A

2D:4D *See* **hand, relative length of the digits**.

3′ One of the two ends of a single strand of DNA. It is called the 3′ (or "three prime") end because the third carbon of the **nucleotide** at that end has a hydroxyl group attached. The other end, the **5′** (or "five prime") end, is so-called because the fifth carbon of the deoxyribose sugar of the nucleotide at that end has a terminal phosphate group attached to it. The direction towards the 3′ end of a single strand of DNA is called the **downstream** direction because as you move in that direction the number of carbon molecules in the sugars in the DNA backbone decreases. The significance of the directionality of a DNA sequence is that the processes of **replication** and **transcription** only occur in the 5′ to 3′ direction. *See also* **DNA**.

5′ One of the two ends of a single strand of DNA. It is called the 5′ (or "five prime") end because the fifth carbon of the deoxyribose sugar of the **nucleotide** at that end has a terminal phosphate group attached to it. The other end, the **3′** (or "three prime") end, is so-called because the third carbon of the nucleotide at that end has a hydroxyl group attached. The direction towards the 5′ end is called the upstream direction because as you move in that direction the number of carbon molecules in the sugars in the DNA backbone increases. The significance of the directionality of a DNA sequence is that the processes of **replication** and **transcription** only occur in the 5′ to 3′ direction. *See also* **DNA**.

23 ka world *See* **astronomical time scale**.

41 ka world *See* **astronomical time scale**.

100 ka world *See* **astronomical time scale**.

1939 mandible *See* **Sangiran 5**.

1941 mandible *See* **Sangiran 6a**.

a The abbreviated form of annum. The joint IUPAC-IUGS Task Group (2006-016-1-200) in 2006 urged that the SI unit a be used for both ages and time spans (i.e., 36 ka for 36 thousand years and 2.3 Ma for 2.3 million years). The IUPAC-IUGS Task Group discourage the use of y, yr and yrs in combination with k, K, m, M, etc.

AAC *See* **alcelaphine plus antilopine criterion**.

AARD *See* **amino acid racemization dating**.

AAS *See* **Aurora archaeostratigraphic set**; **Gran Dolina**.

abduction (L. *ab* = away and *ducere* = to lead) Limbs Refers to moving a limb away from the midline (i.e., the true **sagittal** plane) when the body is in the **anatomical position**. Digits In the case of the hands and feet abduction means moving fingers or toes away from the reference digit. The reference digit of the hand is the middle finger; the reference digit of the foot is the second toe. Thus, the muscles that move the limbs away from the midline (e.g., the deltoid and the gluteus medius) and those that move a digit away from the reference digit (e.g., the dorsal interosseus muscles of the hand) are referred to as abductors. *See also* **abductor**; **reference digit**.

abductor Any muscle that contributes to moving 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).

Abdur (Location 15°09′N, 39°52′E Eritrea; etym. the name of a nearby village) History and general description Faure and Roubet (1968) had reported finding Acheulean artifacts on the surface of marine

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Wiley-Blackwell Encyclopedia of Human Evolution, First Edition. Edited by Bernard Wood.

deposits on the African shore of the Red Sea. Abdur is a Pleistocene reef terrace on the western shore of the Buri Penisula, and is northeast of the Danakil Depression. The terrace, comprised of a 6.5 km/4 mile by 1 km/0.6 mile exposure of the Abdur Reef Limestone (or ARL), is divided into three sections: Abdur North (AN), Abdur Central (AC) and Abdur South (AS). Obsidian and quartz artifacts have been found in AN and AS, with most of the evidence coming from AN and the artifacts coming from the "basal cobble zone," the "lower part of the lower shell zone" and the "beach facies" (Walter et al. 2000, p. 67). Temporal span and how dated? Five of six dates based on **uranium-series dating** (uranium-thorium) performed on coral aragonite suggest the ARL was deposited between 136 and 118 ka, with a mean age of *c*.125 ± 7 ka. Hominins found at site None. Archeological evidence found at site Bifaces made from chert and quartz and flake and blade tools mainly from obsidian. The artifacts are consistent with the early **Middle Stone Age**. Key references: Geology, dating, and fauna Walter et al. 2000; Hominins N/A; Archeology Walter et al. 2000.

"Abel" The informal name given by Michel **Brunet** to a hominin mandibular fragment recovered in 1994 by the **Mission Paléoanthropologique Franco-Tchadienne** (French-Chadian Paleoanthropological Mission, or MPFT) at a site in Chad called **Koro Toro**. Brunet and his colleagues assigned the specimen to a new species, ***Australopithecus bahrelghazali***. He gave the specimen the name Abel to honor the memory of Abel Brillanceau, a colleague and close friend who died while doing field research.

abiotic (Gk *a* = not and *bios* = life) In relation to hominins this term subsumes all the "non-living" factors (e.g., climate and physical catastrophies such as massive volcanic eruptions, tsunamis, etc.) that might have influenced the outcome of human evolution.

Abri Bourgeois-Delaunay *See* **La Chaise**.

Abri d'Aurignac *See* **Aurignac**.

Abri Moula-Guercy (Location 44°52′59″N, 4°50′51″E, France; etym. Fr. *abri* = rock-shelter, Moula = the name of the discoverer, Guercy = the limestone outcrop in which the cave lies) History and general description This site, sometimes referred to as Baume Moula-Guercy (*baume* is Provençal for cave) or just Moula-Guercy, lies 80 m above the right bank of the Rhône river, in the east side of the Serre de Guercy, a small limestone outcrop in the town of Soyons, in the Ardeche region of southeast France. Discovered in 1970, the site was not excavated until 1991, when a team led by Alban Defleur began to explore the rock-shelter and deep cave beneath. They uncovered 20 layers, all of which are exclusively **Middle Paleolithic**. This site is best known for the abundant evidence of defleshing and disarticulation on bones assigned to ***Homo neanderthalensis***, which the authors have suggested is due to cannibalism. It is also one of the few well-preserved sites with hominin fossils of Eemian age. Temporal span and how dated? The site represents the period between **Oxygen Isotope Stages** 6 and 4. Most of the site is dated using **biostratigraphy**, but an ash layer near the top of the site has been dated using thermo**luminescence dating** to 72 ± 12 ka. The hominin layer is estimated to be between 100 and 120 ka. Hominins found at site Neanderthals are the second most abundant taxon recovered from layer XV; 78 bone fragments were recovered, representing at least six individuals. The majority of these bones show cutmarks and intentional fractures that have been interpreted as attempts at marrow extraction; the patterns are similar to those found on deer bones found at the same site. Archeological evidence found at site The artifacts from the layer containing the fossil hominins are attributed to the Ferrassie **Mousterian**. Key references: Geology, dating, and paleoenvironment Sanzelle et al. 2000, Defleur et al. 1998, 2001; Hominins Defleur 1995, Defleur et al. 1998; Archeology Defleur 1995, Defleur et al. 1998.

Abri Pataud (Location 44°56′N, 1°00′E, France; etym. Fr. *Abri* = rock-shelter, and Pataud after the name of the family who owned the land) History and general description One of several rock-shelter sites along the Vézère River in southwest France. The site was obscured by farm buildings until 1953 when Hallam Movius began exploring the site, and it was systematically excavated between 1958 and 1964 by a joint French and American team led by Movius. Temporal span *c*.34–19 ka. How dated? Conventional **radiocarbon dating**. Hominins found at site Partial skeletons of three adult and two adolescent modern human skeletons were found in the Proto-Magdalenian layer. Archeological evidence found at site Thirteen numbered archeological layers represent an almost complete **Upper Paleolithic** sequence, from basal **Aurignacian** to a possibly lower **Solutrean** level, separated by unnamed sterile layers. Abundant fauna and some pollen suggest a cold environment consistent with the **Last Glacial Maximum**, but with local river valleys providing **refugia** for warm-climate species. Key references: Geology, dating and paleoenvironment Donner 1975, Movius Jr. 1975, Wilson 1975, Bricker and Mellars 1987; Hominins Billy 1975; Archeology Movius Jr. 1975.

Abri Peyrony *See* **Combe-Capelle**.

Abri Suard *See* **La Chaise**.

abridged life table A complete **life table** gives mortality per individual year of age, while an abridged life table lumps various ages together. It is common in **paleodemography** to use age classes starting at 0, 1, 5, 10, 15, 20, 25, 30, 40, and 50, where the end of an age class is implied by the next age class. For example, the first few age classes in the above list would be 0–0.9973 (where 0.9973 is 364/365 days, 1–4.9973, and 5–9.9973. The last age class is considered to be open, so that the last age class in the above list is 50+. Any life table function which involves person-years will require that the last age interval be closed, which is usually done by continuing the age progression so that 50+ becomes 50–60. Using the notation ${}_nD_x$ to represent the number of deaths between age x and age $x+n$, the symbols for the abridged life table example here would be: ${}_1D_0$, ${}_4D_1$, ${}_5D_5$, ${}_5D_{10}$, ${}_5D_{15}$, ${}_5D_{20}$, ${}_5D_{25}$, ${}_{10}D_{30}$, ${}_{10}D_{40}$, and ${}_{10}D_{50}$.

absolute dating (L. *absolutus* = free or unrestrained) In physics, "absolute" means being free, or independent, of arbitrary standards. Thus, absolute dating methods were so labeled because they were regarded as not being arbitrary in that they are based on physical or chemical systems whose dynamics are predictable. This predictability means they can be used to calibrate events or measure the passage of geological time. Very few of the current techniques can be used to determine the age of the fossils or artifacts themselves; in most cases they are used to date surrounding sediments or associated igneous rocks, which have a known stratigraphic relationship to the fossils in question. **Radiocarbon dating** is perhaps the best-known absolute dating method, but several others (e.g., **potassium-argon dating**, thermo**luminescence dating**, **uranium-series dating**) are used to provide age estimations for fossil hominins beyond the age range of radiocarbon dating (i.e., older than approximately 50 ka). All absolute dates have various associated errors. Occasionally these are errors in the measurement of the physical parameter used [i.e. the amount of carbon-14 (^{14}C) **isotope** present in the sample]. Errors can also arise from imperfect calibration of the physical parameter to the geological time scale or from various alterations of the dated material after it was deposited. Thus, whenever the age of a tuff, cave deposit, directly dated fossil, etc. is cited it should include its error term expressed either in standard deviation units or as years, depending on the dating technique being utilized. Geochronologists are moving away from the old divisions of absolute and relative methods, and tend to refer to absolute dating methods as methods that provide a "numerical age estimate". *See also* **geochronology**.

AC Acronym for Abdur Central. *See* **Abdur**.

acceleration (L. *accelerationem* = a hastening) A heterochronic process that produces peramorphic results by dissociating ancestral patterns of ontogeny. Specifically, shape change is accelerated and progresses further for a given size in descendants relative to ancestors; adult size and duration of growth found in the ancestor remain unchanged in the descendant.

accelerator mass spectrometer (AMS) A specialised mass spectrometer that can extend the range of carbon dating back to 50–60 ka. This technique uses an accelerator to produce ions with very high kinetic energies; this is done to increase the ionization state of the ions from the sample in order to facilitate the removal of potential contaminants (particularly ^{14}N and $^{13}CH^-$) that would interfere with the counting of ^{14}C ions in the detector. The technique is referred to as **AMS radiocarbon dating**, to distinguish it from conventional radiocarbon dating. *See also* **radiocarbon dating**.

accentuated line A pronounced line within a tooth corresponding to the temporary slowing of movement of the developing **enamel** or **dentine** front, or to a change in chemical composition, that does not result from an intrinsic rhythm (*see* **incremental features**), but rather relates to a (non-specific) stressor event. The **neonatal line** found in teeth developing just prior to, during, and immediately after birth is the best-known example. Accentuated lines are sometimes found in association with enamel **hypoplasia**s, but they can occur without there being any surface manifestation of developmental stress (syn. pathological lines, **Wilson bands**, or accentuated striae of Retzius).

accentuated striae of Retzius *See* **Wilson bands**.

accessory cusp A cusp on a maxillary (upper) or mandibular (lower) molar tooth that is not one of the main cusps (i.e., not the **proto-**, **para-**, **meta-**, or **hypocone** on a maxillary molar, and not the **proto-**, **ento-**, **meta-**, or **hypoconid**, or **hypoconulid**, on a mandibular molar). For example, the **metaconule** is an accessory cusp between the metacone and protocone on a maxillary molar, and the **tuberculum sextum** is an accessory cusp between the **entoconid** and the **hypoconulid** on the **talonid** component of the crown of a mandibular molar. *See also* **cusp**.

accessory olfactory system *See* **olfactory bulb**.

accretion model (L. *accrescere* = to grow) Refers to the mode of origin of the Neanderthals. The model suggests that the distinctive morphology of *Homo neanderthalensis* did not arise suddenly, but emerged gradually, or grew (i.e., accreted), over a period of several hundred thousand years (Hublin 1998). Although Jean-Jacques **Hublin** (1982, 1986, 1998, 2009) is its contemporary proponent, this type of evolutionary scenario was first proposed by Piveteau (1970), and then developed by Vandermeersch (1978b). The model proposes that initially there were relatively few distinctive features (e.g., facial recession and a wide occipital torus) and what features there were occurred at a relatively low frequency, but through time the number and frequency of distinctive features increased. Dean et al. (1998) provided the most comprehensive explanation of the model. They suggested that Neanderthal evolution occurred in four stages (*ibid*, Table 1, p. 487): Stage 1 or the early pre-Neanderthal stage, Stage 2 or the pre-Neanderthal stage, Stage 3 or the early Neanderthal stage, and Stage 4 or the classic Neanderthal stage. Examples of Stage 1 Neanderthal specimens include those from **Arago**, **Mauer**, and **Petralona**. Specimens from **Sima de los Huesos**, **Reilingen**, **Steinheim**, and **Swanscombe** have been assigned to Stage 2, with **Bilzingsleben** and **Vérteszöllös** considered as Stages 1 or 2. Examples of specimens assigned to Stage 3 include **Ehringsdorf**, **Biache**, **Saccopastore**, and **Shanidar**, with **Amud**, **Monte Circeo**, **La Chapelle-aux-Saints**, **La Ferrassie**, **La Quina**, **Neanderthal**, and **Spy** examples of specimens included in Stage 4. As for the morphological features that emerge at each stage, the Stage 2 morphology includes an incipient **suprainiac fossa**, a small **juxtamastoid eminence**, and an incipient occipital bun. The changes that occur at Stage 3 include a smaller mastoid process, a larger **juxtamastoid process**, an anterior **mastoid tubercle**, and a more exaggerated occipital bun. At Stage 4 the additions include greater midfacial **prognathism**, a more exaggerated suprainiac fossa, and a larger piriform, or nasal, aperture. However, Hublin (1998, 2009) emphasized that there is a shift in the frequencies of these features and that stages primarily result from discontinuity in the fossil record. He proposed that the taxon name *Homo neanderthalensis* should be used for *all four stages*. Other researchers support the accretion model, but they would confine the hypodigm of *H. neanderthalensis* to the later stages, and would use *Homo heidelbergensis* for the early stages (e.g., the hominins from **Sima de los Huesos**). *See also* ***Homo heidelbergensis***; ***Homo neanderthalensis***.

acculturation The adoption by one group of a large number of cultural behaviors from another group. Thus, in the terminology of dual inheritance theory, acculturation is a form of group-level horizontal cultural transmission.

accuracy (L. *accurare* = to do with care) Accurate refers to something that is true, or close to the truth. Thus, accurate estimates of measurements or dates are ones that are very close to the real dimensions or ages. A series of accurate measurements are not necessarily close to each other, however. Imagine a dartboard with three darts placed equidistant on a circle around the bull's eye. Each dart is close to the bull's eye, but not particularly close to the other darts. *See also* **precision**.

acetabulocristal buttress *See* **acetabulocristal pillar**.

acetabulocristal pillar (L. *acetum* = vinegar, *abulum* = small receptacle, and *crista* = crest) Thickening of mostly the outer table of the iliac blade part of the pelvic bone between the acetabular fossa and the iliac crest about one-third of the way between the anterior and posterior superior spines. The thickening is seen in pre-modern *Homo*, but not in anatomically modern humans (Stringer 1986b). It presence is interpreted as evidence that the gluteal muscles were playing a significant abducting role (i.e., working isometrically to prevent the pelvis from dipping down on the side where the leg is no longer in contact with the ground because it is in the swing phase of the **walking cycle**). For example, Day (1971) refers to the acetabulo cristal pillar as the "vertical iliac pillar" or "vertical iliac bar" and suggests that its presence in **OH 28** is evidence that "the alternating pelvic tilt mechanism of striding bipeds was well developed" (*ibid*, p. 384). *See also* **pelvis**.

Aché A group of foragers (also known as the Guayaki) living in eastern Paraguay, an environment of mixed broadleaf evergreen forest and grassland. There are four main groups of Aché who distinguish themselves based on language, customs, and geographic range, and all contrast themselves from the neighboring sedentary farmers with whom they usually have only hostile interactions. All four Aché groups have been studied by ethnographers, and the northern group has been the particular subject of subsistence studies by behavioral ecologists. Most of the northern Aché were full-time foragers until the 1970s; now roughly 130 of this group live in an agricultural settlement. Some of these 130 people still spend a considerable amount of time in the forest on extended foraging trips, where they hunt a wide range of animals with bows, and gather plant foods. Studies of their diet have enabled several researchers to test hypotheses about evolutionary ecology in the absence of agriculture, and to use them as analogues for pre-agricultural human ancestors. Studies of the Aché have suggested that both plant and animal foods are important in an optimal diet, that men and women have different foraging goals which must be accounted for in behavioral ecology studies (Hill et al. 1987), and that hunting may be a social signal as well as a method of provisioning (Wood and Hill 2000).

Acheulean Originally proposed in the 19thC by Gabriel de Mortillet; takes its name from the French village of Saint-Acheul in the Somme River Valley where numerous **handaxe**s had been recovered. In 1872 Gabriel de Mortillet named the **industry** "l'Epoque de St Acheul", but in 1925 the name was changed to Acheulean. Earlier mention of handaxes was made by John Frere who in 1797 sent two examples from Hoxne, Suffolk, UK, to the Royal Academy in London claiming that "they belonged to a very ancient period indeed" and had been produced by "people who had not the use of metals." Given the general lack of knowledge of evolution in those times his claims were mostly ignored. The oldest and youngest reported Acheulean sites were in Africa from 1.6–0.16 Ma. Acheulean sites are found in a substantial portion of Eurasia (but they are generally absent from Asia east of **Movius' Line**). Most Eurasian Acheulean sites date from the Middle Pleistocene (i.e., they are *c*.500 ka). Handaxes and similar implements (such as **cleaver**s and picks) define the Acheulean; these tool types are not *confined* to the Acheulean, but when they occur at other sites they are rare and are typically outnumbered by **flake**s, **core**s, and other smaller modified tools such as **scraper**s. The Acheulean is preceded by the **Oldowan**, and many of the non-handaxe Acheulean tools are Oldowan-like, emphasizing the retention of an older but effective stone tool technology. Similarly, some later Acheulean sites, including for example those in the Somme River Valley and in the **Kapthurin Formation** of Kenya, show evidence for the use of **Levallois** technology for large flake production. This technique is seen more commonly in later **Middle Paleolithic** or **Middle Stone Age** sites, and this also suggests local technological continuity. The Acheulean site of **Gesher Benot Ya'akov** in Israel documents the earliest controlled use of fire, as well as nut fragments and processing equipment (Goren-Inbar et al. 2002a, 2002b). Meat was very likely an important component of the hominin diet, but Acheulean hunters may have been relatively ineffective compared with later populations at bringing down large game (Klein et al. 2007). Although traditionally associated with ***Homo erectus***, Acheulean tools were likely made and used by more than one hominin taxon. Interpretations of the Acheulean vary widely. Its seemingly static nature is usually attributed to **social learning** and **cultural transmission**, in combination with functional constraints (cutting, scraping), repeated resharpening, and raw-material constraints (e.g., large tabular chunks versus small elongated pebbles). Some workers have speculated that the quite unchanging basic features of Acheulean implements were genetically determined, and that the variability of the final products may have signaled the genetic qualities of the maker. The Acheulean is unique in the evolution of hominins in that neither before nor since has such a singular technology dominated the activities of hominins for so long over so much of the planet.

Acheulian Alternative spelling for **Acheulean** (*which see*).

Acheulian industrial complex *See* **Acheulean**.

actualistic studies (L. *actus* = an act) Such studies, which reconstruct activities to understand the role or function of that activity, are used in archeology and paleontology. For example, in archeology, researchers use tools in controlled circumstances to help determine what paleolithic artifacts were used for. For example, if an artifact made by a skilled knapper is used to whittle wood, the wear on the modern tool can be compared with the wear on ancient artifacts to see if the wear facets show the same macro- and microwear. 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 uniformitarian in the sense that they assume that processes observed in the present are same as those that took place in the past (*see* **uniformitarianism**). In turn, inferences about the past are interpreted in terms of processes operating in the present. Actualistic research methodologies range from naturalistic to experimental. In a naturalistic context, the analyst observes and records natural processes and their resulting effect on bone assemblages. In an experimental context, the analyst controls some or all of the taphonomic processes affecting bone assemblages. Actualistic research provides the basis for most taphonomic and zooarcheological analysis and interpretation and is thus central to reconstructing the behavioral and paleoenvironmental signals encoded in the fossil record.

acute margin Another term for a sharp edge on a stone tool.

adaptation (L. *adaptare* = to fit) A useful feature or trait that (a) promotes survival and reproduction and (b) is shaped by natural selection, and formulating and testing hypotheses of adaptation is a major focus of paleoanthropological research. Adaptations are therefore heritable and perform functions. The term is also used to describe the process by which features that promote or enhance fitness evolve under **natural selection**, which can be **directional selection** or **balancing selection** (also known as stabilizing selection). Evolutionary biologists differ as to whether understanding the genesis of a trait is important in determining its adaptive status, some noting the importance of distinguishing between current function and original function(s). In some cases the function of a current trait can be assessed experimentally, but in most cases in evolutionary biology describing a phenotypic trait as a current or previous adaptation should be seen as an hypothesis. The frequency of a heritable variant, the **trait**, predominates or becomes fixed in a population because the individuals possessing it enjoy greater reproductive success (**fitness**) than those that lack it. It is common for workers to think of adaptive traits as being **derived** (i.e., **apomorphic**), but this need not be the case if a **primitive** trait has been retained in a population as a result of stabilizing selection. 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"). So, what needs to be done to strengthen an hypothesis that a trait in a **hominin** taxon is an adaptation in the non-historical sense? If a trait seems to have an obvious function (e.g., the **acetabulocristal buttress** of the pelvic bone functions in bipedal hominins as a bony strut that links the proximal attachment of the hip abductors with the acetabulum of the hip joint) then all well and good. But just because our present knowledge does not allow us to assign a function to a trait, it does not follow the trait has no function; we may not yet understand what its function is. For example, if we did not know about the way the specialized receptors in the **semicircular canals** of the **membranous labyrinth** of the **inner ear** respond to motion, we would perhaps be inclined to assume that the shape of that part of the bony labyrinth of a fossil **hominid** was not adaptive. Therefore, adaptation will tend to be under-recognized (i.e., it is prone to **type I error**). It can be difficult, if not impossible, to firmly establish whether or not a given trait has been subjected to natural selection in fossil hominins, so the identification of adaptations in paleoanthropology is inevitably conjectural. *See also* **phylogenetic lag**; **structure–function relationships**.

adaptive landscapes *See* **fitness landscapes**.

adaptive radiation (L. *adaptare* = to fit and *radius* = ray) The relatively rapid diversification of a lineage into **species** that evolve a range of new **adaptive strategies** that facilitate their occupation of a range of new **adaptive zone**s. An example is the simultaneous appearance (at least in geological time) of multiple pig species at the same site(s) at several times during the **Pliocene** and **Pleistocene**. During the last 4 Ma approximately six pig species have coexisted at the same locality (i.e., **sympatric**ally) at the same time (i.e., **synchronic**ally). A number of these species exhibit M_3 hypsodonty and craniofacial elaboration (bosses, crests, tusks). This is usually interpreted as an adaptive response to more open, grassland environments.

adaptive strategy (L. *adaptare* = to fit and *strategos* = general) Sewall-Wright's term for the set of traits that enables organisms of a species to survive and reproduce. The origin of these trait sets can vary; they may have been inherited from a recent common ancestor or they may be the result of independent adaptation to similar environmental conditions (i.e., **parallel evolution** or **convergent evolution**). An adaptive strategy can be shared by more than one species (syn. organizational plan). *See also* **adaptive type**; **adaptive zone**; **grade**.

adaptive type (L. *adaptare* = to fit, *typus* = image) According to Huxley (1958) an adaptive type is a fossil taxon with a more derived **phenotype**, or organizational plan, that replaces an older fossil taxon with a less derived organizational plan. In some cases the replacement is straightforward, involving just two taxa. In others, the old organizational plan is replaced by several new organizational plans, which are then reduced in number by extinction, until only one is left. Regardless of the mode of replacement, the new taxon is called an adaptive type because, according to neo-Darwinian principles, it must have been more successful than the taxa it superseded. The rise and success of a new organizational plan is evidence that it was better adapted than the older one, and that it was also better adapted than any potential competitor. The terms adaptive type and grade are interchangeable. Huxley's (1958) term "organizational plan" is equivalent to Sewell-Wright's adaptive strategy (syn. grade). *See also* **adaptive strategy**; **adaptive zone**; **grade**.

adaptive zone (L. *adaptare* = to fit and *zona* = girdle) Taxa that occupy the same adaptive zone survive and reproduce in a similar manner. That is, they have the same adaptive strategy. The relationship between adaptive strategies and adaptive types, or grades, is such that some adaptive zones are occupied by taxa that have the same adaptive strategy and so represent an adaptive type or grade. Occasionally, a lineage will rapidly diversify into several species that occupy a range of new adaptive zones. This is referred to as an adaptive radiation. *See also* **adaptive radiation**; **adaptive strategy**; **adaptive type**; **grade**.

adduction (L. *adducere* = to bring towards) Limbs Adduction refers to moving a limb towards the midline (i.e., the true **sagittal** plane) when the body is in the **anatomical position**. Digits In the case of the hands and feet, adduction means moving fingers or toes towards the reference digit. The reference digit of the hand is the middle finger; the reference digit of the foot is the second toe. Thus, the muscles that move the limbs towards the midline (e.g., teres major and obturator internus) and those that move a digit towards the reference digit (e.g., the palmar interosseus muscles of the hand) are referred to as adductors. *See also* **adductor**; **reference digit**.

adductor Any muscle that contributes to moving a limb towards the midline reference plane (e.g., teres major, obturator internus), or a digit towards the reference digit (e.g., palmar interossei of the hand). *See also* **reference digit**.

aDNA *See* **ancient DNA**.

adolescence (L. *adolescentia* = youth) Adolescence is the stage of modern human life history that follows the juvenile stage and the event of puberty. The length of adolescence varies across modern human populations; it ends when adult skeletal lengths, dental development, and sexual maturation are attained (e.g., the age range of its ending is from 17 to 25 years). The defining characteristic of adolescence is a spurt in height (unique to modern humans among extant higher primates; several nonhuman primate species undergo growth spurts in craniofacial dimensions) and mass (shared with many nonhuman primates). The intensity and duration of this spurt shows much variation among and within modern human populations. The onset of menstruation (**menarche**) in modern human girls usually follows within 1 year of the peak velocity of the growth spurt, and for 1–3 years they experience a period of "adolescent subfecundity" (where menstrual cycles are often irregular or anovulatory). Sexual maturation in modern human boys precedes the time of peak growth velocity, but the full development of modern human male secondary sexual characteristics takes much longer to manifest. This results in subfecund, adult-looking girls, and fecund, non-adult-looking boys. It has been proposed that this is an adaptation that enables each sex to learn as much as possible about their adult social, economic, and sexual roles in society, with as little risk as possible. It has been suggested that the adolescent stage evolved either in archaic or anatomically modern ***Homo sapiens***, but it is difficult to determine, at the current time, whether extinct hominin taxa underwent a growth spurt and, if so, whether it was more similar to that of modern humans or that of nonhuman primates.

adolescent growth spurt (L. *adolescere* = to grow up, from *ad* = forward and *alescere* = to grow) Adolescence in modern humans is the period of **life history** between puberty and maturity. During the adolescent stage of modern human development rapid gains in height and weight usually occur beginning on average between ages of 10 (females) and 12 (males). This period of the highest growth velocity, second only to that experienced in infancy, usually lasts between 8 and 10 years. There is significant variation in the onset and intensity of the adolescent growth spurt within and among modern human populations, with some showing a clear and marked spurt in stature while others demonstrate no clear evidence of such a spurt. While many species of nonhuman primates have been shown to have growth spurts in mass, modern humans are the only primates that show evidence for a spurt in linear skeletal dimensions. This intense growth is seen in almost all skeletal elements, with the exception of the female pelvis (instead of experiencing a major spurt in growth, the female pelvis grows slowly until adulthood). The later onset and longer duration combined with the generally higher growth velocity experienced during the adolescent growth spurt in modern human males when compared with females is largely responsible for their greater average adult height.

adrenarche (L. *ad* = near, *renal* = kidney, and Gk *arkhe* = beginning) The onset of prepubertal adrenal androgen production (specifically of dehydroepiandrosterone, or DHEA, and dehydroepiandrosterone sulfate, or DHEAS) after a post-infancy period of very little adrenal activity. While circulating levels of adrenal androgens in nonhuman primates are generally higher than those in nonprimate mammals, none show the same pattern that is seen in modern humans and chimpanzees: a sharp postnatal decline in levels from birth with subsequent elevations before sexual maturation usually around 6–10 years of age. It has been suggested that differences in patterns of adrenal androgen secretion may be due to differences in the timing of the regression of the fetal zone and development of the *zona reticularis* (or ZR), the region of the adult adrenal gland where these hormones are produced. Specifically, these two events occur in closer temporal proximity in primates other than chimpanzees, such as baboons, whose DHEAS levels peak shortly after birth and decline steadily thereafter. It has been proposed that the decline in serum DHEA/DHEAS prior to adrenarche acts as a mechanism to delay skeletal maturation in concert with prolonged prepubertal growth (Bogin 1997). The outward effects of adrenarche (e.g., changes in body fat distribution, growth of body hair) noticeably alter an individual's physical appearance. It has been suggested that adrenarche and the slowed growth prior to it is critical to the development of an individual's cognitive function. It also aids the perception by others that an individual is transitioning from a child to a juvenile.

ADU Abbreviation of Aduma, a site in the **Middle Awash study area**, Ethiopia. *See* **Aduma**.

ADU-VP Acronym for **Adu**ma – **V**ertebrate **P**aleontology. Prefix for fossils from the site of **Aduma**.

ADU-VP-1/3 Site **Aduma**. Locality Aduma. Surface/*in situ* Surface collection from **lag deposits**. Date of discovery 1996. Finder Timothy Douglas **White**. Unit N/A. Horizon Bed B. Bed/member Ardu Beds. Formation **Bouri Formation**. Group Middle Awash. Nearest overlying dated horizon Bed A, Ardu Beds. Nearest underlying dated horizon Bed C, Ardu Beds, followed by the **Herto Formation**.

