



**WILEY-BLACKWELL
STUDENT DICTIONARY OF**

HUMAN EVOLUTION

Edited by
BERNARD WOOD

WILEY Blackwell

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PREFACE AND ACKNOWLEDGMENTS

Not long ago the only information a student needed in order to do well in a course about human evolution was an appreciation of general evolutionary principles, a familiarity with a relatively sparse fossil record and its context, and knowledge of a few simple analytical methods. But times have changed. The fossil record has grown exponentially, imaging techniques allow researchers to capture previously unavailable gross morphological and microstructural evidence in previously unimaginable quantities, analytical methods have burgeoned in scope and complexity, phylogeny reconstruction is more sophisticated, molecular biology has revolutionized our understanding of genetics, evolutionary history, modern human variation, and development, and a host of different advances in biology, chemistry, earth sciences, and physics have enriched evidence about the biotic, climatic, and temporal context of the hominin fossil record. In short, the fossil evidence and the range of methods used to study human evolution have grown by several orders of magnitude in the past six decades. Yet there is no single reference source where students can go to find out about topics as diverse as sagittal crest, *Sahelanthropus tchadensis*, Saint-Césaire, sampling with replacement, the Sangiran Dome, sapropel, savanna, and satellite imagery.

The *Wiley Blackwell Student Dictionary of Human Evolution* is based on the principles that were used to determine the content of the *Wiley Blackwell Encyclopedia of Human Evolution*, but the layout and content are deliberately different and new. We used our combined student and teaching experience to cull the entries in the *Encyclopedia*, select the ones most relevant to students, and then rewrite them with an emphasis on explaining the relevance of each entry to studies of human evolution. We are indebted to all the editors and contributors who were involved in the assembly of the *Encyclopedia*, for without that as a template, our task would have been much more difficult.

Kelvin Matthews at Wiley Blackwell, and Nik Prowse, our freelance copy editor and project manager, made substantial and important contributions to any success this student dictionary enjoys. We are also grateful to those who helped us improve the text. Laurel Poolman, a George Washington University undergraduate archeology major, read through an early draft and alerted us to topics we needed to explain more clearly or where we needed to do a better job of explaining why they were included in the *Dictionary*. After BW and AH responded to these

suggestions the revised text was read in its entirety by two students in George Washington University's hominid paleobiology graduate program, Kevin Hatala and Laura Reyes. Their comments were invaluable, in terms of both catching errors and making many constructive suggestions for improvement. Charlotte Krohn's help with the final stages of preparing the manuscript is greatly appreciated. However, despite the best efforts of Laurel, Kevin, and Laura, in a project like this errors will have been made. If you see one, please contact us (bernardawood@gmail.com, amanda_henry@eva.mpg.de) and we will make sure it is corrected in later editions.

Bernard Wood
Amanda Henry
July 2014

WILEY-BLACKWELL ENCYCLOPEDIA OF HUMAN EVOLUTION

This comprehensive A to Z encyclopedia provides extensive coverage of important scientific terms related to improving our understanding of how we evolved. Specifically, the 5,000 entries cover evidence and methods used to investigate the relationships among the living great apes, evidence about what makes the behavior of modern humans distinctive, and evidence about the evolutionary history of that distinctiveness, as well as information about modern methods used to trace the recent evolutionary history of modern human populations. This text provides a resource for everyone involved in the study of human evolution.

Visit the companion site www.woodhumanevolution.com to browse additional references and updates from this comprehensive encyclopedia.

HOMININ FOSSIL ABBREVIATIONS

A.L. (or AL)	Lower Awash River, Hadar, Ethiopia
ALA-VP	Al ayla – Vertebrate Paleontology, Western Margin, Middle Awash, Ethiopia
ARA-VP	A ramis – Vertebrate Paleontology, Middle Awash, Ethiopia
ATD	A tapuerca – Gran Dolina, Sierra de Atapuerca, northern Spain
ATE	A tapuerca – Sima del Elefante, Sierra de Atapuerca, northern Spain
BAR	prefix for the fossils recovered at Lukeino, Tugen Hills, B aringo District, Kenya from 2000 onwards (e.g., BAR 1000'00, the holotype of <i>Orrorin tugenensis</i>)
BBC	B lombos Cave, South Africa
BC	B aringo Chemeron Formation, Kenya
BEL-VP	B elohdelie – Vertebrate Paleontology, Ethiopia
BK	B aringo – Kapthurin, Kenya, and Blimbingkulon, Indonesia
BOD	B odo, Ethiopia
BOU	B ouri, Middle Awash, Ethiopia
BOU-VP	B ouri – Vertebrate Paleontology, Middle Awash, Ethiopia
BS	B usidima Formation, Gona, Ethiopia
DIK	D ikika, Ethiopia
DNH	D rimolen hominid, Drimolen, South Africa
HCRP UR	H ominid Corridor Research Project, Uraha, Malawi
KBS	K ay Behrensmeyer site, Koobi Fora, Kenya
KHS	K amoya's Hominid Site, Kibish, Omo Basin, Ethiopia
KNM-ER	K enya National Museum followed by the site code for E ast R udolf (now referred to as Koobi Fora), Kenya
KNM-KP	K enya National Museum followed by the site code for K anapoi, Kenya
KNM-LT	K enya National Museum followed by the site code for L othagam, Kenya
KNM-LU	K enya National Museum followed by the site code for L ukeino, Tugen Hills, Baringo region, Kenya
KNM-TH	K enya National Museum followed by the site code for the T ugen H ills, Baringo region, Kenya

KNM-WT	K enya N ational M useum followed by the site code for W est T urkana, Kenya
L.	prefix used by the American contingent of the International Omo Research Expedition for localities in the Shungura Formation (e.g., L. 396). The prefix is also used for fossils found within one of the L. localities (e.g., L. 40-19).
LB	L iang B ua, Flores, Indonesia
LH (or L.H.)	L aetoli h ominin, Tanzania
MH	M alapa h ominin
MLD	M akapansgat L imeworks D eposit, South Africa
MKM	M akha M era collection area, Woranso-Mille study area, Central Afar, Ethiopia
OH (or O.H.)	O lduvai h ominid, Tanzania
Omo	prefix for fossils collected by the French-led group from the Shungura Formation, O mo Basin, Ethiopia
SK	S wart k rans hominin, South Africa
Sts	fossil hominins recovered from the S terkfontein type site between 1947 and 1949, South Africa
Stw or StW	S terkfontein W itwatersrand, South Africa
TD	T rinchera D olina, Gran Dolina, Sierra de Atapuerca, Spain
TM	T ransvaal M useum, South Africa
UA	U adi A alad, Ethiopia
UR	U raha, Malawi
WLH	W illandra L akes h ominid, Australia

a

The abbreviated form of annum (from L. *annus* = year). In 2006 the joint IUPAC-IUGS Task Group urged that the Syst me International (SI) unit “a” be used for both ages and time spans (e.g., 36 ka for 36 thousand years and 2.3 Ma for 2.3 million years). The same report discouraged the use of y, yr, and yrs in combination with k, K, m, M, etc.

