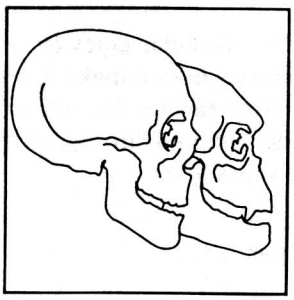

Evolution, Human

HENRY M. MCHENRY, *University of California, Davis*

Glossary

Australopithecus Extinct forms of humans who lived in Africa from about 5 to 1.3 million years ago. They were characterized by human-like bipedal posture, brain size about one third that of modern people, and relatively large cheek teeth. One species of this genus probably evolved into the genus *Homo*

Hominid Organisms belonging to the zoological family Hominidae which include both extinct and modern forms of humans such as *Australopithecus, Homo erectus,* and the Neanderthals

Hominoid Organisms belonging to the zoological superfamily Hominoidea including modern and fossil species of humans and apes

Molecular clock A method of computing the time of divergence between evolutionary lineages based on the genetic distances among living species

Pongid Organisms belonging to the zoological family Pongidae including modern great apes (chimpanzee, gorilla, and orangutan) and closely related fossil species

THE HUMAN EVOLUTIONARY lineage originated in Africa in the late Miocene, 8 to 5 million years ago, from an ancestor shared with the African great apes (chimpanzee and gorilla). Probably by 5 but certainly by 4 million years ago, our ancestors walked bipedally, had front teeth intermediate in shape between modern apes and people, and had a relative brain size about one-third that of *Homo sapiens*. By 2 million years, the teeth were basically human-like (except for the large size of the cheek teeth), and the relative brain size was about 50% larger than its predecessor. The species *Homo erectus* first appear 1.6 million years ago with a brain nearly twice the size of the first hominids. Not until about 1 million years ago did our family disperse out of Africa to colonize Asia and Europe, and not until about 300,000 years ago were brains expanded into the modern human range. Anatomically modern *H. sapiens* appears to have originated in Africa about 100,000 years ago. By about 35,000 years this form had occupied all the Old World including Australia. Although some people may have reached the Americas earlier, the first substantial population there dates to about 12,000 years ago.

This brief outline of current knowledge derives from the remarkably successful cooperation of molecular biologists, comparative morphologists, geologists, paleontologists, archaeologists, biological anthropologists, geneticists, ecologists, and individuals from many other fields. Such a sketch is, of course, tentative, pending further information and interpretation, but a great deal of hard evidence lies behind it.

I. Place in Nature

A. Taxonomy of *Homo sapiens*

Homo sapiens is one of about 180 living species within the order Primates, which is one of 18 mammalian orders. The order Primates contains prosimians (such as lemurs), monkeys, and apes. Our species is placed in the suborder Haplorhini along with tarsiers, monkeys, and apes. Within Haplorhini we are grouped with Old World monkeys, and apes in the infraorder Catarrhini, which in turn is divided into two superfamilies [i.e., Cercopithecoidea (Old World monkeys) and Hominoidea (apes and people)]. Traditionally the Hominoidea are divided into three families (i.e., Hylobatidae (gibbons and siamangs), Pongidae (orangutans, gorillas, and

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chimpanzees), and Hominidae (humans), but research since the 1960s has clearly demonstrated that this classification does not reflect the true phyletic relations. Several lines of evidence, especially molecular systematics, show that the African great apes (gorilla and chimpanzee) are more closely related to humans than to the Asian apes (gibbons, siamangs, and organutans). Some authors believe that the classification should reflect that fact by placing the African apes in the family Hominidae. By this scheme, the Hominidae is divided into subfamilies Paninae (gorilla and chimpanzee) and Homininae (humans). There are several other recently proposed revisions in the classification, but the most widely used is still the traditional division of Pongidae (great apes) and Hominidae (humans), with the understanding that this does not reflect the phyletic relations.

B. Genetic Relations

As early as 1904, G. H. F. Nuttall published "Blood Immunity and Blood Relationships," which explored the genetic relations among animals using immunological techniques. More than half a century lapsed before M. Goodman showed the power of molecular biology in clarifying our place in nature. Using the method of immunodiffusion he published in 1962 and 1963 what has become established fact: *H. sapiens* is much more closely related to African great apes than either is to the Asian great ape. Subsequent tests using a variety of methods (e.g., amino-acid sequencing, microcomplement fixation, DNA hybridizations, electrophoresis, and nucleotide sequencing) confirm the surprisingly close relations among humans, chimpanzees, and gorillas. The genetic similarity among these three is of a similar magnitude to the similarity between dog and fox, cat and lion, sheep and goat, and only slightly more than that between horse and donkey.