Geological age **Late Pleistocene**, associated with **Middle Stone Age** artifacts and sediments dated between 79 and 105 ka (Yellen et al. 2005). Developmental age Adult. Presumed sex Unknown. Brief anatomical description The most complete of five fragmentary crania from Aduma, ADU-VP-1/3 preserves part of the frontal squame and much of the parietals and occipital. The occipital is rounded and the parietals have a strong sagittal curvature, indicating a globular **neurocranium**. Announcement Haile-Selassie et al. 2004b. Initial description Haile-Selassie et al. 2004b. Photographs/line drawings and metrical data Haile-Selassie et al. 2004b. Detailed anatomical description Haile-Selassie et al. 2004. Initial taxonomic allocation ***Homo sapiens***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Homo sapiens*. Informal taxonomic category Anatomically modern human. Significance The Aduma crania are clearly anatomically modern and even though their dating is not precise they add support to the hypothesis that modern humans evolved in Africa. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

Aduma (Location 10°25′N, 40°31′E, Ethiopia; etym. named after a nearby Afar village) History and general description A region in the **Middle Awash study area** with **Early**, **Middle**, and **Later Stone Age** archeological sites. The locality was briefly surveyed by John Kalb in 1976, but excavations were not undertaken until John Yellen and Alison Brooks excavated there between 1993 and 1998 under the aegis of the **Middle Awash Research Project**. A variety of **lacustrine**, **fluvial**, and **tuffaceous** sediments crop out in the area; the majority of the *in situ* (Middle Stone Age) archeological sites occur within the Ardu Beds (informally subdivided into Ardu A–C from bottom to top). The archeological sites in the Ardu Beds are important for documenting temporal trends within the Middle Stone Age, and are associated with fossil fauna (including hominins) that suggest use of a range of habitats, but with a strong reliance on riverine resources. Temporal span Multiple radiometric methods provide a general estimate of the age of the Ardu Beds. An **argon-argon dating** age estimate on pumice of *c*.180 ka from the base of the sequence and a **radiocarbon dating** result of 10.50±0.07 ka on *Unio* sp. shell from sterile sediments capping the sequence provide bracketing ages. Although there are inconsistencies and stratigraphic reversals, thermoluminescence dating and optically stimulated **luminescence dating** (single and multiple-grain) ages on silt and sand and **uranium-series** estimates on fossilized mammal and *Clarias* sp. bone and crocodile teeth suggest an age range of *c*.80–100 ka for most of the archeological sites. How dated? ^{40}Ar/^{39}Ar, ^{14}C, optically stimulated luminescence dating, thermoluminescence dating, and U-series. Hominins found at site Four adult hominins, a cranium (**ADU-VP-1/3**), parietal fragments (ADU-VP-1/1 and 1/2), and unidentified cranial fragments (ADU-VP-1/6), all attributed to ***Homo sapiens***, were recovered from the surface of Aduma (likely from Ardu B sediments). Archeological evidence found at site The approximately 16,200 **lithic** artifacts are made of **lava** (including **obsidian**), **quartz**, and **chert**, and include cores for the production of **blades**, **bladelets**, **Levallois** and other flakes, diverse **retouch**ed pieces dominated by **points** and **scrapers**, and rare **grindstones**. The assemblages are notable for showing temporal variation among Middle Stone Age assemblages, particularly a decrease in core and flake/blade size with increased stratigraphic height. More than 30 taxa are recognized among the recovered fauna. Rare cutmarks implicate the role of hominins in the accumulation of at least some of this fauna. The combination of taxa that are water-dependent (e.g., *Crocodylus niloticus*, *Clarias* sp., and *Unio* sp.) and water-independent (e.g., *Oryx*) suggest the presence of steep ecological gradients away from a forested river margin to a **savanna** grassland; soil isotopic and pollen data also support the latter suggestion. Key references: Geology and dating Yellen et al. 2005; Hominins Haile-Selassie et al. 2004b; Archeology Yellen et al. 2005.

Aduma cranium *See* **ADU-VP-1/3**.

aeolian (Gk *Aeolus* = god of the winds) Deposited primarily by wind action. Clay-sized aeolian material is often difficult to recognize, being readily integrated into soils or sedimentary deposits. The large volumes of glacially derived silts subject to aeolian transport are responsible for **loess** deposits. Sand-size aeolian material commonly forms dunes in dry environments and coastal areas. Volcanic ash can be subjected to aeolian transport and reworking prior to deposition. At **Laetoli**, most of the sediments comprising the **Laetoli Beds** are either primary airfall tuffs, or they are formed from airfall tuffs that have been reworked by aeolian processes.

Afalou *See* Afalou-Bou-Rhummel; Iberomaurusian.

Afalou-Bou-Rhummel (Location 36°45′N, 5°35′E, Algeria) History and general description Site discovered by Camille **Arambourg** in April 1928. It is a rock-shelter located on the southern shore of the Gulf of Bejaïa. The hominin fossils found at this site were described as a distinctive type or race similar to those found only at other North African sites, now called the Afalou or Mechta-Afalou type. Temporal span and how dated? Late Pleistocene/Holocene *c*.15–11 ka. Hominins found at site At least 50 *Homo sapiens* individuals (26 male, 14 female, six juvenile) buried in cemeteries. Archeological evidence found at site **Iberomaurusian**, backed microlithic blades of La Mouillah type and anthropomorphic and zoomorphic clay figurines. Key references: Geology, dating, and paleoenvironment Hachi 1996; Hominins Hachi 1996; Archeology Hachi 1996, Hachi et al. 2002. *See also* **Iberomaurusian**.

Afar Rift System This is part of the **East African Rift System**, which comprises a series of river valleys and basins that extends from the Afar Rift System in the northeast, via the **Main Ethiopian Rift System**, to the **Omo Rift Zone** in the southwest. The Afar Rift System includes the **Gona**, **Middle Awash**, and the **Dikika study areas**.

Afar Triangle *See* **Awash River Basin**.

aff. Abbreviation of affinity. It is a term used in taxonomy to suggest that a specimen belongs to a hypodigm that is closely related to, but not necessarily synonymous with, a known taxon. Thus, a small piece of thick cranial vault might be assigned to "*Homo* aff. *H. erectus*."

Africanthropus* Dreyer, 1935** (Gk *anthropos* = human being; this name refers to a "human-like" creature from Africa) A new **genus** established by Weinert (1939) to accommodate the species ***Palaeoanthropus njarasensis that Kohl-Larsen and Reck (1936) had proposed for the **Eyasi 1** calvaria. Type species ***Africanthropus njarasensis* Weinert, 1939**.

Africanthropus njarasensis* Weinert, 1939 (Reck and Kohl-Larsen, 1936)** Weinert (1939) transferred the **species** previously known as ***Palaeoanthropus njarasensis to a new **genus**, ***Africanthropus***, as *Africanthropus njarasensis*. First discovery **Eyasi 1**. Holotype Eyasi 1. Paratypes N/A. Main sites Eyasi.

Afro-European hypothesis *See* ***Homo heidelbergensis*** **Schoetensack, 1908**.

Afro-European sapiens hypothesis *See* **replacement with hybridization**; **out-of-Africa hypothesis**.

age at maturity This is generally taken to mean age at reproductive maturity. It has been proposed that there is a relationship between life span and age at maturity and specifically that the ratio of adult life span to age at maturity differs among lineages but is fixed within them (Charnov and Berrigan 1990). The relationship between these two variables has been proposed to relate to the cost of reproduction (i.e., older mothers produce offspring that are more likely to survive than younger mothers).

age at weaning Weaning is most often defined as a process that begins with the introduction of supplemental foods to the nursing infant and ends with the complete termination of breast feeding. The length of this process is extremely variable, both within and among species. The end of the weaning process represents a time when offspring are, to varying degrees, responsible for their own foraging, ingestion, and food supply. However, in modern humans and many nonhuman primates, weaned juveniles forage either in different circumstances from adults, or continue to receive provisioning in some way from adults in the group. This is called the period of "postweaning dependency" and it is also seen in other nonprimate mammals, specifically the social carnivores. Among many large-bodied mammalian taxa, the timing of the end of the weaning period coincides with the attainment of a critical body weight by offspring. This weight is measured variably as a multiple of birth weight or as some proportion of adult (specifically maternal) weight.

age estimate In paleoanthropology, an age estimate indicates the number of years that are thought 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**.

age-heaping A common problem in reported ages, where the ages are rounded up or down to particular values, for example ages that end in zeroes or fives. This results in the histogram for ages having "heaps" (higher bars) on the particular ages. Age-heaping is viewed as problematic when using "known-age" samples to work out aging methods, as the age-heaping is a clear sign that the ages are not actually known. As a consequence, some researchers will only use reference skeletal collections that have documented birth and death dates.

agenesis (Gk *a* = absence, without and *genesis* = birth or origin) Absence or lack of development of an anatomical structure. Agenesis is one of the most common dental anomalies seen in modern humans, especially in the third molars. Agenesis of other teeth has been estimated at a frequency of 2–10% depending on the population, with most of these cases involving only one or two teeth. Agenesis also occurs in fossil hominins. For example, at least one individual of ***Homo floresiensis*** (**LB1**) appears to show agenesis of the lower right second premolar (RP_4) and upper right third molar (RM^3). It has been suggested that this may be a consequence of the small size of the individual (Brown et al. 2004), but **KNM-WT 15000** also has agenesis of the M_3s.

agglomerate A coarse-grained clastic rock formed during volcanic activity. The **clast**s range in size from small pebbles to large boulders and tend to be angular in shape; they are usually enclosed in a fine-grained matrix. Examples include the fronts of lava flows where cooling lava on the surface of the flow is broken up and deposited by the underlying still molten portion of the flow; agglomerates also occur within actual volcanic vents where episodes of explosive release of volcanic gases fracture the pre-existing rocks.

aggressive scavenging *See* **scavenging**.

Ahmado The name used by **International Afar Research Expedition** for the **collecting area** now known as **Am-Ado** within the **Woranso-Mille study area**, Central Afar, Ethiopia.

AHOB *See* **Ancient Human Occupation of Britain Project**.

AHS Acronym for Awoke's hominid site at **Omo-Kibish** in the **Omo-Turkana Basin**. It was named after Awoke Amzahe, an Ethiopian scientist who found the fossil. *See also* **Omo-Kibish**.

Ailuropoda-Stegodon* fauna** A cave fauna named after two consistent components, *Ailuropoda*, which is the only genus in the subfamily Ailuropodinae of ursids (i.e., bears) and *Stegodon*, a genus of proboscideans within the extinct subfamily Stegodontinae. The *Ailuropoda-Stegodon* fauna is found in caves in southern China, Vietnam, and Laos, but the existence of distinct lithologies in the caves suggest different environmental settings, the faunal elements also indicate a mixed environmental signal (e.g., ***Pongo indicates a rainforest environment, whereas the presence of horses indicates a more open landscape), and many layers contain a temporal mix of genera (e.g., *Mastodon*, *Stegodon*, and *Elephas*). Most observers now consider the *Ailuropoda-Stegodon* fauna to be a faunal palimpsest (i.e., a mixed assemblage containing elements from several different faunas).

Ain Hanech (also written as Aïn Hanech) (Location 36°16′39’N, 8°19′0’E, Algeria; etym. local settlement name) History and general description Archeological site located within the Ain Hanech Formation in the Ain Boucherit and Ain Hanech areas of northeastern Algeria. The site was discovered and initially excavated by Camille **Arambourg** in 1947 during the course of a paleontological survey conducted between 1931 and 1948; further excavations took place in 1992–3 and 1998–9. This Algerian site has yielded some of the oldest stone tools in North Africa. Temporal span A *terminus post quem* for the site is provided by the Ain Boucherit fossil-bearing stratum, which is estimated to be 2.4–2.0 Ma. The site itself has been estimated to 1.8 Ma. How dated? **Biostratigraphy** and **magnetostratigraphy**. Hominins found at site None. Archeological evidence found at site **Lithic** artifacts have been recovered from layers A (youngest), B, and C within Unit T. These artifacts are considered a North African variant of the **Oldowan** industrial complex. Artifacts recovered from overlying calcretes, paleosols, and colluvia have been attributed to the **Acheulean**. At one time the **Oldowan** and Acheulean artifacts were thought to be associated, but this is now known not to be the case. Key references: Geology and dating Sahnouni et al. 2002; Hominins N/A. Archeology Sahnouni and de Heinzelin 1998, Sahnouni et al. 2002.

A.L. (also written as AL) Acronym for Afar Locality. Prefix for fossils recovered from the **Hadar** study area, Ethiopia.

A.L. 129-1 Site **Hadar**. Locality Afar Locality 129. Surface/*in situ* Surface. Date of discovery

October 30, 1973. Finder Donald **Johanson**. Unit N/A. Horizon N/A. Bed/member Sidi Hakoma. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Basalt. Nearest underlying dated horizon Sidi Hakoma Tuff. Geological age *c*.3.3 Ma. Developmental age Adult. Presumed sex Female, based on small size. Brief anatomical description Well-preserved right distal femur (A.L. 129-1a) and proximal tibia (A.L. 129-1b), with an associated proximal femoral fragment (A.L. 129-1c) broken inferior to the lesser trochanter (NB: A.L. 128-1, a left proximal femur fragment, may belong to the same individual). Announcement Johanson and Taieb 1976. Initial description Johanson and Coppens 1976. Photographs/line drawings and metrical data Johanson and Coppens 1976. Detailed anatomical description Johanson and Coppens 1976. Initial taxonomic allocation Specimen bears morphological similarities to proximal femora assigned to ***Australopithecus*** sp. Taxonomic revisions ***Australopithecus afarensis***. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance One of the first hominin specimens to be recovered from Hadar, its functional morphology was interpreted as evidence of adaptations to **bipedalism**. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 162-28 Site **Hadar**. Locality Afar Locality 162. Surface/*in situ* Surface. Date of discovery 1974. Finder N/A. Unit N/A. Horizon Kada Hadar Tuff. Bed/member Denen Dora. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon BKT-2. Nearest underlying dated horizon Kada Hadar Tuff. Geological age *c*.3.15 Ma. Developmental age Adult. Presumed sex Female. Brief anatomical description Partial calvaria composed of left and right parietals and occipital. Announcement Kimbel et al. 1982. Initial description Kimbel et al. 1982. Photographs/line drawings and metrical data Kimbel et al. 1982. Detailed anatomical description Kimbel et al. 1982. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance Compared to other larger calvariae (e.g. **A.L. 333-45, A.L. 444-2**), the small size of A.L. 162-28 suggests a high level of cranial **sexual dimorphism** in *Au. afarensis*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 199-1 Site **Hadar**. Locality Afar Locality 199. Surface/*in situ* Surface. Date of discovery October 17, 1974. Finder Ato Alemayehu Asfaw. Unit N/A. Horizon N/A. Bed/member Sidi Hakoma. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Basalt. Nearest underlying dated horizon Sidi Hakoma Tuff. Geological age *c*.3.3 Ma. Developmental age Adult. Presumed sex Female, based on small size. Brief anatomical description Right half of the maxilla bearing C–M^3. Announcement Johanson and Taieb 1976. Initial description Johanson and Taieb 1976. Photographs/line drawings and metrical data Kimbel et al. 1976. Detailed anatomical description Johanson and Coppens 1976. Initial taxonomic allocation Specimen bears morphological similarities to ***Australopithecus*** sp. and ***Homo***. Taxonomic revisions ***Australopithecus afarensis***. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance Found within 15 m of, and in the same horizon as, **A.L. 200-1**. Although both bear adult dentitions, A.L. 199-1 is smaller than A.L. 200-1. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 200-1a Site **Hadar**. Locality Afar Locality 200. Surface/*in situ* Surface. Date of discovery October 17, 1974. Finder Ato Alemayehu Asfaw. Unit N/A. Horizon N/A. Bed/member Sidi Hakoma. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Basalt. Nearest underlying dated horizon Sidi Hakoma Tuff. Geological age *c*.3.4 Ma. Developmental age Adult. Presumed sex Uncertain. Brief anatomical description Complete maxilla containing both left and right I^1–M^3. The maxilla has I^2/C diastemata, extensive ribbon-like wear on the incisors and premortem enamel chipping of the C and P^3. Announcement Johanson and Taieb 1976. Initial description Johanson and Taieb 1976. Photographs/line drawings and metrical data Kimbel et al. 1976. Detailed anatomical description Johanson and Coppens 1976. Initial taxonomic allocation It was assessed as bearing morphological similarities to ***Australopithecus*** sp. and ***Homo***. Taxonomic revisions ***Australopithecus afarensis***. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance First complete australopith maxilla from Hadar. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 288-1 Site **Hadar**. Locality Afar Locality 288. Surface/*in situ* Surface. Date of discovery 1974. Finders Donald **Johanson** and team. Unit N/A. Horizon Kada Hadar 1. Bed/member Kada Hadar. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon BKT-2. Nearest underlying dated horizon Kada Hadar Tuff. Geological age *c*.3.2 Ma. Developmental age Adult. Presumed sex Female. Brief anatomical description A.L. 288-1 (or "Lucy") is a remarkably complete **associated skeleton** of a fossil hominin. The cranial vault remains include portions of the parietals, occipital, left zygomatic, and frontal bones. The mandible includes the right P_3–M_3, LP_3, M_3, and two M_1 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 is represented 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. Announcement Johanson and Taieb 1976. Initial description Johanson and Taieb 1976. Photographs/line drawings and metrical data Johanson et al. 1982. Detailed anatomical description Johanson et al. 1982. Initial taxonomic allocation Specimen bears morphological similarities to ***Australopithecus*** sp. Taxonomic revisions ***Australopithecus afarensis***. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance A.L. 288-1 was the first relatively complete hominin associated skeleton of this antiquity, and it remains the best preserved associated skeleton of *Au. afarensis*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 333-1 Site **Hadar**. Locality Afar Locality 333. Surface/*in situ* Surface. Date of discovery 1975. Finder N/A. Unit N/A. Horizon Denen Dora 2. Bed/member Denen Dora. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Kada Hadar Tuff. Nearest underlying dated horizon Triple Tuff-4. Geological age *c*.3.2 Ma. Developmental age Adult. Presumed sex Male, based on canine size. Brief anatomical description Partial facial skeleton, and maxilla containing the right P^3–P^4, left C–P^3. Announcement N/A. Initial description Kimbel et al. 1982. Photographs/line drawings and metrical data Kimbel et al. 1982. Detailed anatomical description Kimbel et al. 1982, 2004. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance This specimen shares the maxillary morphology demonstrated in other *Au. afarensis* specimens (e.g., **A.L. 444-2**) and it was used in the reconstruction of a composite skull of *Au. afarensis*. Along with smaller specimens (e.g., **A.L. 200-1** and **A.L. 417-1**) it demonstrates the extent of the **sexual dimorphism** of the maxillary region and the palate. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 333-45 Site **Hadar**. Locality Afar Locality 333. Surface/*in situ* Surface. Date of discovery 1975. Finder N/A. Unit N/A. Horizon Denen Dora 2. Bed/member NA. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Kada Hadar Tuff. Nearest underlying dated horizon Thin Tuff 4. Geological age *c*.3.2 Ma. Developmental age Adult. Presumed sex Male, based on size and robusticity. Brief anatomical description A cranium that preserves the posterior portion of the cranial vault together with a well-preserved cranial base. Announcement Johanson et al. 1982. Initial description Kimbel et al. 1982. Photographs/line drawings and metrical data Kimbel et al. 1982, 1984. Detailed anatomical description Kimbel et al. 1982. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance First complete adult cranium of *Au. afarensis*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 333-105 Site **Hadar**. Locality Afar Locality 333. Surface/*in situ* Surface. Date of discovery 1975. Finder N/A. Unit N/A. Horizon Denen Dora 2. Bed/member Denen Dora. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Kada Hadar Tuff. Nearest underlying dated horizon Triple Tuff-4. Geological age *c*.3.2 Ma. Developmental age Juvenile. Presumed sex Unknown. Brief anatomical description Distorted, partial juvenile cranium. The cranial vault is represented by the frontal, the right temporal, the posterior portion of the left temporal, parts of the parietals, and fragments of the sphenoid and occipital. The face is represented by the right side of the maxilla (including the right dm$^{1\text{-}2}$, an unerupted M^1, and a di), plus fragments of the nasal, lacrimal, zygomatic, vomer, and palatine bones. Announcement N/A. Initial description Kimbel et al. 1982. Photographs/line drawings and metrical data Kimbel et al. 1982. Detailed anatomical description Kimbel et al. 1982. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance Despite being a juvenile it shows the taxonomically distinctive craniofacial morphology of *Au. afarensis*, and it is the first partially complete juvenile cranium of that taxon. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 333-115 Site **Hadar**. Locality Afar Locality 333. Surface/*in situ* Surface. Date of discovery 1975. Finder N/A. Unit N/A. Horizon Denen Dora. Bed/member Denen Dora 2. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Kada Hadar Tuff. Nearest underlying dated horizon Triple Tuff 4. Geological age *c.*3.2 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description A partial left foot including portions of all five metatarsals, all five proximal phalanges, and the fourth and fifth intermediate phalanges. Announcement Johanson et al. 1982. Initial description Latimer et al. 1982. Photographs/line drawings and metrical data Latimer et al. 1982. Detailed anatomical description Latimer et al. 1982. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance The first articulated foot skeleton of *Au. afarensis*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 400-1a&b Site **Hadar**. Locality Afar Locality 400. Surface. *in situ* Surface. Date of discovery 1976/77. Finder Dato Adan. Unit NA. Horizon Sidi Hakoma 2. Bed/member Sidi Hakoma. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Basalt. Nearest underlying dated horizon Sidi Hakoma Tuff. Geological age *c.*3.3 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description A mandible that includes the left I$_1$–M$_3$ and the right I$_2$–M$_3$ (A.L. 400-1a) and a maxilla with the right canine (A.L. 400-1b). Announcement Johanson et al. 1982. Initial description White and Johanson 1982, Johanson et al. 1982. Photographs/line drawings and metrical data White and Johanson 1982, Johanson et al. 1982. Detailed anatomical description White and Johanson 1982, Johanson et al. 1982. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance One of the most complete and best preserved mandibles of *Au. afarensis*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

A.L. 417-1a–d Site **Hadar**. Locality Afar Locality 417. Surface/*in situ* Surface. Date of discovery 1990–3, 1999. Finders Dato Adan and team. Unit N/A. Horizon Sidi Hakoma. Bed/member 33 m above the Sidi Hakoma Tuff. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon Basalt. Nearest underlying dated horizon Sidi Hakoma Tuff. Geological age *c.*3.3 Ma. Developmental age Adult. Presumed sex Female. Brief anatomical description Skull comprising the well-preserved left side of the mandible including C–M$_3$ (A.L. 417-1a), part of the right side of the mandible with M$_2$–M$_3$ (A.L. 417-1b), the basioccipital, basisphenoid, and right alisphenoid (A.L. 417-1c), and a maxilla including the right I^2–M^3 and the left C–M^3 (A.L. 417-1d). Announcement Kimbel et al. 1994. Initial description Kimbel et al. 1994. Photographs/line drawings and metrical data Kimbel et al. 1994, 2004. Detailed anatomical description Kimbel et al. 1994, 2004. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance This presumed female skull of *Au. afarensis* enabled researchers to assess the extent of cranial **sexual dimorphism** in *Au. afarensis*. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

A.L. 438-1a–v Site **Hadar**. Locality Afar Locality 438. Surface/*in situ* Surface and *in situ*. Date of discovery February 24, 1992. Finders Donald **Johanson** and team. Unit N/A. Horizon Kada Hadar-2. Bed/member 10–12 m below the BKT-2. Formation **Hadar Formation**. Group N/A . Nearest overlying dated horizon BKT-2. Nearest underlying dated horizon KHT. Geological age *c*.3.0 Ma. Developmental age Adult. Presumed sex Male, based on skeletal size and robusticity. Brief anatomical description An **associated skeleton** consisting of a frontal fragment (A.L. 438-1b), the right side of the mandible (A.L. 438-1g) and a fragment of maxilla (A.L. 438-1s). Preserved dental elements consist of the right I_1, P_4 fragment, M_1, M_3 (A.L. 438-1h–k), upper molar root fragment (A.L. 438-1q), and a lower molar root (A.L. 438-1u). The forelimb fossils include a fragment of a clavicle (A.L. 438-1v), a right proximal humeral shaft and two shaft fragments (A.L. 438-1c, n, o), a left ulna (A.L. 438-1a), a right ulna shaft fragment (A.L. 438-1m), a right proximal radial fragment (A.L. 438-1l), and several metacarpals including the right MC2 (A.L. 438-1f) and the left MC2-3 (A.L. 438-1d, e). Announcement Kimbel et al. 1994. Initial description Kimbel et al. 1994. Photographs/line drawings and metrical data Kimbel et al. 1994, 2004, Drapeau et al. 2005. Detailed anatomical description Kimbel et al. 2004, Drapeau et al. 2005. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance The A.L. 438-1 associated skeleton has the most complete ulna of *Au. afarensis*, and it is the first specimen to possess metacarpals in association with forelimb remains. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

A.L. 444-2a–h Site **Hadar**. Locality Afar Locality 444. Surface/*in situ* Surface. Date of discovery February 26, 1992. Finder Yoel Rak. Unit N/A. Horizon N/A. Bed/member Kada Hadar-2. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon BKT-2. Nearest underlying dated horizon Kada Hadar Tuff. Geological age *c*.3.0 Ma. Developmental age Adult. Presumed sex Male. Brief anatomical description Well-preserved (75–80% complete) hominin skull, including the frontal bone (A.L. 444-2d), portions of the right and left parietals (A.L. 444-2d, e, g), a fragment of the left squamous temporal (A.L. 444-2f), the posterior parts of both temporal bones (A.L. 444-2f), the occipital squama (A.L. 444-2f), the right zygomatic (A.L. 444-2c), the maxilla with the right I^1, C, and P^4–M^3 and left I^1, C, and P^3–M^3 (A.L. 444-2a), fragments of the nasal bones (A.L. 444-2h), and the right side of the mandibular corpus and the symphyseal region with left and right incisors, the right canine, and damaged right P_4–M_1 (A.L. 444-2b). Announcement Kimbel et al. 1994. Initial description Kimbel et al. 1994. Photographs/line drawings and metrical data Kimbel et al. 1994, 2004. Detailed anatomical description Kimbel et al. 2004. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current convention taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance First complete adult skull of *Au. afarensis*. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

A.L. 666-1 Site **Hadar**. Locality Afar Locality 666. Surface/*in situ* Surface. Date of discovery November 2, 1994. Finders Ali Yesuf and Maumin Allahendu. Unit N/A. Horizon N/A. Bed/member N/A. Formation **Busidima Formation**. Group N/A. Nearest overlying dated horizon BKT-3. Nearest underlying dated horizon BKT-2. Geological age *c*.2.35 Ma. Developmental age Adult. Presumed sex Male. Brief anatomical description The maxilla, broken along the intermaxillary suture, with the left P^3–M^3, the right P^3–M^1 with M^2 and M^3 roots, and other isolated dental fragments. Announcement Kimbel et al. 1996. Initial description Kimbel et al. 1996. Photographs/line drawings and metrical data Kimbel et al. 1996, 1997. Detailed anatomical description Kimbel et al. 1996, 1997. Initial taxonomic allocation ***Homo*** sp. Taxonomic revisions *Homo* aff. ***Homo habilis***. Current convention taxonomic allocation *H.* aff. *H. habilis*. Informal taxonomic category Transitional hominin. Significance A.L. 666-1 was found in the same layer as **Oldowan flake**s and **chopper**s, and it is the first evidence of a *Homo habilis* facial morphotype in the middle **Pliocene**. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

A.L. 822-1 Site **Hadar**. Locality Afar Locality 822. Surface/*in situ* Surface. Date of discovery October 26, 2000. Finders Dato Adan and team. Unit N/A. Horizon Kada Hadar 1. Bed/member N/A. Formation **Hadar Formation**. Group N/A. Nearest overlying dated horizon BKT-2. Nearest underlying dated horizon KHT. Geological age *c*.3.1 Ma. Developmental age Adult. Presumed sex Female. Brief anatomical description A well-preserved skull that includes a well-preserved mandible with portions of the dentition preserved; most of the calvaria is preserved along with the zygomatics, and the maxilla including the right C–M^3. Announcement Kimbel et al. 2003. Initial description Kimbel et al. 2003. Photographs/line drawings and metrical data N/A. Detailed anatomical description N/A. Initial taxonomic allocation ***Australopithecus afarensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *Au. afarensis*. Informal taxonomic category Archaic hominin. Significance First relatively complete female skull of *Au. afarensis*. Its postcanine dentition is large compared to other inferred female australopith specimens (e.g., **A.L. 417-1**), and the specimen allows for a systematic evaluation of **sexual dimorphism** in *Au. afarensis*. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

^{26}Al/^{10}Be ratio *See* **cosmogenic nuclide dating**.

ALA Abbreviation of Alayla, and the prefix for fossils recovered from Alayla in the **Western Margin**, **Middle Awash study area**, Ethiopia.

ALA-VP-2/10 Site **Alayla**. Locality Alayla VP Locality 2. Surface/*in situ* Surface. Date of discovery July, 1999. Finder Yohannes **Haile-Selassie**. Unit N/A. Horizon N/A. Bed/member Asa Koma Member. Formation **Adu-Asa Formation**. Group N/A. Nearest overlying dated horizon Witti Mixed Magmatic Tuff. Nearest underlying dated horizon Ladina Basaltic Tuff. Geological age *c*.5.2–5.8 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Right side of the mandibular corpus with M_3, together with associated teeth (left I_2, C, P_4, M_2, and part of the M_3 root). Announcement Haile-Selassie 2001. Initial description Haile-Selassie 2001. Photographs/line drawings and metrical data N/A. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus kadabba***. Taxonomic revisions ***Ardipithecus kadabba*** (Haile-Selassie 2004). Current conventional taxonomic allocation *Ar. kadabba*. Informal taxonomic category Possible primitive hominin. Significance **Holotype** of *Ar. kadabba*. Location of original **National Museum of Ethiopia**, Addis Ababa, Ethiopia.

albumin (L. *alba*=white) A **protein** given its name because it turns white when it is heated, or coagulated (it is coagulated albumin that gives the non-yolk part of a cooked egg its white color). Albumin is produced by the liver, and is the most abundant protein in the clear, plasma, component of fresh blood. Its molecular weight is relatively small (67 kDa) and it only contains 585 **amino acid**s in its active form. Its main function is to attract and maintain water in the bloodstream, but it also transports hormones (e.g., thyroid hormone), fatty acids, and bilirubin. The importance of albumin for human evolution is that it was one of the first molecules to be used to measure the closeness of the relationships between the extant **great ape**s. Morris Goodman (1962) obtained albumin from modern humans, **chimpanzee**s, **gorillas**, orangutans, and other primates, and injected it into woolly monkeys. It did not harm the monkeys, but because it was not their own albumin they reacted by generating **antibodies** to the injected **antigen** (i.e., the foreign albumin). Goodman then used the antiserum made when modern human albumin was injected into the woolly monkey to investigate the similarity of albumin antigens between pairs of taxa (e.g., modern human and chimpanzee albumins vs modern human antiserum; modern human and gorilla albumins vs modern human antiserum; chimpanzee and orangutan albumins vs modern human antiserum, etc.). When the modern human antiserum and the fresh albumins from the extant great apes other than *Pan* meet and react with the antiserum, they coagulate and form a white spur. Goodman showed that the reactions between the modern human antiserum and modern human and chimpanzee albumin were so similar there was no spur, yet when modern human antiserum was used to compare the albumins from modern humans and gorillas, there was a definite spur. In 1962 this was a novel use of immunochemistry, and along with Emil Zuckerkandl's (1960) use of chromatography to compare the structure of the hemoglobins of the extant great apes it represented the first use of biomolecules (e.g., albumin and hemoglobin) to compare the molecular affinities of the extant great apes. Jerold Lowenstein (1981) spearheaded attempts to see if it was possible to detect albumin in fossils, and then use this preserved albumin in a form of radioimmunoassay in much the same way that Goodman had used the albumins from living taxa. However, it was never possible to be sure that any albumin extracted from the fossils was undamaged, and this once promising technique has since fallen into disuse. *See also* **immunochemistry**; Morris **Goodman**.