abductor

A muscle that moves a limb away from the midline reference plane (e.g., deltoid, gluteus medius) or a digit away from the reference digit (e.g., dorsal interossei of the hand).

abiogenic

All “nonliving” factors (e.g., climate, physical catastrophes such as massive volcanic eruptions or tsunamis, etc.) that might have influenced the outcome of human evolution. (Gk *a* = not and *bios* = life.) *Compare to* **biogenic**.

absolute dating

Dating methods (e.g., potassium-argon, radiocarbon, thermoluminescence, and uranium-series) that are based on physical or chemical systems with predictable dynamics. Geochronologists are moving away from the old categories of absolute and relative dating methods. Instead, they refer to absolute dating methods as methods that provide a “numerical age estimate.” (L. *absolutus* = free or unrestrained.) *See also* **geochronology**.

acceleration

A technical term used in growth and development studies. It refers to a change in the relative timing of events that results in the acceleration of shape change without any corresponding increase in the rate of change in the size of the individual. Adult size and the duration of growth are unchanged. (L. *accelerationem* = a hastening.) *See also* **heterochrony**; **neoteny**; **pedomorphosis**; **peramorphosis**.

A

accessory cusp

A cusp on a maxillary (upper) or mandibular (lower) molar tooth that is not one of the main cusps. Examples of accessory cusps are the metaconule, which is between the metacone and protocone on a maxillary molar, and the tuberculum sextum, which is between the entoconid and the hypoconulid on a mandibular molar. *See also* **cusp**.

accretion model

A model that suggests that the distinctive morphology of *Homo neanderthalensis* emerged gradually (i.e., accreted) over a period of several hundred thousand years. Fossils with different levels of expression of these features are divided into stages, with Stage 1 being the most primitive and Stage 4 being the most derived. (L. *accrescere* = to grow.) *See also* **Homo heidelbergensis**.

Aché

A group of modern human foragers (also known as the Guayaki) that lives in eastern Paraguay. Behavioral ecological studies of their diet suggest that both plant and animal foods are dietary staples and the different foraging goals of men and women reflect this. Among the Aché hunting may be a social signal as well as a method of provisioning.

Acheulean

A stone tool industry proposed in the 19thC by Gabriel de Mortillet that takes its name from the French village of Saint-Acheul in the Somme river valley. It is defined by handaxes and similar implements (e.g., cleavers and picks), but these tool types are not confined to the Acheulean. However, when they occur in other contexts they are rare and are typically outnumbered by flakes, cores, and other smaller modified tools such as scrapers. The Oldowan industry preceded the Acheulean and many of the nonhandaxe Acheulean tools are Oldowan-like. Similarly, some later Acheulean sites (e.g., the Somme river valley and in the Kapthurin Formation of Kenya) show evidence of the use of Levallois technology for the production of large flakes. The Acheulean, which is also known as the Acheulean industrial complex, is unique in the sense that neither before nor since has such a distinctive technology dominated the activities of hominins for so long over so much of the planet. Currently the earliest evidence of the Acheulean is found at the 1.76 Ma site of Kokiselei, in West Turkana, Kenya; the most recent sites date to c.0.16 Ma.

Acheulian

See **Acheulean**.

actualistic studies

Studies in which researchers try to recreate objects and circumstances encountered by archeologists and paleontologists. For example, in archeology, researchers use replicas of ancient tools in controlled circumstances to help determine what the ancient tools were used for. In paleontology, actualistic research involves studying the factors that determine the formation and nature of present-day bone assemblages and then applying that knowledge to the paleontological record. Actualistic studies are explicitly uniformitarian in that they assume that the objects and processes used in the past and the present have the same functions, products, or outcomes. (L. *actus* = an act.) *See also* **uniformitarianism**.

adaptation

A useful feature or trait that (a) promotes survival and reproduction and (b) is shaped by natural selection. Adaptations must be heritable *and* perform a function. Adaptation can also be used as an adjective in connection with a taxon, as in “the dentition of *Paranthropus boisei* is better adapted for chewing than for slicing food.” In such usage, adaptation is being used in an informal sense (i.e., “better adapted” can be read to mean “functions better”). Adaptations will tend to be under-recognized (i.e., the process of recognizing adaptations is prone to Type I error). It can be difficult to establish whether a given trait has been subjected to natural selection in fossil hominins, so the identification of adaptations in paleoanthropology is inevitably conjectural. Formulating and testing hypotheses of adaptation is a major focus of paleoanthropological research. (L. *adaptare* = to fit.) *See also* **structure–function relationship**.

adaptive radiation

The rapid diversification of a lineage into species that evolve a range of new adaptive strategies that enable them to occupy new adaptive zones. An example is the simultaneous appearance of multiple pig species at the same sites at several times during the Pliocene and Pleistocene. During the last 4Ma approximately six pig species have coexisted at the same locality (i.e., they are sympatric) at the same time (i.e., they are synchronic). A number of these species exhibit tall (hypsodont) third molar crowns and craniofacial elaboration (bosses, crests, tusks). Such changes are usually interpreted as an adaptive response to more open grassland environments. Archaic hominins may be an example of an adaptive radiation. (L. *adaptare* = to fit and *radius* = ray.)

adaptive strategy

Any set of traits that enables the members of a species to survive and reproduce. When different species have similar adaptive strategies, it could be because (a) they were inherited from a recent common ancestor or (b) they may be the result of independent adaptations to similar environmental conditions (i.e., parallel evolution or convergent evolution). In the latter case the morphology involved would be a homoplasy. (L. *adaptare* = to fit and *strategos* = general.) *See also* **grade**.

adductor

Any muscle that moves a limb towards the midline reference plane (e.g., teres major, adductor longus), or a digit towards the reference digit (e.g., palmar interossei of the hand).

aDNA

See **ancient DNA**.

adolescence

The period of life history in modern humans between puberty and maturity. Adolescence ends when skeletal lengths and dental development reach their adult state, and when sexual maturation is attained. This usually occurs between 17 and 25 years in modern human populations. The defining characteristic of human adolescence is a rapid height increase; nonhuman primate species undergo growth spurts in craniofacial dimensions and overall body mass, but not height. The intensity and duration of this height spurt varies among and within modern

human populations. It has been suggested that the adolescent stage evolved in either pre-modern *Homo* or anatomically modern *Homo sapiens*. It is difficult to determine whether extinct hominin taxa underwent a growth spurt and, if so, whether it was more similar to that of modern humans or to that of nonhuman primates. (L. *adolescentia* = youth.)

aeolian

Sediments deposited primarily by wind action. The large volumes of glacially derived silts subject to aeolian transport are responsible for the loess deposits that are common in central China. Some of the sediments in the Laetolil Beds at Laetoli, Tanzania, are formed from airfall tuffs that have been reworked by aeolian processes. (Gk *Aeolus* = god of the winds.)

