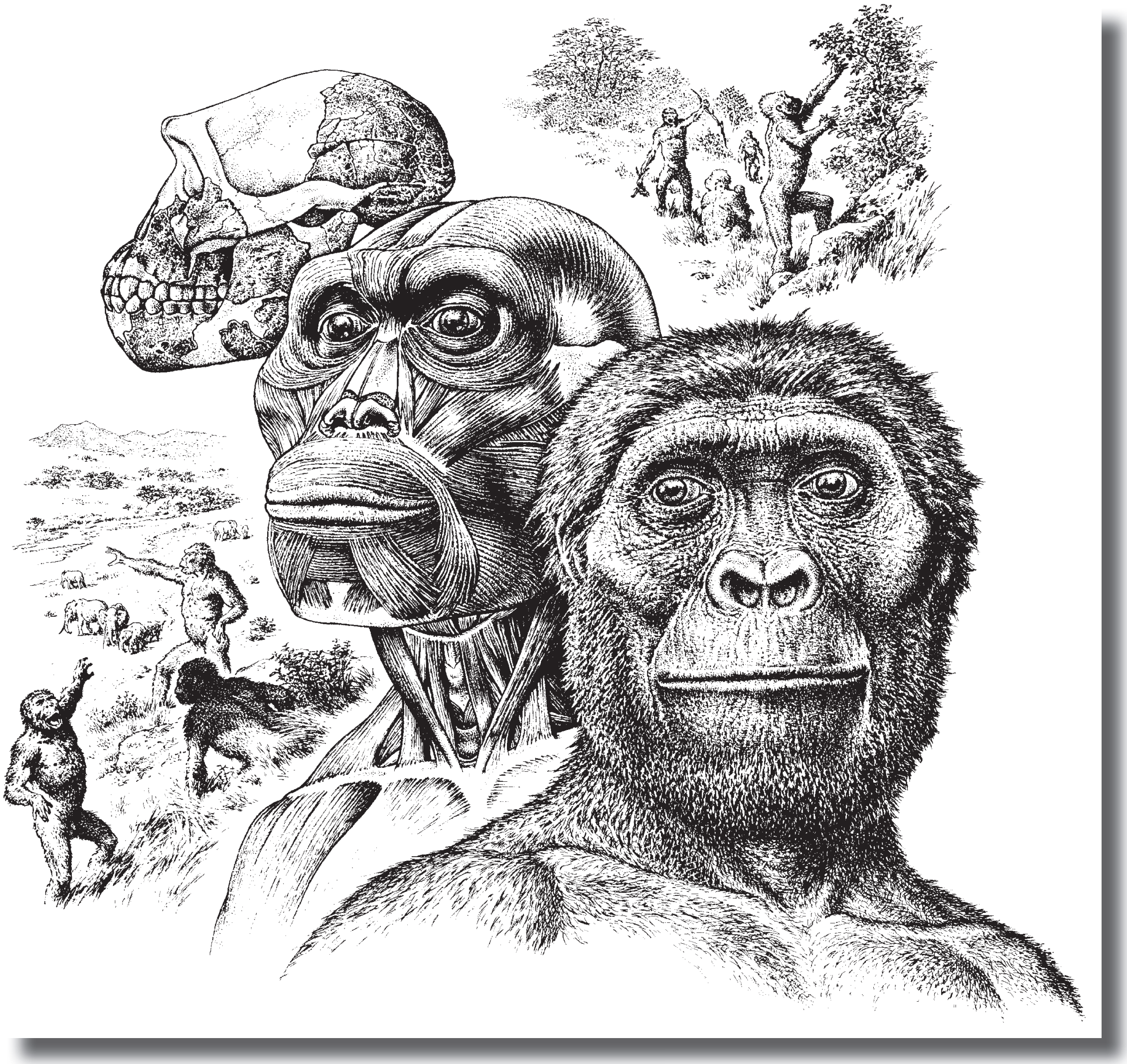
CHAPTER 11

Human Evolution



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KEY QUESTIONS IN THIS CHAPTER

1 What are the oldest primates?
2 Does the old division of modern primates into prosimians and anthropoids make sense?
3 How do the diverse Eocene primates such as adapiforms and omomyids relate to modern primates?
4 How long have the Old World and New World monkeys had a separate existence?
5 What is the oldest ape, and what were the Miocene apes like?
6 How do humans differ from the other apes?
7 What came first – bipedalism or the large brain?
8 What is the oldest human being, and why is it so difficult to gain agreement among experts?
9 How do palaeoanthropologists reconstruct the appearance and palaeobiology of the early hominids?
10 To what extent were the Neanderthals our ancestors?
11 Are all the modern human races closely related, and when did they split apart?
12 How and when did humans populate the world?

INTRODUCTION

A key theme in palaeontological research is human origins. Indeed, this goes much deeper, because people have been intrigued about the origins of humanity for thousands of years, and it could be counted as one of the core questions any intelligent person might ask. Unfortunately, the fossil evidence for human evolution is patchy. There has been a great deal of controversy over primate and human relationships, partly because of the limited number of good fossils, but also because of the numbers of researchers involved, and the high stakes associated with each new discovery. There are almost as many palaeoanthropologists as there are good fossils, and each researcher of course has his or her own theories!

In this chapter, the fossil evidence for primate evolution is presented, with critical assessments of the key fossils and some of the major controversies over relationships.

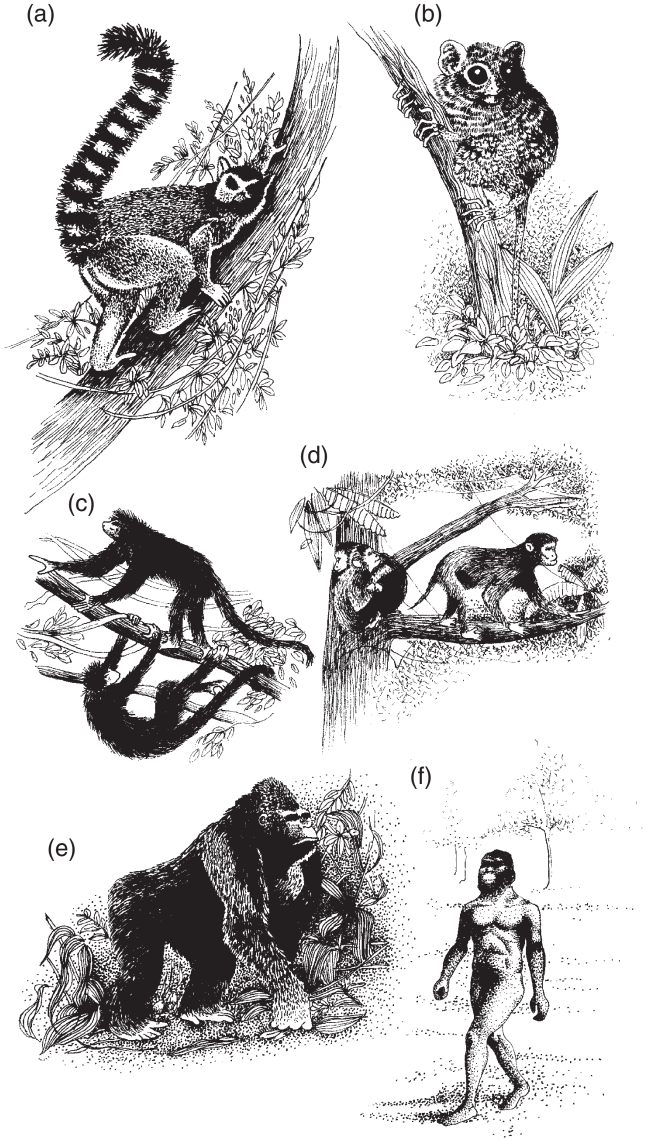


Figure 11.1 A selection of modern primates shown in their natural habitats: (a) the ring-tailed lemur, *Lemur catta*; (b) the spectral tarsier, *Tarsius*; (c) the spider monkey, *Ateles*; (d) the rhesus monkey, *Macaca*; (e) the gorilla, *Gorilla*; (f) the early hominin *Australopithecus*. Source: Adapted from various sources.