Alcel+A+C *See* **alcelaphine plus antilopine criterion**.

Alcelaphinae (L. *alces* = elk and Gk *elaphus* = deer) In this alternative interpretation of bovid taxonomy, the tribe Alcelaphini is elevated to a subfamilial level. It is a subfamily of antelopes, family **Bovidae**, which comprises hartebeest (the eponymous *Alcelaphus* sp.), wildebeest (*Connochaetes* sp.), and their allies. This subfamily likely arose during the late middle Miocene but it is extremely common in fossil assemblages by the later Pliocene. Modern alcelaphines prefer open grassland habitats and are restricted to Africa, although at least some examples (e.g., *Damalops*) have been recovered from the Asia. The relative proportion of alcelaphine fossils at hominin sites has been used as an important indicator of the presence of open habitats in the past as part of the **alcelaphine plus antilopine criterion** developed by Elisabeth Vrba. *See also* **Alcelaphini**.

alcelaphine Informal name for any antelope belonging to the subfamily **Alcelaphinae**.

alcelaphine plus antilopine criterion (AAC or Alcel+A+C) Developed by Elisabeth Vrba, this is a method of **paleoenvironmental reconstruction** that relies on the relative abundance of **alcelaphine bovids** and **antilopine bovids**. Vrba found that in modern African game reserves characterized by closed habitats, the bovid tribes **Alcelaphini** and **Antilopini** make up a low percentage (<40%) of the bovid sample, whereas in more open habitats they make up a high percentage (>60%) of the bovid sample. The AAC has been widely used in paleoenvironmental studies at **Olduvai Gorge** in Tanzania and at sites in the **Blaauwbank valley** in South Africa.

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 and are characterized by hypsodont teeth and **cursorial** limb adaptations. Most alcelaphine bovids are of medium to large size (about 60–230 kg) and are highly gregarious, often forming large migratory herds. In attempts at the **paleoenvironmental reconstruction** of fossil assemblages, frequencies of alcelaphine bovids are often used to track the presence of open grasslands. For example, in the **Turkana Basin**, changes in the frequencies of fossil alcelaphines, together with other open habitat taxa, has been interpreted as evidence for an expansion of grassland environments associated with the origin of the genus ***Homo***. *See also* **Alcelaphine plus Antilopine Criterion**.

Alemseged, Zeresenay (1969–) Born in Axum, Ethiopia, Zeresenay Alemseged attended Addis Ababa University, graduating in 1990 with a BSc in geology. Thereafter he worked from 1991 to 1993 as a junior geologist in the Paleoanthropology Laboratory of the National Museum of Ethiopia in Addis Ababa. In 1993 he moved to France to enroll as a graduate student in the Institute of Evolutionary Sciences, University of Montpellier II, where in 1994 he obtained an MSc in paleontology. Alemseged stayed in France, but moved to the University of Paris VI for his PhD, which was awarded in 1998 for a thesis entitled "*A. aethiopicus*-*A. boisei* transition and paleoenvironmental changes in the Omo Ethiopia." Alemseged worked from 1998 to 2000 as research associate in the French Center for Ethiopian Studies in Addis Ababa, Ethiopia, then from 2000 to 2003 as postdoctoral research associate in the **Institute of Human Origins** at Arizona State University, and then from 2004 to 2008 as senior researcher in the Department of Human Evolution at the **Max-Planck Institute for Evolutionary Anthropology**, in Leipzig, Germany. Since 2008 he has held the Irvine Chair of Anthropology at the California Academy of Sciences. Zeresenay Alemseged began his investigation of the **Dikika study area** in 1999, and he and Denis Geraads reported **Acheulean** and **Middle Stone Age** tools from the Asbole area. During initial surveys the team identified extensive fossil deposits in the central Dikika area and in 2000 they recovered the first evidence of **DIK-1-1**, the most complete early hominin infant skeleton known and DIK-2-1, the earliest hominin from the **Hadar Formation**. In 2010 the same team also claimed to have discovered the earliest known evidence for tool use and meat consumption. *See also* **DIK-1-1**; **Dikika study area**.

alkenones Complex molecules produced by a limited number of types of algae, used as **biomarkers** in **paleoclimate** research. Alkenones are well-preserved in marine sediments and first appeared in the Cretaceous. They are useful for **paleoclimate** reconstruction because their molecular structure varies with environmental conditions, with warmer **sea**

surface temperatures favoring the diunsaturated over the triunsaturated form. Sea surface temperature reconstructions are computed from a paleoclimate index ($U^{k}37'$) which is based upon the abundance ratio of the diunsaturated to the triunsaturated form of the alkenones. Calibrations are based on *Emiliani huxleyii* which first appeared 250 ka (Pagani et al. 1999). In some lakes, including several in Africa, alkenones have been used to reconstruct lake surface temperature. The carbon isotopic composition of alkenones is also used to reconstruct past carbon dioxide concentrations in the atmosphere, beyond the range of the ice cores (*c*.800 ka). While there are large uncertainties, carbon dioxide levels appear to have been below 500 parts per million since the Oligocene.

allele (Gk *allos* = another) Refers to alternate forms of a **gene** at a specified site, or **locus**, in the **genome**, or alternate forms of a particular **DNA** sequence. For example, if you think of a locus in the genome as the "street address," the allele at that locus is analogous to the type of house present at that address. All houses serve the same purpose of providing shelter but the types of house can differ quite radically (i.e., one may be a luxury mansion while another is a modest bungalow). The genome is arranged into units called **chromosomes**, and with certain exceptions every chromosome is present as a pair in the cell; therefore, for each gene there is a pair of alleles (the exception is the X chromosome in males). 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 (s) in the **heterozygous** form (i.e., Ss). However, if both copies of the beta globin allele are the S type, as in the **homozygous** dominant form (i.e., SS), a person will suffer from sickle-cell anemia.

Allen's Rule This concept (probably better described as a trend) is attributed to Joel Allen (1877). It states that animals living at lower average temperatures tend to have smaller appendages (i.e., shorter limbs or tails). **Neanderthal**s 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 (Trinkaus 1981, Ruff 1994, 2002). These body proportions appear, at least in part, to have resulted from climatic influences (Holliday 1999, Ruff 1994, 2002). This hypothesis is given support by research indicating that limb bone **robusticity** in modern humans might be more influenced by temperature than by habitual activity (Pearson 2000), although others have argued strongly that behavior affects the skeleton more strongly than climate (Finlayson 2004). Relatively early in hominin evolutionary history there is evidence of a relationship between temperature and postcranial morphology, for example the **KNM-WT 15000** associated skeleton has been interpreted as having tropical body proportions (Ruff and Walker 1993). However, it has been argued that KNM-WT 15000 shows signs of skeletal pathology (Ohman et al. 2002) and caution should be exercised before extrapolating from it to other members of the species.

Allia Bay (Location 3°35′4″N, 36°16′4″E, Kenya; etym. takes its name from the bay in Lake Turkana, just south of Koobi Fora) History and general description The site comprises an isolated set of exposures that forms the most southerly subregion of the **Koobi Fora** complex of sites. It includes a *c*.4.2 Ma "bone bed" that was most likely in a meander of a channel of the ancestral Omo River. The first fossil hominins were found in 1982. The collecting areas at Allia Bay are numbered in the same way as they are in other parts of the Koobi Fora site complex, with the numbering starting at 200. Fossil specimens from the site are given the **KNM-ER** prefix. All the fossil hominins from Allia Bay have been assigned to ***Australopithecus anamensis***, although in some respects the fossils from this site resemble younger specimens attributed to ***Australopithecus afarensis*** more than they do conspecifics from the older site of **Kanapoi**. Temporal span All the hominin specimens come from *c*.3.9–4.1 Ma sediments beneath or within the Moiti Tuff which has been dated to 3.97±0.034 Ma (McDougall and Brown 2008). A hominin radius, KNM-ER 20419, was initially described as having been found at a younger locality "east of Allia Bay" (Heinrich et al. 1993, p. 139). However, this specimen's location has since been reported as being "Sibilot" (Ward et al. 1999b, p. 198). How dated? **Argon-argon dating**, **potassium-argon dating**, and **magnetostratigraphy**. Hominins found at site Thirteen hominin specimens found between 1982 and 1995 were described by Leakey et al. (1995); a further 11 found between 1995 and 1997 were announced by Leakey et al. (1998). Archeological evidence found at site None. Key references: Geology and dating Heinrich et al. 1993, Leakey et al. 1995, 1998; Hominins Heinrich et al. 1993, Leakey et al. 1995, 1998, Ward et al. 1999b.

allocortex (Gk *allos* = other and L. *cortex* = bark, thus the "outer covering" of the cerebral cortex) Refers to the parts of the cerebral cortex that have fewer than six layers of cells. Allocortical areas are concerned with the processing of olfaction (i.e., the piriform cortex, which is also called the paleocortex), as well as memory and spatial navigation (i.e., the hippocampus, which is also called the archicortex). *See also* **cerebral cortex**.

allometric *See* **allometry**.

allometry (Gk *allos* = other and *metron* = measure) Towards the end of the 19thC several researchers (e.g., Dubois 1898, 1914, Lapicque 1898, Snell 1891) recognized that there is a predictable relationship between brain size and body size. In the early part of the 20thC, Pezard (1918) and Huxley (1924) introduced the terms "heterogonic" and "constant differential growth," respectively, for this relationship. Huxley (1927, 1931) went on to show that the phenomenon was widespread, and that such a relationship could apply to dimensions of the same individual at different stages in its development, or to the same dimensions of different individuals of the same species at the same or different stages of development. Subsequently, Huxley and Tessier (1936) proposed the term allometry for 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 which is taken as a **proxy** for the whole) of the same organism. Today, the term allometry is used in two senses, which can be a source of confusion. Allometry 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 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 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 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 refers to examples when shape is maintained as size increases. In other words, an isometric variable increases in size at the same rate as body size. *See also* **scaling**.

allopatric *See* **allopatry**; **speciation**; **vicariance biogeography**.

allopatric speciation A mode of speciation in which new species evolve as a consequence of the original species population being divided by a geographic barrier. The resulting physical isolation leads to a loss of gene flow, and the accumulation of genetic differences in the new populations is due to **genetic drift**, **natural selection**, and **mutation**. Eventually, these genetic differences lead to reproductive isolation, such that even if the physical barrier between the populations disappears they remain genetically isolated. Note that peripatric speciation can be thought of as a special case of allopatric speciation.

allopatry (Gk *allos* = other and *patris* = fatherland) When two organisms have geographic ranges that are entirely separate and distinct, and do not overlap anywhere. Given the nature of the fossil record it is difficult to be certain which hominin species were truly allopatric, but, for example, ***Australopithecus africanus*** (southern Africa) and ***Australopithecus afarensis*** (East Africa) were probably allopatric. Allopatric speciation, in which a single species splits into two separate species after a subsection of the ancestral population is geographically and reproductively isolated, is thought to be the most common cause of speciation. Geographic barriers that might promote allopatric speciation include mountain ranges, rifts formed by plate tectonics, substantial rivers, and rising sea levels that form islands out of areas that were previously connected. Forest fragmentation may also cause geographic isolation and hence allopatric speciation. It is likely that allopatric speciation was the mechanism by which many hominin species arose. *See also* **speciation**; **vicariance biogeography**.

alluvial (L. *alluere* = to wash against) 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. *See also* **riverine**.

alpha taxonomy (Gk *alpha* = first, and *taxis* = to arrange or "put in order") Mayr et al. (1953) is one of the few sources that defines the terms "alpha" (and "beta" and "gamma") taxonomy; for example, these terms do not appear in the index of Simpson's (1961) *Principles of Animal Taxonomy*. Mayr et al. (1953) suggest that "the taxonomy of a given group, therefore, passes through several stages...informally referred to as alpha, beta, and gamma taxonomy" (*ibid*, p. 19). The distinction made by Mayr et al. is that alpha taxonomy is about species being "characterized and named," beta taxonomy involves arranging species in "a natural system of lesser and higher categories," and gamma taxonomy involves the "analysis of intraspecific variation" (*ibid*, p. 19). If you subscribe to the philosophy that the reconstruction of phylogeny in the form of a **cladogram** should inform how higher-order taxa are arranged in a classification, then what alpha taxonomy refers to is taxonomy minus **phylogeny reconstruction**, and what Mayr et al. (1953) called beta taxonomy is the process of phylogeny reconstruction. But Mayr et al. (1953) also caution that it is "quite impossible to delimit alpha, beta and gamma taxonomy sharply from one another, since they overlap and intergrade" (*ibid*, p. 19). While it is common for reference to be made to alpha taxonomy, you very seldom read, or hear, any reference to beta or to gamma taxonomy. *See also* **systematics**; **taxonomy**.

Altamura (Location 40°52′21″N, 16°35′17″E, Italy; etym. named after Altamura, a nearby town) History and general description The hominin partial skeleton including a cranium known as Altamura 1 was found in 1993 in a cavity in the Grotta di Lamalunga, a karstic limestone cave near Altamura, Bari, Apulia, in southern Italy. The bones are covered in a variably thick coating of calcareous material. Temporal span and how dated? Biostratigraphic evidence points to a Late Pleistocene date. Hominins found at site **Altamura 1**, most likely belonging to ***Homo neanderthalensis***. Archeological evidence found at site None. Key references: Geology and dating N/A; Hominins Pesce Delfino and Vacca 1993, Vacca and Pesce Delfino 2004; Archeology N/A.

Altamura 1 Site **Altamura**. Locality Grotta di Lamalunga. Surface/*in situ* *In situ*. Date of discovery October 1993. Finders Members of Centro Altamurano Ricerche Speleologiche (C.A.R.S.), the local speleological society and Eligio Vacca of the University of Bari. Unit N/A. Horizon N/A. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Estimated to be **Middle Pleistocene**. Developmental age Adult. Presumed sex? Male. Brief anatomical description Fairly complete skeleton covered with flowstone. Announcement Pesce Delfino and Vacca 1993. Initial description Pesce Delfino and Vacca 1993. Photographs/line drawings and metrical data Pesce Delfino and Vacca 1993, 1996, Vacca and Pesce Delfino 2004. Detailed anatomical description N/A. Initial taxonomic allocation ***Homo neanderthalensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *H. neanderthalensis*. Informal taxonomic category Pre-modern *Homo*. Significance The skeleton purportedly exhibits a mix of Neanderthal and anatomically modern human characteristics, but it is difficult to be sure because its detailed morphology is obscured by a thick layer of **flowstone**. Location of original The skeleton is still *in situ* in Grotta di Lamalunga except for a portion of the scapula that has been removed for DNA analysis.

altricial (L. *alere* = to nourish) The whereabouts of taxa along the altricial–**precocial** spectrum depends upon the state of the newborn. Taxa with newborn that are at a relatively early stage of development at the time of birth are called altricial. Altricial offspring usually have their eyes and ears closed, and they lack fur or feathers and they possess little to no ability to move independently. They are thus reliant on parental units for varying lengths of time after birth for temperature regulation, food, and transport. For instance, domestic cats are altricial because newborn kittens are unable to move on their own, and they rely on the mother to clean them, transport them, and direct them to the nipple. Compared to nonhuman primates, most of which are considered relatively precocial at birth, modern humans are described as secondarily altricial (Portmann 1941) for modern human babies require intensive parental care. The various manifestations of modern human newborn altriciality (e.g., poor temperature regulation, reliance on parents for feeding, poor motor control and coordination) are thought to have evolved as a consequence of a combination of a relatively large **neonate** and a relatively large neonatal brain size that caused the length of gestation to be reduced to increase the likelihood of a successful birth through the modern human birth canal. The high "catch-up" rates of brain growth during the first year of postnatal life are also likely to be consequence of this strategy.

Alu The name given to a **restriction enzyme** cut site with the sequence AGCT. This particular cut site was named "Alu" because it has a sequence recognized by an endonuclease (an enzyme that acts like scissors on specific DNA sequences) isolated from the bacterium *Arthrobacter luteus*. *See also* **Alu repeat elements**.

Alu elements *See* **Alu repeat elements**.

Alu repeat elements A family of short interspersed nucleotide elements (or **SINEs**) of **DNA**, and they are common in all primates, including the **great apes** and modern humans. Each Alu repeat element is approximately 300 **base pairs** (bp) in length, and the origin of **Alu** elements has been traced back to the 7SL RNA gene. Alu repeat elements are a class of retrotransposons (i.e., sequences that are transcribed from DNA to mRNA and then the mRNA is copied back into DNA, which is inserted elsewhere in the genome) and were originally named for the Alu restriction enzyme cut site (with the sequence AGCT) that is typically found within the element. Alu elements account for as much as 10% of the modern human genome (Smit 1996) but less than 0.5% vary (i.e., they are **polymorphic**). Alu repeat elements can help regulate the **transcription** of the DNA sequence by binding regulatory proteins, and they influence evolution via unequal **recombination** of chromosomes and **gene duplication**. They are useful for phylogenetic analyses and for studies of population history because (a) the insertion of an Alu element has a known ancestral state (i.e., no Alu insertion), (b) each Alu insertion is almost certainly homologous since the probability of two insertions at the same location within the genome is very small, (c) Alu insertions are stable, and (d) they are easy to analyze (Batzer et al. 1996, Sherry et al. 1997, Stoneking et al. 1997, Watkins et al. 2001). The most recently active Alu subfamilies in modern humans are the Ya5 and Ya8 subfamilies. Alu elements that are polymorphic within modern humans are especially useful for studies of population history while fixed Alu insertions are useful for phylogenetic studies within primates (Salem et al. 2003).

Alus *See* **Alu repeat elements**.

alveolar process (L. *alveolus* = small hollow, dim. of *alveus* = hollow, and *processus* = to go forward or advance) 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**). The maxillary and the mandibular alveolar processes are where the roots of the upper and lower teeth, respectively, are embedded.

alveoli Plural of **alveolus** (*which see*).

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

AMA Prefix for fossils recovered from the Am-Ado collecting area, **Woranso-Mille study area**, **Afar Rift System**, Ethiopia. *See* **Am-Ado**.

Am-Ado Collecting area initially identified by the **International Afar Research Expedition**, but now within the **Woranso-Mille study area**, **Afar Rift System**, Ethiopia.

Amba East Collecting area within the **Central Awash Complex**, **Middle Awash study area**, Ethiopia.

Amboseli live/dead study This is an elegant use of contemporary data to validate the assumption that bone assemblages at fossil sites are an accurate reflection of the types of animals that lived in and around that site. Two researchers, David Western and Kay Behrensmeyer, collected live/dead census data (i.e., census data for live animals and for animal carcasses in the same location) in the Amboseli National Park across four periods ranging from 5 to 6 years. During each of the four periods, and across the four decades that separated the beginning of the first period and the end of the last, a period that showed "rapid ecological change" (Western and Behrensmeyer 2009, p. 1063), they found highly significant correlations for variables such as **relative taxonomic abundance** between the live and dead data sets. They also found similar values for "standard ecological measures of community structure" (*ibid*, p. 1063). Thus, the study suggests that as long as post-depositional taphonomic biases are taken into account, then at least in tropical settings fossil animal **assemblage**s can be used to make inferences about paleohabitats. *See also* **paleoenvironmental reconstruction**; **taphonomy**.

Ambrona (Location 41°09′34″N, 2°29′55″W, Spain; etym. named after a nearby town) History and general description This site lies along the Masegar River, and it, along with the nearby site of **Torralba**, was originally excavated by Clark **Howell** and Les Freeman in the early 1960s. They believed the sites to be contemporaneous, and presented their finding of many faunal remains, particularly from elephants, and a quantity of stone tools, as the earliest evidence of hunting. Later researchers, including Lewis **Binford** and Richard Klein, argued that the faunal profiles from these sites suggested scavenging, not hunting. The most recent analysis by Santonja and Pérez-González has shown that, first, Ambrona is significantly older than Torralba, and second, there is a mix of natural and human components to the site, and thus too little evidence of actual interaction between the hominins and fauna that it is impossible to say anything more than some butchery occurred at the site. Temporal span and how dated? Based on the **uranium-series dating** of a nearby river terrace, and on fauna and stratigraphic correlation, the site is thought to be from **Oxygen Isotope Stage** 12 (*c*.470–430 ka). Hominins found at site None. Archeological evidence found at site Large quantities of fanual remains, a very few of which have cutmarks, and a few stone tools. Key references: Geology, dating, and paleoenvironment Villa et al. 2005, Freeman 1994, Villa et al. 2005; Hominins N/A; Archeology Freeman 1994, Villa et al. 2005.

AME Prefix for fossils recovered from **Amba East**, **Central Awash Complex**, **Middle Awash study area**, Ethiopia. *See* **Amba East**.

ameloblast [obsolete *amel* = enamel (ME, ultimately from OF *esmail*) and Gk *blastos* = germ] The name given to secretory and maturational (i.e., functional) enamel-forming cells. Ameloblasts are derived from the inner enamel epithelium. As they mature, they become elongated, with their long axis at approximately right angles to the future **enamel-dentine junction** (or EDJ). During enamel formation, secretory ameloblasts move away from the EDJ and secrete enamel matrix from the Tomes' process located on the end of the cell facing the EDJ. The secreted matrix forms elongated **enamel prisms** approximately 5 μm in diameter. Think of the way a long bead of toothpaste is extruded from a toothpaste tube when the latter is squeezed. The free end of the bead is at the EDJ and the longer the tube is squeezed the further away from the EDJ the tube moves. Secretory ameloblasts cease to lay down enamel matrix when the final thickness of enamel is completed. They then switch function and become maturational ameloblasts. These alternately remove water and degraded proteins or pump in calcium to facilitate the final mineralization of enamel. Finally, ameloblasts become the reduced enamel epithelium that covers the crown and then lies dormant until the tooth erupts, after which it is shed. **Short-period** and **long-period incremental lines** produced by ameloblasts are believed to represent interruptions in the secretion or mineralization of the matrix. *See also* **enamel development**; **incremental features**.

amelogenesis [obsolete *amel* = enamel (ME, ultimately from OF *esmail*) and Gk *genesis* = birth or origin] The process of enamel formation by **ameloblast**s. *See also* **enamel development**.

American Institute of Human Paleontology In 1949 the Viking Fund was instrumental in the establishment of this institute. Its aim was to provide a forum to increase knowledge of early humans, and the founding members were Loren C. Eiseley (President), Joseph Birdsell, Paul Fejos, Theodore McCown, Hallam Movius, Dale Stewart, and Sherwood **Washburn**. An important accomplishment of the Institute was to acquire, with financial support from the Wenner-Gren Foundation for Anthropological Research, the Barlow/Damon collection of molds of hominin fossils. The collection was deposited with the University of Pennsylvania Museum of Archaeology and Anthropology and it provided the basis of that museum's hominin casting program. The Barlow/Damon molds were at the Penn Museum from 1952 to 1964 when they were returned to the the Wenner-Gren Foundation for Anthropological Research and put into storage. They were sent back to the University of Pennsylvania Museum of Archaeology and Anthropology in 1980 and they remain there. During the 1950s the Wenner-Gren Foundation supported the research of the plastics engineer, David Gilbert, to develop a new and highly accurate molding technique. This led to the establishment of the Anthrocast program in 1965. The first molds were made in the field in 1962 and molding continued until 1974. Between 1968 and 1976 Anthrocast provided over 16,000 replicas of 180 different fossil specimens to institutions and researchers worldwide. The Anthrocast molds are currently curated in the University of Pennsylvania Museum of Archaeology and Anthropology and casts continue to be available on a limited basis through their casting program. *See also* **Viking Fund**; **Wenner-Gren Foundation for Anthropological Research**.

American Museum of Natural History (or AMNH) In 1869 Albert Smith Bickmore was successful in his proposal to create a natural history museum in New York City. He gained the support of William E. Dodge, Jr, Theodore Roosevelt, Sr, Joseph Choate, and J. Pierpont Morgan. On April 6, 1869 the museum became a reality when the Governor of New York, John Thompson, signed a bill creating the American Museum of Natural History. The collections relevant to paleoanthropology are the extensive collections of northwest coast Native Americans as well as great ape remains. There are 11 *Gorilla gorilla beringei* skeletal specimens all of which are from Zaire (present-day Democratic Republic of the Congo). Most of the 68 *Gorilla gorilla gorilla* skeletal specimens come from the Central African Republic or Cameroon; one comes from the Congo and the rest are unlabelled. None of the 21 skeletal specimens labeled *Gorilla gorilla* have any information about location; there is one *Gorilla* sp. The AMNH also holds the remains of 86 specimens of *Pongo pygmaeus*: 44 of these comprise skeletal remains with the remaining samples comprising soft tissues. The records simply list "Borneo" as the collection location. The great apes are part of the mammals collection. Contact Department of Mammalogy. Tel +1 202 769 5474. E-mail mammvisits@amnh.org.

AMH Acronym for **anatomically modern humans**. *See* ***Homo sapiens***.

amino acid (Gk *ammoniacos* = the pungent resin that is the source of ammonia, NH_3, was first collected from near the temple of Amen in Libya) Relatively small **molecules** that are the components of proteins. There are 20 different standard amino acids. Chemically, amino acids are distinctive in having amine (NH_2) and carboxyl (COOH) groups. If they are attached to the alpha carbon they are called alpha amino acids, and these are the ones that make up the larger protein molecules. Differences in the side chains among amino acids determine their properties (i.e., whether they are acids or bases, hydrophilic or hydrophobic). Amino acids are transported by specific **transfer RNA**s (or tRNAs) and they are joined together in a sequence encoded by messenger **RNA** (mRNA) to form a **polypeptide** chain. The latter process occurs in a reaction catalyzed by **ribosome**s and is referred to as translation. Proteins consist of one or more of these polypeptide chains. *See also* **protein**; **translation**.

amino acid racemization Amino acids exist in two **antimeric** forms, 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**. This apparently regular and predictable process has been used as a **molecular clock** for dating. *See also* **amino acid racemization dating**.

amino acid racemization dating (AARD) The apparently regular and predictable process of **amino acid racemization** has been used as a **molecular clock** for dating, 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 develop **ostrich egg shell dating** but the problem of temperature-dependency persists.

AMOC *See* **Atlantic Meridional Overturning Circulation**.

AMS *See* **accelerator mass spectrometer**.

AMS radiocarbon dating First used in 1977, this is a direct ion-counting method of radiocarbon dating. It uses a particle accelerator to produce ions with a $^{+}3$ charge state and in this state many of the ions that interfere with the counting of ^{14}C can be easily removed, thus allowing the accurate measurement of very low concentrations of ^{14}C. Because this method, called **accelerator mass spectrometry** (or AMS), enables the direct measurement of individual ^{14}C atoms much smaller samples can be processed than with other techniques; AMS can routinely date samples of 1 mg of carbon. This means that previously undateable samples, such as single hominin teeth and individual grains of domesticated cereals, can now be dated. Typical starting weights required for AMS (e.g., 10–20 mg of seed/charcoal/wood, 500 mg of bone, 10–20 mg of shell carbonate) are about 1000 times less than the weights required by conventional counting systems. 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 (Location 32°52′N, 35°30′E, Israel; etym. named after the Wadi Amud) History and general description Amud cave is approximately 5 km northwest of the Sea of Galilee, and is situated in a steep cliff face above the Wadi Amud. Excavations sponsored by the University of Tokyo began in the early 1960s under H. Suzuki. The researchers quickly found **Amud 1**, a fairly complete but poorly preserved adult, presumed male, ***Homo neanderthalensis***, and further excavations by the team recovered fragments of at least three other individuals. The lithic evidence and the morphological affinities of the hominin remains suggested the site represents the transition between the **Middle** and **Upper Paleolithic**. Work was resumed in 1991 by a joint Israeli-American team led by Erella Hovers, Yoel Rak, and William Kimbel. The results of these excavations include a greatly expanded understanding of the lithic industry, the identification and study of fire places and fire-related behavior, the secure dating of the site, and more hominin remains, including an associated skeleton of a neonate, **Amud 7**, that may have been intentionally buried. Temporal span Early comparative analysis of the **Mousterian** lithic industry gave a date of *c*.30 ka, but recent thermo**luminescence dating** on a number of burned lithic artifacts for the various stratigraphic horizons indicates two occupation events, dated to 70 and 55 thousand years ago. A smaller sample of age estimates by electron spin resonance yielded comparable dates. The hominin remains are associated with the younger ages. How dated? Electron spin resonance spectroscopy dating, and thermoluminescence dating. Hominins found at site The remains of 18 hominins have been found, of which seven appear to be under the age of 2 years. They include a fairly complete skeleton of an adult male (Amud 1) and the skeleton of an infant (Amud 7). Archeological evidence found at site The Middle Paleolithic layer, Level B, has been divided into four stratigraphic units, all of which contain lithic assemblages roughly equivalent, but not identical, to those found at Tabun B. Hovers (1998) argues that the dates and appearance of the assemblages from these layers at Amud show that there was not a single sequence of technological change within the Levantine later Middle Paleolithic, as suggested from the archeological sequence at **Tabun**. **Phytolith** studies from sediment samples collected at the site provide evidence of the use of several kinds of plants and suggest that dates, figs, and grass seeds may have been part of the diet of the Amud hominins. Faunal evidence suggests hunting and transport into the site of mostly gazelle and fallow deer. Lithic production activities were differentially organized in the cave's space. Fire places were common features and ashes constitute the majority of the sediment bulk. Key references: Geology and dating Suzuki and Takai 1970, Grün and Stringer 1991, Schwarcz and Rink 1998, Valladas et al. 1999, Rink et al. 2001. Hominins Suzuki and Takai 1970, Rak et al. 1994, 1996, Hovers et al. 1995, Arensburg and Belfer-Cohen 1998; Archeology Suzuki and Takai 1970, Hovers 1998, Hovers et al. 2000, Madella et al. 2002, Rabinovich and Hovers 2004, Alperson-Afil and Hovers 2005, Hovers 2007, Shahack-Gross et al. 2008.