By the late 1960s V. Sarich and A. Wilson accumulated enough genetic comparisons among primates to show that immunologically detected differences in albumin (i.e., their ability to interact with certain antibodies) likely changed at a constant rate through time. By calibrating this change with a widely accepted date for the evolutionary divergence of two lineages, they derived a molecular clock for primate evolution that placed the origin of the hominid lineage at 4.2 million years ago. Subsequent studies by a variety of methods by numerous individuals, including the direct comparison of DNA, have shown that the molecular clock is generally correct, but irregularities in rate make it necessary to give significant error ranges. Recent estimates of the origin of the hominid lineage range from about 8 to 4 million years ago.

C. Traits Shared with Apes

Despite the obvious fact that *H. sapiens* is profoundly different from all other animals in many respects, we share a number of traits uniquely with apes that show our phylogenetic affinity with them. These shared and unique characteristics are most conspicuous in the forelimb and trunk anatomy. Apes and humans share exceptionally short lumbar regions of the spine, the lack of a tail, highly mobile shoulder and elbow joints, broad chests that are flattened from front to back, reduced ulnar olecranon processes, a vertebral column that protrudes into the chest cavity, long clavicles and acromial processes, a broad sternum, a diaphragm that is perpendicular to the spine, an obliquely positioned heart that adheres closely to the diaphragm, and abdominal organs that are closely attached to the posterior wall of the body cavity. These and other traits are probably related to the orthograde posture (upright) of the trunk. The molar teeth show detailed similarity in cusp number, fissure pattern, and overall form. A few traits are uniquely shared by humans and the African great apes, such as the presence of a frontal sinus that develops from the ethmoid bone and the fusion of the os centrale in the wrist. In addition, African apes and humans share certain molecular similarities such as a unique substitution of amino acids in the myoglobin chain at positions 23 and perhaps 110; two shared substitutions in the fibrinopeptide A and B chains; three transversions, eight transitions, and three deletions in the nuclear DNA sequence; and 16 substitutions in the mitochondrial DNA. [*See* COMPARATIVE ANATOMY.]

D. Unique Traits of Hominidae

As Lamarck, Huxley, Haeckel, Darwin, and other nineteenth century evolutionists pointed out, bipedalism was probably the primary change in the origin of our evolutionary lineage. Twentieth century discoveries of fossils confirm this. Habitually walking on the hindlegs with the forelimbs free for carrying and perhaps wielding weapons is the first fundamental change away from our common ancestors with the apes. This change required a major reor-

ganization of the hindlimb and back away from the pattern common to most mammals. The most conspicuous anatomical differences are the shortened pelvic blade and the reorientation of the foot from a grasping organ to one in which the sole function is propulsion.

Modern human brain size is about three times greater than that of apes of the same body size. From the fossil record it is clear that brain size evolution occurred after the adoption of bipedalism. Most of the change occurred during the last 2 million years of evolution. Why the brain expanded is the subject of much speculation, but certainly the origin of language is related to this process.

II. Evolutionary History

A. The Stock from which Our Family Arose

The first substantial fossil evidence of the origin of the evolutionary lineage leading to modern catarrhines (Old World monkeys, apes, and humans) occurs in geological strata dating to 37 to 31 million years ago in the Fayum deposits of Egypt. Unfortunately, no fossil localities in Africa have produced sufficient mammalian remains before the rich and diversified primate fauna of the Fayum, so little is known about what came before. Primates are abundant in European and North American localities dated before 37 million years ago, but no catarrhines are present. A few mandibular fragments from Burma dating to about 40 million years ago hint at the possibility of catarrhines in Asia, but the evidence is tenuous so far.