11.1 WHAT ARE THE PRIMATES?

There are over 430 species of living primates, classified in 16 families, of which modern humans, *Homo sapiens*, are but one. Primates include a wide array of morphological types, from bush babies and tarsiers to gorillas and humans (Figure 11.1), and they range in size from the pygmy mouse lemur weighing 30 g to the gorilla at more than 175 kg. Primates are diagnosed by 30 or so characters that relate to three major sets of adaptations: (1) agility in the trees; (2) large brain and acute daylight vision; and (3) parental care (Kirk, 2013).

Primates are essentially tree-dwellers, although many lack the remarkable agility seen in certain South American monkeys and the gibbons. Anatomical changes to permit this kind of activity include grasping hands and feet in which the big toe may be opposable, flat nails instead of claws and sensitive tactile pads on all digits, and in hominoids, a very mobile shoulder joint and elbow so that the arm can be rotated in a complete circle.

Primates have larger brains, in proportion to body size, than all other terrestrial mammals. In addition, their eyes are generally large and close together on the front of the face, and the snout is reduced. The flattened face of most primates allows them to look forwards and to have a large amount of overlap between the fields of vision of both eyes, which makes stereoscopic, or three-dimensional, sight possible. Primates use their binocular vision to judge distances when they leap from branch to branch, and the enlarged brain allows them to cope with the variety of forest life and social interactions.

Turning to the cranium, primates have a postorbital bar (see Figure 11.4(a,b)), a strut between the orbit and lower temporal fenestra (= fossa), which is absent in related mammals (see Section 10.13). Furthermore, the auditory bulla, the bony capsule that encloses the middle ear and other structures (see Figure 11.4(d)) in primates, is large and it is composed of the petrosal bone (see Section 10.2.1).

The third set of derived characters of the primates relates to improved parental care of their offspring. Primates usually have only one baby at a time, the foetus is retained longer in the womb than in other mammals of the same body size, and there is an extended period of parental care of the offspring. In addition, primates usually have only two mammary glands. Sexual maturity comes late and the total life span is long relative to other similar-sized mammals. Primates have opted for high parental investment, which may have been essential so that the young could learn the complexities of forest life.

There have been many suggestions about why primates adopted their tree-climbing characteristics. For at least 100 years, primatologists have emphasized that primates reduced the sense of smell that is typical of most other mammals, and noted the improvements in their vision, brains, and branch-grasping abilities, all of which form parts of the 'arboreal theory' for primate origins. This has been extended (Sussman *et al.*, 2013) as the 'primate/angiosperm coevolution theory', that the earliest primates, presumably in the latest Cretaceous, and certainly in the early Palaeocene, made their move into the trees to exploit a unique new food source, the fruits and flowers of angiosperms. In order to do this, they had to become especially adept at manoeuvering themselves to the ends of the thinnest branches of trees to snatch the flowers and berries, hence their tiny body sizes, long, slender limbs, sensitive, grasping fingers, and excellent binocular vision.

11.2 THE FOSSIL RECORD OF EARLY PRIMATES

The fossil record indicates that primates radiated in the Palaeocene and Eocene. Older records from the Cretaceous are doubtful, although molecular evidence (see Section 10.4) suggests that the order might have originated in the latest Cretaceous. Could our distant ancestor, a small squirrel-like animal, have seen the last dinosaurs as it peered nervously from behind some branches?

The earliest primates include plesiadapiforms (possibly), adapiforms, omomyids, and tarsiids. The relationships of these 'pre-monkey' primates are currently hotly debated: are plesiadapiforms primates at all, are adapiforms on the line to humans or lemurs, and how do lemurs and tarsiers relate to each other?

11.2.1 Plesiadapiforms

Plesiadapiformes are a group of eleven families that radiated in the Palaeocene and Eocene of North America, western Europe, and Asia (Rose, 2006; Bloch *et al.*, 2007; Sussman *et al.*, 2013). Their oldest representative is *Purgatorius*, known from teeth and jaw fragments from the early Palaeocene. A supposed Late Cretaceous record, once billed as the first true primate, is discounted now. The best known plesiadapiform is *Plesiadapis* itself from the late Palaeocene of North America and France (Figure 11.2), a squirrel-like animal with strong claws on its digits and adaptations for tree-climbing. The eyes are large, but face sideways, a plesiomorphic character suggesting this animal did not have binocular vision. The long snout bears large rodent-like incisors, with large gaps behind and broad cheek teeth for grinding plant food.

Plesiadapiforms have brachiated in and out of the primate tree over the years, but recent cladistic analyses (e.g. Seiffert *et al.*, 2005; Rose, 2006; Bloch *et al.*, 2007; Gunnell and Silcox, 2010) generally confirm that they are sister clade to all other primates. However, this is opposed by a comprehensive phylogenetic

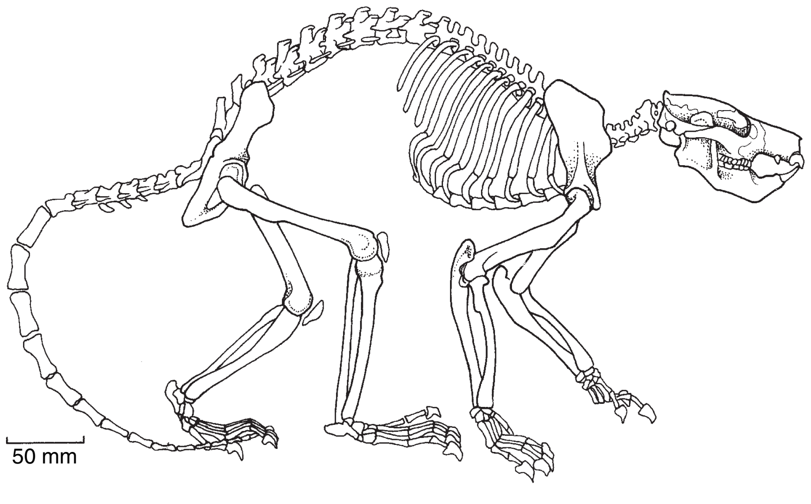


Figure 11.2 Skeleton of the early Eocene plesiadapiform *Plesiadapis*. Source: Adapted from Tattersall (1970).

study by Ni *et al.* (2013), who place plesiadapiforms within Archonta, but between Scandentia and Dermoptera.

11.2.2 Strepsirhini: lemurs and their kin

All other primates belong to the clade Euprimates (see Box 11.1), which radiated extensively during the early Eocene (Rose, 2006; Hartwig, 2008). Euprimates are divided into Strepsirhini, lemurs and lorises, and Haplorhini, the tarsiers, monkeys and apes, and among the most abundant Eocene euprimates, the adapiforms are strepsirhines and the omomyids are haplorhines.

The most abundant of the early primates were the lemur-like adapiforms. The adapiforms arose in the early Eocene and survived until the late Miocene, and during that time they spread from Europe and North America to Africa and Asia. *Smilodectes* from the mid-Eocene of North America (Figure 11.3(a,b)) has a long snout and small orbits, distinguishing it from the contemporary omomyids. The long hindlimbs, grasping hands and feet and long tail were presumably used for balancing during climbing. The teeth of adapiforms suggest a diet of fruit and leaves.

The most famous, or infamous, adapiform is *Darwinius* from the middle Eocene Messel Formation in Germany (see Box 10.8). This little primate is known from a complete specimen preserved as slab and counter-slab, originally found in 1982. In 2007, one of the slabs was sold for $1 million to the Oslo Natural History Museum in Norway, amidst enormous publicity and claims that it was the definitive 'missing link' in human evolution. *Darwinius* is 58 cm long, with a 34 cm tail, and was clearly adapted for scampering around in trees (Figure 11.3(c); Franzen *et al.*, 2009). She lacks a baculum, or penis bone, and so was identified as female, and nicknamed 'Ida'. Her teeth, with sharp edges on the molars, were adapted for a diet of leaves and fruit, as confirmed by her stomach contents.