Afar Rift System

The part of the East African Rift System comprising a series of river valleys and basins that are mainly in modern-day Ethiopia and Eritrea. The Dikika, Gona, and Middle Awash study areas are all in the Afar Rift System.

aff.

Abbreviation of **affinity** (*which see*).

affinity

A term used in taxonomy (usually abbreviated as “aff.”) to suggest that a specimen belongs to a hypodigm that is closely related to, but not necessarily synonymous with, a taxon. Thus, a small piece of thick cranial vault might be assigned to “*Homo* aff. *H. erectus*.”

Afro-European hypothesis

See *Homo heidelbergensis*; **out-of-Africa hypothesis**; **replacement with hybridization**.

age estimate

The number of years that are estimated to have elapsed between an event (e.g., the deposition of a bone or artifact) and the present day. Paleoanthropological age estimates are expressed in thousands (ka) and millions (Ma) of years. See also **geochronology**.

agenesis

Absence or lack of development of an anatomical structure (e.g., third molars). Examples of agenesis in fossil hominins include at least one individual of *Homo floresiensis*, LB1, that shows agenesis of the lower right second premolar (RP₄) and upper right third molar (RM³). The *Homo ergaster* associated skeleton, KNM-WT 15000, has agenesis of both lower third molars (M₃s). (Gk *a* = absence or without, and *genesis* = birth or origin.)

***Ailuropoda-Stegodon* fauna**

A cave fauna named after two consistent components: *Ailuropoda*, the only genus in the subfamily Ailuropodinae of ursids (i.e., bears), and *Stegodon*, a genus of proboscideans (i.e., elephant precursors) within the extinct subfamily Stegodontinae. The *Ailuropoda-Stegodon* fauna is found in caves in southern China, Vietnam, and Laos. The presence of these fossils has been used as a means of dating several East Asian sites.

Ain Hanech

This *c.*1.8 Ma Algerian site (also known as Ain Hanech) contains some of the oldest stone artifacts in North Africa. The artifacts found in the early layers are considered a North African variant of the Oldowan industrial complex. Artifacts recovered from overlying sediments have been attributed to the Acheulean industrial complex. (Location 36°16'39"N, 08°19'00"E, Algeria.)

A.L. 288-1

Also known as "Lucy," this specimen was the first relatively complete hominin associated skeleton of great antiquity and it remains the best preserved associated skeleton of *Australopithecus afarensis*. Its components were found on the surface at Hadar, Ethiopia, in 1974 by Donald Johanson and his team; it is dated to *c.*3.2 Ma. The cranial vault remains include portions of the parietals, occipital, left zygomatic, and frontal bones. The mandible includes the right P₃-M₃, and the left P₃, M₃, and two M₁ fragments. The postcranial skeleton is represented by the right scapula, humerus, ulna, radius, a portion of the clavicle, the left ulna, radius, and capitate, and the axial skeleton by lumbar and thoracic vertebrae and ribs. The left pelvic bone, sacrum, and left femur are well preserved. Remains of the right leg include fragments of the tibia, fibula, talus, and some foot and hand phalanges. This individual has an endocranial volume of 375–400 cm³.

A.L. 444-2a-h

The first well-preserved (75–80% complete) skull of *Australopithecus afarensis* that was found at Hadar in 1992 by Yoel Rak; it is dated to *c.*3.0 Ma. The skull includes parts of the cranial vault, the face, maxillary dentition, the right side of the mandibular corpus, the symphyseal region and part of the mandibular dentition.

A.L. 666-1

The first example of a *Homo habilis*-like morphotype in the middle Pliocene. It was found at Hadar in 1994 in a layer with Oldowan tools; it is dated to *c.*2.35 Ma. It comprises a maxilla, broken along the intermaxillary suture, with the left P³-M³, the right P³-M¹ with M² and M³ roots, plus other isolated dental fragments.

ALA-VP-2/10

The holotype of *Ardipithecus kadabba* was found at Alayla, Ethiopia, in 1999; its age is *c.*5.8–5.2 Ma. It comprises the right side of the mandibular corpus with M₃, together with associated teeth (left I₂, C, P₄, M₂, and part of the M₃ root).

albumin

This protein, which is present in plasma serum, was given its name because it turns white when it is heated or coagulated. It was one of the first molecules that was used to precisely measure the closeness of the relationships between the extant great apes. When fresh albumins from the extant great apes other than *Pan* meet and react with modern human antiserum they coagulate and form a white spur. In contrast, modern human albumin does not create a spur in the presence of modern human antiserum, because the albumin is not recognized as foreign and thus does not prompt a reaction. There is also no spur when modern human antiserum meets and reacts with *Pan* albumin. This suggests that this test, or assay, cannot discriminate between modern human and chimpanzee albumin. (*L. alba* = white.) See also **immunochemistry**.

A

Alcelaphini

A tribe of the family Bovidae that includes wildebeest, hartebeest, bonteboks, and their allies. Alcelaphine bovids are grazers with a preference for open grassland habitats that are characterized by tall (hypsodont) tooth crowns and cursorial (running) limb adaptations. When researchers attempt paleoenvironmental reconstructions of African fossil assemblages, examining the frequencies of alcelaphine bovids is one way to track the presence of open grasslands.

allele

The form of a gene at a specified site, or locus, in the genome, or the form of a particular DNA sequence. If the locus in the genome is a “street address,” the allele at that locus is analogous to the type of house present at that address. All houses share the same basic attributes, although one may be a luxury mansion while another may be a modest single-story residence. The genome is arranged into units called chromosomes, and with one exception (the genes on the X chromosome in males of many types of animal) every chromosome is present as a pair in the cell. Therefore, for each gene there is a pair of alleles. The particular combinations of alleles at a locus can have significant effects on function. For example, in modern humans the S allele at the beta-globin locus is protective against malaria if present with a wild-type allele (A) in the heterozygous form (i.e., AS). However, if both copies of the beta-globin allele are the S type (i.e., the homozygous form, SS) that individual will suffer from sickle cell anemia. (Gk *allos* = another.)