Amud 1 Site **Amud**. Locality N/A. Surface/*in situ* *In situ*. Date of discovery July 1961. Finders H. Suzuki and others. Unit B1/6. Horizon N/A. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age 55 ka. Developmental age Adult. Presumed sex Male. Brief anatomical description A nearly complete but poorly preserved adult skeleton. Announcement Vallois 1962. Initial description Suzuki and Takai 1970. Photographs/line drawings and metrical data Suzuki and Takai 1970. Detailed anatomical description Suzuki and Takai 1970. Initial taxonomic allocation Due to what was seen as its combination of Neanderthal and modern human features, Suzuki (1970) interpreted the skeleton as being intermediate between the **Tabun** and **Shanidar** specimens on the one hand, and the more clearly modern human-like **Skhul** and **Qafzeh** specimens on the other. Taxonomic revisions Hovers et al. (1995) cite a number of cranial and mandibular synapomorphies as evidence that the remains should be assigned to ***Homo neanderthalensis***, but Arensburg and Belfer-Cohen (1998) rejected that proposal. Current conventional taxonomic allocation *H. neanderthalensis*. Informal taxonomic category Pre-modern ***Homo***. Significance At 1740 cm^3, Amud 1 appears to have the largest cranial capacity of any known hominin. Location of original Department of Anatomy, Tel Aviv University, Israel

Amud 7 Site **Amud**. Locality **Middle Paleolithic** layers. Surface/*in situ* *In situ*. Date of discovery 1992. Finders Excavation team led by Yoel Rak, William Kimbel, and Erella Hovers. Unit Layer B2/8, square K3a. Horizon N/A. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age 50–60 ka. Developmental age Neonate (*c*.10 months). Presumed sex Unknown. Brief anatomical description From the cranium, only the occipital, fragmentary parietals, nearly complete mandible, and a few maxillary teeth remain. Several postcranial elements are preserved, including thoracic and limb elements. Announcement Rak et al. 1994. Initial description Rak et al. 1994. Photographs/line drawings and metrical data Rak et al. 1994, 1996. Detailed anatomical description N/A. Initial taxonomic allocation ***Homo neanderthalensis***. Taxonomic revisions N/A. Current conventional taxonomic allocation *H. neanderthalensis*. Informal taxonomic category Pre-modern ***Homo***. Significance The remains of this young individual preserve several morphological features that have been put forward as *H. neanderthalensis* autapomorphies (e.g., an oval foramen magnum and a medial pterygoid tubercule). Location of original Department of Anatomy, Tel Aviv University, Israel.

Amudian (etym. After the site of **Amud**, Israel) A stone tool industry found in the Near East that appears in the late **Middle Paleolithic** or early **Upper Paleolithic**. It is characterized by backed blades and **Levallois**-style flake production.

amygdala (L. *corpus amygdaloideum* from the Gk *amygdalē* = almond) A small almond-shaped complex of neurons in the medial temporal lobe of the **cerebral hemispheres**, located at the tip of the inferior horn of the lateral ventricle, near the tail of the caudate nucleus. It is part of the **limbic system**, and its major function is to attach emotional valence to learning and to consolidate **memory**. The amygdala is reciprocally connected to the **hypothalamus**, **hippocampus**, **neocortex**, and **thalamus**. It also coordinates the actions of the autonomic nervous system and the endocrine system. Barger et al. (2007) showed that the lateral nucleus of the amygdala in modern humans is larger than would be expected based on **allometric** scaling to overall **brain size** in living apes. This relative increase in the volume of the lateral nucleus of the amygdala suggests there has been some reorganization of the amygdala's connections with the orbitofrontal and temporal parts of the **cerebral cortex** in the course of human evolution.

AN Acronym for Abdur North. *See* **Abdur**.

anagenesis (Gk *ana* = up and *genesis* = birth or origin) An evolutionary pattern (or **mode**) in which an ancestral **species** evolves into a descendant species without lineage splitting. Anagenesis is the alternative to **cladogenesis**. For example, it has been claimed that ***Australopithecus anamensis*** and ***Australopithecus afarensis*** are time-successive species in the same lineage (Kimbel et al. 2006) in which case the relationship between them is anagenetic.

anagenetic *See* **anagenesis**.

anagenetic unit *See* **grade**.

analogous (Gk *analogos* = resembling, from *ana* = according to and *logos* = ratio) A trait (i.e., structure, gene, or developmental pathway) in two or more taxa that was *not* inherited from the most recent common ancestor. Analogous traits have similar functions, but not necessarily a similar structure. The eyes of vertebrates and cephalopods (e.g., octopuses) are an example of an analogy. They perform the same basic function, but in the former the retina is inverted (i.e., the receptors are towards the back of the retina, and the nervous connections are deep to them so that the light has to traverse the nervous connections before it reaches the receptors) whereas in cephalopods it is not (i.e., the receptors are towards the front of the retina, and the nervous connections are superficial, so that the light does not have to traverse the nervous connections before it reaches the receptors). *See also* **analogue**; **homologous**; **homoplasy**.

analogue (Gk *analogos* = resembling) An example that serves as an illustration of an organism without being closely related to it. For example, the differences between the masticatory systems of bears and pandas, animals that are distantly related to hominins, has 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*. *See also* **homoplasy**; **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. For example, if cranial capacity and body mass is known for samples of individuals belonging to three different species, ANCOVA can be used to identify whether a significant difference exists between the three species in the scaling relationship between cranial capacity and body mass. The first step determines whether there is a significant interaction between the continuous and categorical independent variables (i.e., do the scaling slopes differ between groups). A significant result indicates the slopes differ significantly from each other, and no further analysis is conducted. A non-significant result indicates that the scaling slope cannot be distinguished statistically between the groups. In that case the next step determines whether the common scaling slope differs significantly from zero, and whether the intercepts differ between groups (e.g., whether cranial size is larger in one species than another at any given body size).

analysis of variance (or ANOVA) A statistical test most 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. A non-significant result indicates that the means of all groups cannot be said to differ from each other significantly. A significant result indicates that the null hypothesis that all means are equal is incorrect; however, when more than two groups are included in the analysis, a significant result does not indicate which group or groups differ from the others. Typically this question is addressed using a series of pairwise tests in which an ANOVA is performed on each possible pair of groups from the total number of groups to identify which groups differ significantly in their means. 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 statistic**al test; an equivalent **non-parametric statistic**al test is the **Kruskal–Wallis test**. ANOVA is appropriate for a single continuous variable, but an extension to the multivariate case is also available. *See also* **multivariate analysis of variance**.

anatomical position The position of the body that is used as a reference when describing the surfaces of the body, the spatial relationships of the body parts, and the movements of the axial and postcranial skeleton. The anatomical position assumes the individual is standing, looking forward, with their legs and feet together, with their arms by their side, and with their palms facing forward. The plane that divides the body into right and left halves is the sagittal plane; it is also called the midline. All the surfaces that face towards the front when an individual is in the anatomical position are called anterior or ventral, and all 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 of the body; lateral is further from the midline of the body. With respect to the limbs, proximal is in the direction of the root of the limb and distal is in the direction of the tips of the fingers or toes. Moving a whole limb forwards is to flex it; moving a whole limb backwards is to extend it. Moving a limb away from the body is to abduct it and 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 reference digit of the hand is the middle finger and the reference digit of the foot is the second toe.

anatomical terminology The first serious systematic study of modern human anatomy in the Western tradition was undertaken by the Greek physicians Herophilus (335–280 BCE) and Erasistratus (304–250 BCE) and the first recorded human dissections were carried out at the Museum and Library of Alexander the Great, in what is now Alexandria, Egypt. However, by the time of Galen, physician to the Roman imperial court in the 2ndC AD, the practice of human dissection had effectively ceased. Its revival was largely due to the efforts of a young anatomy teacher called Andreas Van Wesele (who is better known by the latinized version of his family name, Andreas Vesalius). His seven-volume treatise *De Humani Corporis Fabrica Libri Septem* ("On the Fabric of the Human Body", or just the *Fabrica*) must rank among the foremost contributions to biology. In the Preface to the *Fabrica* Vesalius chronicles his dissatisfaction with his own anatomy teaching and writes that it was during a visit to Bologna in 1540, when he was given the opportunity to compare the skeletons of a monkey and a modern human, that he realized that much of the "human" anatomy described in the Galenic texts was based on monkey and not human anatomy. It was this appreciation that stimulated Vesalius to embark on the dissections on which the *Fabrica* is based. The latter comprises seven "books" totaling approximately 660 pages, or 400,000 words, plus excellent illustrations made by apprentices working in the studio of the painter Tiziano Vecellio, better known as Titian. The *Fabrica* was published in 1543, when Vesalius was still only 29; the scale and pace of Vesalius' achievement is without parallel in biology. This historical preamble explains why the original anatomical terms were Greek, and then why they were subsequently supplemented with Latin terminology. It is important that anatomical terminology transcends the barriers of language so at an early stage it was decided informally that any new anatomical terms should be based on Latin. This policy was formalized in 1895 when the first Basle edition of the *Nomina Anatomica* was produced. In 1950 responsibility for monitoring and maintaining human anatomical nomenclature passed to the International Anatomical Nomenclature Committee (IANC), and in 1989 it was transferred to the Federative Committee on Anatomical Terminology (FCAT). This body, under the aegis of the International Federation of Associations of Anatomists (IFAA), is now responsible for modern human anatomical terminology. The latest version of official modern human anatomical terminology is in a book called *Terminologia Anatomica* (1998). Two versions of each anatomical term are given in the *Terminologia Anatomica*: the Latin version and the approved English language version. English is the official language of anatomical terminology (just as it is the official language for air traffic control). Thus, the English-language version of *corpus mandibulae* is the "body of the mandible" and the English-language version of *facies articularis capitis fibulae* is the "articular facet on the head of the fibula." Some terms are the same in both Latin and English (e.g., sternum, os centrale, tibia, sustentaculum tali). 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". Researchers sometimes use the Latin versions of terms, but if you choose to use *os coxae* instead of the English language terms hip bone or pelvic bone, then logically you should use *os scaphoideum* instead of the scaphoid and *caput ulnae* instead of the head of the ulna. It is best to be consistent and use the English-language term(s) listed in the *Terminologia Anatomica* rather than continuing to use arcane terminology.

ancient DNA (aDNA) (OF *ancien* from the L. *ante*=before and DNA=deoxyribonucleic acid) **Deoxyribonucleic acid**, or DNA, that is extracted from old or poorly preserved bone, teeth, hair, tissue, or coprolites. The analysis of DNA extracted from archeological and paleontological materials is a relatively new area of research that was made possible by the technological revolution in genetics that began in the 1980s. The first experiments to determine whether DNA survived in ancient material used dried tissue, such as skin from a quagga (an extinct form of the plains zebra; Higuchi et al. 1984) and a 2400-year-old Egyptian mummy (Pääbo 1985a), and brain tissue preserved in anoxic conditions under water, such as at Windover Pond and Little Salt Spring, Florida (Doran et al. 1986, Pääbo 1986, Pääbo et al. 1988). A few years later, DNA was extracted from 300 to 5500-year-old modern human bone (Hagelberg et al. 1989). Although early work relevant to hominins primarily demonstrated the presence of DNA in ancient materials, subsequent analyses have addressed questions regarding the relationship between ***Homo neanderthalensis*** 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 (e.g., Krings et al. 1997, Stone and Stoneking 1998, Poinar et al. 2001, Krause et al. 2007a). Most ancient DNA research has targeted **mitochondrial DNA** (mtDNA) because of its high copy number in cells. Several studies have examined nuclear DNA loci, including **Y chromosome** sequences for sex identification and short tandem repeat (STR) loci for determining relatedness among individuals. Most recently, high-throughput emulsion **polymerase chain reaction** (PCR) and pyrosequencing have been used for complete mitochondrial DNA or genome sequencing. One of the major concerns in ancient DNA research is contamination. Precautions must be taken to ensure the authenticity of the results. The so-called criteria of authenticity for ancient DNA results include a physically isolated work area, the extensive use of controls to test reagents, small size of PCR products, cloning of PCR products, assessment of preservation, and reproducibility of results (Handt et al. 1994a, 1996, Richards et al. 1995, Stoneking 1995, Cooper and Poinar 2000). In particular, because ancient DNA analyses are destructive, time-consuming, and expensive, assessments of DNA preservation such as testing the DNA from associated faunal remains or the extent of **amino acid racemization** is recommended. For the latter, high levels of **racemization** are thought to be associated with poor DNA preservation and, specifically, the lower the ratio of the D to L enantiomers of **aspartic acid**, the better DNA preservation is expected to be (Poinar et al. 1996). However, Collins et al. (2009) found no correlation between aspartic acid racemization and DNA preservation in a large sample of ancient specimens from different sites and time periods.

Ancient Human Occupation of Britain Project (AHOB) A project designed to investigate ancient human occupations of Britain and continental Europe from the **Paleolithic** to the Mesolithic. The AHOB project, which has been funded by the Leverhulme Trust, is a multidisciplinary collaborative project directed by Christopher **Stringer** that involves members and associate members from various fields including paleoanthropology, paleontology, archeology, and the earth sciences. The first phase of the AHOB project, which was confined to Great Britain, ran from 2001 to 2006 and its successes included the excavations at **Pakefield**. The second phase extended the scope of investigation from Britain to continental Europe and ran from 2006 to 2009 and included the excavations at **Happisburgh**. The third phase, "Dispersals of Early Humans: Adaptations, frontiers and new territories," began in October 2009, and will run for 3 years, and its members come from Britain, Europe, and North America. The third phase of the AHOB project focuses on four complementary research questions: (a) what is the chronology of human dispersals over the last million years and where were the frontiers of human occupation at different times?, (b) how did the nature of occupation change through time, and what were the factors controlling dispersal into marginal environments: climate, resource availability, and changing geography?, (c) was occupation continuous or episodic, and how viable were human populations at the limits of their range?, and (d) what survival strategies were deployed in these marginal situations: seasonal migration, technological innovation, or physical adaptation? For information about the personnel involved in the AHOB 3 project see www.ahobproject.org/People.php and for the resources and publications produced by the three AHOB projects see www.ahobproject.org/Publications.php.

ANCOVA Acronym for **analysis of covariance** (*which see*).

Andersson, Johan Gunnar (1874–1960) Johan Gunnar Andersson was born in Knista, Sweden, and studied geology at the University of Uppsala. In 1914 Andersson became a geological and mining advisor to the government in China. In this capacity he worked with China's National Geological Survey, led by V.K. Ting (Wenjiang Ding). He became interested in the paleontology and archeology of China and he began searching for fossils in traditional Chinese pharmacies where they were sold for use in traditional medicines. He published a description of some **Neolithic** implements in 1920 and conducted research at a prehistoric site in Hunan in the early 1920s. It was around that time that Andersson learned of a fossiliferous cave site near Peking (now Beijing) called Choukoutien (now **Zhoukoudian**) and in 1919 he published a "Preliminary description of a bone-deposit at Chow-kou-tien in Fang-shan-hsien, Chili Province" in *Geografisker Annaler*. Andersson conducted sporadic excavations at Choukoutien (and at other sites) over the next few years. In 1921 he was joined by the Austrian paleontologist Otto **Zdansky**, and their excavations at Choukoutien began to yield **Cenozoic** fossils, including what was then thought to be the tooth of an anthropoid ape. In 1923 Zdansky left China for Sweden and the fossils he and Andersson had unearthed from Choukoutien were sent to the University of Uppsala for analysis by Zdansky and the paleontologist Carl Wiman. In 1924–5 Wiman and Zdansky found what they interpreted to be a hominin tooth in the collection and this prompted them to suggest that a tooth found in 1921 might have belonged to a hominin and not to an ape. Andersson learned of Wiman and Zdansky's conclusions by letter and with support from the Swedish industrialist Axel Lagrelius the China Fund (which in 1921 became the Swedish China Research Committee) was established to fund and organize paleontological exploration in China, including at Choukoutien. By this time Andersson had enlisted the help of Canadian anatomist Davidson **Black** (they had first met in 1919). Black was initially the Professor of Embryology and Neurology at the newly created **Peking Union Medical College**, and only later did he hold the Chair of Anatomy. He joined forces with Weng Wenhao, who was the director of China's Geological Survey, to conduct large-scale excavations at Choukoutien. In 1926 Andersson founded the Museum of Far Eastern Antiquities in Stockholm, Sweden, to house part of the paleontological and archeological remains he collected in China; the remaining portion stayed in China. Andersson left China in 1925 to become director of the museum, a position he held until 1938, and the excavations in China were left to Black and Weng. The hominin teeth identified by Zdansky (possibly also Wiman), along with subsequent material discovered by Black and his Chinese colleagues at Choukoutien, resulted in the recognition of a new hominin species that Black named *Sinanthropus pekinensis* Black, 1927 (now *Homo erectus*). *See also* ***Sinanthropus pekinensis***; ***Homo erectus***.

Andresen lines The eponymous name recognizes Viggo Andresen's (1898) description of the microstructure of **dentine**. Andresen's name is used for the long-period (greater than **circadian**) incremental features in dentine, which correspond to **striae of Retzius** in enamel (Dean et al. 1993a). They are the 2D manifestation of a 3D structure, namely the surface of the developing dentine. Counts and measurement of Andresen lines have been used to infer the rate of dentine secretion and extension, as well as the age at death in developing teeth (e.g., Dean et al. 1993a, Smith et al. 2006). *See also* **dentine development**; **incremental features**.

androgens (Gk *andro* = male and *gennan* = to produce) A class of steroids with 19 carbon atoms ("C19 steroids") that are produced by conversion of pregnenolone (itself produced from cholesterol) in various tissues in the body but mainly in the gonads and adrenal glands. Androgen steroids include testosterone, dihydrotestosterone (or DHT), and the adrenal androgens dehydroepiandrosterone (or DHEA), and dehydroepiandrosterone sulfate (or DHEAS). Contrary to popular understanding, androgens, while responsible for many aspects of masculine phenotype and behavior, are not strictly "male" hormones. In addition to their importance in normal male fetal and postnatal development, androgens are implicated as playing key potentiating roles in various behaviors in both modern humans and nonhuman primates and their levels are themselves affected by behavior and emotion. For example, seasonal shifts in reproductive behavior and associated agonistic interactions and territorial aggression are associated with changes in gonadal androgen levels. Similarly, gonadal androgens are elevated in modern humans preceding physical or mental contests and they remain elevated in winners of these contests but decline in the losers. Levels of circulating gonadal androgens vary substantially among modern human populations, potentially related to differences in diet and body composition. Prolonged, chronically elevated levels of androgens may be associated with a number of health consequences, including prostate cancer.

Anglian *See* **glacial cycles**.

angular gyrus (L. *angulus* = angle and Gk *gyros* = ring, circle) The angular gyrus of the **cerebral cortex** corresponds to **Brodmann's area** 39, which is part of the inferior parietal cortex. It lies immediately posterior to the **supramarginal gyrus**. The cortex of the angular gyrus is involved in processing the spatial relationships among objects, the semantics of words, and mathematical problems. The cortex of the angular gyrus is also involved in the memory of meaningful gestures and the sequence of actions of the upper limb; hence the angular gyrus, like the supramarginal gyrus, has been implicated in the neural basis of the production and use of **tools**.

angular unconformity *See* **unconformity**.

anisognathous *See* **chewing**.

anisotropy (Gk *an* = not, *iso* = equal, and *tropus* = direction) Meaning directionally dependent. In paleoanthropology, anisotropy is used most commonly either in reference to the material properties of a substance (e.g., **bone** or **enamel**) or to dental microwear textures. Materials are anisotropic when their material properties, particularly their various measures of material behavior (stiffness as reflected by the **elastic modulus** or Young's modulus, shear stiffness as reflected by the **shear modulus**, and the relationship between axial and lateral strains as reflected by **Poisson's ratio**) are different in different directions and/or planes. Bone, like many other biological materials, is anisotropic, although its material properties can approach **orthotropy** or **transverse isotropy**, which can be thought of as special cases of anisotropy. With respect to dental microwear, anisotropy is a term used to describe the orientation of microwear features. Microwear is anisotropic when the features are consistently aligned in a given direction (i.e., as when microwear scratches are parallel). Anisotopic microwear textures are typically found in folivorous primates. *See also* **dental microwear**.

anorthoclase feldspar A mineral of the **feldspar** group in which sodium (Na) and potassium (K) are the dominant cations (i.e., positively charged ions). The chemical formula is (Na or K)$AlSi_3O_8$. Anorthoclase feldspar is common in alkaline (i.e., Na- and K-rich) **lavas** and in the **sediments** derived from them. Older anorthoclase feldspars, especially those with high potassium content, may be suitable for **potassium-argon dating**.

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

antagonistic pleiotropy theory (Gk *pleion* = more) One of several theories put forward to explain the evolution of senescence. The antagonistic pleiotropy theory (Williams 1957) builds upon the premise that a **gene** can have both beneficial and detrimental effects on **fitness**. More specifically, it suggests that genes that confer fitness benefits early in the life cycle and/or at reproductive age may also have deleterious effects later in life. For example, in young males testosterone can benefit fitness through its effects on **body size**, coloration, secondary sexual ornamentation, and competitive behavior. However, later in the life cycle testosterone can have negative effects (e.g., depression of the immune system, or predisposing individuals to prostate cancer, etc.). *See also* **senescence**.

Antarctic Circumpolar Current The ocean current that flows from west to east around Antarctica. It is the strongest ocean current in the world at 125 Sverdrups (or 125×10^6 m^3/s), and it is the dominant feature of the Southern Ocean circulation. It is the cause of the thermal isolation of Antarctica, which has supported a large ice sheet throughout much of the **Cenozoic**.

ante-Néandertalien *See* **pre-Neanderthal hypothesis**.

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

anterior buttress A bony column that begins lateral to the nasal, or piriform, aperture and then runs inferiorly to the **canine eminence**.

anterior cingulate cortex (L. *cingulum* = collar and *cortex* = shell, husk) The cingulate cortex is part of the limbic lobe, the portion of the **cerebral cortex** that wraps around the **corpus callosum**. The cingulate cortex is involved in regulating emotional and cognitive behavior. Its anterior portion is home to a class of large spindle-shaped neurons called **von Economo neurons**, which occur in high densities exclusively among large--brained and social mammals (e.g., whales, dolphins, great apes, modern humans, and elephants). The anterior cingulate cortex has been implicated in emotional self-control, focused problem solving, error recognition, and adaptive responses to changing conditions.

anterior condylar canal *See* **hypoglossal canal**.

anterior fovea *See* **fovea**; **fovea anterior (mandibular)**; **fovea anterior (maxillary)**.

anterior fovea (mandibular) *See* **fovea anterior (mandibular)**.

anterior fovea (maxillary) *See* **fovea anterior (maxillary)**.

anterior pillars Columns of bone described by Yoel Rak that run from the side of the nasal, or piriform, aperture down to the **alveolar process** of the upper jaw. Rak (1983) makes the point that the anterior pillars are found in many (e.g., **Sts 5**, **Sts 71**, Sts 17, Stw 13), but not all (e.g., Sts 52a), of the faces of ***Australopithecus africanus*** (anterior pillars are also present on **Stw 252**, a specimen found subsequent to Rak's 1983 study). They are also present in a reduced form in ***Paranthropus robustus***, but they are not seen as distinct structures in ***Australopithecus afarensis***, in most ***Paranthropus boisei*** specimens (but note that the presumed *P. boisei* female, **KNM-ER 732**, has an anterior pillar), or in **KNM-WT 17000**. Some ***Homo*** specimens are also said to have an anterior pillar (e.g., **Stw 53**, **OH 24**). The anterior pillar is often confused with, but is distinct from, the **canine jugum** that covers the root of the upper canine, and some specimens (e.g., Sts 5) display both structures.

anterior teeth Refers to the two incisors and the canine in each quadrant of the jaws; the balance of the teeth in the tooth row are referred to as the posterior, or **postcanine teeth**.

anterior transverse crest Term used by Korenhof (1960) for a structure on the crowns of the maxillary postcanine teeth that others call the **mesial marginal ridge** (*which see*).

anterior trigon crest Term used by Robinson (1956) and Tobias (1967a) for a structure on the crowns of the maxillary postcanine teeth that others call the **mesial marginal ridge** (*which see*).

anthracothere *See* **Anthracotheriidae**.

Anthracotheriid Unit (AU) The fossiliferous unit at **Toros-Menalla**, one of several "fossiliferous areas" discovered in the **Chad Basin** by the **Mission Paléoanthropologique Franco-Tchadienne**. The Anthracotheriid Unit was initially dated to 6–7 Ma using biochronology, but more recently **cosmogenic nuclide dating** suggests an age range of 6.8–7.2 Ma. *See also* **Anthracotheriidae**; **Toros-Menalla**.

Anthracotheriidae (Gk *anthrax* = coal or carbuncle, *therion* = beast) A family of **artiodactyls** that lived in the Old World and North America. They arose at the end of the middle Eocene in Asia and were extinct in Africa by the late Miocene. Anthracotheres are quite variable in their dental morphology, ranging from bunodont to selenodont in tooth form. Physically, they appear to have been ectomorphic, having relatively big bodies and small heads and limbs. Some forms (e.g., *Bothriogenys*) likely inhabited semi-aquatic habitats. Their dental and body forms, supposed habitats, and the fact that they disappeared as true hippopotamus arose lead many to consider them as stem hippos, but they are not universally accepted as ancestors of the Hippopotamidae.

Anthrocast *See* **American Institute of Human Paleontology**.

anthropogenic bone modification Any alteration of the completeness, structure, or surface of bone resulting from hominin activities. It subsumes bone surface modifications (e.g., cutmarks and hammerstone percussion marks) and fracture/breakage patterns associated with carcass butchery and dismemberment, marrow processing, and grease extraction. Other forms of anthropogenic bone modification include tooth marks and digestion, heating, and burning, and use-wear on bone tools. However, anthropogenic tooth marks and evidence of digestion can be difficult to distinguish from similar modifications produced by other taphonomic agents, such as carnivores. Recognition of anthropogenic bone modifications is central to demonstrating that a fossil bone assemblage has been accumulated by hominins and/or altered by hominin activities, as opposed to other taphonomic agents including carnivores, porcupines, or fluvial processes. *See also* **bone breakage patterns**.

anthropoid (Gk *anthropos* = human being) Primates that are relatively modern-human-like.

It is usually used in one of two senses, either to refer 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 Anthropoidea (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 only correct one.

anthropoid apes *See* anthropoid.

Anthropopithecus* de Blainville, 1839** (Gk *anthropos* = human being and *pithekos* = ape-like) A **genus** created by Henri Marie Ducrotay de Blainville (1839) to accommodate chimpanzee material, but because it postdates Oken's 1816 designation of ***Pan, it is a **junior synonym** of *Pan*. *Anthropopithecus* was sometimes used as the generic name for any great ape, but for much of the 19thC it was the genus name of choice for chimpanzees (e.g., Sutton 1883). It was the genus used by Pilgrim for *Anthropopithecus sivalensis*, a fossil ape from the Siwaliks, and Eugène **Dubois** (1893) used the same genus to accommodate ***Anthropopithecus erectus***, the species he introduced to accommodate the **Trinil 2** skullcap. However, Dubois subsequently abandoned *Anthropopithecus*, replacing it with *Pithecanthropus* (Dubois 1894), and later still Weidenreich (1940) subsumed *Pithecanthropus* into ***Homo***. *See also* ***Pithecanthropus***.

Anthropopithecus erectus* Dubois, 1893** (Gk *anthropos* = human being, *pithekos* = ape-like, and L. *erectus* = to set upright) (*NB: this citation is often given the year 1892, but it should be 1893. Dubois was obliged to submit official reports of his field activities to the government of **Batavia**, and although he first refers to *Anthropopithecus erectus* in the report of his field activities for the third quarter of 1892, the report was not published as a government document until 1893) A **hominin** species established by Eugène **Dubois** (1893) to accommodate the **Trinil 2** skullcap. The sequence of events was as follows: in 1891 Dubois reported that at **Trinil** "The most important find is a molar (upper third molar) of a chimpanzee (Anthropopithecus***). This genus of humanlike apes, now present in West- and Central Equatorial Africa, lived in Pliocene times in British India and, as is clear from the discovery, also during Pleistocene periods in Java" (Dubois 1891, pp. 13–14) (this, and all the subsequent translations from Dutch are by kind favor of John de Vos). Later in the same year (but published in 1892) he reported that "Close to the site at the left bank of the river where the molar was found, a very nice skullcap was found, which, like the the molar, must undoubtedly attributed to the genus *Anthropopithecus* (*Troglodytes*)" (Dubois 1892, pp. 13–14). Later in the same report Dubois wrote that "With the Pliocene *Anthropopithecus sivalensis*, of which only an incomplete upper jaw is known, only the molar is comparable, however in a limited amount. Probably one cannot exclude a close relation between both," and he continued "The above mentioned *Anthropopithecus sivalensis* [originally described under the name of *Palaeopithecus* and then as *Troglodytes*] represented by an incomplete upper jaw in the Pliocene of the Punjab in 1878 discovered by Theobald" (*ibid*, pp. 13–14). However, it was not until 1892, and the discovery of the straight-shafted **Trinil 3** femur, that Dubois decided to name the new taxon *Anthropopithecus erectus*, and in the same year (but published in 1893) he wrote that "The three discovered skeletal elements show that *Anthropopithecus erectus* Eug. Dubois is closer to Man than any other of the anthropoid apes, the most by the femur…" (Dubois 1893, p. 11). In Dubois' report for the last quarter of 1893 (Dubois 1894, p.14) the new taxon was subsequently transferred to the genus ***Pithecanthropus* Haeckel, 1868**, as *Pithecanthropus erectus*, and much later it was transferred to ***Homo*** by Weidenreich (1940). *See also* ***Homo erectus***; ***Homo erectus javanensis***; ***Pithecanthropus erectus***.

antibody (Gk *anti*=opposite and ME *body* = container) Antibodies (also known as immunoglobulins or Igs) are **proteins** that are part of the immune system. They are produced by lymphocytes (a type of white blood cell) when the former react with foreign particles (e.g., bacteria and viruses) collectively called **antigens**. Each antibody reacts to a specific antigen, binding with it and then tagging it for destruction by other parts of the immune system, or blocking it directly from growing or causing damage. Antibodies may be free and soluble, and found in blood and tissue fluids, or they may be bound to the surface of a type of white cell (a type of lymphocyte called B cells, so-called because they mature in the bursa of

Fabricius in birds). Antibodies consist of four chains of **amino acids**, two heavy ones and two light ones. There are five types of antibody: IgA, IgD, IgE, IgG, and IgM. These are defined by differences in the structures, functions, and properties of their heavy amino acid chains. Antibodies raised against foreign albumins are the basis of the experiments undertaken by Morris **Goodman** to investigate the relationships among the **great apes**. *See also* **albumin**.

anticline (Gk *anti* = against and *klinein* = to slope) In structural geology this is a type of fold where the oldest rocks occupy the center of the structure and the rocks become progressively younger towards the margins. The simplest form of anticline is a symmetrical arch-shaped fold, which is open downwards. Such folds are important in geological and paleontological fieldwork, as they will determine the direction in which successively older or younger strata are encountered and will cause a repetition of the **outcrop** pattern on either side of the fold's axis. They are common features in tectonically active areas.

