



(b)

Fig. 1.2. (Continued)

Box 1.1 Some Features Characterizing Living Primates That (in General) Distinguish Them from Other Mammals

1. Lifestyle is typically arboreal; range is mainly restricted to tropical and subtropical forest ecosystems.
2. Extremities are adapted for prehension; sensitive tactile pads are present on the digits.
3. Locomotion is hindlimb dominated, with the center of gravity of the body located closer to the hindlimbs.
4. The visual sense is greatly emphasized, and the olfactory sense is reduced.
5. The bony housing for the middle ear is formed by a separate bone called the petrosal bone.
6. The brain is moderately enlarged relative to body size (at all stages of gestation) and has a true lateral, or Sylvian, sulcus separating the frontal and parietal lobes from the temporal lobe and a triradiate calcarine sulcus.
7. Males are characterized by early descent of the testes into a scrotal sac.
8. Gestation periods are long relative to maternal body size, and small litters of precocial neonates (i.e., infants born with at least a moderate covering of hair and both ears and eyes open at birth) are produced.
9. Both fetal and postnatal growth are characteristically slow in relation to maternal size; sexual maturity is attained late, and life spans are correspondingly long relative to body size (i.e., reproductive turnover is slow).
10. The dental formula exhibits a maximum of two incisors, one canine, three premolars, and three molars in each quadrant of the upper and lower jaws.

SOURCE: Martin (1986).

The unique skeletal adaptations distinguishing humans from other primates are those of the pelvis and lower limb that permit our unusual type of locomotion, bipedalism (Fig. 1.2b). The reason(s) for the origin of bipedalism remain one of the intriguing mysteries of human evolution, and we will discuss it fully in later chapters. For now, let us just note that bipedalism frees the hands from the locomotor functions that characterize all other primates, thereby allowing the hands to be used in other critical roles such as making tools, holding infants, and gathering food.

As noted above, a number of life history variables distinguish humans from other primates. Modern humans have long gestation periods relative to maternal body size as well as prolonged periods of infant dependency. Sexual maturation occurs relatively late and life spans are correspondingly long. Therefore, compared to other primates, human females have a much longer postreproductive phase to their life cycle. Unlike other primates that usually have peak periods of sexual receptivity, or **estrus**, human females remain receptive throughout the duration of their monthly reproductive cycle.

Finally, one of humanity's most distinguishing characteristics is the evolution of language and the type of symbolic thinking associated with it. Without language, much of our social behavior and interactions would be impossible. The evolution of articulate human speech involved major structural reorganization in both the brain and the laryngeal apparatus (i.e., the voice box). As Pilbeam (1992) notes, language "makes possible sharing, exploitation and the delay of reward or punishment; the structuring of relationships; propaganda; art; the division of labour; warfare; and the aggregation and socialisation of masses of people. Its most essential feature is that it allows human behavior to be governed by the complex and subtle rules that together make up human culture."

BASIC PRIMATE MORPHOLOGY

Virtually all human fossil material studied by paleoanthropologists consists of cranial, dental, and/or postcranial (skeletal) remains. For this reason, interpretation of the human fossil record necessarily demands a basic understanding of primate morphology (particularly skeletal biology) and odontology. To better prepare the reader for discussions of the fossil record that follow in later chapters, we begin by reviewing some basic aspects of primate cranial, dental, and skeletal anatomy. Many of the items mentioned in this brief overview will be more fully discussed in later chapters when they become relevant to interpretations of the fossil evidence.

Cranial Morphology

The primate cranium¹ serves a number of critical functions: it houses and protects the brain and special sense organs such as those of hearing, vision, and smell; it forms the anchoring structure for the upper dentition; and it provides the bony surface attachment area for both the chewing (masticatory) muscles and the muscles of facial expression. The main osteological features of the ape and human cranium are compared in Figure 1.3 and the main osteological landmarks of the human mandible are identified in Figure 1.4.

¹By definition, the anatomical term *skull* refers to a specimen containing both the cranium and the lower jaw, or mandible; the term *cranium* refers to the skull without the mandible; and the term *calvaria* refers to the domelike roof of the cranium, or "skullcap." The term *calotte* is sometimes used for *skullcap*. The term *calvarium* is an incorrect term for *calvaria*.