There has been an active debate about the phylogenetic position of *Darwinius* and the adapiforms, with strong claims that they are haplorhines, and hence on the line to humans (Franzen *et al.*, 2009). However, most cladistic analyses (Seiffert *et al.*, 2009; Maiolino *et al.*, 2012; Ni *et al.*, 2013) unequivocally identify adapiforms as strepsirhines. For example, adapiforms share an unusual feature with modern lemurs and lorises (Maiolino *et al.*, 2012), the grooming or toilet claw on their second toe, which is used for raking through the fur to remove plant debris and dead skin, and for scratching. The living forms also have a toothcomb composed of the incisors and canines, which are narrow and point forwards, and these are also used for feeding and for grooming the fur.

The extant lemurs and lorises branched from adapiforms early in the Paleogene. A fossil from the early Eocene of Tunisia, *Djebelemur*, appears to be on the stem to both modern groups, and suggests these animals originated in Africa (Marivaux *et al.*, 2013). *Djebelemur* was a nocturnal animal that walked on all fours through the trees, feeding primarily on insects. Its anterior teeth pointed forwards and may have been used in grooming the fur, but this is not a full tooth-comb as seen in modern lemurs.

There are 100 living species of lemuriforms, which include the lemurs, indriids and the aye-aye, all restricted now to Madagascar. Most of these are cat-sized, but a few are mouse-sized. They have long bushy tails, often striped black and white (see Figure 11.1(a)). Different species of lemurs are diurnal or nocturnal, feeding on insects, small vertebrates and fruit. The incisors and canines of the lower jaw point forwards and form a comb that is used for scooping out soft fruit and for grooming the fur. The indrisids include the woolly lemur, which is nocturnal and lives in trees, whereas the indri and the sifaka are diurnal animals that live in troops and may move about bipedally by leaping along the ground. The aye-aye (*Daubentonia*) is a cat-sized nocturnal animal that probes for insects in tree bark with its slender elongated fingers.

Until the arrival of humans in Madagascar some 2000 years ago, the island was populated by a remarkable array of giant lemurs, ranging up to 200 kg in weight. In the absence of artiodactyls and perissodactyls, the lemurs took on a very wide array of ecological roles, many feeding in the trees, but others chomping vegetation on the ground like horses or cattle. These include the giant lemur, *Megaladapis*, with an elongate almost horse-like skull measuring 0.3 m in length (see Figure 11.3(d)). This would suggest an original body length of 1.3–1.5 m, several times larger than the largest living lemur. Another subfossil lemur, *Hadropithecus*, was baboon-sized, and may have grazed on grass that it grabbed in its hands. The 17 species of giant lemur died out as a result of hunting – there are several sites where butchered lemur bones show they were eaten by humans – and through competition with pigs and other mammals brought by the people. The last giant lemur disappeared about the year 1450 (Crowley *et al.*, 2012). It had been thought that there was fossil evidence for earlier evolution of lemurs in Asia: an enigmatic strepsirhine from the Oligocene of Pakistan, *Bugtilemur*, was interpreted as a lemuriform, by far the oldest of the clade (Marivaux *et al.*, 2001), but this may in fact be an adapiform (Godinot, 2006).

The lorisiforms, 30 species of lorises and galagos (bushbaby) from Africa and southern Asia, have a more substantial fossil record, with teeth and jaw remains representing a galago and a possible loris from the middle Eocene of Egypt (Seiffert *et al.*, 2003). Later fossil lorises include Miocene forms from East Africa and from Pakistan.

11.2.3 Tarsiiformes: tarsiers and their kin

The living tarsier (see Figure 11.1(b)) is a small nocturnal animal that leaps from tree to tree in the forests of south-east Asia, feeding on insects, lizards and small birds. Long classed with lemurs and lorises as a 'prosimian', tarsiers are part of the clade Haplorhini, together with the anthropoids (see Box 10.1). Within Haplorhini, tarsiids are part of the clade Tarsiiformes, which also includes the extinct omomyids.

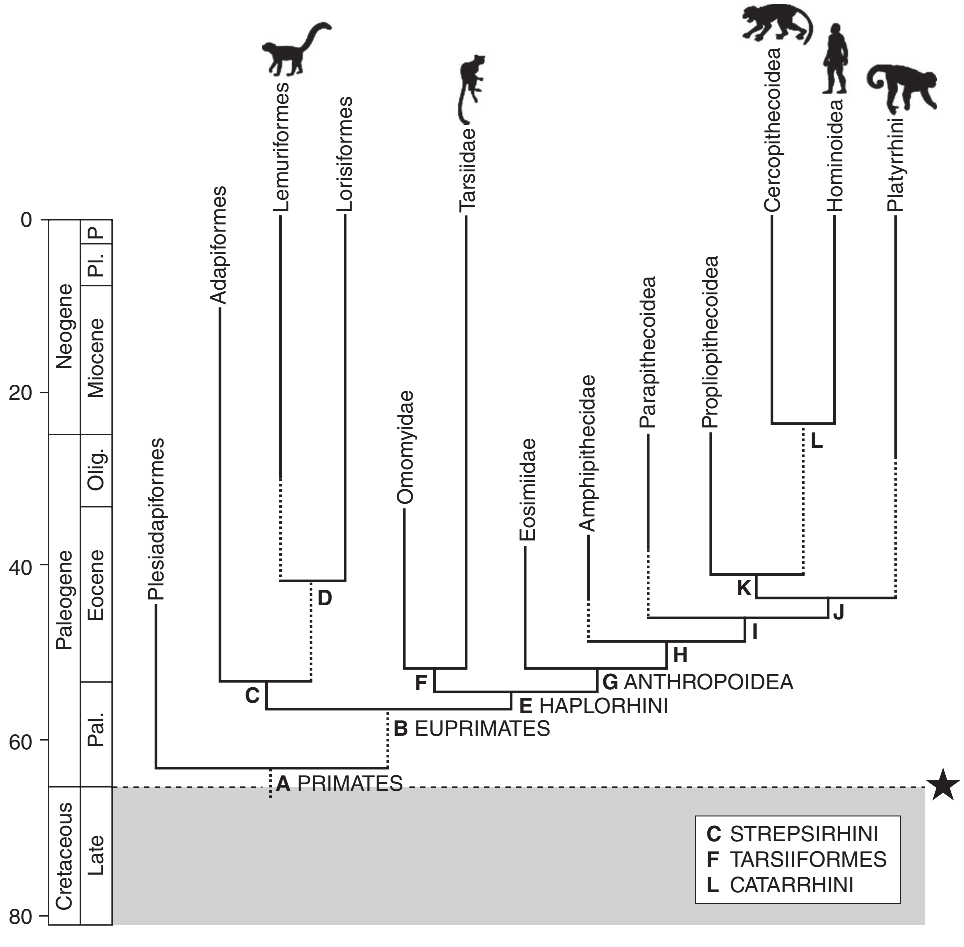
The omomyids, some 50 genera from the Eocene of North America, Europe, Asia, and possibly north Africa (Szalay, 1976),

BOX 11.1 RELATIONSHIPS OF THE BASAL PRIMATES

The traditional classification of the Order Primates was simple: the lemurs, lorises and tarsiers were grouped in the Suborder Prosimii, and the monkeys and apes in the Suborder Anthropoidea. However, the Prosimii were clearly paraphyletic, and they could be diagnosed only with respect to the Anthropoidea, in other words, by the absence of characters. A phylogenetic approach then is bound to break up the classic Prosimii.