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

antigen (from *anti*body *gen*eration) Any foreign molecule capable of stimulating the production of an antibody, or of provoking other responses by the immune system. *See also* **antibody**.

antilopine *See* **Antilopini**.

Antilopini (Gk *antholpos* = a fabulous beast from the orient) A tribe of the family **Bovidae** that includes the gazelles and their allies. Extant members of the tribe include springbok (*Antidorcas marsupialis*), Grant's gazelle (*Gazella granti*), and Thomson's gazelle (*Gazella thomsoni*). Antilopine **bovid**s are of small to medium size (approximately 15–65 kg) and they exhibit adaptations for **cursorial** behavior (i.e., running) suited for the open and arid grasslands they typically inhabit. In **paleoenvironmental reconstruction**s of fossil assemblages, high frequencies of antilopine and **alcelaphine bovids** are generally interpreted as indicating open habitats. *See also* **antilopine and alcelaphine criterion**.

antimere (Gk *anti* = opposite and *meros* = a part) Refers to the version of a bilateral structure that belongs to the opposite side of the body [e.g., "the crown area of the right P_3 of **KNM-ER 992** is larger than its antimere" (i.e., the left P_3)]. Amino acids come in forms that are antimeres (e.g., D- and L-forms) and the rate of conversion from one antimere to the other has been used as a dating method. *See also* **amino acid racemization dating**; **ostrich egg shell dating**.

antimeric *See* **antimere**.

anvil A stationary object against which another object, such as 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). Anvils can also be used in combination with a hammer, made of stone (a **hammerstone**) or wood. The object to be fractured (e.g., bone, core, nut) is rested on the anvil surface and struck from above with the **hammer**. Bones fractured with the "hammer-and-anvil" technique frequently have opposing load points and surface damage attributable to both the hammerstone and the anvil. Stone cores flaked using a hammer-and-anvil or bipolar technique usually have flakes removed from both ends. *See also* **bipolar**; **chimpanzee tool-use**.

Anyskop Blowout (Location 32°58′11.6″S, 18°06′50.66″E, South Africa; etym. in Afrikaans *anyskop* translates to "anise hill") History and general description This open-air archeological locality is located within the boundaries of the West Coast Fossil Park, approximately 1 km/0.6 miles south of the site of **Langebaanweg**. Discovered in the late 1970s, this site was extensively collected and excavated in 2001 and 2002 by researchers from the University of Tübingen, Germany. The archeological remains provide clear evidence that archaic and modern humans occupied this elevated setting during all of the southern African archeological periods, including the **Early Stone Age**, the **Middle Stone Age**, and the **Later Stone Age**. Temporal span and how dated? Allocation to the Early, Middle and Late Stone Ages is based on the types of artifact. Hominins found at site None. Archeological evidence found at site Stone tools (see above), **Late Pleistocene** and **Holocene** fauna, ceramics, and hearths. Key references: Hominins N/A; Archeology Conrad

2001, 2002, Dietl 2004, Dietl et al. 2005, Kandel 2006. *See also* **Later Stone Age**.

apatite (Gk *apate* = deceit, because of apatite's reputation for being confused with other minerals) Apatite is one of the common names (hydroxyapatite and bioapatite are others) used for the dominant mineral phase of **bone**, **cementum**, and **dentine**, as well as **enamel**. The proper name for bioapatite or hydroxyapatite is apatitic calcium phosphate, chemical formula $Ca_{10}(PO_4)_6(OH)_2$. Bioapatite or hydroxyapatite makes up approximately 96% of the mineral phase of mature enamel, and this high proportion is responsible for the latter's extreme hardness and resilience to **diagenesis**.

ape (OE *apa* = ill-bred and clumsy. Groves (2008) suggests that *apa* became *apan* (pl.), *apan* became *apen*, and then approximately 1350 years BP *apen* became apes. Before the apes had been investigated scientifically and appreciated on their own terms, they were regarded as being "clumsy" because they lacked **dexterity**) Refers to an informal taxonomic category that includes extant and fossil taxa and it is coincident with the superfamily **Hominoidea**. The extant taxa in this superfamily are chimpanzees/bonobos, gorillas, orangutans and gibbons/siamangs; the fossil taxa are all the extinct forms that are more closely related to chimpanzees/bonobos, gorillas, orangutans and the gibbons/siamangs than to any other living taxon. In the traditional, pre-molecular, taxonomy the informal term ape was equivalent to the families Pongidae and Hylobatidae. syn. hominoid.

ape hand All extant apes are capable of specialized suspensory and climbing behaviors and thus the ape hand, more so than the modern human hand, is well adapted for grasping by hook-like flexed fingers. Extant ape fingers are relatively long and the phalanges are curved to facilitate hanging and grasping. The thumb is relatively short and is not usually used during these locomotor behaviors. These adaptations, and others such as a highly mobile midcarpal joint, are particularly accentuated in orangutans, gibbons, and siamangs to facilitate suspension and, in the hylobatids, ricochetal brachiating (Lewis 1989). The gorilla, in contrast, has relatively shorter and straighter phalanges compared to other apes because of its frequent use of terrestrial locomotion. African apes differ from Asian apes in having **scaphoid-os centrale fusion**, extra bony ridges, and the bevelling of articular surfaces that make the wrist and finger joints more stable. This increased stability has been interpreted as being advantageous for knuckle-walking locomotion (Tuttle 1969, Richmond et al. 2001).

apical closure The developmental condition that signifies the closing of the root canal at its distal, or apical, end. At this point the growth in length of the root (also called extension) ceases, although secondary dentine secretion continues within the pulp cavity. Apical closure, which is traditionally taken as the final stage of **tooth formation**, can be evident macroscopically, microscopically, or radiographically.

apical tuft (L. *apex* = point and OF *tof(f)e* = projection) The most distal part of the distal phalanx of a **manual digit**. The fingers of the primate **hand** each comprise three bones, called the **proximal**, intermediate, and distal phalanges. The small distal phalanx has a base, a shaft, and an apex. In higher primates the apex is rounded and takes the form of a bony excrescence called an apical tuft. The edges of this apical tuft extend more proximally than does its mid-part, and they are referred to as ungual spines. The apical tuft provides bony support for the nail and for the soft tissue, or pulp, that lies beneath the nail. The apical tuft is markedly enlarged in modern humans and in ***Homo neanderthalensis***, and it is relatively enlarged in chimpanzees and gorillas compared to other primates. In modern humans, the expanded apical tuft supports the elaboration of a pulpy pad (the "ungual pulp") on the palmar side of the distal phalanx. This palmar pad is functionally compartmentalized such that only the distal end is tethered by ligaments to the bone while the proximal end is more flexible, allowing for deformation in various ways during grasping of objects (Marzke and Marzke 2000) (syn. ungual process, tuberosity, or tuft) (Susman 1979).

Apidima (Location Mani peninsula, Southern Greece; etym. local dialect of Greek for "jump", probably referring to the steep sea-side cliff face where the caves are located) History and general description Discovered in 1978 and partially excavated between 1978 and 1985, the site comprises four limestone caves accessible only by sea.

Temporal span Dating investigations have proved to be inconclusive. Cave A is probably **Middle Pleistocene**, and Cave Γ possibly **Late Pleistocene**. How dated? **Biostratigraphy**, lithic typology, and morphology of the hominin remains. Hominins found at site Cave A: Apidima 1 and 2; Cave Γ: Apidima 3. Archeological evidence found at site Stone artifacts reported from Cave Γ, possibly **Upper Paleolithic**. Key references: Geology and dating Lax 1995, Liritzis and Maniatis 1995; Hominins Pitsios 1985, Harvati and Delson 1999; Archeology Darlas 1995. *See also* **Apidima 1 and 2**; **Apidima 3**.

Apidima 1 and 2 Site **Apidima**. Locality Cave A. Surface/*in situ* *In situ*. Date of discovery 1978. Finders Team from National Kapodistrian University. Unit N/A. Horizon N/A. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Probably **Middle Pleistocene** on morphological grounds. Developmental age Adult. Presumed sex Apidima 2 proposed Female. Brief anatomical description Two crania; Apidima 2 is largely complete, whereas Apidima 1 lacks a face and the superior part of the cranial vault. Announcement Pitsios 1985. Initial description Koutselinis et al. 1995. Photographs/line drawings and metrical data Koutselinis et al. 1995. Initial taxonomic allocation No proper classification or description exists. Taxonomic revisions N/A. Current conventional taxonomic allocation **Pre-Neanderthal** (Harvati and Delson 1999). Significance These specimens represent two out of the total of three fossil hominin crania from the Middle Pleistocene of southeastern Europe. Location of original Anthropological Museum, National Kapodistrian University, Athens, Greece. *See also* **Apidima**.

Apidima 3 Site **Apidima**. Locality Cave Γ. Surface/*in situ* *In situ*. Date of discovery 1984. Finders Excavating team from the National Kapodistrian University. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Possibly Late-Terminal Pleistocene. Developmental age Young adult. Presumed sex Female. Brief anatomical description Largely complete skeleton of a modern human, presumably female and possibly a burial. Announcement Pitsios 1985. Initial description Mompheratou and Pitsios 1995. Line drawings Mompheratou and Pitsios 1995. Initial taxonomic allocation ***Homo sapiens***. Significance Possible **Upper Paleolithic** burial. The brief description of the stone artifacts suggests they may be **Aurignacian**. The **Upper Paleolithic**, and the Aurignacian in particular, is almost completely absent from the fossil and archeological records of Greece. Location of original Anthropological Museum, National Kapodistrian University, Athens, Greece. *See also* **Apidima**.

Apollo 11 Cave (Location 27°45′S, 17°06′E, Namibia; etym. named after the 1969 return flight and landing of Apollo 11 spacecraft, which occurred the day excavations commenced) History and general description A large (28 m×11 m) limestone cave on the western slopes of the Huns Mountains. W.E. Wendt excavated 12 m^2 to a maximum depth of approximately 2 m, recovering more than 50,000 lithic and faunal remains. The site contains a number of **Middle Stone Age** strata including Howieson's Poort and Still Bay levels. Stone slabs with painted representations of a rhinoceros and an animal, or perhaps modern human, form are among the earliest known examples of ***art mobilier***, with age estimates using all the available data ranging from *c*.20 to 59 ka. Temporal span Wendt recognized eight strata (A–H from top to bottom) separated by unconformities; Jacobs et al. (2008) further subdivided the strata, although correlations with Wendt's scheme are not provided. The sediments have been dated by single-grain optically stimulated **luminescence dating** on **sand**, conventional **radiocarbon dating** of charcoal, and **accelerator mass spectrometry** age estimates and **amino acid racemization dating** on ostrich egg shell. The pooled samples of age estimates suggests discontinuous hominin occupation of the cave from *c*.0.3 ka to more than 83 ka. Excluding conventional radiocarbon age estimates from the 1970s, the stratum containing the painted slabs (Layer E of Wendt 1976) has an estimated age of 41–59 ka. How dated? ^{14}C, amino acid racemization dating, accelerator mass spectrometry, and optically stimulated luminescence dating. Hominins found at site None. Archeological evidence found at site More than 27,000 stone artifacts and more than 23,000 faunal elements have been recovered from the Apollo 11 Cave excavations. The former have been divided by Wendt and later researchers into (from bottom to top) early Middle Stone Age, Still Bay, Howieson's Poort, late Middle Stone Age, early **Later Stone Age**, Later Stone Age, and pottery-bearing strata. Apollo 11 Cave reflects the northernmost and westernmost limit of known Still Bay sites, and in addition to the distinctive bifacial points, the Still Bay stratum there (Layer G of Wendt 1976, Komplex 2 of Vogelsang 1998) also contains worked **hematite** and **bone tools**. Incised and perhaps painted ostrich egg shell fragments also occur in overlying levels (i.e., Layers F and E of Wendt 1976, and Komplex 3 and 4 of Vogelsang 1998). The associated fauna is interpreted as primarily the result of hominin accumulation, with the notable selective transport of high-utility elements of large **antelope**s that were subsequently discarded in the cave. Key references: Geology and dating Wendt 1976, Vogelsang 1998, Miller et al. 1999, Jacobs et al. 2008; Archeology Wendt 1976, Thackeray 1979, Vogelsang 1998, Jacobs et al. 2008.

apomorphic (Gk *apo* = different from and *morph* = form) A term used in **cladistic analysis** to refer to the state of a **character** that is different from the ancestral or **primitive** condition of that character. Hence it is a "catch-all" word that refers to any derived **character state**. For example, within the hominin clade there are two morphoclines for anterior lower premolar (P_3) root morphology. One leads from the primitive condition [i.e., two roots, one mesiobuccal and one distal (2R: MB+D)] to a derived morphology of root reduction [i.e., a single conical root (1R)], whereas the other leads to a derived morphology of further root complexity [i.e., two plate-like roots, one mesial and one distal (2R: M+D)]. Both of these character states are apomorphic. 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. *See also* **autapomorphy**; **synapomorphy**.

apomorphy (Gk *apo* = different from and *morph* = form) *See* **apomorphic**.

apoptosis (Gk *apo* = from, and *ptosis* = falling) A process (also called programmed cell death) whereby cells in a multicellular organism die according to a program determined by the cell. Apoptosis plays important roles in development, homeostasis, the removal of damaged cells, and the prevention of cancer. There is much apoptosis during the development of the brain, and most of the tubes of the body (e.g., the tear duct) start as a solid core of cells that becomes tubular when the cells in the middle of the core undergo apoptosis.

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

appositional enamel (L. *appositus* = to put near) Strictly speaking, all enamel is appositional, but this term usually refers to the enamel formed during the initial phase of enamel formation, or cuspal enamel. *See also* **cuspal enamel**; **enamel development**.

appositional growth *See* **ossification**.

approximal wear *See* **interproximal wear**.

aptation (L. *adaptare* = to fit) There are two main categories of aptations. 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 what is now a functional trait was non-functional prior to its being co-opted for its current function, then the trait is referred to as an exaptation (*sensu* Gould and Vrba 1982). *See also* **adaptation**; **exaptation**.

^{40}Ar/^{39}Ar *See* **argon-argon dating**.

ARA *See* **Aramis**.

ARA-VP Acronym for Aramis – Vertebrate Paleontology. Prefix for fossils recovered from **Aramis**, **Middle Awash study area**, Ethiopia.

ARA-VP-1/1 Site **Aramis**. Locality Aramis VP Locality 1. Surface/*in situ* Surface. Date of discovery December 17, 1992. Finder Gen Suwa. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation **Sagantole Formation**. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Right M^3. Announcement White et al. 1994. Initial description White et al. (1994). Photographs/line drawings and metrical data White et al. 1994, Suwa et al. 2009a. Detailed anatomical description N/A. Initial taxonomic allocation ***Australopithecus ramidus***. Taxonomic revisions ***Ardipithecus ramidus***. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance First specimen of *Ar. ramidus* to be discovered. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-1/300 Site **Aramis**. Locality Aramis VP Locality 1. Surface/*in situ* Surface. Date of discovery December 26, 1993. Finder Unknown. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Associated permanent dentition that includes the crowns and roots of at least one side of all the upper teeth (ARA-VP-1/300A–M) and of all the lower teeth (ARA-VP-1/300N–ZA). Announcement White et al. 2009a. Initial description Suwa et al. 2009a. Photographs/line drawings and metrical data Suwa et al. 2009a. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus***. Taxonomic revisions None. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance Excellently preserved dentition of a single *Ar. ramidus* individual. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-1/401 Site **Aramis**. Locality Aramis VP Locality 1. Surface/*in situ* Surface. Date of discovery December 27, 1993. Finder Unknown. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description The symphysis and both sides of the corpus of a subadult mandible containing the crowns and roots of the left and right I_1–M_1, plus the left M_2. Announcement White et al. 2009a. Initial description N/A. Photographs/line drawings and metrical data Suwa et al. 2009b. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus***. Taxonomic revisions None. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance The best preserved mandible of *Ar. ramidus*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-1/500 Site **Aramis**. Locality Aramis VP Locality 1. Surface/*in situ* Surface. Date of discovery December 28, 1993. Finder Unknown. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Three pieces (right and left temporal and occipital) of a partial adult cranium. Announcement White et al. 2009a. Initial description Suwa et al. 2009b. Photographs/line drawings and metrical data Suwa et al. 2009b. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus***. Taxonomic revisions None. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance The three pieces (right and left temporal and occipital) of this partial adult cranium were used in the reconstruction of the cranium of the **ARA-VP-6/500** associated skeleton. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-1/701 Site **Aramis**. Locality Aramis VP Locality 1. Surface/*in situ* Surface. Date of discovery December 20, 1994. Finder Unknown. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Proximal end of a left femur. Announcement White et al. 2009a. Initial description Lovejoy et al. 2009b. Photographs/line drawings and metrical data Lovejoy et al. 2009b. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus***. Taxonomic revisions None. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance A fragment of the proximal end of the left femur, one of only two proximal femoral fragments (the other is **ARA-VP-6/500**–5) in the *Ar. ramidus* hypodigm. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-6/1 Site **Aramis**. Locality Aramis VP Locality 6. Surface/*in situ* Surface. Date of discovery December 29, 1993. Finder Gada Hamed. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Several associated teeth, including the left I^1, $\underline{C}$, P^3, and P^4, and right, I^1, $\underline{C}$, P^4, M^2, P$_3$ and P$_4$. Announcement White et al. 1994. Initial description White et al. 1994. Photographs/line drawings and metrical data White et al. 1994, Suwa et al. 2009a. Detailed anatomical description N/A. Initial taxonomic allocation ***Australopithecus ramidus***. Taxonomic revisions ***Ardipithecus ramidus***. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance **Holotype** of *Ar. ramidus*. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-6/500 Site **Aramis**. Locality Aramis VP Locality 6. Surface/*in situ* Surface. Date of discovery November 5, 1994 and thereafter. The first evidence of ARA-VP-6/500 were two fragments of a second right metacarpal found on the surface by Yohannes **Haile-Selassie**. Thereafter further evidence of the ARA-VP-6/500 partial skeleton was recovered by sieving and surface prospecting and from excavations. Finders Yohannes Haile-Selassie and members of the **Middle Awash Research Project**. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Female. Brief anatomical description One hundred and thirty recognizable fragments belonging to a single individual were recovered. Most were in perilous condition and much of the cranial morphology has been recovered from micro-CT scans of unconsolidated cranial fragments still in matrix. Much of the cranial vault and the face have been reconstructed. The crowns and roots of all of the upper teeth on the right side, and the left lower canine through to the M$_3$, 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. All that remains of the thorax that can be identified precisely are two vertebrae (a cervical and a thoracic) and the left first rib. Much of the left innominate 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. Of the long bones of the lower limb, all that remains 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. Endocranial volume: “300 ± 10 cm^3, with a larger range of 280 to 350 cm^3” (Suwa et al. 2009b, p. 68e6). Announcement White et al. 2009a. Initial description Lovejoy et al. 2009a–c, Suwa et al. 2009a, 2009b. Photographs/line drawings and metrical data Lovejoy et al. 2009a–c, Suwa et al. 2009a, 2009b. Detailed anatomical description N/A. Initial taxonomic allocation ***Ardipithecus ramidus***. Taxonomic revisions None. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance An associated skeleton whose exceptional completeness and eventual preservation is a testament to the many hours of painstaking work, in both the field and laboratory, that went into its recovery, restoration, and reconstruction. This associated skeleton is the centerpiece of the **hypodigm** of *Ar. ramidus*, and functional interpretations based on it form the main evidential platform for the assumption that *Ar. ramidus* is a basal hominin. Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

ARA-VP-7/2 Site **Aramis**. Locality Aramis VP Locality 7. Surface/*in situ* Surface. Date of discovery December 30, 1993. Finder A. Asfaw. Unit N/A. Horizon N/A. Bed/member Lower Aramis Member. Formation Sagantole Formation. Group N/A. Nearest overlying dated horizon Daam-Aatu Basaltic Tuff. Nearest underlying dated horizon Gaala Vitric Tuff Complex. Geological age *c*.4.4 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description Fragments of the long bones of an arm of a single individual; the humeral fragment includes the proximal end. Announcement White et al. 1994. Initial description White et al. 1994. Photographs/line drawings and metrical data White et al. 1994. Detailed anatomical description N/A. Initial taxonomic allocation ***Australopithecus ramidus***. Taxonomic revisions ***Ardipithecus ramidus***. Current conventional taxonomic allocation *Ar. ramidus*. Informal taxonomic category Possible primitive hominin. Significance The first associated postcranial remains of *Ar. ramidus*, and the size of the humeral head was the source of the initial body mass estimate of approximately 40 kg. Its discovers claimed that "the arm displays a mosaic of characters usually attributed to hominids and/or great apes" and "a host of characters usually associated with modern apes" (White et al. 1994, p. 311). Location of original National Museum of Ethiopia, Addis Ababa, Ethiopia.

Aragai (Location 00°34′N, 35°50′E, Kenya; etym. local, Tugen, name for the area) History and general description Site within the **Lukeino Formation** in the foothills of the Tugen Hills, Baringo District, Kenya. Along with **Cheboit**, **Kapcheberek**, and **Kapsomin**, Aragai is one of four localities from which remains attributed to ***Orrorin tugenensis*** have been recovered. Temporal span *c*.6–5.7 Ma. How dated? **Argon-argon dating**, **potassium-argon dating**, and **magnetostratigraphy**. Hominins found at site The only specimen recovered to date is BAR 1215'00, a proximal right femur found by M. Pickford in 2000 which has been assigned to *O. tugenensis*. Archeological evidence found at site None. Key references: Geology and dating Hill et al. 1985, Pickford and Senut 2001, Deino et al. 2002, Sawada et al. 2002; Hominins Senut et al. 2001; Archeology N/A.

Arago *See* **Caune de l'Arago**.

Arago II Site **Caune de l'Arago**. Locality N/A. Surface/*in situ In situ*. Date of discovery July 21, 1969. Finders Henry and Marie-Antionette de Lumley. Unit N/A. Horizon Layer G. Bed/member Middle Stratigraphic Complex. Formation N/A. Group N/A. Nearest overlying dated horizon Speleothem floor just above dates to *c*.350 ka. Nearest underlying dated horizon N/A. Geological age **Arago XXI** from the same layer was directly dated to *c*.400 ka. Developmental age 40–55 years. Presumed sex Female. Brief anatomical description A nearly complete mandible with six teeth and lacking the left ramus. Announcement de Lumley and de Lumley 1971. Initial description de Lumley and de Lumley 1971. Photographs/line drawings and metrical data de Lumley et al. 1982. Detailed anatomical description de Lumley et al. 1982. Initial taxonomic allocation Pre-Neanderthal/*Homo erectus tautavelensis*. Taxonomic revisions Rightmire 1998. Current conventional taxonomic allocation ***Homo heidelbergensis***, pre-Neanderthal, or transitional form. Informal taxonomic category Pre-modern *Homo*. Significance The most complete mandible from Arago. Location of original Institut de Paléontologie Humaine, Paris.

Arago XXI Site **Caune de l'Arago**. Locality N/A. Surface/*in situ In situ*. Date of discovery July 1971. Finders Henry and Marie-Antionette de Lumley. Unit N/A. Horizon Layer G. Bed/member Middle Stratigraphic Complex. Formation N/A. Group N/A. Nearest overlying dated horizon Speleothem floor just above dates to *c*.350 ka. Nearest underlying dated horizon N/A. Geological age Directly dated using **uranium-series dating** to *c*.400 ka (but this is near the maximum limit of this dating method, so the fossil may be older). Developmental age Young adult. Presumed sex Male. Brief anatomical description A deformed cranial fragment with a complete frontal, sphenoid and all of the face. **Arago XLVII**, a right parietal, fits with the frontal and was recovered from the same layer in 1979. Announcement de Lumley and de Lumley 1971. Initial description de Lumley and de Lumley 1971. Photographs/line drawings and metrical data de Lumley and de Lumley 1971, 1973, Spitery 1982a, 1982b, Bouzat 1982. Detailed anatomical description Spitery 1982a, 1982b, Bouzat 1982. Initial taxonomic allocation Pre-Neanderthal/*Homo erectus tautavelensis*. Taxonomic revisions Rightmire 1998. Current conventional taxonomic allocation ***Homo heidelbergensis***, pre-Neanderthal or transitional form. Informal taxonomic category Pre-modern *Homo*. Significance One of the most complete pre-Neanderthal or *H. heidelbergensis* fossil faces.

Location of original Institut de Paléontologie Humaine, Paris.

Arago XLVII Site **Caune de l'Arago**. Locality. Surface/*in situ* *In situ*. Date of discovery July 1979. Finders de Henry and Marie-Antionette de Lumley. Unit N/A. Horizon Layer G. Bed/member Middle Stratigraphic Complex. Formation N/A. Group N/A. Nearest overlying dated horizon Speleothem floor just above dates to *c*.350 ka. Nearest underlying dated horizon N/A. Geological age This piece likely joins with **Arago XXI**, which has been directly dated to *c*.400 ka. Developmental age 20 years. Presumed sex Male. Brief anatomical description Right parietal. Announcement Grimaud 1982. Initial description Grimaud 1982. Photographs/line drawings and metrical data Grimaud 1982. Detailed anatomical description Grimaud 1982. Initial taxonomic allocation Pre-Neanderthal/*Homo erectus tautavelensis*. Taxonomic revisions Rightmire 1998. Current conventional taxonomic allocation *Homo heidelbergensis*, pre-Neanderthal, or transitional form. Informal taxonomic category Pre-Neanderthal. Significance This parietal fits with Arago XXI. Location of original Institut de Paléontologie Humaine, Paris.

aragonite *See* **calcium carbonate**.

Aralee Issie A collection area initially identified by the **International Afar Research Expedition** but now within the **Woranso-Mille study area**, Central Afar, Ethiopia.

Arambourg, Camille Louis Joseph (1885–1969) Camille Arambourg was born in Paris, France. He graduated from the private school of Sainte-Croix de Neuilly in 1903, and later that year he entered the Institut National Agronomique (National Agronomic Institute) where he completed a degree in agricultural engineering in 1908. Arambourg left France after graduation to join his family in Oran, Algeria, where his father had moved to establish a vineyard. While improving irrigation around the family vineyard Arambourg found specimens of fossil Miocene fish and so began to excavate and collect fossils in the area. As Arambourg's paleontological interests grew he made contacts at the geological laboratory of the Algiers Faculty of Sciences, which allowed him to expand his knowledge of geology and paleontology. When WWI broke out Arambourg left Algeria to join the French army and fought in the Dardanelles Campaign in 1915 and was stationed in Macedonia from 1916 to 1918. While in Macedonia, Arambourg collected Miocene mammalian fossils from the region around Salonika. At the end of the war Arambourg sent this collection to the **Muséum National d'Histoire Naturelle** (National Museum of Natural History) in Paris and he returned to Algeria. In 1920 Arambourg accepted a position as Professor of Geology at the Institut Agricole d'Alger (Agricultural Institute of Algiers) and over the next decade he collected fossil Miocene fish and Pleistocene vertebrates in Algeria and North Africa. These researches offered Arambourg opportunities to visit the renowned French paleontologist Marcellin **Boule** at the Muséum National d'Histoire Naturelle in Paris, and in 1930 Arambourg moved to Paris to become Professor of Geology at the Institut National Agronomique. Arambourg continued to conduct paleontological research in Africa, and while excavating the **Upper Paleolithic** site of Bejaia, in northern Algeria, between 1928 and 1930, he found six skeletons of early ***Homo sapiens***. Soon thereafter he organized an expedition, the Mission Scientifique de l'Omo, to the Omo river valley in Ethiopia from 1932 to 1933 where he collected Pleistocene fossils and explored along portions of Lake Rudolf (now called Lake Turkana). The research conducted during this expedition on the geology, paleontology, and anthropology of the region was later published as *Mission scientifique de l'Omo, 1932–1933* (3 vols., 1935–48). Arambourg was appointed Professor of Paleontology at the **Muséum National d'Histoire Naturelle** in Paris in 1936 and during the 1938–9 field season he explored Cretaceous deposits in Lebanon and Oligocene deposits in Iran. In 1943 Arambourg published a short work on prehistory titled *La genèse de l'humanité* (*The Genesis of Humanity*), which went through eight editions by 1969. After WWII, Arambourg excavated the Villafranchian site of **Ain Hanech**, near the village of Sétif in northeastern Algeria. In 1947–8 where he discovered Lower Pleistocene mammal fossils and **Lower Paleolithic** artifacts including **spheroid** stones. Even greater success came during excavations at **Ternifine** (now called **Tighenif**) during 1954–5 where he found crude **Acheulean** tools and several mandibles that he attributed to a "pithecanthropoid" form of early human that he called ***Atlanthropus mauritanicus*** (now subsumed into ***Homo erectus***). Arambourg's last major work, *Vertébres villafranchiens d'Afrique du nord* (*Villafranchian Vertebrates of*

North Africa) was published posthumously in 1979. Arambourg retired from the Muséum National d'Histoire Naturelle in 1955, but he continued to write and conduct research. He served as President of the Société Géologique de France (Geological Society of France) in 1950, President of the Société Préhistorique Française (French Prehistoric Society) in 1956, and he was President of the Fourth Pan-African Congress on Prehistory held in Leopoldville, the Belgian Congo, in 1959. When the **International Omo Research Expedition** was established in 1966 Arambourg became the leader of the French contingent and participated in a limited fashion in its first three field seasons from 1967 until his death in 1969. Regarding human evolution, Arambourg argued that there were long periods of relative biological stability as well as stability in the stone tool industries as seen in the archeological record, punctuated by periods of rapid change. Moreover, he believed that human biological and cultural evolution was progressive and proceeded along successive stages. As a result, Arambourg considered what he referred to as **australopithecine**s, **pithecanthropine**s, **Neanderthal**s, and ***Homo sapiens*** to represent successive stages of human evolution.