The Fayum presents an extraordinary window on the early stages of the evolution of the primates between 37 and 31 million years ago. The climate was warm, the habitat forested, and a major river moved slowly through the site. Primates constituted a major component of the mammalian fauna. A tarsier-like form is represented (by a jaw fragment) as well as a loris-like creature (known only from one tooth). The most common primates are grouped under the family name of Parapithecidae (*Parapithecus* and *Apidium*), which are not catarrhines (i.e., they retain the primitive characteristic of having three premolar teeth). There are several species of catarrhines divided by their original describers into two genera, *Propliopithecus* and *Aegyptopithecus*, although some authorities recognize only one genus. *Propliopithecus* was small (2–3 kg), aboreal, quadrupedal, and sexually dimorphic. *Aegyptopithecus* was larger (about 6 kg), diurnal, and arboreal. Its postcrania show an adaptation for slow and deliberate branch climbing and quadrupedal walking. It had strong sexual dimorphism in body size, canines, and skull morphology. The teeth indicate fruit-eating. The best-preserved cranium shows a long, almost lemur-like snout, but other facial skeletons are much less prognathic. The brain is relatively small compared with modern catarrhines but catarrhine-like in having relatively smaller olfactory bulbs, larger visual cortex, and a more complex sulcal pattern.

By current paleontological evidence, catarrhines were confined to Africa until about 16 million years ago. Until this date Africa and Arabia were separated from Eurasia by the Tethys Sea. Unfortunately, there is a gap in the primate fossil record in Africa between 31 and 22 million years. By early Miocene times (21–17 million years ago) there was a rich sample of catarrhines in East Africa during a period when tropical forests extended much further east and north than they do now, although there are some indications that woodland or brushland grassland habitats existed as well.

The early Miocene primates of East Africa show the earliest evidence for the divergence between the two catarrhine superfamilies Cercopithecoidea (Old World monkeys) and Hominoidea (apes and people). Cercopithecoid fossils are relatively less abundant than hominoids. The hominoids are quite different from any living species and are best placed in one or more separate families. There are at least seven genera. The adaptive diversity among these hominoids is considerable. Body sizes range from 4 to 40 kg. Their diets were primarily of fruit, but some species were leaf eaters. Most were arboreal quadrupeds, but some may have been capable of forelimb suspensory behavior as well. The postcranium does not, however, reveal many (if any) of the distinctive traits that are shared by all the living hominoids. In fact, the early Miocene hominoids share very few derived traits with living hominoids, although two recently discovered genera, *Afropithecus* and *Turkanopithecus,* show greater resemblance to later hominoids.

Between 15 and 13 million years ago there was a major faunal change in the Old World because of the exchange of species between Africa and Eurasia. This event was apparently triggered by the breaking down of the Tethys Sea barrier, which had kept Afro-Arabian faunas isolated. Although forests were much more abundant than today, there is evidence for some open habitat and possibly grassland.

particularly in the northern latitudes. There is evidence of climatic cooling at this time.

The first hominoids outside Africa occurred at this time (15–18 million years ago) in both Europe and Asia. The adaptive and phyletic diversity was much higher than among modern hominoids. Between 15 and 12 million years ago, at least four genera and nine species of large-bodied hominoids were in Eurasia, and possibly the African diversity was equally great, although fewer African fossil primates are known during this period. Most of these hominoids had thick molar enamel similar to that seen in modern orangutans and fossil hominids. They were apparently frugivorous, had marked sexual dimorphism, and looked somewhat like modern apes. Although the postcranial fossils are rarer and unassociated, they appear to share the suite of characteristics unique to modern hominoids. The divergence of the evolutionary lineage leading to the orangutan probably occurred by 12 million years ago, as shown by the remarkable discovery of a facial skeleton of *Sivapithecus* in Pakistan. This specimen shares numerous derived traits with the Asian great ape. There is a wealth of new material from Europe and especially China that shows the rich diversity of these ape-like forms in the Miocene compared with the impoverished diversity of modern ape species.

At about 10 or 11 million years ago, there is evidence for increasing open habitat in the Old World and another major faunal turnover. By about 7 million years, forest and woodland-adapted fauna were replaced by more open-country species in South Asia. In Africa the record is less well documented, but certainly the abundant forests by the early Miocene gave way to more and more patchy woodland and grassland habitats in the middle to late Miocene. The collection of middle to late African hominoids is rapidly expanding in recent years, but the picture is still far from clear. Yet no fossils are clearly linked uniquely to any of the living African great apes, although a palate from 8 million-year-old beds in Kenya shows some gorilla-like traits. There is a sprinkling of tantalizing bits of hominoid fossils in the late Miocene but nothing that can be linked specifically to living species until possibly 5 and certainly 4 million years ago when some fossils distinctly belong to the human evolutionary lineage.