There is wide agreement that the old 'prosimians' are divided into lemurs and lorises on the one hand, which together form the clade Strepsirhini, and the tarsiers and anthropoids on the other, which form the clade Haplorhini, distinguished from each other by characters of the nostrils and skeleton. Among Haplorhini, tarsiers are outgroup to Anthropoidea, comprising the Catarrhini and Platyrrhini (New World monkeys). The Catarrhini comprise two extant subclades, the cercopithecoids (Old World monkeys) and hominoids (apes, including humans).

There are numerous extinct clades of primates, and we include only some major clades here. Adapiformes is a large clade, generally assigned to Strepsirhini, and so close relatives of lemurs and lorises (Seiffert *et al*., 2005; Rose, 2006; Ni *et al*., 2013). A second large clade of early primates, the Omomyidae, is widely classed as sister group to Tarsiidae, forming together with them the clade Tarsiiformes (Seiffert *et al*., 2005; Rose, 2006; Ni *et al*., 2013). There then follow a number of stem anthropoid clades, the Eosimiidae, Amphipithecidae, and Propliopithecoidea, among many smaller clades, probably outgroups to crown Anthropoidea (Seiffert *et al*., 2005; Rose, 2006).



Cladogram showing postulated relationships of the major primate clades. Animal silhouettes are mostly from the PhyloPic website, and we acknowledge the work of Gareth Monger, T. Michael Keesey, Smokeybjb, Mateus Zica, and Sarah Werning. Synapomorphies from Kay *et al*. (1997), Seiffert *et al*. (2005), and other sources: **A PRIMATES**, postorbital bar, large orbits, orbits are located close together and on the front of the face, large braincase, modifications of the elbow to allow extra flexibility, modifications of the tarsus, opposable thumb; **B EUPRIMATES**, petrosal bulla, nails on the digits and terminal tactile pads, grasping hind feet; **C STREPSIRHINI**, ring-shaped tympanic bone enclosed within the tympanic cavity, posterolateral and dorsal position of the posterior carotid foramen, as well as characters of the hand and foot such as the grooming claw on the second toe; **D**, grooming claw on second toe, dental tooth comb made from forwards-projecting lower incisors and canines; **E HAPLORHINI**, haplorhine nose (nostrils have complete margins and are not slit-like), short face placed largely below the braincase, narrow and simplified bony bar between orbits, olfactory lobes of brain reduced and optical lobes enlarged, haemochorial placenta (invades uterine wall and chorion directly bathed by maternal blood); **F TARSIIFORMES**, greatly enlarged orbits, tubular ectotympanic bone (external auditory meatus), elongate tarsal bones, closely apposed tibia and fibula; **G ANTHROPOIDEA**, large inferior orbital fissure, large sinuses in the maxilla and sphenoid, fused mandibular symphysis, expanded quadratic molars, molarization of the premolars (especially P_4), strong development of the hypocone, canine occlusion, relatively large canines compared with incisors, lateral incisors larger than central incisors; **H**, no synapomorphies; **I**, no synapomorphies; **J**, no synapomorphies; **K CATARRHINI**, orbits small, forward facing and convergent, bony lamina separates orbit from adductor fossa, tympanic bone fused to bony sidewall of middle ear, relatively deep mandible; **L CROWN CATARRHINI**, two premolars, sexual dimorphism is marked, males have larger canines than females. Abbreviations: Olig, Oligocene; P, Pleistocene; Pal, Paleocene; Pl, Pliocene. Dashed lines and star symbols indicate extinction events.

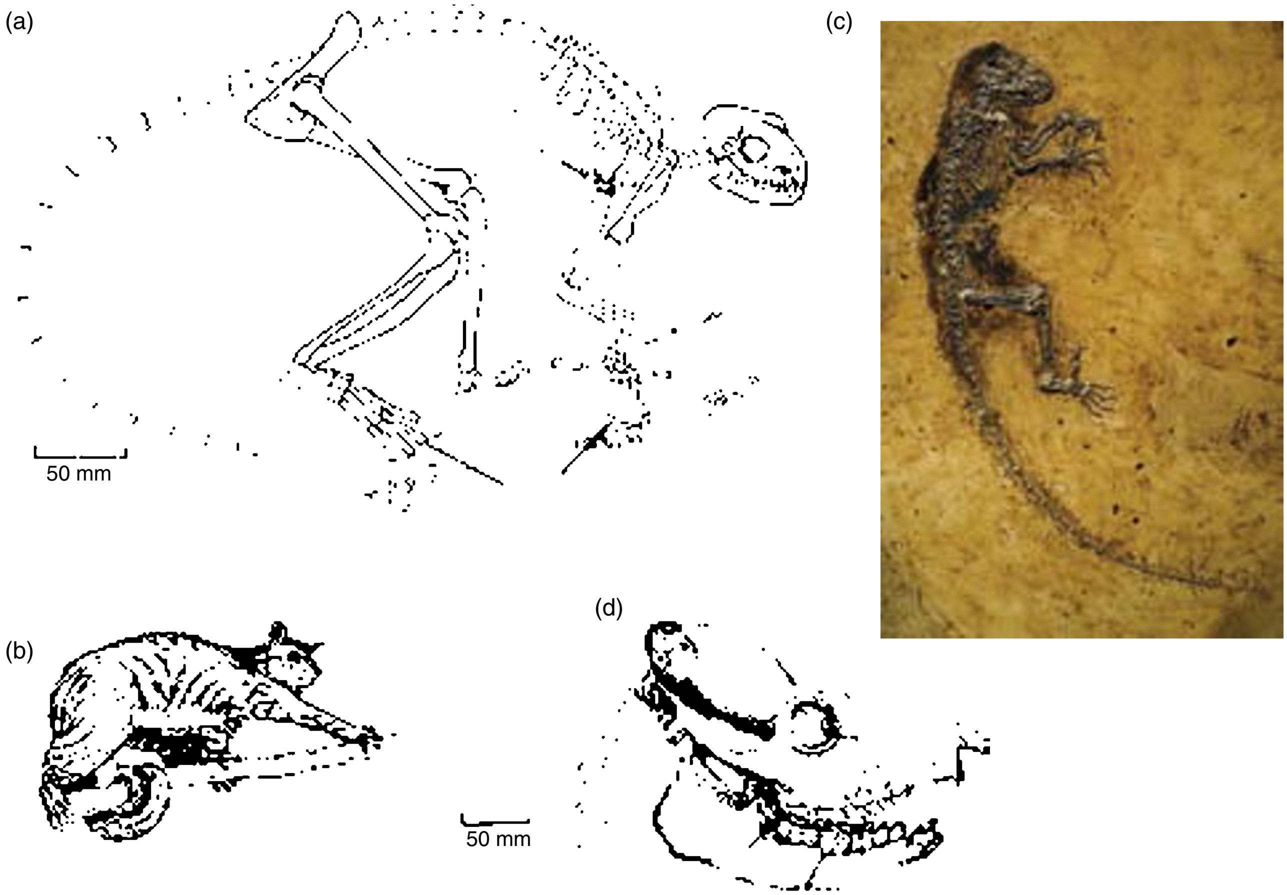


Figure 11.3 Fossil strepsirhine primates: (a b) the middle Eocene adapiform *Smilodectes*, skeleton and restoration of life appearance; (c) the type specimen of the adapiform *Darwinius*; (d) the Pleistocene giant lemur *Megaladapis*, lateral view of skull. See Colour plate 11.1. Source: (a) Adapted from Simons (1964). (b) Adapted from Rose (2006). (c) © Jens L. Franzen, Philip D. Gingerich, Jörg Habersetzer1, Jørn H. Hurum, Wighart von Koenigswald, B. Holly Smith/CC-BY-SA-2.5/GFDL. (d) Adapted from Zapfe (1963).

were all small tarsier-like tree-dwellers, mostly weighing less than 500 g, but some later forms reached 2.5 kg. They generally have large orbits, shortened snouts and tooth rows, loss of the anterior premolars in later forms, and cheek teeth adapted for insect- and fruit-eating diets. For example, *Tetonius* (Figure 11.4(a–c)) has a short snout, a bulbous braincase and an obvious postorbital bar. The orbits face forwards and it is likely that these early primates already had stereoscopic vision. Another omomyid, *Shoshonius* from Wyoming, USA, known from several tiny crania (Figure 11.4(d)), also has very large orbits and a short snout. Omomyids show adaptations in their limb skeletons for climbing, grasping branches with thumbs and large toes and leaping from branch to branch (Rose, 2006).