Basic Primate Morphology

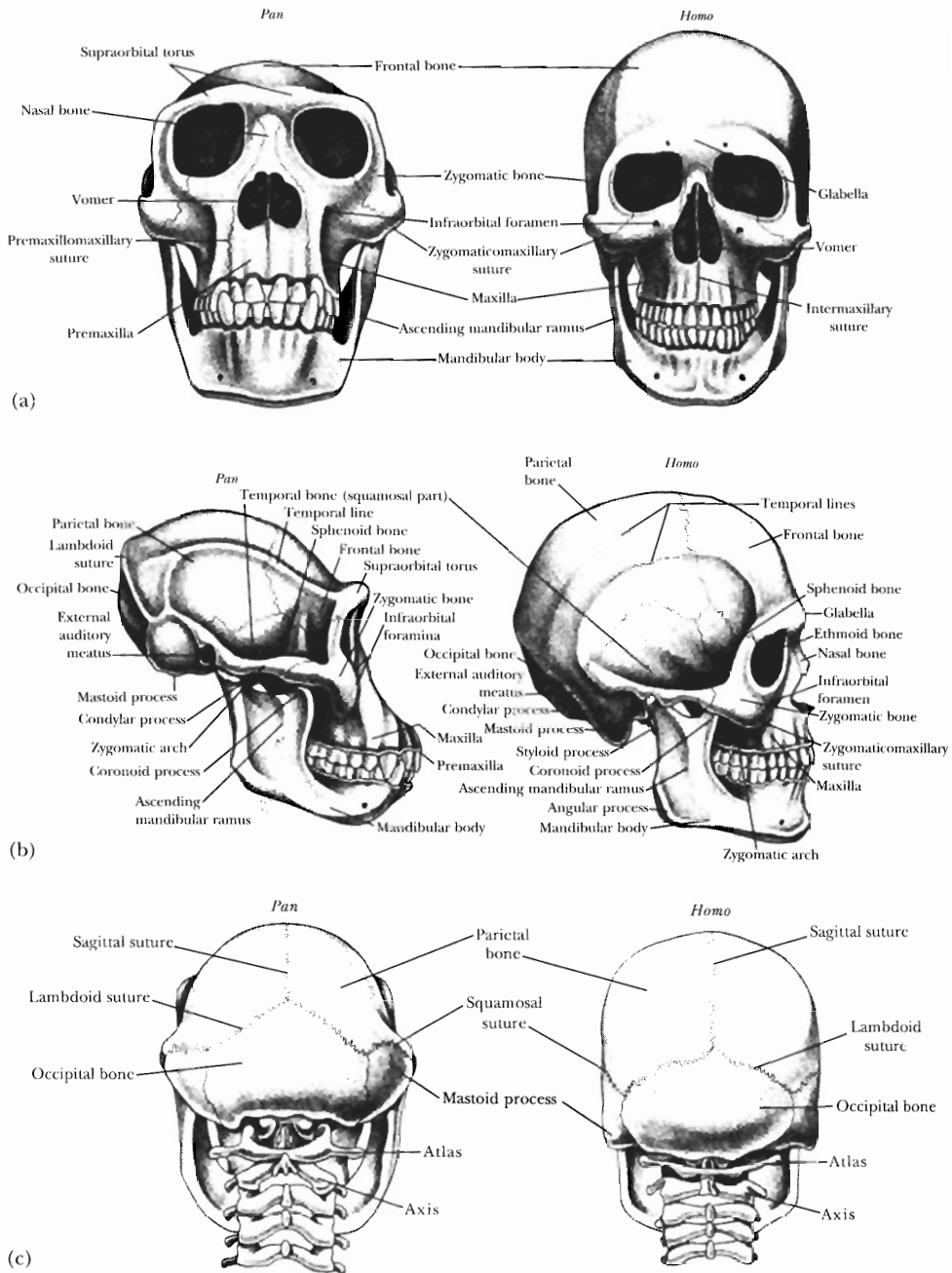


Fig. 1.3. Comparison of the skull in chimpanzees (left) and modern humans (right), with the major bones and bony landmarks identified. (a) Frontal view. (b) Lateral view. (c) Posterior view. (d) Basal or occlusal view.