Allen’s Rule

Attributed to Joel Allen in the late 19thC, it states that animals living in locations with lower average temperatures tend to have smaller appendages (i.e., shorter limbs or tails). *Homo neanderthalensis* and some other high-latitude archaic *Homo* specimens have the type of body proportions (i.e., relatively shorter distal limb lengths and larger bi-iliac breadths) that would be predicted from Allen’s Rule.

allometry

The study of the growth, or size, of one part of an organism with respect to the growth, or size, of the whole (or another part that is taken as a proxy for the whole) of the same organism. The term allometry is used in two senses. It is often used to refer generally to the study of the “consequences of differences in size.” In this sense, allometry is equivalent to the term scaling. However, allometry can also be used in a more specific sense to refer to changes in shape of a part or the whole of an organism that are associated with changes in the overall size of the organism. When a variable increases in size more slowly than overall body size, this is called negative allometry (i.e., the variable becomes proportionally smaller as overall body size increases). The term used when a variable increases in size more quickly than overall body size is positive allometry (i.e., the variable becomes proportionally larger as overall body size increases). In both negative and positive allometry any change in size will result in a change in shape. When used in this sense, the opposite of allometry is isometry, which is when shape is maintained as size increases. In other words, an isometric variable increases in size at the same rate as body size. (Gk *allos* = other and *metron* = measure.) *See also scaling.*

allopatric speciation

A mode of speciation in which new species evolve as a consequence of the original species population being subdivided by a geographic barrier. The resulting physical isolation leads to loss of gene flow, and the accumulation of genetic differences in the new populations is due to genetic drift, natural selection, and mutation. Allopatric speciation is thought to be the most common cause of speciation in mammals, including hominins. *See also* **parapatric speciation**; **sympatric speciation**.

allopatry

When two organisms have geographic ranges that are entirely separate and distinct (i.e., there is no overlap). Given the nature of the fossil record it is difficult to be certain whether hominin species were truly allopatric, but, for example, *Australopithecus africanus* (known only from southern Africa) and *Australopithecus afarensis* (known only from East Africa) were probably allopatric. (Gk *allos*=other and *patris*=fatherland.) *See also* **speciation**; **vicariance biogeography**.

alluvial

Nonmarine sediments deposited by water that is flowing. If there is evidence to attribute the sediments to a more specific depositional mechanism (e.g., fluvial, lacustrine, etc.) then the term alluvial should be avoided. (L. *alluere*=to wash against.) *See also* **riverine**.

alpha taxonomy

According to Ernst Mayr alpha taxonomy is the process of “characterizing and naming” species. Beta taxonomy involves arranging species in “a natural system of lesser and higher categories,” and gamma taxonomy involves the “analysis of intraspecific variation.” (Gk *alpha*=first and *taxis*=to arrange or “put in order.”) *See also* **systematics**; **taxonomy**.

altricial

Taxa with newborn offspring that are still at a relatively early stage of development at the time of birth. Altricial offspring possess little to no ability to move independently and are reliant on parents or relatives for varying lengths of time after birth for temperature regulation, food, and transport (e.g., newborn kittens rely on the mother to clean them, transport them, and direct them to the nipple). Compared to nonhuman primates, most of which are relatively precocial at birth, modern human babies are altricial and require intensive parental care. (L. *alere*=to nourish.) *See also* **precocial**.

Alu repeat elements

A family of short interspersed nucleotide elements (or SINEs) of DNA that are common in all primates including the great apes and modern humans. Each Alu repeat element is approximately 300 base pairs (bp) in length. Alu repeat elements, which are a class of retrotransposons (i.e., sequences that are transcribed from DNA to messenger RNA (mRNA) and then the mRNA is copied back into DNA, which is inserted elsewhere in the genome), were originally named for the Alu restriction enzyme cut site that is typically found within each element. Alu elements, which account for as much as 10% of the modern human genome,

A

are useful for phylogenetic analyses and for studies of population history. This is because (a) the insertion of an Alu element has an unequivocal ancestral state (no Alu insertion), (b) each Alu insertion is almost certainly homologous, as the probability of two insertions at the same location within the genome is very small, (c) they are stable, and (d) they are relatively easy to analyze.

alveolar process

The inferior part of the upper jaw (i.e., the maxilla) and the superior part of the body, or corpus, of the lower jaw (i.e., the mandible) into which the roots of the upper and lower teeth, respectively, are embedded. (L. *alveolus* = small hollow, dim. of *alveus* = hollow, and *processus* = to go forward or advance.)

alveolus

The name for the socket in the alveolar process of the maxilla or mandible into which the root of a tooth is embedded. (L. *alveolus* = small hollow, dim. of *alveus* = hollow; pl. *alveoli*.)

ameloblast

The name given to secretory and maturational (i.e., functional) enamel-forming cells. During enamel formation, secretory ameloblasts move away from the enamel–dentine junction, secreting enamel matrix as they go. The secreted matrix forms elongated enamel prisms approximately 5 μm in diameter. Secretory ameloblasts cease to lay down enamel matrix when the final thickness of enamel is completed. The subsequent mineralization of the matrix is a separate process. Short-period and long-period incremental lines produced by ameloblasts represent interruptions in the secretion or mineralization of the matrix. (Gk *amel* = pertaining to enamel and *blastos* = germ.) See also **enamel development**.

amelogenesis

The process of enamel formation by ameloblasts. (Gk *amel* = pertaining to enamel and *genesis* = birth or origin.) See also **enamel development**.

amino acid

A relatively small molecule that is the building block of proteins. There are 20 different standard amino acids. Amino acids are transported by specific transfer RNA (tRNA) and then they are joined together in a sequence encoded by messenger RNA (mRNA) to form a polypeptide chain. The latter process, which is catalyzed by ribosomes, is referred to as translation. Proteins consist of one or more polypeptide chains. (Gk *ammoniacos* = the pungent resin that is the source of ammonia, NH_3 , which was first collected from near the temple of Amen in Libya.) See also **protein**.

amino acid racemization

Amino acids exist in two forms called antimeres: a “right-handed” or D form and a “left-handed” or L form. When proteins are assembled in cells the component amino acids are all in the L form, but they convert at a predictable rate by a process called racemization to the D form. Racemization is also known as epimerization. See also **amino acid racemization dating**.

amino acid racemization dating

The apparently regular and predictable process of amino acid racemization has been used as a molecular clock for dating biological specimens, but because the process proved to be temperature-dependent, the dates were found to be unreliable and the method fell into disuse. Recently, the principle has been revived and applied to the epimerization of isoleucine, an amino acid preserved within the calcite crystals of ostrich eggshell, to estimate the age of those shells. However, the problem of temperature-dependency persists.