The tarsiids until recently had a limited fossil record. At times, omomyids such as *Shoshonius*, were assigned to Tarsiidae, but the oldest accepted tarsier records include fossils from middle Eocene cave sediments from China, a jaw named *Xanthorhysis* and teeth assigned to *Tarsius*, the living genus (Rose, 2006). Further, a supposed tarsier from the early Oligocene of Egypt, *Afrotarsius*, is more likely a stem anthropoid. This means the tarsiids had an exclusively Asian history. This is confirmed by a remarkable tarsier fossil from the early Eocene of China, *Archicebus* (see Box 11.2).

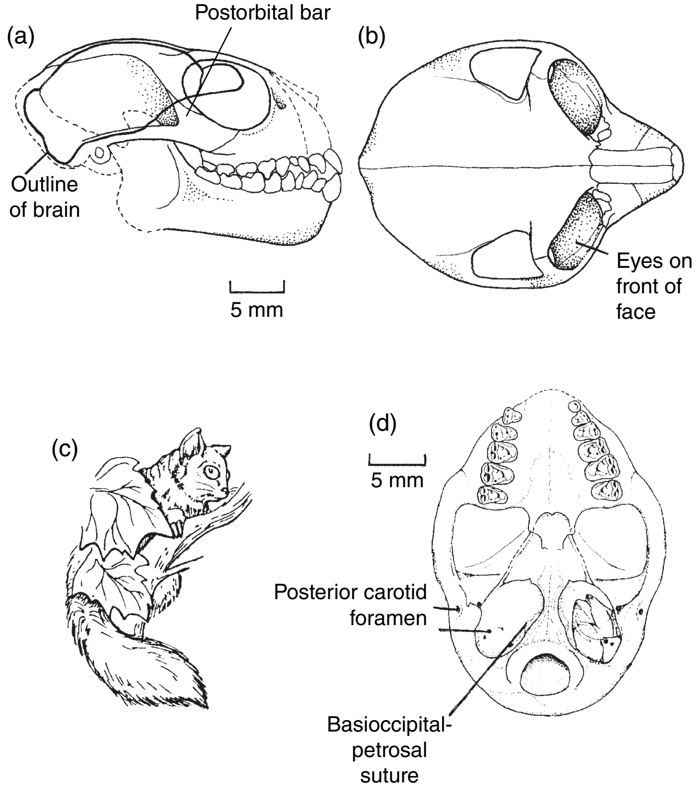


Figure 11.4 Tarsiiform primates: (a–c) the early Eocene omomyid *Tetonius*, skull in lateral and dorsal views, and restoration of life appearance; (d) the early Eocene omomyid *Shoshonius*, ventral view of skull. Source: (a,b) Adapted from Szalay (1976). (c) Adapted from Rose (2006). (d) Adapted from Beard *et al.* (1991).

BOX 11.2 THE WORLD'S FIRST TARSIER

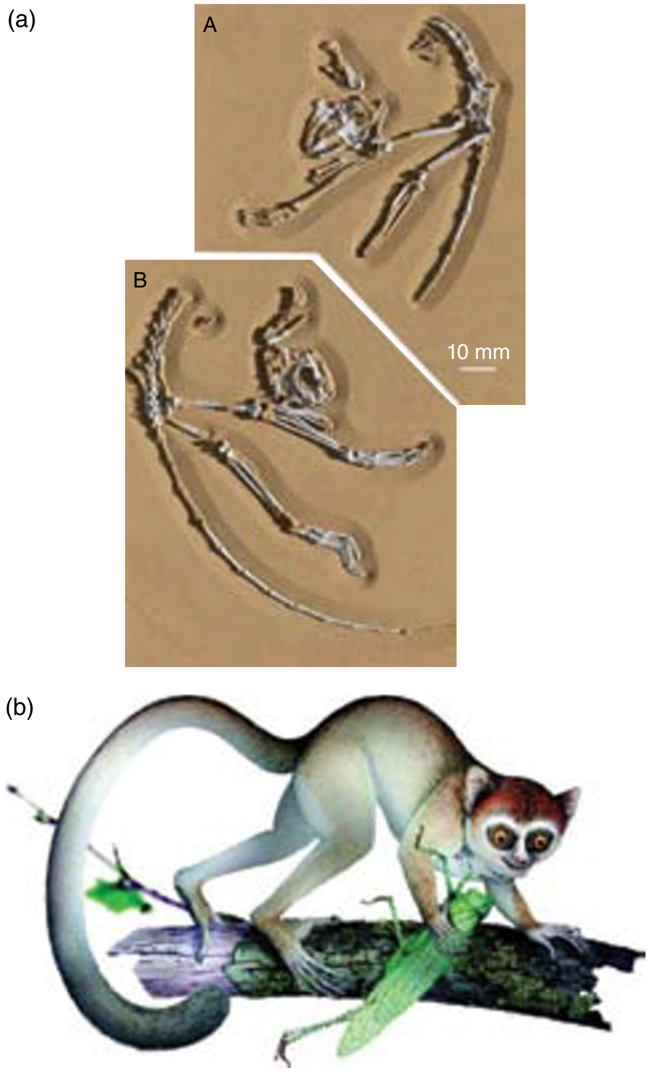
Occasionally, a single complete fossil can resolve decades of debate. The relationships of a broad array of Eocene primates had been hotly debated since the 1960s, and the discussions focused on the adapiforms and omomyids, and the old split of the Order Primates into so-called 'prosimians' and anthropoids, or strepsirhines and haplorhines (see Box 11.1). Humans are haplorhines, and we trace our ancestry back to Eocene forms such as *Eosimias* and *Amphipithecus* (see Section 11.3.1). But what of the highly abundant early and middle Eocene adapiforms and omomyids?

According to some cladistic analyses (e.g. Franzen *et al*., 2009), adapiforms were haplorhines and so in some way ancestral to humans. On the other hand, other recent phylogenetic analyses (e.g. Seiffert *et al*., 2009; Maiolino *et al*., 2012; Ni *et al*., 2013)have shown a great deal of convergence among the different Eocene clades, and that adapiforms are strepsirhines (see Section 11.2.2) and omomyids are tarsiiforms (see Section 11.2.3).

The discovery of the oldest essentially complete primate skeleton in the early Eocene of China then caused a sensation. Not only can it tell us about the adaptations and mode of life of an early primate, it can also help resolve these long-running phylogenetic debates. *Archicebus* is known from a skeleton preserved on slab and counterslab (Ni *et al*., 2013). It was tiny, weighing an estimated 20–30 g, the size of the modern mouse lemur, or indeed the size of a mouse. Its large canine teeth and pointed premolars show it fed mainly on insects. Its eyes are close together, and so *Archicebus* may have had binocular vision, but the eyes are not enlarged, as in most tarsiiforms, so it probably operated in daylight.

In the skeleton *Archicebus* shows adaptations for leaping among tree branches, its long legs, the semi-cylindrical femoral head with a stout and less oblique femoral neck, the tall knee, and the closely apposed tibia and fibula. However, it shows primitive limb features that made it less adept in the trees than modern galagos and tarsiers, such as the long cornoid process of the scapula, the moderately rounded humeral head, the long and straight ischium, the high crural index (ratio of tibia to femur), and the long metatarsals and toes. *Archicebus* likely walked along branches and jumped, but could not cling to vertical trunks.