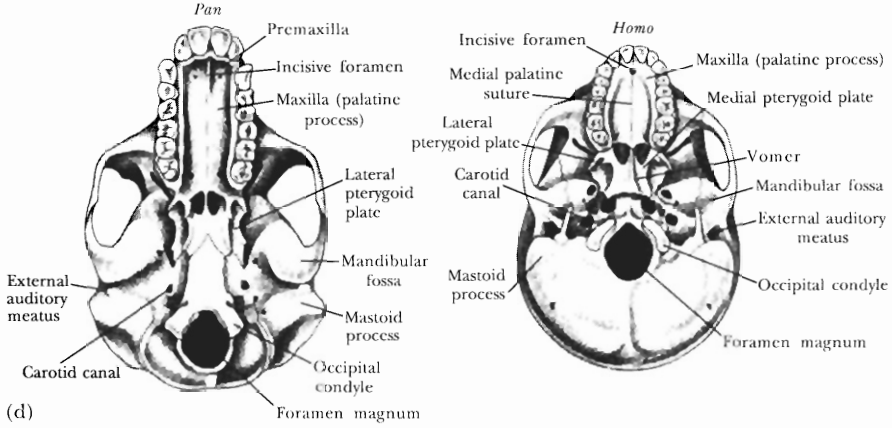


Fig. 1.3. (Continued)

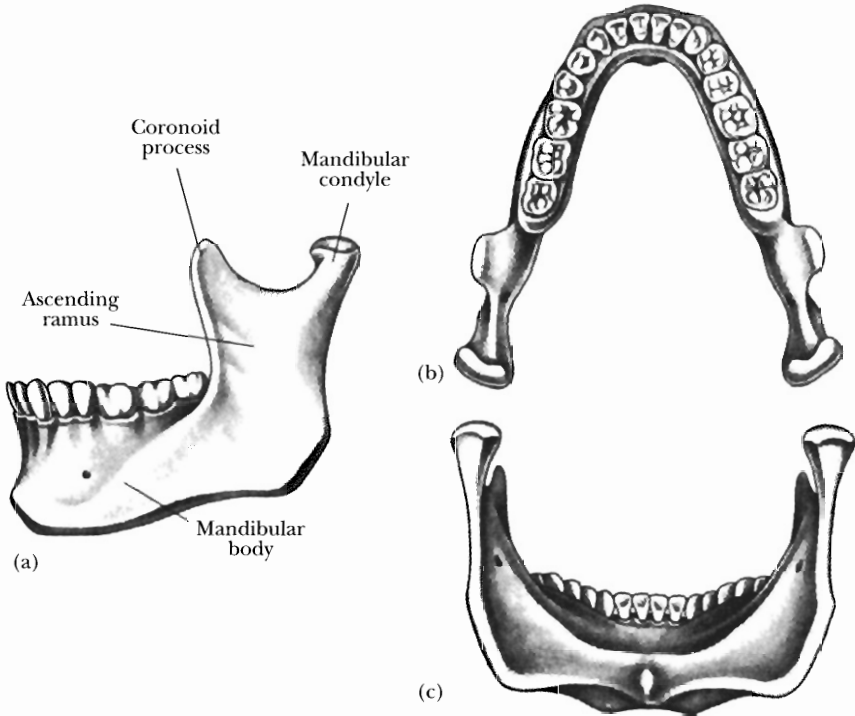


Fig. 1.4. Important bony landmarks of the human mandible. (a) Lateral view. (b) Occlusal view. (c) Posterior view.

To a large extent, the overall shape of the cranium in various primates reflects the relative degree of enlargement or specialization of these various functions. For example, primates that rely more on the sense of smell, or olfaction, tend to have longer snouts than those that rely more on vision. Likewise, those primates with well-developed chewing muscles often have accentuated bony crests or muscular markings on the cranium, for instance temporal lines or sagittal crests marking the origin of the temporalis muscle, that serve as sites of attachment for those powerful muscles.

Posture, or how the head is carried on top of the vertebral column, may also affect cranial morphology. For example, the hole at the base of the cranium for passage of the spinal cord, the **foramen magnum**, tends to face more inferiorly than posteriorly in primates that routinely hold their trunk more erect in both resting and locomotor postures. There are, however, other factors affecting the relative position of the foramen magnum. In humans such factors may include (1) the relatively large degree of cranial base flexion that brings the face to a position below, rather than in front of, the brain case and (2) the relative enlargement of the **occipital lobes** of the brain that results from an expansion of the visual cortex of the cerebral cortex.