Aramis (Location 10°28′N, 40°26′E, Ethiopia; etym. the site is named after a tributary of the Awash River) History and general description Aramis, the type site of ***Ardipithecus ramidus***, 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**. All of the localities (**ARA-VP**) are on exposures of the approximately 300 m-thick Sagantole Formation. Temporal span *c*.4.2–4.1 Ma. Hominin-bearing localities in the Aramis Member are dated by **argon-argon dating** to 4.419 ± 0.058 Ma and 4.416 ± 0.031 Ma. The hominin-bearing locality in the Adgantole Member is constrained by argon-argon dates of 4.041 ± 0.060 Ma for an overlying volcanic stratum (MA 94–55C), and 4.317 ± 0.055 for the underlying Kullunta basaltic tuff (KUBT). An age of approximately 4.12 Ma has been assigned based on additional dating through **biostratigraphy** of the Aramis Member and from **magnetostratigraphy**. How dated? Argon-argon dating, biostratigraphy, magnetostratigraphy. Hominins found at site Specimens recovered from the Aramis Member attributed to *Ar. ramidus* include the **holotype ARA-VP-1/1** and the associated skeleton, **ARA-VP-6/500**. A left maxilla, ARA-VP-14/1, has been attributed to ***Australopithecus anamensis***. Archeological evidence found at site None. Key references: Geology and dating WoldeGabriel et al. 1994, 2009, Renne et al. 1999, White et al. 2006b; Hominins White et al. 1994, 2006, 2009; Archeology N/A.

arboreal (L. *arbor* = tree) The term used to describe animals that live in trees. Some of the defining features of primates (binocular vision, generalized limb structure retaining a clavicle) are important for life in the trees (e.g., binocular vision helps animals to judge distances). Although Elliott Smith and Wood Jones' arboreal theory, in which they argued that tree living was key to primate origins, has now fallen out of favor, arboreality remains an important trait within the order. Today and in the past many primates use trees for moving, foraging, and resting. Indeed, the vast majority of primates are dependent on trees, and the platyrrhines are 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 this 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 (Thorpe et al. 2007). *See also* **locomotion**.

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

"archaeomorphous" *Homo sapiens* *See* **Reilingen calvaria**.

Archanthropinae (Gk *arch* = first or primary and *anthropos* = man) A subfamily apparently introduced by Franz **Weidenreich** in 1946. In the second of his five 1945 Hitchcock Lectures entitled the "The Development of the Specifically Human Form" Weidenreich refers to the introduction by Sir Arthur **Keith** (1925) of the terms "neoanthropic man" and "paleoanthropic man", for modern humans "with all its variants" and Neanderthal man, respectively (Weidenreich 1946, p. 28). Weidenreich proposes that "...only a small step is required to alter the terms in use and to designate all the groups or subfamilies represented by these types as Neoanthropinae and

Paleoanthropinae, respectively" (*ibid*, pp. 28–9). He then goes on to suggest that "…when ***Sinanthropus*** and ***Pithecanthropus*** are measured according to the characteristics of the Paleoanthropinae, they reveal new features which are not found in this group and, therefore, have to be classified as a more primitive subfamily, for which the name Archanthropinae ("primary man") seems to be adequate." (*ibid*, p. 29). In a subsequent publication Weidenreich (1951) referred ***Homo soloensis*** to the Archanthropinae. Robert **Broom** was presumably interpreting Archanthropinae in a different way when he used it as a higher taxon for ***Australopithecus prometheus*** (Broom 1950), but thereafter the subfamily Archanthropinae fell into disuse.

Archi (Location 38°08′20″N, 15°39′38″E in Calabria, Italy; etym. from the nearby village) History and general description Roadwork on the hill of San Francesco d'Archi yielded an immature hominin mandible in 1970. The stratigraphic and geological context were subsequently investigated and published along with an initial description of the specimen. Temporal span and how dated? **Uranium-series dating** on marine molluscs in overlying level suggests an age of more than 40 ka. Hominins found at site Archi 1, a mandible, was found in layer C-3, a gravelly layer containing numerous vertebrate faunal remains. The specimen was mostly likely about 3 years old at the time of death and can be confidently assigned to ***Homo neanderthalensis***. Archeological evidence found at site None. Key references: Geology, dating, and paleoenvironment Ascenzi and Segre 1971; Hominins Mallegni and Trinkaus 1997; Archeology N/A.

arcuate fasciculus (L. *arcuatus* = bent like a bow and L. *fascis* = bundle) A bundle of axons in each cerebral hemisphere that connects Wernicke's area and **Broca's area** on the dominant side, as well as other areas of the temporal cortex and frontal cortex in both hemispheres. In modern humans, damage to this pathway can cause a language deficit known as conduction aphasia, which is a difficulty in repeating words that have been heard; otherwise language comprehension and production are intact. Comparative neuroimaging studies have shown that the arcuate fasciculus in modern humans is larger and makes more extensive interconnections, and thus links a greater number of areas in the temporal cortex and frontal cortex, as compared with chimpanzees and macaque monkeys. These specializations of the modern human arcuate fasciculus may be important in conveying the stored meaning of words in the temporal cortex to the frontal cortical areas that are involved in sentence comprehension and construction.

Arcy-sur-Cure (Location 47°35′N, 3°45′E, France; etym. after a nearby town) The many caves that constitute the site of Arcy-sur-Cure lie in the limestone cliffs above the Cure river in central France. They were originally excavated for saltpeter, and then since the 1850s they have been excavated with different levels of competence by amateur and professional archeologists. The site comprises a complex of more than 10 named caves, including the **Grande Grotte**, the **Grotte du Renne**, the **Grotte du Hyène**, the **Grotte des Fées**, and the **Grotte du Loup** among others (Leroi-Gourhan 1958). 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 isolated 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. A mandible attributed to *Homo neanderthalensis* was found in the Grotte des Fées by de Vibraye in 1859, but researchers at the site have argued on morphological and stratigraphic grounds that this mandible likely represents a Neolithic burial. The Grotte du Loup is a minor site, preserving only a few Châtelperronian and Mousterian tools, but contains evidence of a possible Neanderthal burial. For more information, see the individual entries about each cave.

Ardipithecus **White et al., 1995** (etym. *ardi* = ground or floor in the Afar language and Gk *pithekos* = a postfix that means ape or "ape-like") A genus established in 1995 by White et al. (1995) to accommodate the species *Ardipithecus ramidus*. The authors claimed the new genus was justified because the type species, *Ar. ramidus* (*c*.4.4 Ma), was significantly more primitive than species previously assigned to ***Australopithecus***. Subsequently a second more primitive and temporally older (*c*.5.8–5.2 Ma) species, *Ardipithecus kadabba*, was recognized and included in the same genus (Haile-Selassie 2001). Type species *Ardipithecus ramidus* (White et al., 1994) White et al., 1995. *See also* ***Ardipithecus ramidus***; ***Ardipithecus kadabba***.

Ardipithecus kadabba* Haile-Selassie, 2001** (etym. *see Ardipithecus*, and *kadabba* = a "family ancestor" in the Afar language) A hominin subspecies with the same name was established by **Haile-Selassie** (2001), but it was subsequently elevated to species rank by Haile-Selassie et al. (2004b). The new species was established to accommodate the original cranial and postcranial remains announced in 2001 and six new dental specimens announced 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, **Saitune Dora**, Alayla, **Asa Koma**, and Digiba Dora, are in a region called the **Western Margin**, and one, **Amba East**, is in the **Central Awash Complex** of the Middle Awash study area. The main differences between *Ar. kadabba* and ***Ardipithecus ramidus are that the apical crests of the upper canine crown of the former taxon are longer and the P_3 crown outline of *Ar. kadabba* is more asymmetrical than that of *Ar. ramidus*. The morphology of the postcranial evidence is generally ape-like. Haile-Selassie et al. (2004) suggest 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 (see Fig. 1D in Haile-Selassie et al. 2004). The proximal foot phalanx (AME-VP-1/71) combines an ape-like curvature with a proximal joint surface that is like that of *Au. afarensis* (Haile-Selassie 2001). Some researchers have suggested that because of its ape-like dental morphology the case for *Ar. kadabba* being a hominin is a relatively weak one. The fossil evidence for *Ar. kadabba* and its context are reviewed in Haile-Selassie and Wolde-Gabriel (2009). First discovery **ALA-VP-2/10** (1997). Holotype ALA-VP-2/10 (1997). Paratypes ALA-VP-2/11, -2/101; ASK-VP-3/78, -3/160; DID-VP-1/80; STD-VP-2/62, -2/63, -2/893; AME-VP-1/71. Main sites Middle Awash study area, Ethiopia.

Ardipithecus ramidus* (White et al., 1994) White et al., 1995** (etym. *see Ardipithecus* and *ramid* = "root" in the Afar language) Hominin species established in 1994 by White et al. 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 authors claimed *Ar. ramidus* shares some features with living species of ***Pan, has other features that are shared with the African apes in general and, crucially, has several dental and cranial features that are shared only with later hominins such as ***Australopithecus afarensis***. The taxon was initially included within the genus ***Australopithecus***, but it was subsequently transferred to a new genus, ***Ardipithecus*** (White et al. 1995). Fossils recovered from four localities (**Saitune Dora**, Alayla, **Asa Koma**, and Digiba Dora) in the **Western Margin** region of the Middle Awash study area were initially assigned to *Ar. ramidus* as a separate subspecies, ***Ardipithecus ramidus kadabba*** (Haile-Selassie 2001), but these and additional specimens were subsequently transferred to separate species, ***Ardipithecus kadabba*** (Haile-Selassie et al. 2004). The first reported additions to the *Ar. ramidus* **hypodigm** came from the **Gona Paleoanthropological study area** (Semaw et al. 2005), but subsequently more fossils, including the **ARA-VP-6/500** associated skeleton, recovered from the Aramis locality (White et al. 2009a), as well as from two other localities, Kuseralee Dora and Sagantole, in the Central Awash Complex have also been reported (White et al. 2009a). Initial estimates based on the size of the shoulder joint suggested that *Ar. ramidus* weighed about 40 kg, but researchers claim the enlarged hypodigm indicates an estimated body mass of approximately 50 kg (Lovejoy et al. 2009d). The chewing teeth of *Ar. ramidus* are relatively small and 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 gait of *Ar. ramidus* were respectively more upright and bipedal than is the case in the living apes. The enamel covering on the teeth is not as thin as that of chimpanzees/bonobos, but it is not as thick as that seen in archaic hominins such as *Au. afarensis* (Suwa et al. 2009a).

White et al. (2009a) claim that *Ar. ramidus* is a basal hominin, but this assessment implies that "dental and locomotor specializations evolved independently in each extant great ape genus" (Suwa et al. 2009a, p. 99), and the researchers who judged *Ar. ramidus* to be a basal hominin suggest that its discovery "highlights the alacrity with which similar anatomical structures can emerge,"..."resulting in convergent adaptations" (White et al. 2009a, p. 81). However, by including *Ar. ramidus* in the hominin clade the researchers who found and described it are implicitly assuming there is little, or no, evidence of such "convergent adaptations" (i. e., convergent evolution) in the hominin clade. Yet the inclusion of *Ar. ramidus* in the hominin clade necessitates substantial amounts of convergent evolution in the closely related clades that include the extant great apes. Indeed, 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. First discovery **ARA-VP-1/1** (1993) (N.B.: but if either a 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). Holotype **ARA-VP-6/1** (1993). Paratypes ARA-VP-1/1–4, -1/125, -1/127–9, -1/182, -1/183, -1/200, -1/300, -1/400, -1/401, -1/500, -7/2. Main sites Localities in the Gona and Middle Awash study areas, Ethiopia.

Ardipithecus ramidus kadabba* Haile-Selassie, 2001** A new subspecies of *Ardipithecus ramidus* proposed by Haile-Selassie (2001) to accommodate 11 fossils recovered from localities in the Western Margin of the **Middle Awash study area**. When additions were made to the hypodigm Haile-Selassie et al. (2004b), the subspecies was elevated to the level of a separate species as *Ardipithecus kadabba* Haile-Selassie et al., 2004. *See* ***Ardipithecus kadabba **Haile-Selassie et al., 2004**.

Arene Candide (Location 44°10′N, 8°20′E, Italy) History and general description A large cave site located on the Ligurian coast of Italy, about 90 m above sea level. Excavations by Bernabo Brea and Cardini began in the early 1940s and culminated in 1942 when the burial of Arene Candide I was discovered; WWII halted work shortly thereafter and it did not resume until 1970, under the direction of Cardini. Temporal span and how dated? Using **radiocarbon dating**, Arene Candide I assigned an age of 23,440 ± 190 years BP. The upper layers (3–4) were radiocarbon dated to 11,750 ± 95 years BP. Hominins found at site The ceremonial burial of an adolescent ***Homo sapiens*** male, Arene Candide I, was found in layer 10. The ornate nature of the burial prompted workers to nickname the skeleton "Il Principe" or the prince. At least seventeen other burials dating from the latest Pleistocene have been recovered, many of which are also ornately decorated. Archeological evidence found at site Arene Candide I was found in a bed of red **ochre**, with a probable cap made of perforated shells and deer bones on its head. Mammoth ivory pendants, a long flint blade, and four perforated elk antler batons also adorned the skeleton. The later burials of the site similarly include ochre and perforated shells, but also have painted pebbles and bone ornaments. A **Gravettian** industry characterizes the lower layers, whereas the upper layers have a late Epigravettian microlithic industry. Key references: Geology, dating, and paleoenvironment Pettitt et al. 2003; Hominins Cardini 1980, Sergi et al. 1974; Archeology Bietti 1994.

argon-argon dating An isotopic dating method based upon the K/Ar system, in which radioactive ^{40}K is driven to ^{40}Ar in a reactor, and used as a proxy of K content. Subsequent analyses can be done in a single experiment, by measuring isotopes of Ar in a mass spectrometer. This approach avoids the necessity of separate measurements of K and Ar (in different aliquots of a sample), thus reducing potential error. As a result, single-crystal age determinations have become a possibility. The method has been used to date materials as young as the 79 AD eruption of Vesuvius (Renne et al. 1997) but most applications are to much older rocks. The analytical methods are so sensitive they can be applied to single crystals of feldspar or volcanic glass, and this more precise version is referred to as single-crystal laser fusion ^{40}Ar/^{39}Ar dating (e.g., McDougall and Brown 2008).

ARI The acronym for the Aralee Issie collection area. ARI is used as the prefix for fossils recovered from the Aralee Issie collection area, **Woranso-Mille study area**, **Afar**, Ethiopia. *See also* **Aralee Issie**.

Aristotle University of Thessaloniki, Department of Geology Description The School of Geology belongs to the Faculty of Sciences of the Aristotle University of Thessaloniki founded in 1925. Hominin fossil collections **Petralona cranium**. Contact information Professor Dimosthenis Mountrakis (e-mail dmountra@ geo.auth.gr; tel +30 2310 998481) or Dimitra Christou (e-mail dimitra@geo.auth.gr; tel +30 2310 998558; fax +30 2310 998482). Website www.geo.auth.gr/en_tomeis_gewlogias.htm.

arithmetic mean A method for calculating the average of a set of numbers, it is the method commonly referred to simply as the mean. A sample of n values are summed and divided by n. For example, the arithmetic mean of X_1, X_2, X_3, and X_4 is $(X_1+X_2+X_3+X_4)/4$. There are alternative methods to calculate the mean of a set of numbers, such as the **geometric mean**.

ARL Acronym for Abdur Reef Limestone. *See* **Abdur**.

armature (L. *armatura* = armor or equipment) A term used to refer to any item used for offense or defense. In archeology the term armature refers to most **point**s and any other obvious hunting equipment (e.g., the wooden spears from **Schöningen**).

array (L. *arredare* = to arrange) An array has two meanings in molecular biology. First, it can be an "orderly arrangement" of repetitive **DNA** in the genome that has a similar sequence. Such arrays include **microsatellites** and **satellite DNA**. Second, an array is also used in the sense of a microarray, which is a piece of glass that has molecules of DNA, RNA, or protein affixed to it in an orderly arrangement. These microarrays are used to capture molecules of interest. For example, they can be used to identify copy-number variants (or CNVs), DNA expression, or proteins.

Arsuaga Ferreras, Juan Luis (1959–) Born in Madrid, Spain, Juan Luis Arsuaga displayed an early interest in human evolution and prehistory and he earned both his masters and doctoral degree in biological sciences at the Complutense University of Madrid. In 1982 Arsuaga became a member of the excavation team, headed by Emiliano Aguirre, that was investigating potential hominin cave sites in the Sierra de Atapuerca, which is 14 km/8.7 miles east of Burgos in northern Spain. The Sierra de Atapuerca contains many caves and its two most famous sites, the **Sima de los Huesos** and **Gran Dolina**, have yielded some of the earliest hominin fossils and stone tools in Western Europe. Access to the Sima de los Huesos was particularly hazardous, but by 1991 the infrastructure needed to access the cave was in place and the team began excavations with Arsuaga codirecting the effort, together with José María Bermúdez de Castro and Eudald Carbonell i Roura. The Sima de los Huesos has proved to be a rich source of well-preserved pre-modern *Homo* fossils, all of which are assigned to either ***Homo neanderthalensis*** or ***Homo heidelbergensis***. Arsuaga also helped explore and excavate the TD6 level at the Gran Dolina site where six individuals and 268 lithic artifacts were recovered; the hominins from Gran Dolina cave have been assigned to ***Homo antecessor***. In 1997, the Atapuerca team won the Prince of Asturias Award for Technical and Scientific Research and the Castilla y León Prize in social sciences and humanities, and in 2000 UNESCO added the Pleistocene sites of the Sierra de Atapuerca to their list of World Heritage Sites. Currently, Arsuaga is a professor at the Complutense University of Madrid in the Faculty of Geological Sciences in the Paleontology Department where he serves as the Director of the Center of Evolution and Human Behavior (UCM-ISCIII). Arsuaga is vice-president of the Commission of Human Paleontology and Paleoecology of the International Union Quaternary Research (INQUA). He is a Foreign Member of the US National Academy of Sciences and a member of the Real Academia de Doctores de España.

art (L. *art* = art) The term art refers to 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).

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, but the latter will require additional finds of comparable age for wide acceptance. Because they preserve well, stone tools form the largest part of the early archeological record, although comparison with extant primates suggests that artifacts of perishable materials (e.g., wood or fiber) remain difficult to detect and their origins may well remain in the realm of speculation. Artifacts are one of the fundamental units of analysis for archeologists.

artiodactyl The informal name for the Artiodactyla, the mammalian order that includes all the taxa with an even number of hoofed toes. *See also* **Artiodactyla**.

Artiodactyla (Gk *artios* = even and *daktulos* = toe; literally, the "even-toed") The name of the mammalian order that includes all the taxa with an even number of hoofed toes. Artiodactyl fossils are common within some hominin faunal communities. The order Artiodactyla is now often subsumed within the clade Cetartiodactyla, named to reflect the recent **DNA** studies showing that whales and artiodactyls are closely related (e.g., Ursing and Arnason 1998). There are both ruminating, called ruminants, and non-ruminating groups of artiodactyls. 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), although in Africa other common families within this order are the Suidae (pigs), the Hippopotamidae (hippopotamus), 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). There are other artiodactyl families, both extant and extinct, but these are not known from hominin sites. The earliest known artiodactyl, *Diacodexis*, is from the early Eocene of Portugal.

AS Acronym for Abdur South. *See* **Abdur**.

As Duma (Location 11°10′N, 40°20′E, Ethiopia; etym. named after a local drainage) History and general description Site on the west side of the Awash River in the **Gona Western Margin** sector of the **Gona Paleoanthropological Research Project** study area in the Afar Depression. Located in the headwaters of the Busidima and Gawis drainages. Temporal span Sediments are *c*.4.4 Ma. Hominins found at site Remains of ***Ardipithecus ramidus*** have been recovered from several localities. Archeological evidence found at site None. Key references: Geology, dating, and hominins Semaw et al. 2005.

Asa Issie (Location 11°10′N, 40°20′E, Ethiopia; etym. named after a local drainage) History and general description An area of fossiliferous sediments 10 km/6 miles west of **Aramis**. The hominin-bearing localities called Asa Issie and Hana Hari are in exposures of the Adgantole Member of the Sagantole Formation. Temporal span The sediments have been dated using **biochronology** to *c*.4.2–4.1 Ma. Hominins found at site The hominin fossils recovered there, that include a partial maxilla (ARA-VP-14/1), two sets of associated teeth (ASI-VP-2/2 and -2/334), and three postcranial specimens (ASI-VP-2 and -5, and ASI-VP-5/154), have all been assigned to ***Australopithecus anamensis***, but are claimed to be transitional between ***Ardipithecus ramidus*** and *Au. anamensis*. Archeological evidence found at site None. Key references: Geology, dating, and hominins White et al. 2006b.

Asa Koma An area of fossiliferous exposures that lies against the **Western Margin** of the Afar Depression section of the **East African Rift System** in the **Middle Awash study area**, Ethiopia.

ascertainment bias (L. *ad* = near and *certus* = to determine, so certain came to mean "indisputable"; ascertainment is the process of discovering something indisputable by experimentation, so ascertainment bias is a synonym for experimental bias) Refers to the circumstances when nonrandom sampling produces false results. Such biases can lead to incorrect inferences about an entire **population** either because of distorted or non-typical sampling of the population, or because the data (i.e., a specific marker) used for the analysis were identified in a biased way. For example, in modern humans many of the first **polymorphic** markers were identified through surveys of Europeans. When these markers were examined, Europeans were found to be the most diverse of the limited numbers of modern humans included in the sample. However, when the modern human samples were expanded to better reflect modern humans across the world (i.e., the geographic representation of "modern humans" was unbiased) the results then showed that modern humans from Africa and not

Europeans are the most diverse (Rogers and Jorde 1996, Wakeley et al. 2001).

Asfaw, Berhane (1954–) Born in Gondar Province, Ethiopia, Berhane Asfaw taught chemistry and physical science in high school in Gondar before moving in 1978 to Addis Ababa to work in the Centre of Research and Conservation of Cultural Heritage in the Ministry of Culture and to attend Addis Ababa University, graduating with a BSc in geology in 1980. He then moved to the University of California, Berkeley, USA where he studied for an MA and PhD, gaining the latter in 1988 for a thesis entitled "New perspectives on the evolution of the hominid frontal bone." He returned to Addis Ababa where he became paleoanthropology coordinator at the Centre for Research and Conservation of Cultural Heritage and then in 1990 he was appointed the Director of the National Museum of Ethiopia, a post he held until 1992. Since 1997 he has managed the Rift Valley Research Service. Berhane Asfaw's paleoanthropological fieldwork began in 1980 when he worked at **Melka Kunturé**, but his important involvement with the **Middle Awash Research Project** began in 1981. In 1983 he reported the discovery of a parietal fragment from **Bodo** and since then he has been either the first author, or a co-author, of papers that have reported the discovery of hominin fossil evidence from **Olduvai Gorge** (Johanson et al. 1987), **Belohdelie** (Asfaw 1987), **Maka** (White et al. 1993), **Konso** (Suwa et al. 1997), **Bouri** (Asfaw et al. 2002), **Herto** (White et al. 2003), and **Aramis** (White et al. 2009a), and announced new taxa, including *Australopithecus ramidus* (White et al. 1994) and *Australopithecus garhi* (Asfaw et al. 1999). He was also the lead organizer of the Paleoanthropological Inventory of Ethiopia. In recognition of his contributions to paleoanthropology, in 2008 Berhane Asfaw was elected as a foreign associate of the US National Academy of Sciences and in 2010 a fellow of the Ethiopian Academy of Sciences. *See also* **Paleoanthropological Inventory of Ethiopia**.

ASI Acronym for the Asa Issie collection area. It is used as the prefix for fossils recovered from **Asa Issie**, **Middle Awash study area**, Ethiopia.

ASK Acronym for the Asa Koma collection area. It is used as the prefix for fossils recovered from **Asa Koma**, **Western Margin**, **Middle Awash study area**, Ethiopia.

aspartic acid (etym. a non-essential amino acid found in asparagus, hence its name) It is an empirical observation that fossil bones in which (a) the amino acid content is more than 30,000 parts per million, (b) the ratio of glycine to aspartic acid is between 2 and 10, or (c) the amount of racemized aspartic acid is low (D/L ratios <0.10) are likely to contain sufficient DNA to warrant further analysis (Poinar et al. 1996). *See also* **amino acid racemization dating**.

ASPM *See* **brain size evolution, molecular basis of**.

assemblage Generally, any collection of objects. For archeologists, an assemblage is a stratigraphically-bounded, spatially associated, set of **artifact**s. For example, a single archeological site may contain several artifact assemblages (e.g., as is the case at 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 within an assemblage in the range of tool types found have been used to infer past site function(s) (e.g., Binford and Binford 1969 for French **Mousterian** sites). Also used as an inclusive term to describe all the paleontological evidence from a site.

assimilation model A model for the origin of modern humans that accepts an African origin for the biologically complex characteristic of modern humans but rejects a total replacement of local archaic populations, including ***Homo neanderthalensis***, by modern humans as they spread into Eurasia. This perspective grew out of morphological observations suggesting the archaic contribution to modern human populations throughout Eurasia (and possibly parts of Africa) was always relatively small, though not insignificant, and was limited to morphological details rather than fundamental morphological gestalt. First fully articulated in 1989 (Smith et al. 1989), aspects of the assimilation model were emerging by the mid-1980s. Beginning at this time, the application of thermoluminescence dating and **electron spin**

resonance spectroscopy dating to fossil samples in Africa, the Near East, and Europe began to show that modern human anatomy clearly was established earlier outside of Europe than within that continent and also that Neanderthals survived until relatively late in some portions of Europe. This, along with early observations on the origin of extant human mitochondrial DNA, appeared to weaken the possibility of a classical **multiregional hypothesis** for modern human origins. Some "intermediate models," such as the **replacement with hybridization** model accept the theoretical possibility of admixture but reject any morphological evidence for it. In contrast, the assimilation model has consistently held that evidence for continuity in morphological details is demonstrable in late archaic and early modern human samples in various portions of Eurasia. The assimilation model is consistent with the mostly out-of-Africa genetic model of modern human origins and with the recent evidence from the Neanderthal genome project indicating low levels of Neanderthal contribution to modern Eurasian populations. Recent statements of the assimilation model are found in Smith et al. (2005), Trinkaus (2005, 2007), Smith (2010).

associated skeleton (L. *associare* = to join with) Refers to a fossil specimen that includes more than one skeletal element from the same individual. The term is sometimes used in a more restricted sense to refer to specimens that include evidence of *both* the **skull** and the postcranial skeleton, or *more than one* part of the postcranial skeleton. Associated skeletons are particularly valuable specimens for several reasons. First, most fossil **hominin** taxa are diagnosed and identified on the basis of skull morphology, so associated skeletons that include skull and postcranial elements help sort out which limb bones go with which skulls. For example, the lack of a securely associated skeleton of ***Paranthropus boisei*** that preserves both taxonomically distinctive skull evidence *and* evidence of the postcranial skeleton is hampering attempts to sort postcranial fossils from East Africa into taxa. Second, because the evidence is from a single individual 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. Examples of associated skeletons include **A.L. 288-1** (*Australopithecus afarensis*), **KNM-WT 15000** (*Homo ergaster*), and **Dederiyeh 1** (*Homo neanderthalensis*).

association cortex (L. *cortex* = husk, shell) This term refers to areas of the **neocortex** that are *not* concerned with the primary processing of sensory or motor information. The association cortex comprises part of the **prefrontal cortex**, the limbic cortex, and large regions of the parietal cortex, temporal cortex, and occipital cortex. The association cortices are concerned with the higher-order processing and integration of sensory modalities, abstract thinking, and the planning of movements.

asterionic notch (Gk *aster* = star) The asterion is a bilateral bony landmark on the **cranial vault** where the lambdoidal, parietomastoid, and occipitomastoid sutures meet. In modern human crania the mastoid angle of the parietal, the lateral margin of the occipital squame, and the posterior angle of the mastoid portion of the temporal bone articulate in an "edge-to-edge" fashion. But in the African apes, in which **compound temporal-nuchal crest**s frequently dominate this part of the vault, the mastoid angle of the parietal is a laterally flaring, nearly horizontal, shelf of bone that fits into a narrow, reciprocal slot in the temporal bone between the base of the squamous and the mastoid portion; the mastoid fits between the flared mastoid angle superiorly and the lateral margin of the nuchal plane (occipitomastoid suture) medially (Kimbel and Rak 1985). Kimbel referred to this morphology as the "asterionic notch" (White et al. 1981, p. 456), whereas Delattre and Fenart (1960) called the tip of the mastoid angle the "angle incisural du parietal," and the deepest (i.e., most lateral) part of the female part of the bevel in the temporal the "point incisural externe". This type of asterionic notch articulation is also seen in most crested ***Australopithecus afarensis*** crania (e.g., **A.L. 333-45**, **A.L. 444-2**), including some small, presumably female, individuals (e.g., A.L. 162-28). Large, presumed male, ***Paranthropus boisei*** crania exhibit different anatomy in this region: the posterior part of the temporal squame overlaps the non-flared mastoid angle of the parietal, which, in turn, overlaps the occipital squame in a beveled imbrication of these bones. In this species the overlap of the temporal squame on the parietal is superiorly extensive further anteriorly, as evidenced in specimens with missing or damaged temporal bones by rugose ridges running superomedially high up on the exposed parietal surface toward the midline of the vault. *See also* **striae parietalis**.

astrochronology *See* **astronomical time scale**.

astronomical theory (Gk *astron* = star and *kronos* = time) Joseph Adhemar, James Croll, and John Murphy each suggested the intensity of the sun's rays could drive glacial cycles, but it was Milutin Milanković, a Serbian astronomer, who provided the mathematical foundation for what became known as astronomical theory. The theory suggests that cyclic changes in three important aspects of the Earth's **orbital geometry** (**precession**, **obliquity**, and **eccentricity**) largely determine long-term changes in **climate**. Evidence supporting the theory of astronomical pacing of Earth's climate came from cyclical events in ocean sediments (Hays et al. 1976). *See* **astronomical time scale**.

astronomical time scale (Gk *astron* = star and *kronos* = time) A geological time scale based on regular changes involving three aspects of the Earth's orbital geometry (i.e., the way it rotates about its axis and the shape of its orbit around the sun), namely **precession**, **obliquity**, and **eccentricity**. Precession, or the "wobble" of the Earth's axis of rotation, has a cycle that completes every 19–23 ka. Precession controls the seasonality of the intensity of the sun's rays on the Earth's surface (called **insolation**). For example, stronger summer insolation means stronger **monsoon** intensity. Obliquity, or the tilt of the Earth's axis, has a dominant periodicity of *c*.41 ka and it controls the length of the winter polar darkness. Eccentricity, or the elliptical nature of the Earth's orbit, has *c*.100 and *c*.400 ka cycles. It is thought that obliquity determines the timing (the pacing) of the northern hemisphere glacial cycles with less summer insolation at 65°N resulting in less summer melting and more glacier growth. Note that only eccentricity changes insolation, and even then by a very small amount; the other orbital cycles change only the seasonality or latitudinal distribution of insolation. The climate has not always been uniformly sensitive to these ongoing orbital cycles. Precession has had a long-term influence on the strength of the monsoons (the "23 ka world"). Only at times of global cooling and **northern hemisphere glaciation**, as has been the case for the last 3 Ma, do strong signals of obliquity (the "41 ka world") emerge; obliquity paces the timing of glacial/interglacial cycles. For the last 1 Ma, *c*.100 ka-long cycles appear to dominate (called the "100 ka world"). Eccentricity might be driving these cycles, or ice-sheet dynamics might instead be responding to multiples of two or three obliquity cycles. The regularity of these various cycles is such that astrochronology can be used to calibrate, or "tune," other forms of age estimation. (syn. astrochronology). *See also* **orbital tuning**.