AMS radiocarbon dating

Accelerator mass spectrometry (or AMS) dating enables the direct measurement of individual ^{14}C atoms; AMS can routinely date samples of 1 mg of carbon. This means that smaller and previously undatable samples, like single hominin teeth and individual grains of domesticated cereals, can now be dated. The AMS method also allows for more thorough chemical pretreatment of samples. This is particularly important for older samples (>25 ka BP) where small amounts of modern carbon contamination may have a large effect on the measured ^{14}C fraction and hence the date. *See also radiocarbon dating.*

Amud

A cave approximately 5 km/3 miles northwest of the Sea of Galilee, in Israel. Excavations recovered Amud 1, a fairly complete but poorly preserved, presumed male, adult of *Homo neanderthalensis*. Also recovered were fragments of at least three other individuals including Amud 7, an associated skeleton of a *H. neanderthalensis* neonate that may have been intentionally buried. Recent thermoluminescence dating on a number of burned lithic artifacts for the various stratigraphic horizons indicates two occupation events, one c.70 ka and the other c.55 ka; the hominin remains are associated with the younger age. Archeological evidence includes Middle and Upper Paleolithic lithics and signs of fire-related behavior. (Location 32°52'N, 35°30'E, Israel.)

anagenesis

An evolutionary pattern (or mode) in which an ancestral species evolves into a descendant species without lineage splitting. For example, it has been claimed that *Australopithecus anamensis* and *Australopithecus afarensis* are time-successive species in the same lineage and are therefore an example of an anagenetic relationship. Anagenesis is the alternative to cladogenesis. (Gk *ana*= up and *genesis*= birth or origin.) *See also cladogenesis.*

analogous

A trait (structure, gene, or developmental pathway) in two or more taxa that was *not* inherited from their most recent common ancestor. Analogous morphology is the cause of homoplasy. (Gk *analogos*= resembling, from *ana*= according to and *logos*= ratio.) *See also analogue; homoplasy.*

analogue

An organism that is a functional proxy for another organism without being closely related to it. For example, the differences between the masticatory systems of bears and pandas, animals that are only distantly related to hominins, have been compared to the differences between the masticatory system of *Australopithecus africanus* or *Australopithecus afarensis*, on the one hand, and

that of *Paranthropus robustus* or *Paranthropus boisei*, on the other. In this case, pandas serve as an analogue for *P. robustus* and *P. boisei*. (Gk *analogos*=resembling, from *ana*=according to and *logos*=ratio.) See also **homology**.

analysis of covariance

(or ANCOVA) A variant of multiple regression in which a continuous variable is dependent on continuous and categorical variables (where the categorical variables are converted to binary dummy variables). It is typically used to determine whether the slopes and/or intercepts of scaling relationships between continuous variables differ between groups.

analysis of variance

(or ANOVA) A statistical test commonly used to determine whether there is a significant difference in the mean of a continuous variable between two or more groups. For example, if cranial capacity is known for samples of crania belonging to three different species, ANOVA can be used to identify whether a significant difference exists between the three species in mean cranial capacity. Results from an ANOVA performed for two groups (as opposed to three or more) are equivalent to the results of a *t* test. ANOVA is a parametric statistical test; the equivalent nonparametric statistical test is the Kruskal–Wallis test.

anatomical position

The position of the body used as a reference when describing the surfaces of the body, the spatial relationships of the body parts, or the movements of the axial and postcranial skeleton. In modern human anatomy, the anatomical position assumes an individual is upright, looking forward, with their legs and feet together, their arms by their side, and with the palms facing forward. All the surfaces that face towards the front are called anterior or ventral. All of the surfaces that face towards the back are called posterior or dorsal. Superior is nearer to the crown of the head; inferior is nearer to the soles of the feet. Medial is nearer to the midline; lateral is further from the midline. With respect to the limbs, proximal is in the direction of the root of the limb, where it is attached to the torso; distal is in the direction of the tips of the fingers or toes. Moving a whole limb forward is to flex it; moving it backwards is to extend it. Moving a limb away from the body is to abduct it; moving it back towards the midline is to adduct it. These latter terms also apply to movements of the fingers and toes, except that the movements are described relative to one of the digits rather than to the whole body (NB: the reference digit of the hand is the middle finger and the reference digit of the foot is the second toe).

anatomical terminology

Many anatomical terms were based on the everyday Latin (and sometimes Greek) vocabulary. Thus, the “cup-like” articular surface of the hip joint on the pelvis is called the acetabulum because Pliny thought it resembled a Roman vinegar (*acetum*) receptacle (*abrum*) and the condylar process of the mandible takes its name from the Greek word for a knuckle. The latest version of official modern human anatomical terminology is the *Terminologia Anatomica* (1998). See also **paleoanthropological terminology**.

ancient DNA

(or aDNA) Deoxyribonucleic acid (DNA) that is extracted from old bone, teeth, hair, tissue, or coprolites. Current problems addressed by ancient DNA research include the relationships among *Homo neanderthalensis*, the Denisovans, and modern humans, the initial colonization of the Americas, regional population history, social organization at a particular site, diet, the sex of individuals, and relationships among individuals within a cemetery. Ancient DNA research initially targeted mitochondrial DNA (mtDNA) because of its high copy number in cells, but as methods have improved ancient nuclear DNA has become a tractable source of evidence. (OF *ancien* from the L. *ante*=before and DNA = deoxyribonucleic acid.)