The thin bones forming the roof of the cranium, the **calvaria**, consist of the frontal bone anteriorly, the occipital bone posteriorly, and the parietal, temporal, and sphenoid bones laterally. These bones are joined to one another by fibrous joints called **sutures**. All of the upper teeth are housed in the maxilla except for the incisors, which are housed in the premaxilla. All the lower teeth are contained in the mandible.

Dental Morphology

The dentition is one of the most informative parts of the human body as far as paleoanthropologists are concerned. Of all the skeletal elements teeth are the most resistant to biological, chemical, and/or physical destruction and, therefore, are generally the most common skeletal element found in fossil assemblages. The important clues about past and present human adaptations provided by the dentition pertain to diet, age, sex, health, and phylogenetic relationships.

A major characteristic of the human dentition is that our teeth are regionally differentiated to serve special functions, a condition known as **heterodonty**. Thus, on each side of the upper and lower jaws, starting at the front, are two teeth adapted for cutting and cropping, the **incisors**, followed by a single-pointed, tusk-like tooth, the **canine**, which in turn is followed by the postcanine dentition consisting of two **premolars** and three **molars**, teeth whose complex chewing surfaces are adapted for grinding and crushing. Therefore, all adult fossil and modern humans normally have 8 teeth in each quadrant of the upper and lower jaws, giving a total of

heterodonty

32. A shorthand way to write the **dental formula** for humans is 2.1.2.3. Teeth in the upper and lower jaws are usually identified with superscripts and subscripts, respectively. For example LM^1 is shorthand for a left upper first molar, whereas RM_1 is shorthand for a right lower first molar. One point of potential confusion is that the two premolars in each quadrant of the upper and lower jaws are usually referred to as the third and fourth premolars (P_3 and P_4) and not as the first and second premolars as one might expect. Actually, there is a good evolutionary reason for this terminology; more ancient primates once had four premolars in each quadrant, but during the course of primate evolution the ancestors of higher primates, including humans, lost the first and second premolars. Thus the two remaining premolars are actually premolars three and four of the original set of four.

The adult dentition is preceded by the milk, or **deciduous**, dentition consisting of two incisors, one canine, and two premolars, sometimes referred to as "milk molars," in each quadrant. The three permanent adult molars are not preceded by any deciduous teeth. Shorthand notation for the deciduous dentition would be, for example, Rdi_2 and Ldm^1 for the right deciduous lower second incisor and left deciduous upper first molar, respectively.

The proper anatomical orientation is very important when referring to teeth. A crown, or **occlusal**, view refers to the chewing surface of the tooth. The **buccal** side of the tooth faces laterally toward the cheek and the **lingual** side of the tooth faces medially toward the tongue. The side of the tooth facing the front of the mouth is the **mesial** surface, and the side facing the back of the jaw is the **distal** surface. These orientations are labeled in Figures 1.5 and 1.6.

Teeth consist of two main parts: crowns and root(s). The crowns project into the oral cavity and the roots are anchored in the bony socket, or **alveolus**, of the mandible or maxilla. The crowns are covered by an avascular layer of mineralized tissue called **enamel** (Fig. 1.5). Enamel is the hardest biological structure in the human body. Roots are covered by a thin bone-like layer, the **cementum**. Beneath these surface layers, and forming much of the tooth's bulk, is another very resilient connective tissue, the **dentine**. Dentine differs from enamel in that it is not as highly mineralized a tissue (approximately 70% versus 97% mineralization by weight). The **pulp cavity** is the neurovascular space deep to the dentine that extends for a variable distance into the roots.

In humans the incisors are relatively simple, single-rooted teeth having a somewhat spatulate crown. The single-rooted canine is still a somewhat pointed, tusk-like tooth, but it is not the long, sharp weapon that it is in some other primates like baboons. Functionally, the human canine has become more incorporated into the incisor tooth row. Humans use these teeth in diverse ways, from cutting and cropping foods to holding objects.