B. First Bipeds

The molecular clock predicts the divergence of the human and African ape evolutionary lineages to be some time between 5 and 8 million years. During this period and later, the African habitats were drastically changing, with increasing seasonality of rainfall and spreading grassland. Areas of tropical rainforest were reduced, creating isolated pockets of forest in a sea of grass. Unfortunately, few fossil primates are known from this period: a *Sivapithecus*-like tooth at 9 million years ago, a palate with some gorilla-like features combined with unique traits at 8 million years, an ape-like molar crown at 7 million years, and a mandibular fragment with one molar tooth at 5–6 million years ago. The latter specimen from Lothagam in Kenya has some derived traits that appear to be shared with later hominoids (e.g., a relatively decreased molar length, entoconid size, and mandibular depth). It is associated with open-country fauna. By 4 million years, the presence of humans is more secure with fragments of a jaw, two arms, and a thigh. The thigh is reported to have an internal arrangement of trabeculae characteristic of later bipeds.

By 3.8–3.6 million years, the record of hominids becomes much richer by the discoveries at Laetoli in Tanzania. The site produced the remains of 23 hominids including jaws, associate dental rows, an infant skeleton, and three sets of footprint trails made by bipeds. The footprints are clearly hominid with distinctly convergent big toes and human-like proportions. The dental remains are said to be very similar to those found at Hadar in Ethiopia dating between 2.8 and 3.1 million years ago. The Hadar collection is wonderfully complete with one associated skeleton (A.L. 288-1, "Lucy"), the fragmentary remains of at least 13 individuals who apparently died together at one spot, and numerous other skeletal parts. The combined sample of Laetoli and Hadar yields an excellent picture of what the first human species, *Australopithecus afarensis,* looked like.

Australopithecus afarensis was fully bipedal as indicated by the Laetoli footprints and the Hadar postcranial skeletons. The pelvic blades are low, the sacrum wide, and the pelvic basin quite human-like in shape, although it is not identical to modern humans. The knees are characteristically human and not ape. The toes are relatively shorter than any ape but not reduced as much as they are in modern humans. The forelimbs are relatively quite small, and the wrists and hands show no adaptation for ape-like knuckle-walking. The skeleton retains many ape-like traits, but in most fundamental respects, it is adapted for bipedality. Its long, curved toes and fingers and many other ape-like features

may imply that this first human species was a more adept tree-climber than later species of hominid. Although its pelvis and hindlimb are fundamentally human-like, basic differences imply a somewhat different form of bipedality from that seen in modern *H. sapiens*. The pelvic blades, for example, face more posteriorly; the thighs are relatively short; the knees appear to lack a human-like meniscus attachment; the ankle, in at least one specimen, slopes in an ape-like direction; the foot architecture has many ape-like traits; and the toes are relatively long and curved.

In other characteristics *A. Afarensis* possesses a mixture of hominid and pongid qualities. There was strong sexual dimorphism in body size, females weighing about 30 kg and males close to 45 kg. The brain size was about that of a modern chimpanzee (415 cc), which is about one-third the size of a modern human of the same body size. The skull is quite pongid-like, with a prognathic muzzle, an unflexed cranial base, and a strong development of the posterior fibers of the temporalis muscle. The canine is considerably reduced from the size seen in modern apes, but it is larger than that of modern humans. The lower first premolar is variable, but in many specimens it is quite ape-like in orientation and cusp number.

A similar form of hominid occurs at about 2.5 million years in South African cave deposits, *Australopithecus africanus*. In many postcranial parts it is remarkably similar to the Hadar hominids, although there are some differences, particularly in the hand. *A. africanus* is distinct from the Hadar and Laetoli hominids in having many cranial and dental traits more similar to later *Homo* (e.g., a reduced muzzle, a more flexed cranial base, and a biscuspid first premolar). Females appear to be as small as those from Hadar, but males are not quite as large. The average cranial capacity is slightly larger (442 cc), and there are no specimens as small as the smallest one from Hadar. The cheek teeth are relatively larger.