Andresen lines

Long-period (greater than circadian) incremental features in dentine that correspond to striae of Retzius in enamel. *See also incremental features.*

Anglian

See glacial cycles.

anisotropy

Materials (e.g., bone or enamel) are anisotropic when their material properties (e.g., stiffness) are sensitive to direction. Isotropy is when material properties are the same in all directions. (Gk *an* = not, *iso* = equal, and *tropus* = direction.) *See also dental microwear.*

ANOVA

Acronym for **analysis of variance** (*which see*).

antelope

The informal name for a member of any of the taxa within the Antilopini, the tribe of the family Bovidae that includes the gazelles and their allies. (Gk *antholops* = a fabulous beast from the orient.)

anterior teeth

The two incisors and canine in each quadrant of the jaws. The rest of the teeth in each quadrant are called postcanine teeth.

anthropogenic bone modification

Any alteration of a bone resulting from hominin activity. It includes bone surface modifications (e.g., cutmarks and hammerstone percussion marks), fracture/breakage patterns, heating, burning, and use wear on bone tools. Recognition of anthropogenic bone modifications is central to demonstrating that a fossil bone assemblage has been accumulated and/or altered by hominins, as opposed to other taphonomic agents such as carnivores, porcupines, or fluvial processes. *See also bone breakage patterns.*

A

anthropoid

Primates that are relatively modern human-like. This term is usually used in one of two senses: to refer either to the nonhuman higher primates (i.e., chimpanzee, gorilla, and orangutan and their immediate ancestors), as in “anthropoid apes,” or to all the members of the Anthroidea (i.e., living anthropoids include all the extant New World monkeys, Old World monkeys, and apes, plus modern humans). Strictly speaking the latter use is the correct one. (Gk *anthropos* = human being.)

antibody

Antibodies (also known as immunoglobulins) are proteins produced by lymphocytes (a type of white blood cell) when the latter react with foreign particles collectively called antigens (e.g., bacteria, pollen, and viruses). Each antibody reacts to a specific antigen, binds with it, and then tags it for destruction by other parts of the immune system. In the case of an organism the antibody prevents it from growing or causing damage. Antibodies raised against foreign albumins were the basis of one of the experiments undertaken to investigate the relationships among the great apes. (Gk *anti* = opposite and ME *body* = container.) See also **albumin**.

anticline

A type of fold in structural geology in which the oldest rocks occupy the center and rocks become progressively younger towards the margins. (Gk *anti* = against and *klinein* = to slope.)

anticodon

A sequence of three nucleotides in a transfer RNA (tRNA) molecule that is complementary to a codon (i.e., a sequence of three nucleotides) in a messenger RNA (mRNA) molecule. See also **genetic code**.

antigen

Any foreign molecule capable of stimulating the production of an antibody or of provoking other responses by the immune system. (From *antibody generation*.) See also **antibody**.

Antilopini

A tribe of the family Bovidae that includes the gazelles and their allies. In paleoenvironmental reconstructions of fossil assemblages, high frequencies of antilopine bovids are generally interpreted as indicating open habitats. (Gk *antholops* = a fabulous beast from the orient.)

antimere

Refers to the version of a bilateral structure that belongs to the opposite side of the body. For example “the crown area of the right P₃ of KNM-ER 992 is larger than its antimere” (i.e., the crown of the left P₃). (Gk *anti* = opposite and *meros* = a part.)

anvil

A stationary object against which another object (e.g., a bone or core) can be struck to fracture it. Anvils are generally made of stone although materials such as wood may be used when stone is not available (e.g., Tai forest nut-cracking chimpanzees). Stone cores flaked using hammer-and-anvil or bipolar techniques usually have flakes removed from both ends. See also **bipolar percussion**.

apatite

Apatite is one of the common names (hydroxyapatite and bioapatite are others) for the mineral phase of bone, cementum, dentine, and enamel. Apatite makes up approximately 96% of the mineral phase of mature (i.e., fully mineralized) enamel, and this high proportion is responsible for enamel's extreme hardness and resilience to diagenesis. (Gk *apate* = deceit, because of apatite's reputation for being confused with other minerals.)

ape

An informal taxonomic category that is coincident with the superfamily Hominoidea. The extant taxa in this superfamily are chimpanzees, bonobos, gorillas, orangutans, gibbons, and siamangs. The fossil taxa are all the extinct forms that are more closely related to chimpanzees, bonobos, gorillas, orangutans, gibbons, and siamangs than to any other living taxon. (OE *apa* = ill-bred and clumsy; before apes had been investigated scientifically and appreciated on their own terms they were regarded as being "clumsy" because they lacked dexterity; syn. hominoid.)

apical tuft

The distal part of the distal phalanx of a digit (finger or toe). The apical tuft provides bony support for the nail and the soft tissue (pulp) that lies beneath the nail. [L. *apex* = point and OF *tof(f)e* = projection; syn. unguis process, tuberosity, or tuft.]

apomorphic

A "catch-all" word that refers to any derived character state. Apomorphic is used in cladistic analysis to refer to the state of a character that is different from the ancestral or primitive condition of that character. Apomorphy is one of several terms used in cladistics that is relative. The same morphology can be derived, or apomorphic, in one context and primitive, or symplesiomorphic, in another; it depends on the taxa used as comparators. (Gk *apo* = different from and *morphe* = form.) See also **autapomorphy**; **synapomorphy**.

appendicular skeleton

The hard-tissue (bone and cartilage) components of the upper and lower limbs. In the upper limb it comprises the pectoral or shoulder girdle (scapula and clavicle), the bone of the arm (humerus), and the bones of the forearm (radius and ulna) and hand (carpals, metacarpals, and phalanges). In the lower limb it comprises the pelvic girdle (pelvic bone made up of the ilium, ischium, and pubic bones, but not the sacrum), the bone of the thigh (femur), the patella, and the bones of the lower leg (tibia and fibula) and foot (tarsals, metatarsals, and phalanges). (L. *appendere* = to hang upon.)

appositional enamel

Although all enamel is technically appositional because it is deposited in layers, this term usually refers to the cuspal enamel formed during the initial phase of enamel formation (i.e., it excludes imbricational enamel). Striae of Retzius do not reach the surface of appositional enamel. (L. *appositus* = to put near.) See also **cuspal enamel**; **enamel development**.

appositional growth

See **ossification**.

approximal wear

See **interproximal wear**.

aptation

There are two main categories of aptation. If a functional trait was fixed in a population by natural selection and it still performs that function, then it is referred to as an *adaptation*. But if there is evidence the trait now performs a *different* function, or if a functional trait was non-functional prior to being co-opted for its current function, then the trait is referred to as an *exaptation*. (L. *adaptare* = to fit.) See also **adaptation**; **exaptation**.

Arago

See **Caune de l'Arago**.

aragonite

See **calcium carbonate**.

Aramis

The type site of *Ardipithecus ramidus*. It is situated between the headwaters of the Aramis and Adgantoli drainages on the west side of the Awash River in the Middle Awash study area in the Afar Depression in the Afar Rift System in Ethiopia. All of the localities (ARA-VP) are in the Sagantole Formation. Specimens recovered from the *c.*4.4 Ma Aramis Member include the holotype of *Ar. ramidus* ARA-VP-1/1 and a remarkably complete associated skeleton, ARA-VP-6/500. A left maxilla from the site, ARA-VP-14/1, has been attributed to *Australopithecus anamensis*. No archeological evidence has been found. (Location 10°28'N, 40°26'E, Ethiopia.)