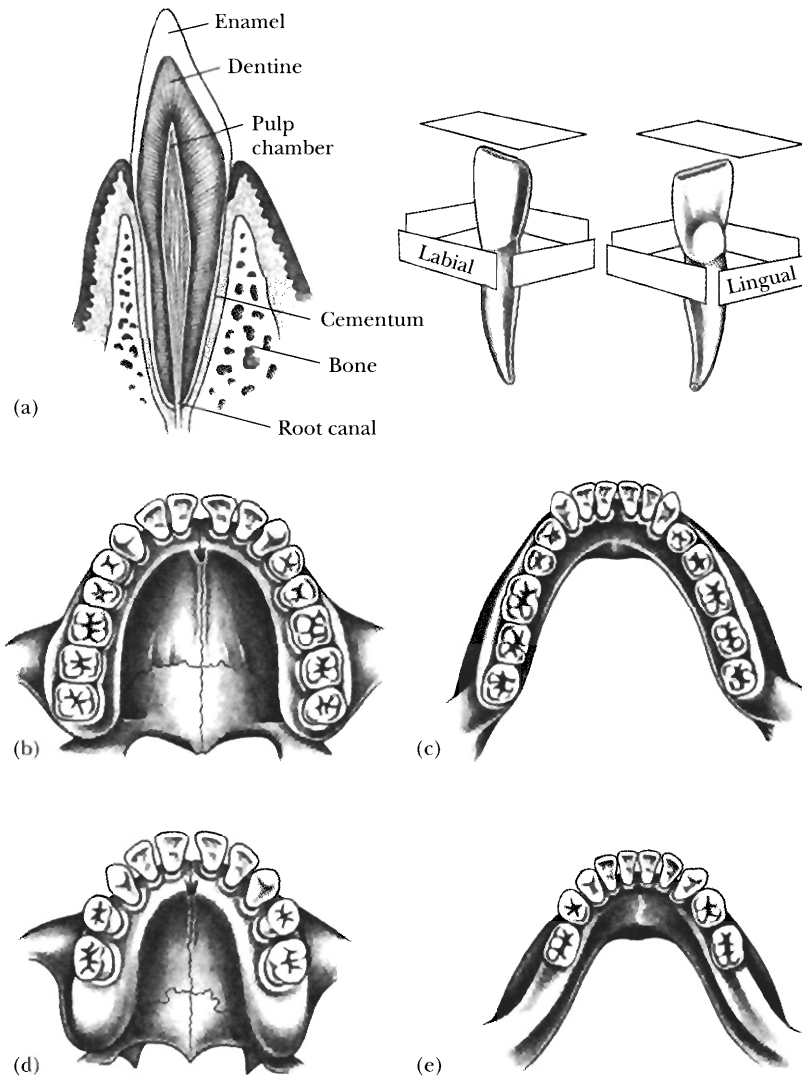


Fig. 1.5. (a) Cross section through a human incisor tooth to show the different tissues (*left*) and its proper orientation (*right*). (b) Occlusal view of the upper permanent dentition. (c) Occlusal view of the lower permanent dentition. (d) Occlusal view of the upper deciduous dentition. (e) Occlusal view of the lower deciduous dentition.