C. Extinct Cousins: The Robusts

From about 2.5 to 1.3 million years lived a variety of hominids referred to as "robust" australopithecines because of their hypertrophied masticatory system. At least two and probably four species are known so far. The earliest, referred to by some as *Australopithecus aethiopicus,* is known from East African sites dating to 2.5 million years ago. Its cheek teeth are enormous, as are all the supporting structures related to heavy chewing (i.e., massive jaws, strongly buttressed skull, enormous area of attachment for the muscles of mastication). In many ways the skull shares primitive characteristics with *A. afarensis* and pongids, (e.g., an unflexed cranial base, a prognathic muzzle, and a strong development of the posterior fibers of the temporalis muscle). In the later robust species, these traits are lost, and they appear more *Homo*-like. These species include *A. boisei,* found abundantly in East Africa between 2.3 and 1.3 million, and *A. robustus* of South Africa. Although body size is no greater than that in earlier hominid species, the brain size is about 100 cc larger. The postcrania are fragmentary and difficult to associate with these species, but what specimens there are indicate a remarkably human-like form. It is generally assumed that the massive development of the chewing apparatus was an adaptation to a vegetarian diet, perhaps consisting primarily of hard fruits and bulbs but not grass.

D. The Appearance of *Homo*

The first abundant evidence of what most investigators would refer to as *Homo* occurs in strata dated to about 2 million years ago, although fragmentary material is known slightly before that date. Between 1.9 and 1.6 million years ago, many specimens probably belong to the genus *Homo,* but the variability is higher than would be expected from a single species. Whether this variability indicates more than one species has not been resolved. The species name associated with this material is *habilis*. The *Homo*-like traits include an expanded brain (about 50% larger than *A. africanus* in relative size) and reduced cheek teeth. The smallest postcranial specimen was probably less than 1 m tall and may have weighed less than 25 kg. The largest probably weighed more than 60 kg. Relative to joint size, the hindlimbs were much less robust than those of *Australopithecus*. Stone tools first appeared in the archaeological record at 2.5 million years, and it is often inferred that *Homo* was responsible for them. Well-preserved living floors occur at least by 1.8 million years and show that these hominids were using tools for several activities including butchering, plant processing, and wood carving.

The species *H. erectus* first appeared at 1.6 million years ago in East and South Africa. Brain size in the larger specimens is twice that of *Australopithecus*. Relative cheek-tooth size was considerably reduced from the large size seen in earlier hominid species. Body size of the larger specimens probably

exceeded 60 kg. It may be that body size sexual dimorphism was not as marked in early *H. erectus* as it apparently was in *H. habilis*, but as yet, no associated female skeletons are complete enough to be certain. At about the same time as the origin of *H. erectus* is the first appearance of the Acheulean material culture characterized by bifacially flaked large stone tools ("handaxes"), which are found throughout most of the Old World for the next 1.5 million years. There is a great deal of evidence supporting the hypothesis that the origin of *H. erectus* marked the beginning of major change in the adaptive strategy of Hominidae, although it remained a numerically minor part of the vertebrate fauna collected in Pleistocene beds despite strong bias of collectors.

E. Colonizing the Old World

By at least 1 million years ago, some populations of *H. erectus* had left their African homeland and colonized Eurasia. The best known of the early hominids outside of Africa are those from Java, dating to about 1 million years, although dating is much less precise than it is for earlier parts of the record. The imprecision is a result of the fact that the best-established method of establishing geological dates older than 1 million years is by the radioactive decay of potassium 40, but between that date and 40,000 years ago there are less precise methods of dating. One major clue is the shifting of the earth's magnetic polarity from north to south at specific times that can be detected in geological sediments. The last "reversal" (when the magnetic pole shifted back to the north) occurred 750,000 years ago.

The *H. erectus* of Java was found in 1893. The famous discovery of Eugene DuBois consisted of a skull cap with an estimated cranial capacity of 940 cc associated with a thigh that was well within the range of variation of *H. sapiens*. This association lead DuBois to name the creature *Pithecanthropus erectus* (erect ape-man). Unfortunately, few other specimens came to light until the 1930s. Between 1930 and the outbreak of the Asian part of World War II came a pulse of discovery in Java and China that established *H. erectus* as a well-documented species preceding our own. A wealth of new Javanese and Chinese fossils were discovered and later described, which gave a picture of a hominid of intermediate brain size (about 800–1000 cc, compared with the average for *H. sapiens* of 1,300 cc) with large brow ridges, a low cranial vault, teeth of intermediate size, and robust but modern-looking postcrania. Several fire layers are present in the best-known *H. erectus* site in China (Zhoukoudien), leading most investigators to infer the controlled use of fire. The first appearance of humans in the rest of Eurasia is less well documented. Some archaeological sites may date back to as early as 1 million years, but the dates are problematical. There are only a sprinkling of human remains in Western Europe before about 200,000 years, and they do not resemble *H. sapiens* very closely. Most if not all the European fossils before 35,000 years are best regarded as archaic *H. sapiens*.