The importance of *Archicebus* is especially in what it says about early primate phylogeny. Cladistic analysis (Ni *et al*., 2013) places this new form firmly at the base of Tarsiiformes, and Tarsiiformes as sister clade to Anthropoidea (see Box 11.1). Adapiforms are strepsirhines and omomyids are tarsiiforms. The new fossil pushes the age of the Tarsiiformes-Anthropoidea and the Strepsirhini-Haplorhini splits down to the early Eocene, or older.



The oldest haplorhine primate, the tarsiiform *Archicebus* from the early Eocene of Hubei, China: (a,b) dorsal and ventral views of the skeleton, showing the long tail, hindlimbs, partial trunk and forelimb, and skull, a composite image based on CT scans of the fossil, showing fossil bones (light grey) and restored elements based on impressions in the rock (dark grey); (b) life restoration. See Colour plate 11.2. Source: (a,b) Adapted from Ni *et al*. (2013).

11.3 ANTHROPOIDEA: MONKEYS AND APES

The 'higher' primates, the monkeys and apes, form a clade, the Anthropoidea ('human-like'), which today comprises two groups that evolved separately in the New World (mainly South America) and the Old World (Africa, Asia, Europe). The New World monkeys, the platyrrhines (literally 'broad nose') have broadly spaced nostrils that face forwards, and some have a prehensile tail. The catarrhines (literally 'hooked nose'), or Old World monkeys and apes, have narrow snouts and non-prehensile tails.

Anthropoids have the rounded nostrils of all haplorhines (tarsiiforms and anthropoids), as well as large canines that occlude with the opposite canine and first premolar, the premolars are rather molar-like, and the molars are broad and square. Anthropoids originated surprisingly early, even by the late Palaeocene, and there were several Eocene and Oligocene clades along the stem lineage to the modern monkey groups (see Box 11.1).

11.3.1 Anthropoid adaptations

Anthropoids are distinguished from strepsirhines and tarsiers by numerous features of their body size, diet, locomotion, senses, and brain size (Williams *et al*., 2010). In terms of size, most modern monkeys and apes weigh more than 1 kg (exceptions are the marmosets, tamarins, and squirrel monkeys), whereas some of the Eocene anthropoids were tiny. This affected their diet. Tiny animals can rarely obtain enough nourishment from leaves alone, and so most of the Eocene primates, including the early anthropoids, relied on insects as their main source of protein. As anthropoids became larger (over 500 g), they could become entirely vegetarian, relying on leaves as their main diet.

Eocene primates were all arboreal, even if many were not as agile as some living forms. The first anthropoids show adaptations to a variety of locomotory modes, most being capable of walking quadrupedally along branches, and leaping from tree to tree. Larger forms were probably slower moving.

Anthropoids show many modifications to their visual system. For example, their cornea is smaller than in lemurs, lorises, and most other mammals, giving them a longer focal length, and so improved visual acuity. Such a reduced cornea means that less light can enter the eye, and so this adaptation must have arisen in diurnal species, whereas strepsirhines are primarily nocturnal. Tarsiers, although primarily nocturnal and equipped with enlarged eyes, share other features of the eye (the retinal fovea and a macula lutea) with anthropoids, and so probably became secondarily nocturnal. Anthropoids and tarsiers have postorbital septa, bony divisions between the back of the eye socket and the temporal fossa. This bony barrier separates the eyeball from the adductor jaw muscles, and may have evolved as the haplorhine face flattened, and the eyes converged on the midline. Anthropoids have colour vision and many strepsirhines do not, but the anthropoids resemble other mammals, and lorises and bushbabies with monochromatic vision have seemingly lost the ability. Catarrhines (Old World monkeys, apes, humans) stand out as having three cone types (other mammals, including other anthropoids have two cone types). Catarrhines again show unique aspects of the loss of the sense of smell (Williams *et al.*, 2010); indeed all haplorhines have reduced olfactory lobes of the brain, but tarsiers and platyrrhines retain a large number of functional olfactory receptor protein genes that are lost in catarrrhines.

The final anthropoid characteristic, when compared to tarsiers and strepsirhines, is a step-change in brain size (Williams *et al.*, 2010). Eocene anthropoids had brains in the size range (when corrected for body mass) of living strepsirhines. However, in these early forms, the visual cortex had increased in size, matching the assumed improved visual acuity. Further, in modern monkeys and apes, the neocortex is expanded when compared to tarsiers and lemuriforms. The neocortex is the outer layer of the cerebral hemispheres, the part of the brain associated with sensory perception, the generation of motor commands, spatial reasoning, conscious thought, and language. This is a further step along the road from the initial expansion of the brain when Primates originated (see Section 11.1), and precedes further brain expansions on the line to modern humans (see Section 11.5.2).

11.3.2 The first anthropoids

The prize for the oldest confirmed primate, and perhaps the oldest anthropoid, may go to *Altiatlasius*, based on ten isolated cheek teeth and a dentary fragment of a juvenile from the late Palaeocene of Morocco (Sigé *et al.*, 1990). The teeth (Figure 11.5(a)) show resemblances to plesiadapiform dentitions,

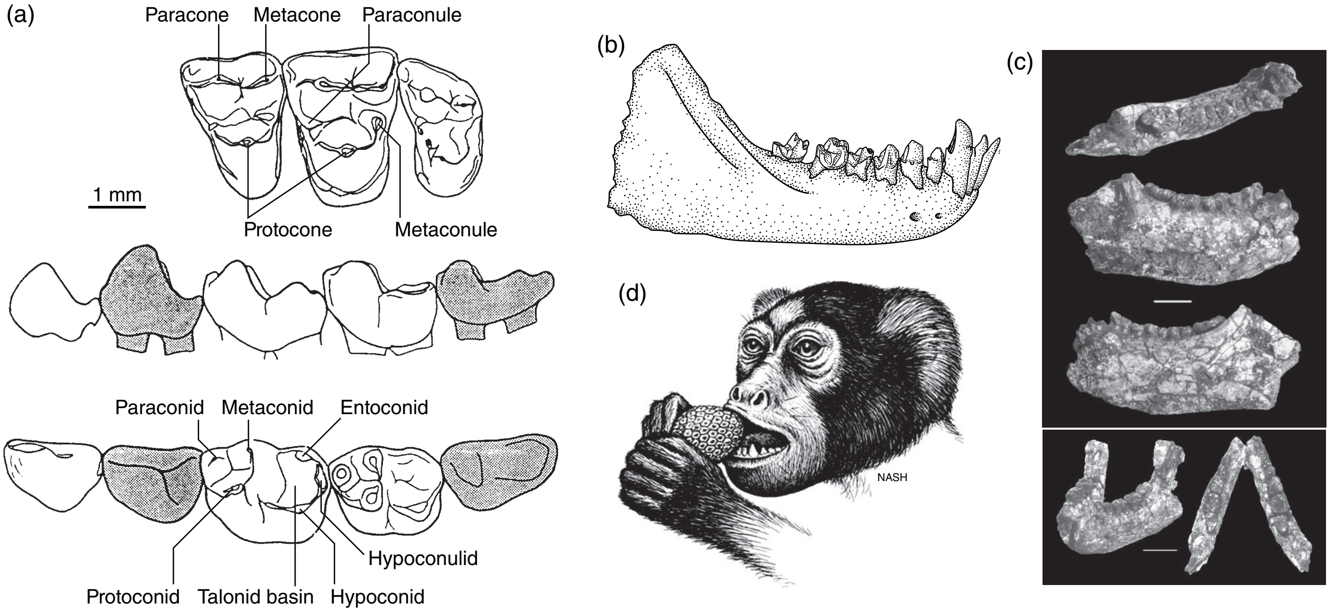


Figure 11.5 Early anthropoids: (a) upper molars 1–3 and lower cheek teeth of *Altiatlasius*, the oldest known primate, from the upper Palaeocene of Morocco; (b) mandible and lower jaw dentition of *Eosimias* from the middle Eocene of China; (c) lower jaw of *Pondaungia*, the original specimen found in 1923, and outline of a second specimen found in 1977; (d) restoration of the head of *Amphipithecus*. Source: (a) Adapted from Rose (2006). (b) Beard and Wang (2004). Reproduced with permission from Elsevier. (c,d) R. Ciochon, University of Iowa, Iowa City, IA, USA. Drawing by S. Nash, Denver Museum of Nature and Science, Denver, CO, USA. Reproduced with permission.