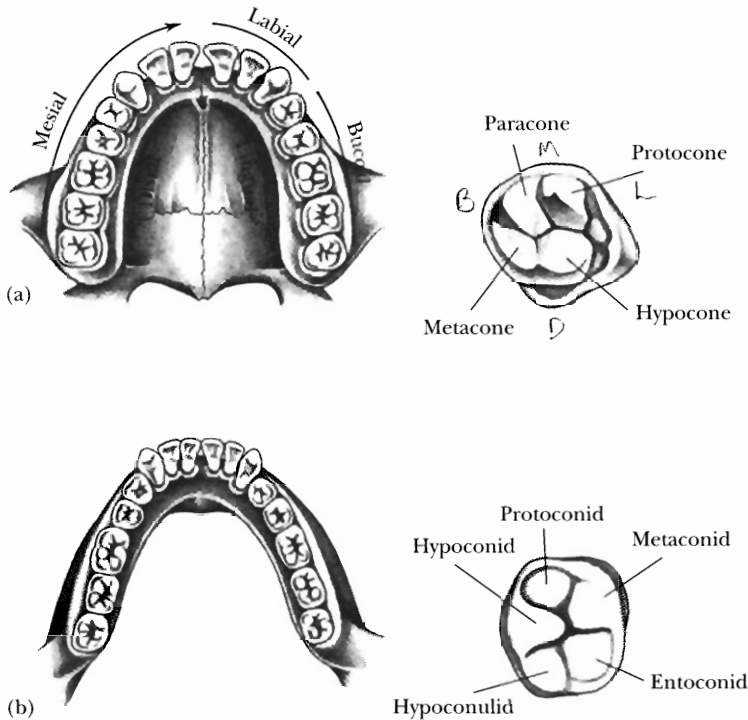


Fig. 1.6. (a) Occlusal view of the upper dentition plus detail showing the major cusps of the right M¹. (b) Occlusal view of the lower dentition plus detail showing the major cusps of the left M₁.

The premolars may have one or more roots and are also relatively simple teeth having two main cusps, which is why they are sometimes referred to as **bicuspid**s. There is often a thickened ring of enamel around the base of the tooth, called the **cingulum**. In some primates with large, stabbing upper canines like baboons, the anterior lower premolar (P₃) acts as a honing stone to sharpen the posterior edge of the upper canine every time the two teeth come into contact. Such an adaptation is referred to as a **sectorial** premolar. The loss of the honing C/P₃ complex is a characteristic of hominins, in contrast to other primates, and evolved very early in human evolution.

The upper molars of humans have four main cusps: **protocone**, **paracone**, **metacone**, and **hypocone**. Looking at the occlusal surface of an upper molar, the protocone is the main cusp on the mesiolingual side, the paracone is the main cusp on the mesiobuccal side, the metacone is the main cusp on the distobuccal side, and the hypocone is the main cusp on

the distolingual side (Fig. 1.6). Enamel crests often connect the main cusps; these crests are adaptations for slicing food between the molars during occlusion.

The lower molars of humans consist of two parts: an anterior portion, the **trigonid**, and a posterior, heel-like projection, the **talonid**. The three main cusps of the trigonid are the mirror image of the cusps of the upper molar trigone: the **protoconid** on the buccal side and the **paraconid** (which is usually absent in higher primates, including humans) and **metaconid** on the lingual side. Note that the names of the lower molar cusps end in *-conid*, whereas those of the upper molars end in *-cone*. The talonid is usually a basin-like structure surrounded by a raised enamel rim with two main cusps: the **hypoconid** buccally and the **entoconid** lingually. Often there is an additional cusp, the **hypoconulid**, toward the middle of the distal margin of the rim, which can be well developed on lower third molars. During chewing, the protocones of the upper molars fit into the talonid basins of the corresponding lower molars, like the action of a pestle in a mortar.

Postcranial Morphology

The postcranial skeleton is composed of an **axial skeleton**, consisting of those bones forming the central axis of the body (including the vertebrae, sacrum, ribs, and sternum) and an **appendicular skeleton**, consisting of those bones making up the upper and lower limbs (including their respective limb girdles). The postcranial skeleton provides the overall scaffolding that holds up the body as well as the site of attachment for the muscles that move the body. The skeleton acts as a system of levers that facilitate, indeed make possible, movement powered by muscles.

In many respects, the primate skeleton retains many basic mammalian postcranial features. For example, primates, including humans, retain five fingers and toes; a relatively mobile shoulder joint for free movement of the upper limb in all directions; grasping, or prehensile, capability in both hands and (in nonhuman primates) feet; a well-developed collarbone, or clavicle; and completely separate bones of the forearm (radius and ulna) and leg (tibia and fibula).

Primates also have developed highly sensitive friction pads on the hands and feet, and in most modern primates the distal finger and toe bones, or phalanges, are covered by flattened nails instead of sharp, curved claws. These nails and friction pads provide an efficient mechanism for both grasping and manipulating objects.

The skeleton of humans and apes consists of the same basic bony elements, although the size and shape of many of these bones, of course, vary, depending on the different functional demands placed on them (Fig. 1.7).