F. Archaic *Homo sapiens*

The term "archaic *Homo sapiens*" refers to a heterogeneous collection of Old World hominids between about 400,000 and 35,000 years ago. The term is not precise, and there is a need for a formal taxonomic reappraisal. The contrast between what is now called archaic *H. sapiens* and anatomically modern *H. sapiens* is greater than that between archaic *H. sapiens* and *Homo erectus* except in one important characteristic, brain size. Brain size is usually within the modern human range of variation (1,000–1,700 cc), although there is one exceptionally small specimen (Sale of North Africa with 860 cc). They resemble *H. erectus* with their large faces, robust skeletons, brow ridges, and long, low skulls. Earlier specimens are associated with Acheulean culture, but by about 200,000 years ago stone tools became more sophisticated, particularly in their manufacture of prepared-core flake tools. The best-known variety of archaic *H. sapiens* is the Neanderthal.

Neanderthals were a relatively homogeneous group of archaic *H. sapiens* who occupied Europe and west Asia between about 200,000 and 35,000 years ago. Their facial morphology was unmistakable, with exaggerated midfacial prognathism leading to what must have been enormously protrusive noses. They were the first prehuman fossils known to science, and consequently they have played a major role in the interpretation of human evolution. Now that much more is known about prehistory, Neanderthals are seen in perspective as a relatively isolated extreme variant of archaic *H. sapiens* that held out against anatomically modern *H. sapiens* until 35,000 years ago when they disappeared.

G. Anatomically Modern *Homo sapiens*

Anatomically modern *H. sapiens* is distinctly different from the archaic form of the species in having small faces, high foreheads, a true chin, and longer and less robust limbs, especially the distal segments (forearm and shin). They are first known in Africa by about 100,000 years ago or slightly earlier. There is some evidence that they were in the Middle East by 90,000 years ago, but remains of archaic *H. sapiens* are much more common in that area until about 35,000 years ago when they disappear from the record. At this time the culture dramatically changes with the introduction of more finely worked stone blades, a wider variety of tools of all kind, and art including cave paintings and stone carvings. There is accumulating evidence that the morphological and behavioral changes between archaic and modern *H. sapiens* are profound enough to warrant changing the taxonomy to restrict the species *H. sapiens* to moderns only. Recent comparisons of nuclear and mitochondrial DNA of living humans appear to show that the ancestors of all modern humans derive from Africa 110,000 to 200,000 years ago. Current fossil and archaeological evidence supports an African origin.

H. Peopling of the Earth

There is no unanimity of opinion concerning the origin and spread of anatomically modern *H. sapiens*. Some scholars emphasize the apparent regional continuity between local forms of fossil hominids and living populations in the same area. For example, several traits characteristic of *H. erectus* in China, such as a high incidence of shovel-shaped incisors, resemble these of some populations of modern Chinese. However, all modern humans are more similar to one another than to archaic *H. sapiens* or *H. erectus;* this similarity may indicate a close genetic relation among modern humans, and a restricted geographical area of origin. Particularly telling is the fact that the maternally inherited mitochondrial DNA of all living people is best interpreted as having a single origin in Africa. Had local premoderns outside of Africa contributed to the modern gene pool, presumably that contribution would be detected in the maternal line. Much more work needs to be done in this area before any certain conclusions can be drawn.

Anatomically modern humans had reached Australia at least by 30,000 years, although some robust and rather archaic hominids are still found there by 10,000 years. Archaeological evidence shows that the colonization of the rest of the Pacific began several thousand years ago from the east, reaching the Marquesas Islands by about AD 300 and New Zealand by about AD 900. Abundant evidence shows that people arrived in the Americas from north Asia by at least 12,000 years ago. Archeological findings before that date are rare, and their authenticity is often challenged. It may be the case that small populations occupied America much earlier, but they remained at low population densities until 12,000 years ago.

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