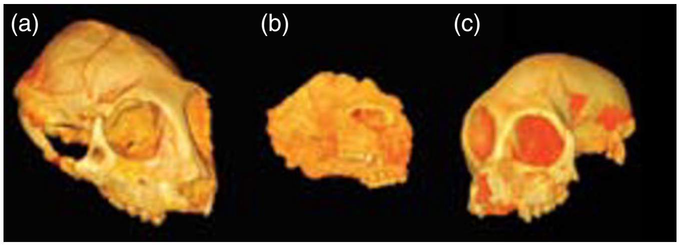


Figure 11.6 Crania of (a) the early Oligocene parapithecid anthropoid *Parapithecus grangeri*; (b) the late Eocene stem catarrhine *Catopithecus browni* (a substantially distorted skull); and (c) the early Oligocene stem catarrhine *Aegyptopithecus zeuxis*. See Colour plate 11.3. Source: Seiffert (2012). Reproduced with permission from John Wiley & Sons.

but *Altiatlasius* was initially identified as an omomyid (Sigé *et al.*, 1990). It has since been assigned many phylogenetic positions, but is generally accepted as the first euprimate, and perhaps even the first anthropoid (Seiffert *et al.*, 2005; Beard, 2006; Rose, 2006; Tabuce *et al.*, 2009). *Altiatlasius* was a tiny animal, about the size of a modern mouse lemur, and weighed perhaps 50–100 g.

Discoveries of early anthropoids during the past twenty years have fostered a heated debate about the geographic area of origin of the clade, whether in Africa or Asia. *Altiatlasius* is too incomplete to be placed confidently in the cladogram, whereas the Eosimiidae from China, Myanmar, and possibly from India (Bajpai *et al.*, 2008) are definitively basal anthropoids (see Box 11.1). *Eosimias* is known from several lower jaws with full dentitions (Beard and Wang, 2004) from the middle Eocene of China. The animal was tiny, weighing perhaps 90–180 g, and small enough to sit on the palm of your hand, and its teeth indicate a probable mixed diet of fruit and insects. The lower jaws (Figure 11.5(b)) show anthropoid characters in the small incisors, large canines, obliquely oriented premolars 3 and 4, molars with broad trigonids, and the relatively deep dentary. Tarsal bones assigned to *Eosimias* suggest anthropoid affinities, the most widely accepted view (Beard and Wang, 2004; Bajpai *et al.*, 2008; Seiffert *et al.*, 2009; Williams *et al.*, 2010; Ni *et al.*, 2013).

Next in the cladogram (see Box 11.1) are the Amphipithecidae, another Asiatic anthropoid family, comprising five or six genera mainly from the middle Eocene of Myanmar (Beard *et al.*, 2009), as well as from the late Eocene of Thailand. Some of these taxa, such as *Pondaungia* and *Amphipithecus* had been named in the 1920s and 1930s, and there are several new forms such as *Siamopithecus*; most are known only from isolated teeth, jaws, and a few other fragments. These were medium-sized to large animals, weighing 5–10 kg, mostly frugivores, and the tooth morphology of *Pondaungia* and *Amphipithecus* (Figure 11.5(c,d)) suggests that they also ate harder food such as nuts and seeds. Other amphipithecids may have fed on leaves, and some smaller animals may have relied on insects. These primates have long been regarded as anthropoids, although some have argued that they were related to adapiforms or omomyids. The anthropoid position has been confirmed in most recent studies, however (e.g. Beard *et al.*, 2009; Seiffert *et al.*, 2009; Coster *et al.*, 2013; Ni *et al.*, 2013), based on similarities in the teeth and jaws, and in the tarsal bones, of the amphipithecids to living anthropoids.

Except for the enigmatic, and unusually early, *Altiatlasius*, the earliest anthropoids come from south-east Asia. The first definitively African clade is the Parapithecoidea from the late Eocene and early Oligocene of Egypt (Seiffert *et al.*, 2005, 2012). These include three species of *Biretia* from the late Eocene, all of which are tiny (<300 g), and may show evidence for enlarged orbits and nocturnality, although this is debated (Seiffert *et al.*, 2005; Seiffert, 2012). Other parapithecoids from the same rock successions in Egypt were diurnal fruit-eaters that moved about in the tropical forest trees by a combination of quadrupedal walking and leaping. *Parapithecus* is known from a reasonably complete skull (Figure 11.6(a)) from the early Oligocene of Egypt, whose small orbits indicate diurnal habits, and size differences in the jaws and teeth may indicate sexual dimorphism between males and females (Simons, 2001). The brain size was smaller than in modern anthropoids of the same size.

11.3.3 Catarrhines: the Old World monkeys

After a to-and-fro between Asiatic and African stem-group anthropoids, the crown-group anthropoids split into Old and New World monkeys in the late Eocene or Oligocene, and the early history of catarrhines is documented by some intriguing, but inevitably controversial, fossils.

Catarrhines share a number of characters. They have only two premolars in each jaw and they generally show considerable sexual dimorphism: males are larger than females and their canine teeth are almost always larger than those of females. The Old World monkeys, the Cercopithecoidea, have long molars with crests (**lophs**) linking transverse pairs of cusps, the bilophodont condition.

Among probable stem catarrhines are a number of small clades, including oligopithecids and propliopithecids. For example, *Catopithecus*, an oligopithecid from the late Eocene of Egypt (Simons, 1995) is relatively completely known. It has two premolars, large upper canines and flattened spatulate incisors. *Catopithecus* specimens show pronounced sexual dimorphism, with males apparently twice the size of females and equipped with much larger canine teeth (Figures 11.6(b), 11.7(a)). *Aegyptopithecus*, a propliopithecid from the Oligocene of Egypt (Figures 11.6(c), 11.7(b,c)), was about the size of a gibbon, with a short snout, large forward-facing eyes and an enlarged braincase. The heavy jaw and broad cheek teeth suggest a diet of fruit, and the limb bones show that *Aegyptopithecus* probably climbed trees and ran along stout branches. *Saadanius* from the Oligocene of Saudi Arabia is close to the split of crown catarrhines (Zalmout *et al.*, 2013).