 $^{40}\text{Ar}/^{39}\text{Ar}$

See **argon-argon dating**.

ARA-VP-6/1

The holotype of *Ardipithecus ramidus*. It was found at Aramis, Ethiopia, in 1993 and it is dated to *c.*4.4 Ma. It comprises several associated teeth, including the left I¹, C, P³, and P⁴, and right I¹, C, P⁴, M², P₃, and P₄.

ARA-VP-6/500

This exceptionally complete *c.*4.4 Ma associated skeleton is the centerpiece of the fossil evidence for *Ardipithecus ramidus*. Functional interpretations of ARA-VP-6/500 form the main evidence for the proposal that *Ar. ramidus* is a basal hominin. The first fragments were recognized at Aramis, Ethiopia, in 1994, but more evidence of it was recovered in subsequent years. One hundred and thirty recognizable fragments belonging to a single individual were recovered, but the fragments are so fragile that the cranial morphology had to be recovered from micro-computed tomography scans of cranial fragments still embedded in matrix. The endocranial volume is estimated at *c.*300 cm³. The crowns and roots of all of the upper teeth on the right side, and the left lower canine through to the M₃, are preserved. The right forearm is intact apart from the distal end of the ulna; the partial right hand includes carpal bones and a complete ray. The only evidence of the left forearm is part of the radial shaft, but much of the

skeleton of the left hand is preserved. Evidence of the thorax includes a few vertebrae and the left first rib. Much of the left pelvic bone is preserved but it is crushed and distorted, as is a piece of the lower part of the body of the sacrum and part of the right ilium. All that remains of the lower limb is a substantial length of the shaft of the right femur, most of the right tibia, and all but the proximal end of the right fibula. Between them the two preserved foot skeletons provide most of the bones of the tarsus and the toes.

ARA-VP-7/2

Fragments of the long bones of an arm, including the proximal end of the humerus, found at Aramis, Ethiopia, in 1993 and dated to *c.*4.4 Ma. It has been assigned to *Ardipithecus ramidus*. Its discoverers used the size of the humeral head to generate the *c.*40 kg estimate for the body mass of this individual. They also concluded that the arm of *Ar. ramidus* had some characters usually associated with great apes.

arboreal

A term used to describe animals that live in trees. Some of the defining features of primates are important for life in the trees (e.g., binocular vision helps animals to judge distances). The vast majority of primates are dependent on trees, with platyrrhines being exclusively arboreal. Nonetheless, many living and extinct primates have successfully radiated into terrestrial niches or have combined life in the trees with life on the ground. The early hominins are a good example of a combination of arboreality and terrestriality and some researchers have suggested that at least one form of hominin bipedalism may have emerged as a way of moving or foraging in trees. (L. *arbor* = tree.) *See also locomotion.*

arboreality

The tendency to live partially, or wholly, in the trees. (L. *arbor* = tree.) *See also arboreal.*

Arcy-sur-Cure

A series of caves in the limestone cliffs above the Cure river in central France, including the Grande Grotte, the Grotte du Renne, the Grotte du Hyène, the Grotte des Fées, and the Grotte du Loup. The Grande Grotte is best known for its *c.*28–33 ka cave paintings, which are the second oldest such paintings in France. The Grotte du Renne is best known for several beads and objects of personal ornamentation found in the Châtelperronian level, alongside a juvenile *Homo neanderthalensis* and several Neanderthal teeth. Researchers debate whether these finds reflect independent Neanderthal invention of so-called modern behaviors, or evidence of acculturation from interaction with modern humans, or if the finds were the product of Neanderthals at all. In the Grotte du Hyène, several hominin remains including a nearly complete mandible with dentition were recovered from the lower Mousterian levels. The other caves also contain Mousterian and some transitional and Upper Paleolithic layers. (Location 47°35'N, 03°45'E, France.)

***Ardipithecus* White et al., 1995**

A genus established in 1995 by White et al. to accommodate the species *Ardipithecus ramidus*. Subsequently a second, more primitive, and temporally older species, *Ardipithecus kadabba*, was recognized and included in the same genus. The type species is *Ardipithecus ramidus* (White

et al., 1994) White et al., 1995. (*ardi* = ground or floor in the Afar language and Gk *pithekos* = a postfix that means ape or “ape-like.”) See also *Ardipithecus kadabba*; *Ardipithecus ramidus*.

***Ardipithecus kadabba* Haile-Selassie, 2001**

A hominin subspecies with this name was established in 2001, and it was subsequently elevated to species rank in 2004. All of the hypodigm was recovered from five c.5.8–5.2 Ma localities in the Middle Awash study area, Ethiopia. Four of the localities are in a region called the Western Margin, and one is in the Central Awash Complex. The main differences between *Ardipithecus kadabba* and *Ardipithecus ramidus* involve the upper canine and the P₃. The postcranial evidence is generally ape-like. Researchers have suggested that there is a morphocline in upper canine morphology, with *Ar. kadabba* exhibiting the most ape-like morphology, and *Ar. ramidus*, *Australopithecus anamensis*, and *Australopithecus afarensis* interpreted as becoming progressively more like the lower and more asymmetric crowns of later hominins. The first discovery was ALA-VP-2/10 (1997). The holotype is ALA-VP-2/10. (*ardi* = ground or floor in the Afar language, Gk *pithekos* = a postfix that means ape or “ape-like,” and *kadabba* = a “family ancestor” in the Afar language.)