AT Abbreviation of Arala Issie Tuff.

Atapuerca (Location 42°21′N, 3°31′W, Spain) The Sierra de Atapuerca is a series of eroded limestone hills 14 km/9 miles east of Burgos in Northern Spain. It is permeated by several sediment-filled cave systems, one of which is the **Cueva Mayor-Cueva del Silo**, and within this system are several cave/fissure complexes including the Sima de los Huesos. The first hominin fossils were recovered from the Sima de los Huesos (or **SH**) in 1976 and since then more than 6500 hominin fossils have been recovered from this location. Just 1 km/0.6 miles away is another system called **Trinchera del Ferrocarril**, which includes several sites (e.g., **Galería**, Gran Dolina, and Sima del Elefante), that have yielded hominin fossils and archeological evidence. Excavations at Gran Dolina (or **TD**) began in 1978 and six levels (TD3–4, 5–7, 10–11) have produced stone artifacts. In 1994 more stone tools and the first hominin fossils were recovered from the **Aurora stratum**, a lithostratigraphic level within **TD6**. The Sima del Elefante site, which may be 1.2 Ma, has provided the oldest hominin remains from the Atapuerca hills. *See also* **Gran Dolina**; ***Homo antecessor***; ***Homo heidelbergensis***; ***Homo neanderthalensis***; **Sima del Elefante**; **Sima de los Huesos**.

atavism (L. *atavus* = ancestor, from *atta* = father plus *avus* = grandfather) The term used for a morphological variant or anomaly that usually appears in what is assumed to be an ancestor (recent or distant). Thus, the occasional appearance as a normal variant of contrahentes muscles in the palm of the hand of modern humans (Cihak 1972) would be an example of an atavism, as would be the presence of a rhomboideus occipitalis (Aziz 1981), or an independent **os centrale** (Cihak 1972) in the carpal bones of the hand of a modern human (in modern humans the os centrale normally fuses with the main part of the scaphoid to form the scaphoid tubercle).

atavistic *See* **atavism**.

ATD Acronym for the Atapuerca – Gran Dolina. It is the prefix for fossils recovered from the **Gran Dolina** site within the Sierra de **Atapuerca**, northern Spain. The prefix ATD is followed by an Arabic number that indicates the **lithostratigraphic** level, then another Arabic number that indicates where in the sequence of **hominins** discovered in the cave that particular specimen was found (e.g., **ATD6-96** is the 96th hominin recovered from the ATD6 lithostratigraphic level).

ATD6-1 through ATD6-12 Site **Gran Dolina**. Locality "6 m^2 planar section" of TD6 (i.e., in the Aurora stratum). Surface/*in situ* *In situ*. Date of discovery July, 1994. Finders Team led by Eudald Carbonell and Jóse Maria Bermúdez de Castro. Unit N/A. Horizon TD6. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Pre-780 ka (TD6 is assumed to be in the **Matuyama chron**) and **uranium-series dating** and **electron spin resonance spectroscopy dating** age is 731 ± 63 ka. Developmental age Young adult. Presumed sex Unknown. Brief anatomical description All of the remains, the mandible ATD6-5, plus the isolated teeth listed as ATD6-1–6-4 and ATD6-6–6-12, belong to a single individual, and they comprise the **holotype** of ***Homo antecessor***. Announcement Carbonell et al. 1995. Initial description Carbonell et al. 1995. Photographs/line drawings and metrical data Carbonell et al. 1995. Detailed anatomical description Bermúdez de Castro et al. 1997, 1999, Rosas and Bermúdez de Castro 1999. Initial taxonomic allocation The holotype of *H. antecessor*. Taxonomic revisions None. Current conventional taxonomic allocation *H. antecessor*. Informal taxonomic category Pre-modern *Homo*. Significance The holotype of *H. antecessor*. Location of original Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain.

ATD6-15 Site **Gran Dolina**. Locality "6 m^2 planar section" of TD6 (i.e., in the Aurora stratum). Surface/*in situ* *In situ*. Date of discovery July, 1994. Finders Team led by Eudald Carbonell and Jóse Maria Bermúdez de Castro. Unit N/A. Horizon TD6. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Pre-780 ka (TD6 is assumed to be in the **Matuyama chron**) and **uranium-series dating** and **electron spin resonance spectroscopy dating** age is 731 ± 63 ka. Developmental age Adolescent. Presumed sex Unknown. Brief anatomical description Frontal bone fragment with part of the right supraorbital torus. Announcement Carbonell et al. 1995. Initial description Carbonell et al. 1995. Photographs/line drawings and metrical data Carbonell et al. 1995. Detailed anatomical description Arsuaga et al. 1999. Initial taxonomic allocation ***Homo antecessor***. Taxonomic revisions None. Current conventional taxonomic allocation *H. antecessor*. Informal taxonomic category Pre-modern *Homo*. Significance Most complete cranial vault fragment of *H. antecessor*. Location of original Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain.

ATD6-69 Site **Gran Dolina**. Locality "6 m^2 planar section" of TD6 (i.e., in the Aurora stratum). Surface/*in situ* *In situ*. Date of discovery 1995. Finders Team led by Eudald Carbonell and Jóse Maria Bermúdez de Castro. Unit N/A. Horizon TD6. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Pre-780 ka (TD6 is assumed to be in the **Matuyama chron**) and **uranium-series dating** and **electron spin resonance spectroscopy dating** age is 731 ± 63 ka. Developmental age Juvenile. Presumed sex Unknown. Brief anatomical description Much of the lower part of the face of a juvenile hominin. It includes the nasal floor and the floor of the right orbit, plus the roots and crowns of the right I^2, P^{3-4}, and M^1, and the left P^3 and M^1. Announcement Bermúdez de Castro et al. 1997. Initial description Bermúdez de Castro et al. 1997. Photographs/line drawings and metrical data Bermúdez de Castro et al. 1997. Detailed anatomical description Arsuaga et al. 1999. Initial taxonomic allocation ***Homo antecessor***. Taxonomic revisions None. Current conventional taxonomic allocation *H. antecessor*. Informal taxonomic category Pre-modern *Homo*.

Significance The most complete specimen in the hypodigm of *H. antecessor*. Location of original Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain.

ATD6-113 Site **Gran Dolina**. Locality Between squares G-13 and F-13. Surface/*in situ In situ*. Date of discovery 2006. Finders Team led by Eudald Carbonell and Jóse Maria Bermúdez de Castro. Unit Silt layer identified as "Pep." Horizon TD6. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon N/A. Nearest underlying dated horizon N/A. Geological age Pre-780 ka (TD6 is assumed to be in the **Matuyama chron**) and **uranium-series dating** and **electron spin resonance spectroscopy dating** age is 731 ± 63 ka. Developmental age Young adult. Presumed sex Male. Brief anatomical description The fragment consists of the left side of the mandibular corpus from the alveolus of the left M_1, the crowns and roots of the left M_{2-3}, and part of the base of the ramus including the lateral prominence. Announcement Bermúdez de Castro et al. 2008. Initial description Bermúdez de Castro et al. 2008. Photographs/line drawings and metrical data Bermúdez de Castro et al. 2008. Detailed anatomical description Bermúdez de Castro et al. 2008. Initial taxonomic allocation By inference it is assigned to ***Homo antecessor***. Taxonomic revisions None. Current conventional taxonomic allocation *H. antecessor*. Informal taxonomic category Pre-modern *Homo*. Significance Resembles the morphology of the more complete ATD6-96 mandible. The combination of a reduced M_3 and a relatively primitive corpus morphology is reminiscent of the hominins from **Dmanisi**. Location of original Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain.

ATE Acronym for Atapuerca – Sima del Elefante. It is the prefix for fossils recovered from the **Sima del Elefante** site within the Sierra de **Atapuerca**, northern Spain. The prefix ATE is followed by an Arabic number that indicates the **lithostratigraphic** level, then another Arabic number that indicates where in the sequence of hominins discovered in the cave that particular specimen was found (e.g., **ATE9-1** is the first hominin recovered from the ATE9 lithostratigraphic level).

ATE9-1 Site **Sima del Elefante**. Locality Square I-31. Surface/*in situ In situ*. Date of discovery 2007. Finders Team led by Eudald Carbonell and Jóse Maria **Bermúdez de Castro**. Unit "c". Horizon TE9. Bed/member N/A. Formation N/A. Group N/A. Nearest overlying dated horizon TE9c (see below). Nearest underlying dated horizon N/A. Geological age A combination of **biostratigraphy** using rodents and insectivores, an observed reversed magnetic polarity (consistent with the TE16 and older **lithostratigraphic** layers being in the **Matuyama chron**), and **cosmogenic nuclide dating** using ^{26}Al and ^{10}Be gives an age of 1.22 ± 0.16 Ma for TE9c suggests the ATE9-1 mandible is 1.2–1.1 Ma. Developmental age Adult. Presumed sex Unknown. Brief anatomical description The mandibular **corpus** fragment extends from the alveolus of the left P_4 to the alveolus of the right M_1. The broken crowns of the right I_2 and C and the left C and P_3 are preserved, as are the roots of the left P_3 and I_2, and the right P_3 and P_4. The crown and root of the left P_4 is also preserved. Announcement Carbonell et al. 2008. Initial description Carbonell et al. 2008. Photographs/line drawings and metrical data Carbonell et al. 2008. Detailed anatomical description N/A. Initial taxonomic allocation Provisionally assigned to ***Homo antecessor***. Taxonomic revisions None. Current conventional taxonomic allocation *H. antecessor*. Informal taxonomic category Pre-modern *Homo*. Significance At the time of its discovery it was the earliest reliably dated hominin from Europe. Location of original Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain.

Aterian (etym. the name is based on Bir el Ater, a community near the **type site** of this industrial complex) An **industrial complex** of the African **Middle Stone Age**. The type site for the Aterian is Oued Djebbana, Algeria (Morel 1974). Aterian sites occur in northern Africa, from the **Maghreb** (i.e., the northern parts of Morocco, Algeria, and Tunisia), south to Niger, throughout the Sahara and east to Egypt. **Tang**ed pieces (especially **point**s and **scraper**s) as well as **bifacially worked points** characterize Aterian sites, and these co-occur with a range of otherwise typical **Mousterian** elements such as side scrapers and diverse **Levallois** flakes and cores, as well as **blade**s (Wendorf and Schild 1992). The tangs are considered an adaptation for hafting, and the tanged (or pedunculate) pieces are sufficiently distinct that Clark (1988) and McBrearty and Brooks

(2000) use the Aterian as one of the strongest cases for early regional diversity in the archeological record of the Middle Stone Age. Aterian sites may be locally contemporary with other assemblages that lack tanged pieces, and the extent to which the tanged pieces reflect temporal or group variation rather than activity-specific elements of a more generalized toolkit remains unclear (Wendorf and Schild 1992). Aterian sites were formerly considered to date to less than 40 ka, but subsequent age estimates by optically stimulated **luminescence dating**, thermoluminescence dating, and **electron spin resonance spectroscopy dating** methods suggests that this age simply represents the upper limit of the conventional **radiocarbon dating** method previously used. New results from **Mugharet el 'Aliya** and other sites suggest an antiquity of approximately 35–90 ka for the Aterian (Garcea 2004). Although limited evidence from some sites suggests occupation during conditions more humid than the present, Aterian populations occupied a range of habitats, including desert areas in the present Sahara (Garcea 2004, Vanhaeren et al. 2006). A perforated *Nassarius gibbosulus* shell from Oued Djebbana was transported more than 200 km/144 miles from the Mediterranean Sea (Morel 1974, Vanhaeren et al. 2006), and green silicified tuff used to make artifacts at Adrar Bous, Algeria, were apparently transported 280 km/170 miles (Clark 1993). Such long-distance transport strongly suggests that Aterian populations were either highly mobile and/or had highly developed exchange networks, and it is consistent with expectations for desert-adapted populations. At **Dar es Soltane II**, Témara (**Smuggler's Cave**), and Zouhrah (El Harhoura), Aterian artifacts are associated with hominin fossils generally considered to be robust examples of ***Homo sapiens***.

Atlanthropus* Arambourg, 1955** (Gk *Atlas* = refers to the proximity of the site to the Atlas Mountains, a system of ranges and plateaus in northwest Africa extending from Morocco to Tunisia, and *anthropos* = human being). The taxonomic name given by Camille **Arambourg** to the genus he established to accommodate a new species he provisionally proposed for three hominin mandibles and a cranial fragment recovered by Arambourg and Hoffstetter in June, 1954 at Ternifine (now called **Tighenif**), near Mascara, Algeria, in the foothills of the Atlas mountains. Although Arambourg noted the new mandibles were "very closely related to the Asiatic *Pithecanthropus* and *Sinanthropus*" and that "some features (are) reminiscent of the australopithecines, *Telanthropus* particularly," (Arambourg 1955, p. 195), he concluded that the fossils "cannot be identified exactly with either *Pithecanthropus* or *Sinanthropus* or *Telanthropus*" so he "assigned to them the provisional name, *Atlanthropus mauritanicus*" (*ibid*, p. 195). Arambourg's paper was published in the same year as the first edition of Wilfrid **Le Gros Clark**'s *The Fossil Evidence for Human Evolution*, but in the second, 1964, edition, when discussing the fossil record for *Homo erectus*, Le Gros Clark concludes his discussion of the remains from what is now called Tighenif by writing that "there can be little doubt...that these remains do belong to the same species (i.e., to *H. erectus*)" (Le Gros Clark 1964, p. 112). Type species ***Atlanthropus mauritanicus* Arambourg, 1955**. *See* ***Homo erectus.

Atlanthropus mauritanicus* Arambourg, 1955** (Gk *Atlas* = refers to the proximity of the site to the Atlas Mountains, a system of ranges and plateaus in northwest Africa extending from Morocco to Tunisia, and *anthropos*=human being; L. *Mauritania*=the name of a province of the Roman Empire that is coincident with Morocco and Algeria). The taxonomic name given by Camille **Arambourg** to three hominin mandibles and a cranial fragment recovered by Arambourg and Hoffstetter in June, 1954 at Ternifine (now called **Tighenif**), near Mascara, Algeria, in the foothills of the Atlas mountains. Although Arambourg noted the new mandibles were "very closely related to the Asiatic *Pithecanthropus* and *Sinanthropus*" and that "some features (are) reminiscent of the australopithecines, *Telanthropus* particularly," (Arambourg 1955, p. 195), he concluded that the fossils "cannot be identified exactly with either *Pithecanthropus* or *Sinanthropus* or *Telanthropus*" so he "assigned to them the provisional name, *Atlanthropus mauritanicus*" (*ibid*, p. 195). In 1964 Wilfrid **Le Gros Clark** formally suggested *Atlanthropus mauritanicus* be sunk into *Homo erectus*. First discovery Ternifine 1, now **Tighenif 1** (1954). Holotype None formally proposed, but *de facto* it is Tighenif 1. Paratypes None proposed. Main site Ternifine (but if the Tighenif material proves to be conspecific with the hominin remains from **Gran Dolina** then *Atlanthropus mauritanicus* Arambourg, 1955 would have priority over ***Homo antecessor, but because it was just a "provisional" name according to the **International Commission on Zoological Nomenclature** (or ICZN) rules it is therefore not an available name.). *See also* ***Homo antecessor***; ***Homo erectus***.

Atlantic Meridional Overturning Circulation (AMOC or MOC) Describes the net northward flow of surface water in the Atlantic associated with the Gulf Stream, then it sinking in the North Atlantic to form a current known as North Atlantic deep water which flows southward until it meets with the Antarctic bottom water current, at which point it rises to the surface and either returns northward or connects via the **Antarctic Circumpolar Current** to currents in other ocean basins. The overturning circulation in the Atlantic can be conceptualized as a conveyor belt carrying warm surface water northwards and cold deep oxygenated water southwards. It is thought that changes in the AMOC could cause large changes in continental climate around the Atlantic and also globally. This is because any reduction or interruption of this "conveyor belt" would drastically reduce the heat transported by the oceans from low to high latitudes.

attrition *See* **tooth wear**.

AU *See* **Anthracotheriid Unit**; **Toros-Menalla**.

auditory cortex *See* **temporal lobe**.

auditory ossicles (L. *audire* = to hear and *ossiculum* = small bone) Three small bones in the **middle ear**, or tympanic cavity, of mammals. They connect the tympanic membrane (which is at the medial end of the external ear) with the oval window (within which is the outer of the two fluid-filled cavities of the **inner ear**). The malleus (L. *malleus* = hammer) has a head (which occupies the epitympanic recess), a handle or manubrium, and a lateral process. The handle attaches to just below the center of the tympanic membrane and the head articulates with the body of the **incus**. The incus (L. *incudere* = to beat upon, hence an anvil) has a body, and two processes, short and long. The long process articulates with the head of the stapes. The stapes (L. *stare* = to stand and *pes* = foot, hence a stirrup) has a head, neck, two limbs (or crurae), and a footplate that fits into the oval window beyond which is the perilymph-filled cochlear part of the inner ear. The footplate is hinged anteroinferiorly and moves like a constrained piston to compress the perilymph. The ossicles articulate via synovial joints; the malleus and incus move as a unit around a horizontal axis that coincides with the anterior ligament of the malleus and the posterior ligament of the incus. Excessive movement of the ossicles is prevented by muscles in the middle ear (the tensor tympani and stapedius attach to the malleus and stapes, respectively) that contract in response to noise above approximately 90 db. Some debate exists about the precise embryological origin of the ossicles, but it is generally believed that most of the malleus and incus develop endochondrally from the Meckel's cartilage of the first **branchial arch** cartilage, while the head, neck, and crurae of the stapes develop from the second arch (hyoid) cartilage and the stapes footplate derives from the mesoderm of the otic capsule. Auditory ossicles attain their adult size prior to birth. They occasionally survive to be recognized as fossils [e.g., a ***Paranthropus robustus*** incus (SK 848), an ***Australopithecus africanus*** stapes (Stw 151)] and at the latest count approximately 25 ear ossicles had been recovered from the **Sima de los Huesos** at **Atapuerca**. *See also* **bony labyrinth**.

auditory tube (L. *audire* = to hear and *tubus* = hollow cylinder) The auditory tube connects the **middle ear** to the nasopharynx. The lateral one-third is bone (so this is the only part that fossilizes) and the medial two-thirds consists of fibrocartilage. The auditory tube is approximately 35 mm long in adult modern humans, and it is oriented 45° to the **sagittal** plane and 30° to the horizontal plane. In infants the auditory tube is shorter and more horizontally inclined; this is one of the reasons children are so prone to middle-ear infections. The auditory tube is inclined more closely to the sagittal plane in extant apes and in archaic hominins, and some specimens of ***Paranthropus robustus*** and ***Australopithecus africanus*** have club-like processes, called Eustachian processes, on the medial ends of the bony auditory tube (syn. Eustachian tube, pharyngotympanic tube, tympanic tube).

Aurignac (Location 43°13′22″N, 0°51′57″E, France; etym. Fr. after the nearby town) <u>History and general description</u> Aurignac cave (or Abri d'

Aurignac) is located the foothills north of the Pyrenees mountains. A road-worker found human bones in a shallow cave. Eight years later Édouard Lartet described its stratigraphic sequence and major artifacts, which later became the basis for establishing the "**Aurignacian**" culture. In 1938–9 Fernand Lacorre investigated Lartet's backfill and excavated the unexplored terrace outside the cave. Temporal span and how dated? The site has not been dated, but the Aurignacian in Western Europe generally dates between 36 and 26 ka. Hominins found at site Apparently 17 individuals were removed from the site by the discoverer and buried in an unmarked grave. Because these fossils were found on the surface of the deposit, it is likely they post-date the Aurignacian. Archeological evidence found at site Lartet recovered stone and bone tools, bone beads, and abundant faunal remains. Key references: Geology, dating, paleoenvironment, hominins, and archeology Lartet 1861.

Aurignacian A material culture named after the site of Aurignac in France. Gabriel de Mortillet was the first to propose an Aurignacian industry for the unique combination of stone tool types, beads, and bone tools, but he abandoned it in his later classification schemes. The Aurignacian was reintroduced and redefined by Henri Breuil in the early 20thC. It is generally thought to be the oldest modern human (or Cro -Magnon) culture in Europe, although there are very few fossils that are securely dated to this time period. The hallmarks of this culture are the use of **blades**, **bone tools**, beads, and other objects of personal decoration, as well as figurines and other figurative art. Its appearance in Eastern Europe around 43 ka and in Western Europe between 40 and 36 ka is consistent with a migration of anatomically modern humans from the Near East. It is replaced by the **Gravettian** culture between 28 and 26 ka. *See also* **Aurignac**.

Aurora archaeostratigraphic set (AAS) Researchers now recognize six layers within the Aurora stratum, which is part of **TD6**, a lithostratigraphic level in Gran Dolina. The latter is one of the sites within the sediment-filled cave system called the **Trinchera del Ferrocarril**, which is in the Sierra de **Atapuerca**, a series of eroded limestone hills 14 km/9 miles east of Burgos in Northern Spain. *See also* **Aurora stratum**; **Gran Dolina**.

Aurora stratum A layer within **TD6**, which is a lithostratigraphic level in **Gran Dolina**, one of the sites within the sediment-filled cave system called the **Trinchera del Ferrocarril**, one of the cave complexes in the Sierra de **Atapuerca**, a series of eroded limestone hills 14 km/9 miles east of Burgos in Northern Spain. Researchers now recognize six lithostratigraphic layers within the Aurora stratum, and they refer to these as the **Aurora archaeostratigraphic set** (AAS).

Australasian strewn-field tektites From time to time the Earth collides with showers of small meterorites, called **tektites**. If the area of impact (the strewn-field) is widespread, and if the tektites are physically or chemically distinctive, and if they can be securely dated at least one location, strewn-field tektites can be used as a dating tool. The Australasian is the largest and the youngest of the major tektite strewn-fields. The *c.*800 ka strewn-field extends across most of Southeast Asia (Vietnam, Thailand, Southern China, Laos, and Cambodia), as well as the Philippines, Indonesia (including Java), and Malaysia. It also stretches into the Indian Ocean and south to the western side of Australia. The identification of Australasian strewn-field tektites in sediments is one of the many ways researchers have tried to date hominins from China and Southeast Asia.

australopith Informal name for some, or all, of the fossil **hominin**s not included in the genus ***Homo***. This term is not used consistently in paleoanthropology. Some workers use this term to categorize *all* non-*Homo* hominins, while others include only non-*Homo* hominins that exhibit **megadontia** (i.e., species typically attributed to ***Australopithecus*** and/or ***Paranthropus***). The term is increasingly used in place of australopithecine, because the latter term should *only* be used if the writer believes that all *Australopithecus* and *Paranthropus* taxa belong in their own hominin subfamily, the **Australopithecinae**. Examples of australopith taxa include the **type species** of *Australopithecus*, ***Australopithecus africanus***, and ***Paranthropus boisei***. *See also* **australopithecine**.

Australopithecinae (L. *australis* = southern and Gk *pithekos* = ape) This formal name should only be used by those who conclude that all *Australopithecus* and ***Paranthropus*** taxa belong in a hominin subfamily separate from the genus ***Homo***. Some researchers have explicitly abandoned its use. For example, Robinson (1972a) sank *Australopithecus* into *Homo* and abandoned Australopithecinae in favor of a more encompassing Homininae. Anyone who supports all hominins being included within a single tribe cannot logically continue to refer to early hominin taxa as "australopithecines." *See also* **australopithecine**.

australopithecine Informal name for the subfamily **Australopithecinae**. Strictly speaking this term should only be employed if the user supports elevating the archaic hominin taxa included in genera such as ***Australopithecus*** and ***Paranthropus*** to the level of a subfamily. More generally, the term has been used in the past to refer to all, or to most, of the early hominins that do not belong to the genus *Homo,* but researchers are increasingly adopting the term **australopith** for this purpose.

Australopithecus* Dart, 1925** (L. *australis* = southern and Gk *pithekos* = ape) Hominin **genus** established by Raymond **Dart** in 1925 to accommodate the **type species** ***Australopithecus africanus. Because it has priority as the genus name for archaic Pliocene hominins, taxa such as *Paranthropus* and ***Plesianthropus***, which were not recognized until 1938, have been sunk into *Australopithecus* by those who recognize only a single genus for these hominins. In the way the taxon is used by **lumper**s, the genus *Australopithecus* includes species that are bipeds with small brains, large cheek teeth, and small, nonhoning canines. However, it almost certainly subsumes taxa representing parts of more than one **clade**. Thus, it is very likely that *Australopithecus* is a **paraphyletic group** (i.e., the taxa it contains represent some, but not all, of the descendants of their most recent common ancestor). The list of species assigned to the genus *Australopithecus* has varied over time. From its discovery up until the seminal publications of John **Robinson**, the genus subsumed three species, *Au. africanus* from the site of **Taung**, ***Australopithecus transvaalensis*** (later, ***Plesianthropus transvaalensis***) from **Sterkfontein**, and ***Australopithecus prometheus*** from **Makapansgat**. Robinson sank *Au. prometheus* and *Pl. transvaalensis* into *Au. africanus,* but he did not include the fossil hominins from **Swartkrans** and **Kromdraai**, which he interpreted as belonging to the genus ***Paranthropus***. In subsequent decades it became conventional to assign all of the above hominins as well as other species such as ***Zinjanthropus boisei*** and ***Meganthropus africanus*** to the genus *Australopithecus*. However, in the 1980s, the researchers who recognized the "robust" species as a monophyletic group revived the genus *Paranthropus* for *P. robustus*, *P. boisei*, and, eventually, *P. aethiopicus,* although many researchers still retain these species in *Australopithecus*. In 1994, a newly identified species, ***Australopithecus ramidus***, was transferred to the genus ***Ardipithecus*** shortly after its initial description, and since that time several early hominin species have been discovered, described, and assigned to genera other than *Australopithecus* (e.g., ***Orrorin***, ***Sahelanthropus***, *Kenyanthropus*). Since 1996, four new species of *Australopithecus* have been described (***Australopithecus anamensis***, ***Australopithecus bahrelghazali***, ***Australopithecus garhi***, and ***Australopithecus sediba***). In recent years, the evident paraphyly of *Australopithecus* has led a minority of researchers to advocate removing species from the genus until there is sound evidence that it is clearly **monophyletic**. This position has not gained widespread support, although some workers have transferred the hypodigm of *Au. afarensis* to the genus *Praeanthropus*. *See also* ***Praeanthropus***.

Australopithecus aethiopicus* (Arambourg and Coppens, 1968)** (L. *australis* = southern, Gk *pithekos* = ape and *aethiopicus* = Ethiopia) A taxon used by researchers who recognize neither ***Paraustralopithecus nor ***Paranthropus*** as separate genera, but who do recognize pre-2.3 Ma **megadont** hominins from the Omo region as a species separate from ***Paranthropus boisei***. No one has formally suggested that this **binomial** be adopted, but Groves (1999) warns that if they did, it would result in **homonymy** because the taxon name *Australopithecus aethiopicus* is preoccupied by Tobias's (1980b) usage of ***Australopithecus africanus aethiopicus*** for the **Hadar** component of the hypodigm of ***Australopithecus afarensis***. *See also* ***Paraustralopithecus aethiopicus***; ***Australopithecus africanus aethiopicus***.

Australopithecus afarensis* Johanson, 1978** (L. *australis* = southern, Gk *pithekos* = ape and *afarensis* recognizes the contributions of the local Afar people) **Hominin species** established in 1978 by Donald **Johanson** and colleagues to accommodate the *c*.3.7–3.0 Ma cranial and postcranial remains recovered from **Laetoli**, Tanzania, and **Hadar**, Ethiopia. White et al. (1981) compared the **hypodigm**s of *Australopithecus afarensis* and ***Australopithecus africanus and made a compelling case for recognizing *Au. afarensis* as a distinct species with generally more primitive craniodental anatomy than *Au. africanus*; Kimbel et al. (1984, 2004), Wood (1991), and Strait et al. (1997) provide supplementary information about the morphological differences between the two hypodigms. Several researchers have drawn attention to dental, facial, and mandibular differences between the early Laetoli component of the hypodigm and the geologically younger Hadar fossils assigned to *Au. afarensis*, and to similarities between the Laetoli remains and those of ***Australopithecus anamensis*** (e.g., Ward et al. 1999, Kimbel et al. 2006). It remains to be seen whether these similarities are sufficient evidence to sustain the hypothesis that *Au. anamensis* evolved via **anagenesis** into *Au. afarensis*. Rak et al. (2007), on the basis of mandibular ramus form, revived the suggestion (originally advocated for part of the Hadar sample by Olson 1981) that *Au. afarensis* may be a primitive taxon of the clade that includes ***Paranthropus boisei***, ***Paranthropus robustus***, and ***Paranthropus aethiopicus***. The main differences between *Au. anamensis* and *Au. afarensis* relate to details of the jaws and dentition, which are generally more primitive in the former taxon. The curved, receding anterior mandibular corpus and more rectangular dental arch of *Au. anamensis* contrasts with the *Au. afarensis* anatomy. In some respects the teeth of *Au. anamensis* are more primitive than those of *Au. afarensis* (for example, the asymmetry of the premolar crowns and the relatively simple crowns of the deciduous first mandibular molars), but in others (for example, the low cross-sectional profiles and bulging sides of the molar crowns) *Au. anamensis* shows some similarities to *Paranthropus* (see below). The upper limb remains are similar to those of *Au. afarensis*, but a tibia attributed to *Au. anamensis* has features associated with **bipedalism**. Most body mass estimates for *Au. afarensis* range from approximately 30 to 45 kg and known endocranial volumes range between 385 and 550 cm^3. This is larger than the average endocranial volume of a chimpanzee, but if the estimates of the body size of *Au. afarensis* are approximately correct then relative to estimated body mass the brain of *Au. afarensis* is not substantially larger than that of *Pan*. It has smaller incisors than those of extant chimps/bonobos, but its premolars and molars are larger. The hind limbs of **A.L. 288-1** are substantially shorter than those of a modern human of similar stature. The appearance of the pelvis and the relatively short lower limb suggests that although *Au. afarensis* was capable of bipedal walking, it was not adapted for long-range bipedalism. This indirect evidence for the locomotion of *Au. afarensis* is complemented by the discovery at Laetoli of several trails of fossil footprints. These provide very graphic direct evidence that a contemporary hominin, presumably *Au. afarensis*, was capable of bipedal locomotion. The upper limb, especially the hand and the shoulder girdle, retains morphology that some workers suggest reflects a significant element of arboreal locomotion. The size of the Laetoli footprints, the length of the stride and stature estimates based on the length of the limb bones suggest that the standing height of adult individuals in this early hominin species was between 1.0 and 1.5 m. Most researchers interpret the fossil evidence for *Au. afarensis* as consistent with a substantial level of **sexual dimorphism**. A few researchers have suggested that sexual dimorphism in *Au. afarensis* is relatively poorly developed (Reno et al. 2003), but most researchers accept that this taxon shows a substantial level of sexual dimorphism. First discovery A.L. 128-1, 129-1 (1973). Holotype **LH 4** (1974). Paratypes (e.g., see Johanson et al. 1978 for a complete list) LH 1, 3 (a–t), 3/6 a, 5, 6 (a–e), 7, 8, 10, 11, 12, 13, 14 (a–h); **A.L.** 128-1, 128-23, **129-1a–c**, 129-52, 137-48a–b, 145-35, 161-40, 166-9, 198-1, 198-17a–b, 198-18, **199-1**, **200-1a**, 200-1b, 207-13, 211-1, 228-1, 241-14, 266-1, 277-1, **288-1**, 311-1, 322-1, **333-1**, 333-2, 333w-1a–e, 333x-1, 366-1, 388-1, **400-1a&b**, 411-1. Main sites **Belohdelie** (tentative), Dikika, **Hadar**, **Maka**, and **White Sands**, Ethiopia, **Koobi Fora**, Kenya, and Laetoli, Tanzania. *See also* ***Praeanthropus afarensis***.