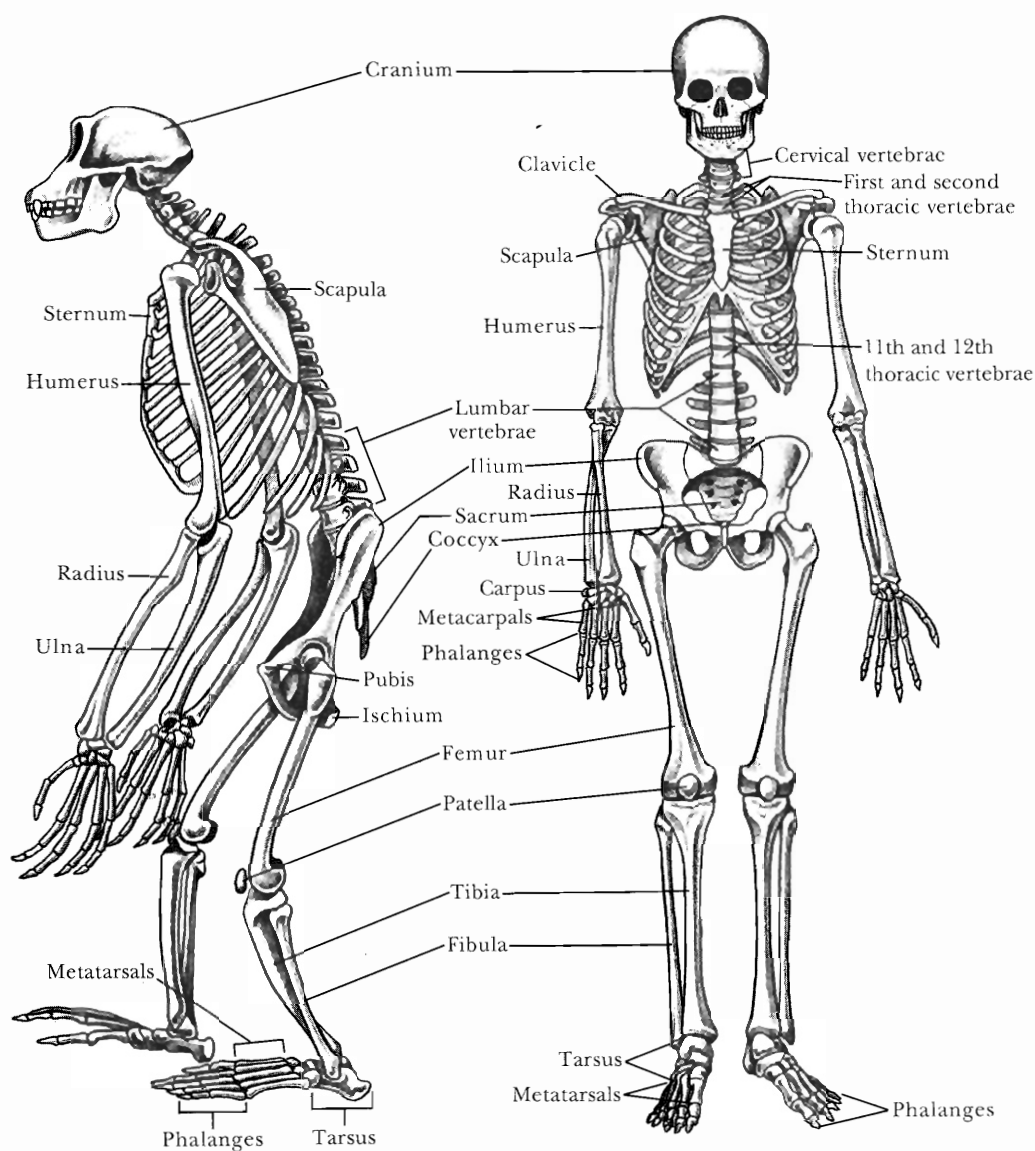


Fig. 1.7. Major bones of the chimpanzee (*left*) and human (*right*) skeleton. Note in the human that the right hand is pronated (palm facing backward), whereas the left hand is supinated (palm facing forward).

These differences are particularly marked in the parts of the skeleton related to locomotion (e.g., the pelvis and lower limb), brain size (e.g., cranial size and shape), and masticatory stresses (e.g., dental size and shape, cranial crests). We will be discussing each of these in much greater detail in later chapters as they pertain to the fossil evidence for human evolution.