***Ardipithecus ramidus* (White et al., 1994) White et al., 1995**

Hominin species established in 1994 to accommodate cranial and postcranial fossils recovered from c.4.5–4.4 Ma localities at Aramis on the northeastern flank of the Central Awash Complex in the Middle Awash study area, Ethiopia. The taxon was initially included within the genus *Australopithecus*, but in 1995 it was transferred to a new genus, *Ardipithecus*. Additions to the *Ardipithecus ramidus* hypodigm have come from the Gona study area, the Aramis locality, and Kuseralee Dora and Sagantole, two other localities in the Central Awash Complex. Initial estimates based on the size of the shoulder joint suggested that *Ar. ramidus* weighed approximately 40 kg, but researchers claim the enlarged hypodigm indicates an estimated body mass of approximately 50 kg. The position of the foramen magnum, the form of the reconstructed pelvis, and the morphology of the lateral side of the foot have all been cited as evidence that the posture and habitual gait of *Ar. ramidus* were respectively more upright and bipedal than is the case in the living apes. Timothy White and his colleagues claim that *Ar. ramidus* is a basal hominin, yet the inclusion of *Ar. ramidus* in the hominin clade necessitates substantial amounts of convergent evolution in the closely related great ape clades. The hypothesis that *Ar. ramidus* is not a hominin, but instead is a member of an extinct ape clade, would, in many respects, be more parsimonious than assuming it is a basal hominin. The first discovery, ARA-VP-1/1 was made in 1993, but if either the mandible KNM-LT 329 from Lothagam, Kenya, or the mandible KNM-TH 13150 from Tabarin, Kenya, prove to belong to the *Ar. ramidus* hypodigm, then they would be the initial discovery. The holotype is ARA-VP-6/1 and the main sites are localities in the Gona and Middle Awash study areas, Ethiopia. (*ardi* = ground or floor in the Afar language, Gk *pithekos* = a postfix that means ape or “ape-like,” and *ramid* = “root” in the Afar language.)

argon-argon dating

An isotopic dating method based upon the potassium-argon (K/Ar) system, in which radioactive ⁴⁰K is driven to ⁴⁰Ar in a reactor, and used as a proxy for the K content. Subsequent analyses can be done in a single experiment, using the same sample, by measuring isotopes of Ar in a mass

spectrometer. This approach avoids the necessity of measuring K and Ar in different aliquots of a sample, thus reducing potential error. The current analytical methods are so sensitive they can be applied to single crystals of feldspar or volcanic glass; this more precise version is referred to as single-crystal laser fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating.

armature

A term used to refer to any body part or implement used for the offense or defense of an organism. In archeology the term armature refers to most points and to any other obvious hunting equipment (e.g., the wooden spears from Schönningen). (L. *armatura* = armor or equipment.)

art

The use of non-utilitarian images for symbolism or self-expression. Prehistoric art is divided into mobile (L. *mobilis* = to move) or portable art (e.g., small figurines), and parietal (L. *paries* = wall) or fixed art (e.g., wall paintings or engravings). (L. *art* = art.)

artifact

Any portable object made, modified, or used by hominins. The earliest artifacts presently known are stone tools and their manufacturing debris from the site of Gona, Ethiopia, dating to 2.55 Ma, although indirect traces of stone tool use may be preserved as cutmarks on bones from the surface at Dikika, Ethiopia dating to 3.39 Ma. Because they preserve well, stone artifacts form the largest part of the early archeological record. Artifacts are one of the fundamental units of data used by archeologists when they reconstruct the behavior of extinct hominins and prehistoric modern humans.

Artiodactyla

The mammalian order that includes all of the taxa with an even number of hoofed toes. Artiodactyls are terrestrial and largely herbivorous, although some artiodactyl taxa (e.g., the Suidae) are more omnivorous. The most diverse family of artiodactyls is the Bovidae (antelopes and their allies). Other artiodactyl families include the Suidae (pigs), the Hippopotamidae (hippopotami), and the Giraffidae (giraffes). Other, less common artiodactyls in African hominin sites are the Camelidae (camels) and the Tragulidae (chevrotains). In Eurasia, the Cervidae (deer) are common at hominin sites, as are the Moschidae (musk deer). (Gk *artios* = even and *daktulos* = toe; literally, the “even-toed.”)

Asa Issie

An area of fossiliferous sediments, which is 10 km/6 miles west of Aramis, Ethiopia, containing hominin fossils assigned to *Australopithecus anamensis*. The fossils, dating to between 4.2 and 4.1 Ma, are claimed to be transitional between *Ardipithecus ramidus* and *Au. anamensis*. No archeological evidence has been found. (Location 11°10'N, 40°20'E, Ethiopia.)

ascertainment bias

Synonymous with experimental bias, ascertainment bias refers to a systemic distortion of results attributable to nonrandom sampling. Such biases can lead to incorrect inferences about an entire population either because of distorted or nontypical sampling of the population or

because the data (i.e., a specific marker) used for the analysis were identified in a biased way. [L. *ad* = near and *certus* (the root of “certain”) = to determine.]

As Duma

Site located on the west side of the Awash River in the Gona Western Margin sector of the Gona Paleoanthropological study area in the Afar Depression, in Ethiopia. It contains several *Ardipithecus ramidus* fossils and dates to *c.*4.4 Ma. No archeological material was found. (Location 11°10'N, 40°20'E, Ethiopia.)

assemblage

An archeological assemblage is a stratigraphically bounded, spatially associated set of artifacts. For example, a single archeological site may contain several artifact assemblages (e.g., many of the excavations at Olduvai Gorge). These may derive from different strata at the site, or from different facies within the same stratum (e.g., from channel and floodplain deposits of the same river system). Assemblages form one of the basic comparative units above the level of single artifacts or artifact types, and variations in the range of tool types found within an assemblage have been used to infer past site function(s). Assemblage is also used as an inclusive term to describe the paleontological evidence from a site.

assimilation model

A model for the origin of modern humans that accepts an African origin but rejects the total replacement of local archaic populations (e.g., *Homo neanderthalensis*) by modern humans as they spread into Eurasia. This model relies on fossil evidence that suggests minor morphological traits show within-region continuity through the transition between the archaic and modern forms. In contrast, the replacement with hybridization model accepts the theoretical possibility of admixture, but rejects any morphological evidence for it. The assimilation model is consistent with the mostly out-of-Africa genetic model of modern human origins. It is also supported by recent evidence from the Neanderthal genome project indicating that Neanderthals made low-level contributions to the genomes of modern Eurasian populations, and evidence that the genomes of modern Melanesian, Oceanian, and Southeast Asian populations contain contributions from Denisovan hominins. *See also* **candelabra model**; **multiregional hypothesis**; **out-of-Africa hypothesis**; **replacement with hybridization**.

associated skeleton

Refers to a fossil specimen that includes more than one skeletal element from the same individual. Most fossil hominin taxa are diagnosed and identified on the basis of skull morphology, so associated skeletons that include skull and postcranial elements can help determine which limb bones go with which skulls. For example, for a long time the lack of a securely associated skeleton of *Paranthropus boisei* that preserves both taxonomically distinctive skull evidence *and* evidence of the postcranial skeleton has hampered attempts to sort into taxa hominin postcranial fossils from East Africa. Well-preserved associated skeletons allow researchers to compare the size of the teeth with the rest of the body, or the relative lengths of the limbs and/or limb segments, or the relative sizes of joint surfaces.