Australopithecus africanus Dart, 1925

(L. *australis* = southern, Gk *pithekos* = ape and L. *africanus* = pertaining to Africa) **Hominin species** established in 1925 by Raymond **Dart** for an immature **skull** recovered from the limeworks at Taungs (now called **Taung**) in 1924. As presently interpreted the taxon *Australopithecus africanus* includes, in addition to the type specimen from Taung, fossils from Member 4 at **Sterkfontein**, fossils initially assigned to ***Australopithecus prometheus*** from Members 3 and 4 at

Makapansgat, and fossils recovered from lime-workers dumps and extracted *in situ* from the breccia exposed at **Gladysvale**; the hypodigm spans the period between *c*.3.0 and 2.5 Ma. It remains to be seen whether the associated skeleton **StW 573** from Sterkfontein Member 2 and 12 hominin fossils recovered from the **Jakovec Cavern** since 1995 (Partridge et al. 2003) belong to the *Au. africanus* hypodigm; Clarke (2008) suggests they belong to a second, so far unnamed, ***Australopithecus*** taxon (see below). The hypodigm of *Au. africanus* is one of the better fossil records of an early hominin taxon. The cranium, mandible, and dentition are well sampled. The postcranium and particularly the axial skeleton are less well represented, but there is at least one specimen of each of the long bones. However, many of the fossils have been crushed and deformed by rocks falling on the bones before they were fully fossilized. The picture emerging from morphological and functional analyses suggests that although *Au. africanus* was capable of walking bipedally it was probably more arboreal than most other archaic hominin taxa. It had relatively large chewing teeth and apart from the reduced canines the skull is relatively ape-like. Its mean endocranial volume is approximately 460 cm^3. The Sterkfontein evidence suggests that males and females of *Au. africanus* differed substantially in body size, but probably not to the degree they did in *Au. afarensis*. For a long time *Au. africanus* was regarded as the common ancestor of all later hominins, but the discovery of the even more primitive ***Australopithecus afarensis*** challenged that interpretation. In most cladistic analyses *Au. africanus* is either the sister taxon of ***Homo*** or ***Paranthropus***, or the sister taxon of the common ancestor of the *Homo* and *Paranthropus* clades. Clarke (e.g., 1988, 1999, 2008) has consistently argued, and others have also suggested (Kimbel and White 1988), that the Sterkfontein Member 4 and Makapansgat hypodigm of *Au. africanus* samples a second, *Paranthopus*-like, *Australopithecus* taxon. Clarke (2008) would include **Sts** 1 and **71**, **StW** 183, **252**, 384, 498 and **505**, and MLD 2 in the second *Australopithecus* species; the differences between the second taxon and *Au. africanus* relate to dental size and craniofacial structure; details are set out by Clarke (2008, p. 448). First discovery **Taung 1** (1924). Holotype As above. Paratypes None. Main sites Gladysvale, Makapansgat (Members 3 and 4), Sterkfontein (Member 4), and Taung.

Australopithecus africanus aethiopicus* Tobias, 1980** Phillip **Tobias** (1980b) made two suggestions about *Australopithecus afarensis*. First, he claimed that *Au. afarensis* was not sufficiently different from ***Australopithecus africanus to merit recognition as a distinct **species**. Second, he considered the **Hadar** and **Laetoli** parts of the **hypodigm** were subspecifically distinct, proposing that the Hadar component of the hypodigm be referred to as *Australopithecus africanus aethiopicus*. *See also* ***Australopithecus afarensis***.

Australopithecus africanus afarensis* Johanson et al., 1978** Phillip **Tobias** (1980b) proposed that the **Laetoli** part of the *Australopithecus afarensis* **hypodigm** be referred to as *Australopithecus africanus afarensis*. Even though Tobias proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., *Australopithecus africanus afarensis* Johanson et al., 1978). The describer of *Australopithecus afarensis* is Johanson et al., 1978, and nothing can alter that, not even the transfer of the type specimen to a subspecies. *See also* ***Australopithecus afarensis; ***Australopithecus africanus aethiopicus***.

Australopithecus africanus africanus* Dart, 1925** John **Robinson** (1954a) proposed that the **Taung 1** skull be referred to a **subspecies** of *Australopithecus africanus* as *Australopithecus africanus africanus*. He did this to distinguish the latter from the "Sterkfontein, Makapan and East Africa" (*ibid*, p. 196) subset of *Au. africanus* which he referred to a separate subspecies, ***Australopithecus africanus transvaalensis. Bernard Campbell (Campbell 1973) subsequently used the same **nomen** to apply to the whole of the **hypodigm** while most other researchers recognize the taxon at the specific level as *Australopithecus africanus*. Even though Campbell proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., *Australopithecus africanus* Dart, 1925). The describer of *Au. africanus* is Dart, 1925, and nothing can alter that, not even the transfer of the type specimen to a subspecies. *See also* ***Australopithecus africanus***; ***Australopithecus africanus transvaalensis***.

Australopithecus africanus habilis **(Leakey, Tobias and Napier, 1964)** A subspecies of *Australopithecus africanus* introduced by Bernard Campbell (Campbell 1973) for the **hypodigm** most other researchers recognize at the specific level as ***Homo habilis***. Even though Campbell proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., *Homo habilis* Leakey, Tobias and Napier, 1964). The describers of *H. habilis* are Leakey, Tobias and Napier, 1964 and nothing can alter that, not even downgrading to a subspecies.

Australopithecus africanus modjokertensis **(von Koenigswald, 1936)** A subspecies of *Australopithecus africanus* introduced by Bernard Campbell (Campbell 1973) for specimens from Indonesian sites Ralph **von Koenigswald** assigned to ***Homo modjokertensis***. Most researchers now regard these specimens as being part of the hypodigm of ***Homo erectus***. Even though Bernard Campbell proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., *Homo modjokertensis* von Koenigswald, 1936). The describer of *H. modjokertensis* is von Koenigswald, 1936, and nothing can alter that, not even the downgrading of *H. modjokertensis* to a subspecies.

Australopithecus africanus robustus **Broom, 1938 (Broom, 1938)** A subspecies of *Australopithecus africanus* introduced by Bernard Campbell (Campbell 1973) for the **hypodigm** most researchers recognize at the specific level as ***Paranthropus robustus***. Even though Bernard Campbell proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., *Paranthropus robustus* Broom, 1938). The describer of *P. robustus* is Broom, 1938, and nothing can alter that, not even the downgrading of *P. robustus* to a subspecies.

Australopithecus africanus tanzaniensis **Tobias, 1980** There is now wide acceptance that *Australopithecus afarensis* is a biologically valid species, but when Don **Johanson**, Tim **White**, and Yves **Coppens** set out the case for recognizing a new species for the hominins recovered from **Hadar** (Johanson et al. 1978) it met with spirited resistance from Phillip **Tobias**. In several publications (Tobias 1980a, 1980b) he laid out the detailed case for his claim that the authors had failed to demonstrate the new species was anything other than an East African variant of *Australopithecus africanus*, and thus should be recognized as a junior synonym of that taxon. In one of these publications, Tobias suggested that what was then called the Laetolil (now **Laetoli**) part of the *Au. afarensis* hypodigm be recognized at the level of a subspecies. He wrote "as we already have two southern African subspecies, ***A. africanus africanus*** and ***A. africanus transvaalensis***, it would perhaps be appropriate to refer to this Tanzanian subspecies as *A. africanus tanzaniensis*" (Tobias 1980b, p. 107).

Australopithecus africanus transvaalensis **(Broom, 1936)** John **Robinson** (1954a) proposed that this **subspecies** of *Australopithecus africanus* should be used to distinguish the **australopith**s from "**Sterkfontein**, Makapan and East Africa" (*ibid*, p. 196) from the **Taung 1** skull, which he referred to a separate subspecies, *Australopithecus africanus africanus*. Even though John Robinson proposed the subspecies, according to the Principle of Coordination in the **International Code of Zoological Nomenclature** (Article 46.1) a name established for a taxon at either rank in the species group (i.e., species or subspecies) retains the name of the author who proposed the species (i.e., ***Plesianthropus transvaalensis*** Broom, 1938). The describer of *transvaalensis* is Broom, 1936, and nothing can alter that, not even the downgrading of *transvaalensis* to a subspecies. *See also* ***Australopithecus africanus***; ***Australopithecus africanus africanus***.

Australopithecus anamensis **Leakey et al., 1995** (etym. *see* ***Australopithecus*** and *anam* = means "lake" in the Turkana language) Hominin species established in 1995 by Meave **Leakey** et al. to accommodate a left distal humeral fragment, **KNM-KP 271**, recovered by Bryan Patterson (Patterson and Howells 1967), and cranial remains recovered from *c*.3.9–4.2 Ma localities at **Allia Bay** and **Kanapoi**, Kenya [additional fossils from the two sites were described 3 years later (Leakey et al. 1998)]. The authors claim *Australopithecus anamensis* teeth are more primitive than those of *Australopithecus afarensis* (e.g., mandibular canine morphology, the asymmetry of the premolar crowns, and the relatively simple crowns of the deciduous first mandibular molars), but in other respects (e.g., the low cross-sectional profiles and bulging sides of the molar crowns) the teeth of *Au. anamensis* show similarities to ***Paranthropus*** (see below). Upper limb remains were also recovered and were described as being australopith-like (Leakey et al. 1998), but a tibia (KNM-KP 29283) attributed to *Au. anamensis*, but not included in the list of paratypes, has features associated with obligate bipedalism. White et al. (2006) reported 31 additional fossils from the **Middle Awash study area**. One, a maxilla, was found at **Aramis**, with the remainder coming from three localities at **Asa Issie**, a collecting area 10 km/6 miles west of Aramis. Biostratigraphic dating suggests an age of *c*.4.2–4.1 Ma for both sets of Middle Awash fossils. Craniodentally (e.g., anterior tooth and postcanine relative tooth size, crown morphology, enamel thickness, etc.) the new material from the Middle Awash is consistent with an attribution to *Au. anamensis* and ASI-VP-5/154, the proximal three-quarters of a right femur shaft, is a slightly more primitive version of the *Au. afarensis* femoral morphology. White et al. (2006) support the proposal made by others (e.g., Ward et al. 1999) that although the hypodigms of *Au. anamensis* and *Au. afarensis* are distinct there is evidence (e.g., relative canine size, upper canine morpohology, enamel thickness, femoral shaft morphology, etc.) of the type of morphological continuity that one would expect to see within an evolving lineage, and Kimbel et al. (2006) provide compelling evidence that *Au. anamensis* and *Au. afarensis* are "parts of an anagenetically evolving lineage, or evolutionary species" (*ibid*, p. 134). Suggestions that *Au. anamensis* might have been a hard-object feeder (e.g., Ward et al. 1999, Teaford and Ungar 2000, Macho et al. 2005, White et al. 2006b) are apparently not supported by dental microwear evidence (Grine et al. 2006). First discovery KNM-KP 271 (1965). Holotype **KNM-KP 29281** (1994). Paratypes KNM-KP 271, 29282-8; KNM-ER 7727, 20419-23, 20427-8, 20432, 22683, 24148, 30202, 30200. Main sites Allia Bay and Kanapoi, Kenya; Aramis and Asa Issie, Ethiopia. *See also* ***Australopithecus afarensis***.

Australopithecus bahrelghazali **Brunet et al., 1996** (etym. *see* ***Australopithecus***, and *bahr el ghazali* = place of discovery) Hominin species established by Michel **Brunet** and colleagues in 1996 to accommodate a tooth-bearing midline mandible fragment that includes the symphysis and an upper premolar tooth recovered from *c*.3.5–3.0 Ma sediments in the **Bahr el Ghazal** region, **Koro Toro**, Chad. The mandibular fragment had been previously assigned to *Australopithecus* aff. *Australopithecus afarensis* (Brunet et al. 1995). The authors claim that it has thicker enamel than ***Ardipithecus ramidus***, a more vertically orientated and more gracile symphysis than ***Australopithecus anamensis***, more complex premolar roots than *Australopithecus afarensis* and ***Australopithecus africanus***, and larger incisors and canines than *Au. africanus*. However, other researchers interpret these differences as geographical variation within *Au. afarensis*. First discovery **KT 12/H1** (1995). Holotype As above. Paratypes KT 12/H2, right P^3. Main site Bahr el Ghazal, Chad. *See also* ***Australopithecus afarensis***.

Australopithecus boisei **(Leakey, 1959)** (etym. *see* ***Australopithecus***, plus *boisei* to recognize the substantial help provided to Louis **Leakey** and Mary **Leakey** by Charles **Boise**) The genus ***Zinjanthropus*** was established by Louis Leakey in 1959 to accommodate fossil hominins recovered in 1955 and 1959 in Bed I, **Olduvai Gorge**, Tanzania. John **Robinson** (1960) suggested it was a synonym of ***Paranthropus***, and Louis Leakey (1963) subsequently sank *Zinjanthropus* into ***Australopithecus***. *See also* ***Zinjanthropus boisei***.

Australopithecus garhi **Asfaw et al., 1999** (etym. *garhi*=surprise in the Afar language) Hominin species established by Asfaw et al. (1999) to accommodate a fragmented cranium and two partial mandibles recovered from the *c*.2.5 Ma Hatayae Member of the **Bouri Formation** at the **Bouri**, **Gamedah**, and **Matabaietu** collection areas,

Middle Awash study area, Ethiopia. *Australopithecus garhi* combines a primitive cranium with large-crowned postcanine teeth. However, unlike ***Paranthropus boisei*** the incisors and canines are large and the enamel apparently lacks the extreme thickness seen in the latter taxon. A partial skeleton combining a long femur with a long forearm was found nearby, but is not associated with the type cranium (Asfaw et al. 1999) and these fossils have not been formerly assigned to *Au. garhi*. The authors claim that despite its large postcanine tooth crowns its cranium lacks the derived features of ***Paranthropus***, and they suggest it may be ancestral to ***Homo***, but what little evidence there is from phylogenetic analyses does not support a close link with *Homo*. The morphology of the mandibles reported in the same publication as *Au. garhi* is in some respects like that of ***Paranthropus aethiopicus***. If it is demonstrated that the type specimen of *P. aethiopicus*, **Omo 18-18**, belongs to the same taxon as the mandibles that appear to match the *Au. garhi* cranium, then *P. aethiopicus* would have priority as the name for the *Au. garhi* hypodigm. First discovery GAM-VP-1/1 (1990). Holotype **BOU-VP-12/130** (1997). Paratypes None. Main sites Bouri, Ethiopia.

Australopithecus prometheus* Dart, 1948** (L. *australis* = southern, Gk *pithekos* = ape and *Prometheus* = in Greek mythology the Titan who stole fire from Olympus. Raymond **Dart** chose this **species** name because organic chemists had confirmed the presence of carbon in the Makapansgat Cave; Dart 1948, p. 201). Hominin species established by Raymond Dart in 1948 to accommodate **MLD 1**, a hominin occipital recovered by the Kitching brothers at the Makapansgat Limeworks Dump. Dart (1948) considered the combination of the large size of MLD 1, the separation of **inion** and opisthocranion, and its distinctive **suture** pattern, to justify his conclusion that MLD 1 "differs vividly" (*ibid*, p. 200) from ***Plesianthropus. Most researchers interpret the Makapansgat hominin remains as being similar enough to those from **Taung** and **Sterkfontein** Member 4, etc. for *Australopithecus prometheus* to be regarded as a junior synonym of ***Australopithecus africanus* Dart, 1925**, and Robinson (1954a) suggested that the hominins from Makapansgat be transferred to *Australopithecus africanus* as *Australopithecus africanus transvaalensis*. However, Aguirre (1970) considered the dental morphology of some of the Makapansgat hominins to be sufficiently like that of ***Paranthropus robustus*** to argue the case for a second hominin at Makapansgat. First discovery **MLD 1** (1947). Holotype As above. Paratypes None. Main site Makapansgat, South Africa. *See also* **Makapansgat**; ***Australopithecus africanus transvaalensis***.

Australopithecus ramidus* White et al., 1994** A new species of *Australopithecus* proposed by White et al. (1994) to accommodate 17 fossils recovered from localities at Aramis in the **Central Awash Complex** of the **Middle Awash study area**. A year later, in a corrigendum to the original paper, the same authors made a new genus name, *Ardipithecus*, available along with a diagnosis. They also noted that "in late 1994 a mandible of *A. ramidus* was found at Aramis associated with a partial postcranial skeleton, 50 m north of the holotype specimen, and at the same stratigraphic level. Analysis of this specimen has begun, and will provide further features with which to characterize *Ardipithecus*" (White et al. 1995, p. 88). Presumably White and his colleagues were referring to ARA-VP-6/500 (White et al. 2009a). *See **Ardipithecus ramidus.

Australopithecus sediba* Berger et al. 2010** (L. *australis* = southern, Gk *pithekos* = ape, and Se Sotho *sediba* = fountain or wellspring) A hominin taxon established by Berger et al. (2010) to accommodate two hominin associated skeletons, **MH1** and **MH2**, recovered from **Malapa** in South Africa. These authors suggest that although the lower limb of *Australopithecus sediba* is like those of other archaic hominins, they claim that it has cranial morphology (e.g., more globular neurocranium, gracile face), mandibular morphology (e.g., more vertical symphyseal profile, a weak **true chin**), dental morphology (e.g., simple canine crown, small anterior and postcanine tooth crowns), and pelvic morphology (e.g., **acetabulocristal pillar**, expanded ilium and short ischium) that is only shared with early and later ***Homo taxa. First discovery MH1 (2008). Holotype MH1. Paratype MH2. Main site Malapa.

Australopithecus transvaalensis* Broom, 1936** (L. *australis* = southern and Gk *pithekos* = ape; literally the "southern ape of the Transvaal") Hominin species established by Robert **Broom** in 1936 to accommodate **TM 1511**, the cranium and endocranial cast of a young adult recovered at **Sterkfontein** from breccia now referred to as being from Member 4. Broom considered the new cranium "agrees fairly closely with the Taungs ape," but that "the molar teeth differ in a number of important details" (Broom 1936, p. 488). The species *Australopithecus transvaalensis* was subsequently transferred to the genus *Plesianthropus* as *Plesianthropus transvaalensis* by Broom (1938), but it is now almost universally regarded as a junior synonym of *Australopithecus africanus*. In any event it is doubtful whether Broom's presentation of the new species complied with the then current (i.e., 1930 revision) version of the Rules of Zoological Nomenclature. First discovery TM 1511 (1936). Holotype As above. Paratypes None. Main site Sterkfontein, South Africa. *See also* ***Plesianthropus; ***Plesianthropus transvaalensis***; ***Australopithecus africanus***.

Australopithecus walkeri **Ferguson, 1989** (L. *australis* = southern and Gk *pithekos* = ape, literally (Alan) Walker's "southern ape") Hominin species established by Walter Ferguson in 1989 to accommodate the "black skull" **KNM-WT 17000** and named "in honor of its discoverer" (*ibid*, p. 231). Ferguson (1989) argued that shape and size differences between **OH 5**, belonging to *Paranthropus boisei*, and KNM-WT 17000 were (a) greater than those between "*Australopithecus boisei*" and "*Australopithecus robustus*" (his terminology) and (b) too great to be subsumed within a single species. For example, he suggested the differences in cranial capacity (410 cm^3 in KNM-WT 17000 and 530 cm^3 in OH 5), both presumed male crania, were beyond what would be expected within one sex in a higher primate taxon. Ferguson's presentation of the new species complied with the **International Code of Zoological Nomenclature** rules, but his proposal is almost universally ignored because researchers who see the need for a second species for the pre-2.3 Ma **megadont** archaic hominins from East Africa use *Paraustralopithecus* or ***Paranthropus aethiopicus*** as the name for such a **taxon**. Groves (1999) has pointed out that the taxon name ***Australopithecus aethiopicus*** is preoccupied by Tobias (1980b), who suggested that *Au. africanus aethiopicus* could be used for the **Hadar** component of the hypodigm of ***Australopithecus afarensis***. First discovery KNM-WT 17000. Holotype As above. Paratypes None. Main site **West Turkana**, East Africa. *See also* ***Paranthropus boisei***; ***Paraustralopithecus aethiopicus***.

Austronesia (L. *australis* = southern and Gk *nesos* = island, literally "southern islands") An inclusive term used for all the island groups in the Pacific (i.e., **Indonesia**, **Melanesia**, **Micronesia**, and **Polynesia**).

autapomorphic *See* **autapomorphy**.

autapomorphy (Gk *autos* = self and *morphe* = shape) A term used in **cladistic analysis** for a derived **character state** that is confined to one of the taxa, or **operational taxonomic units**, used in that analysis. Autapomorphies can be used for taxonomic identification, but because the morphology is by definition confined to a single taxon it cannot be used to explore how closely that taxon is related to another taxon. Examples of probable autapomorphies are the enlarged talonid of the mandibular postcanine teeth of ***Paranthropus boisei*** and the large globular brain case of ***Homo sapiens***.

autecology (Gk *auto* = self) The branch of **ecology** that focuses on the interactions between an individual (or a single species) and its environment. Although autecology is a term used infrequently by paleoanthropologists, many ecological studies of hominins are essentially autecological, as some species are represented by a single fossil and in many cases research focuses on a single species.

autopod (Gk *autos* = self and *pod* = foot) The **distal** of the three compartments of a tetrapod, and therefore of a hominin, limb. The proximal compartment is the **stylopod** (the upper arm or the thigh), the intermediate one is the **zeugopod** (the forearm or the lower leg), and the distal one is the autopod (the hand or the foot).

availability *See* **available**.

available (L. *valere* = to be worthy) In relation to nomenclature a taxonomic name that is available is a name that has been generated according to the rules and recommendations of the **International Code of Zoological Nomenclature**. For example, the rules stipulate that an available name must not have been used in that context before, it must be formed from the 26 letters of the alphabet, and it must not have any commercial connotation. So whereas at the time it was proposed ***Plesianthropus transvaalensis*** was an available name, if it was proposed today it would not be available, and for different reasons neither would the taxon names *Homo 2feet* or *Homo bigmacensis*. To be a **valid** as a taxon name, the name must be available, but among many available names for a taxon, only one is valid. *See also* **International Code of Zoological Nomenclature**.

Aves (L. *avis* = bird) The name of the class that contains all bird taxa. Birds are bipedal tetrapod vertebrates; their forelimbs are specialized as wings, although the capability for powered flight has been lost in some lineages (e.g., ratites and penguins). Birds are warm blooded, lay eggs, and have feathers. Birds have a global distribution and there are both resident and migratory species. Bird bones are extremely fragile, having a lightweight structure to make flight less energetically costly. This makes them less durable in death and bird bones are disproportionally destroyed by perimortem, post mortem, and other **diagenetic** processes. Therefore bird osseous true fossils are relatively rare in the fossil record as are bird trace fossils in the form of prints and trails, but fossil egg shell, especially ostrich egg shell, is relatively common in open-air sites in Africa. Structural fragility means that bird remains are unlikely to be transported far from their place of death since they are especially prone to mechanical destruction. When bird remains are found in the fossil record they can be useful paleoenvironmental indicators (e.g., wading birds indicating the nearby presence of water). The most common bird remains found at early hominin fossil sites is probably ostrich egg shell, which can be used for ostrich egg shell dating as well as for paleoenvironmental reconstruction. *See also* **birds**; **ostrich egg shell dating**; **paleoenvironmental reconstruction**.

Awash River The Awash River runs for approximately 1100 km/700 miles within Ethiopia. It begins in the Ethiopian Highlands west of Addis Ababa, where it shares a watershed with the headwaters of the Blue Nile. It passes south of Addis Ababa and then turns north to run through the Awash National Park which is approximately 240 km/150 miles to the east of the Ethiopian capital. The Awash River then enters the Afar Triangle and runs north–northeast for 320 km/200 miles before turning east and then south–southeast for 120 km/75 miles before coming to an end in the most arid part of the Afar Triangle in Lake Abbé, some 112 km/70 miles west of the deepest part of the western, landward, end of the Gulf of Tadjoura. The Upper, Middle, and Lower Awash regions are informal divisions of the part of the Awash River valley that runs through the Afar Triangle. *See also* **Middle Awash study area**.

Awash River Basin This refers to the approximately 440 km-/275 mile-long part of the Awash River that passes north, then in a southeasterly direction, through the Afar Triangle. Mammalian fossils have been reported in the region since the beginning of the 20thC, but it was not until geologist Maurice Taieb undertook reconnaissance work there in the 1960s that its potential as a source of fossils began to be realized. Taieb, together with Yves **Coppens**, John Kalb, and Don **Johanson**, formed the **International Afar Research Expedition** (or IARE) to explore the northern part of the basin in the early 1970s, but thereafter Kalb shifted his attention to the south and in 1975 and 1976 he formed the **Rift Valley Research Mission in Ethiopia** (or RVRME) to explore the region now known as the **Middle Awash study area**. The RVRME's activities focused on the eastern side of the Awash River, but Kalb and colleagues visited the Bouri Peninsula late in 1975, and located fossils and **Acheulean** artifacts at a locality identified as **Dakanihylo**. In the next year they discovered a hominin cranium (**Bodo 1**) in a region on the eastern side of the river at **Bodo**.

Awirs *See* **Engis**.

awl (ME *aul* = pointed tool) A small pointed tool commonly made of bone or metal for engraving or perforating. Awls are, and presumably were, used for a variety of tasks including sewing, leatherwork, basketry, woodworking, and inscribing brittle materials like ceramic and glass. Awls may be used hafted or hand-held. Bone awls, manufactured by longitudinal splitting of long bones and subsequent sharpening of the pointed tip, occur as components of early bone industries, such as found, for example, at **Blombos Cave**, South Africa.

axial digit (L. *axis* = a straight line around which a body or object rotates, or a line around which something is symmetric) The term used for the **reference digit** of the hand (the middle finger), or the reference digit of the foot (the second toe). *See also* **axis**.

axial skeleton Comprises the **skull**, the vertebral column, the ribs, and the sternum. It is the presence of these components of the hard tissue skeleton that defines the vertebrate subphylum. What unites the components of the axial skeleton is that it is what is left of the skeleton after the limbs and limb girdles have been removed or excluded. The components of the axial skeleton are all either in the midline, or they are connected directly, or indirectly, to midline stuctures.

axis (L. *axis* = a straight line around which a body or object rotates, or a line around which something is symmetric) Four meanings of axis are relevant to human evolution. First, it refers to the midline, or axis, of the body, as in **axial skeleton**. Second, it refers to the straight line, or axis, around which a part of the body rotates. For example, the axis of **pronation** and **supination** of the forearm is a straight line joining the center of the head of the radius and the styloid process of the ulna. Third, it refers to the reference digit of the hand (the middle finger) and foot (the second toe). The fourth meaning refers to the second (C2) of the seven cervical vertebrae. The C2 vertebra is called the axis because it incorporates the odontoid process, which forms the axis around which the atlas [the first (C1) cervical vertebra] plus the cranium, which articulates with the superior aspect of the atlas, rotate.

axon (Gk *axon* = axis) A tubular process that projects from a nerve cell, or **neuron**, and is the way neurons connect to other neurons in a nervous pathway, or with the target structure (e.g., muscle fiber, blood vessel, or sweat gland) or target organ (e.g., heart) being innervated. Axons have diameters that range from 0.2 to 20 μm and they can extend for up to 1 m. Axons are capable of conducting a nerve signal, or action potential, over great distances. Large axons are surrounded by a fatty insulating sheath called **myelin**, which is important for enabling the high-speed conduction of action potentials. The sheath is interrupted at regular intervals by nodes of Ranvier (named after the neuroanatomist Louis Antoine Ranvier who first described them towards the end of the 19thC). Near its end the axon divides into fine branches that have specialized swellings called presynaptic terminals where neurotransmitter molecules are released into the synaptic cleft that lies between the presynaptic terminals and the next neuron, or the structure or organ being innervated. During development, a neuron sends out axons by way of a growth cone. The growth cone appears as an enlargement of the shaft of the axon, and several extensions, called filopodia, project from it and facilitate the migration of the axon through tissue. Maxwell Cowan, Giorgio Innocenti, and their colleagues independently found that neurons send axons to many more targets in the developing brains than are eventually retained in the adult animal, and the projections are focused on discrete areas within the brain (e.g., the **cerebral cortex**) by pruning projections to inappropriate targets.

Azilian A technocomplex that includes small scrapers and distinctive points; the type site is Mas-d'Azil. *See* **Mas-d'Azil**.

Azokh Cave complex (Location 39°37′09″N, 46°59′19″E, Nagorno-Karabagh, an autonomous region within Azerbaijhan in the Lesser Caucasus; etym. named after a nearby village) History and general description The Azokh Cave was discovered in 1960. The initial, 15 year-long, period of excavations at Azokh 1 was brought to an end in 1989, and in that time 2430 m^3 out of an estimated 3400 m^3 total volume of sediment had been removed from that part of the cave complex. Since 2002 the Azokh Cave Project, an international and multidisciplinary program, has been working at the site. Four more entrances were discovered and two of these, Azokh 2 and Azokh 5, contain fossils and artifacts. A hominin mandible was found at Azokh 1 in 1968. Temporal span and how dated? Five beds have been identified at Azokh 1, with Bed V being dated at *c*.200 ka by **uranium-series dating** and *c*.300 ka by **amino-acid racemization dating** and **electron spin resonance spectroscopy dating**. Archeological evidence found at site In Beds II and II "the lithic assemblages are primarily Middle Paleolithic in character" and Bed V contains "retouched scrapers and unretouched flakes" (Fernández-Jalvo et al. 2010, p. 105). Key references: Geology and dating Fernández-Jalvo et al. 2004, 2010; Hominins Kasimova 2001; Archeology Fernández-Jalvo et al. 2004, 2010.