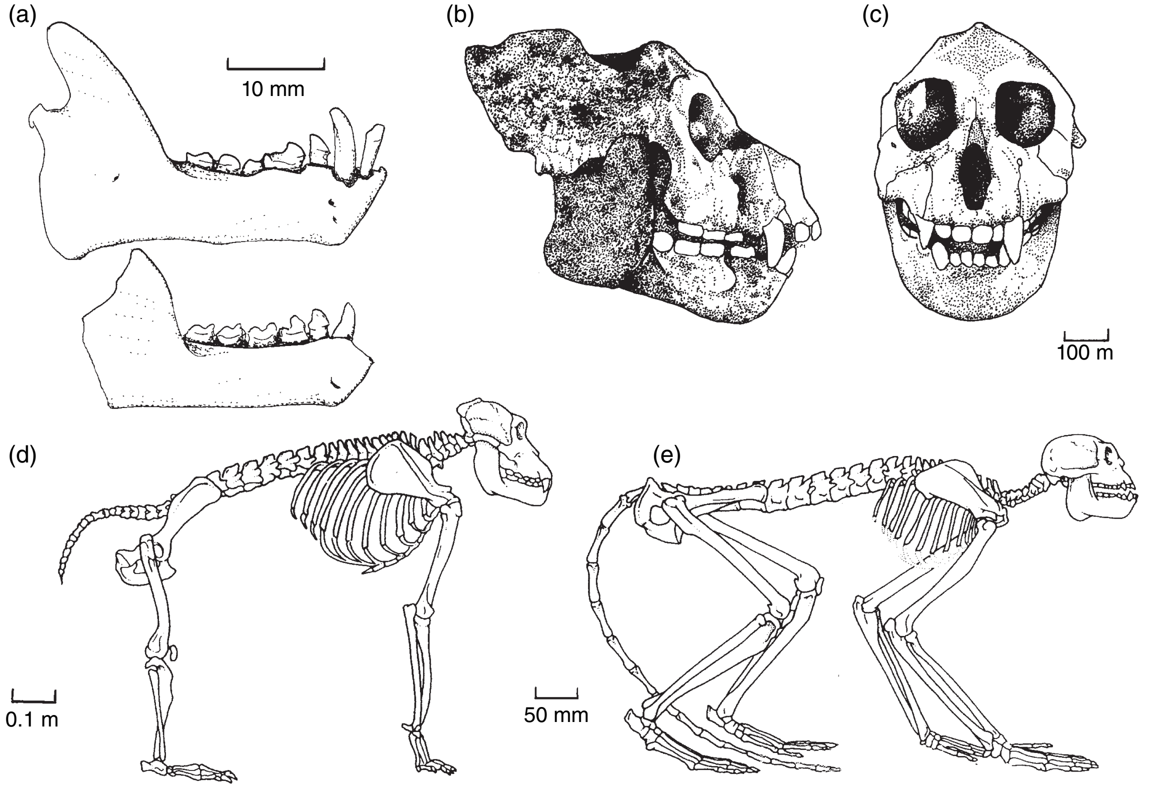


Figure 11.7 Early monkeys: (a) lower jaws of a male and female *Catopithecus*, an early catarrhine, from the upper Eocene of Egypt; (b,c) the skull of *Aegyptopithecus* from the Oligocene of Egypt, in lateral and anterior views; (d) skeleton of the giant baboon *Theropithecus oswaldi* from the Pleistocene of East Africa; (e) skeleton of the tree-dwelling cercopithecoid monkey *Mesopithecus pentelicus* from the upper Miocene of Greece. Source: (a) Adapted from Simons (1995). (b,c) Adapted from Simons (1967). (d,e) E. Delson, CUNY, New York, NY, USA. Reproduced with permission.

The 140 species of modern cercopithecids divide into two groups, the cercopithecines, such as the macaques (see Figure 11.1(d)) of Africa, Asia and Europe (the barbary 'ape' of Gibraltar) and the terrestrial baboons and mandrills, and the colobines, the leaf-eating colobus monkeys and langurs. The oldest fossil evidence of cercopithecids is from the late Oligocene of Africa, a lower third molar (Stevens *et al.*, 2013). More completely known is *Victoriapithecus*, a cercopithecid from the middle Miocene (15–14 Myr ago) of Kenya, which has bilophodont molars and probably fed on fruit (Miller *et al.*, 2009). By the late Miocene, cercopithecids had extended their range across the Old World, as far as China and Java and Europe, and in the Pleistocene such monkeys reached as far north as England. As many as ten cercopithecid lineages took to the ground and they replaced the ground-dwelling apes in parts of Africa.

Modern genera of cercopithecines appeared in Africa during the Pliocene and Pleistocene. The living gelada, *Theropithecus*, a specialized ground-dweller related to the baboon, lives in the Ethiopian highlands and feeds on grass and seeds. Pleistocene relatives were larger than the modern species, some of them much larger (Figure 11.7(d)), and they are common at East African fossil sites and their range extended as far as India and Spain.

Fossils of colobine monkeys also appear first in the Miocene. Colobines entered Asia and Europe before the cercopithecines and diverged into distinctive groups in those continents. *Mesopithecus* from the upper Miocene and Pliocene of Europe and the Middle East (Figure 11.7(e)), is a short-faced form, similar to modern langurs. It has a deep lower jaw, as in all colobines, an adaptation for chomping huge amounts of leaves and other plant material.

11.3.4 Platyrrhines: the New World monkeys

The 130 species of living platyrrhines are divided into three families, the Pitheciidae (titis, saki monkeys and uakaris), the Cebidae (capuchin and squirrel monkeys, tamarins and marmosets) and Atelidae (howler and spider monkeys, owl monkeys; see Figure 11.1(c)). All of these are confirmed tree-dwellers, and they are either herbivores, feeding on fruit and leaves, or omnivores, with the addition of insects and small vertebrates to their diet. Most are small, including the world's smallest monkey, the 120–190 g pygmy marmoset.

Platyrrhine fossil remains are sparse (Perez *et al.*, 2013; Schrago *et al.*, 2013). The oldest fossil platyrrhine is *Branisella* from the late Oligocene, and then good quality fossils of taxa such as *Dolichocebus*, *Tremacebus*, and *Chilecebus* are known from the early Miocene, dating to approximately 20 Myr ago. Some Pleistocene platyrrhines, *Protopithecus* and *Cartelles*, were larger than any living atelid, weighing an estimated 25 kg

(Halenar and Rosenberger, 2013). With longer arms than legs, these large frugivores swung themselves through the trees. *Protopithecus* was named in 1836, based on partial remains from a cave in Brazil; this was the first ever fossil primate to be named.

The platyrrhines probably split from the catarrhines in the Eocene or Oligocene, and they may have reached South America direct from Africa, crossing the opening South Atlantic Ocean. It is currently debated whether the Oligocene and Miocene fossils are part of the modern radiation, or whether they lie on the stem lineage; if the latter is true, then the crown clade, comprising all the living forms, would have diversified only about 20 Myr ago. Molecular evidence strongly supports the multiple expansions model, and a relatively recent diversification of the crown clade (Schrago *et al.*, 2013).

11.4 HOMINOIDEA: THE APES

The apes, Hominoidea, today include the gibbons and orang-utan of southern and eastern Asia, the gorilla and the chimpanzee from Africa, and humans (see Figure 11.1(e,f)). The limited number of living species of ape gives little idea of their great diversity in the past, especially in the Miocene of Africa. For a long time, the timing of divergence of cercopithecoids and hominoids was unclear, but *Nsungwepithecus* and *Rukwapithecus* from the late Oligocene of Tanzania, both based on limited remains, are diagnostic of cercopithecoids and hominoids respectively (Stevens *et al.*, 2013).

11.4.1 Early ape evolution

In the early Miocene of East Africa (23–16 Myr ago), apes were more abundant than anywhere today. Most of these belong to the Proconsulidae, including genera such as *Nyanzapithecus*, *Rangwapithecus* and *Turkanapithecus*. Best known is *Proconsul* (Walker *et al.*, 1983; Walker and Shipman, 2005), which was named in 1933 on the basis of some jaws and teeth from Kenya. The name refers to a chimp named Consul who then lived at London Zoo and entertained visitors with his bicycle riding and pipe smoking. Since the 1930s, evidence of most of the skeleton has been found, including several well-preserved associated skeletons (Figure 11.8). There are four species that differ mainly in body size.

Proconsul has a long monkey-like trunk and the arm and hand bones share the characters of modern monkeys and apes. Many different modes of locomotion have been proposed, ranging from nearly fully bipedal walking (when it was thought to be closer to human ancestry), through knuckle walking, as seen in modern chimps and gorillas, to full **brachiation**, swinging hand over hand through the trees as in modern gibbons. The present view is that *Proconsul* could move on the ground on all fours and run quadrupedally along heavy branches. The elbow and foot anatomy of *Proconsul* is fully ape-like, but the head is primitive, with small molar teeth and long projecting canines (Figure 11.8(b)). Its diet was probably soft fruit.

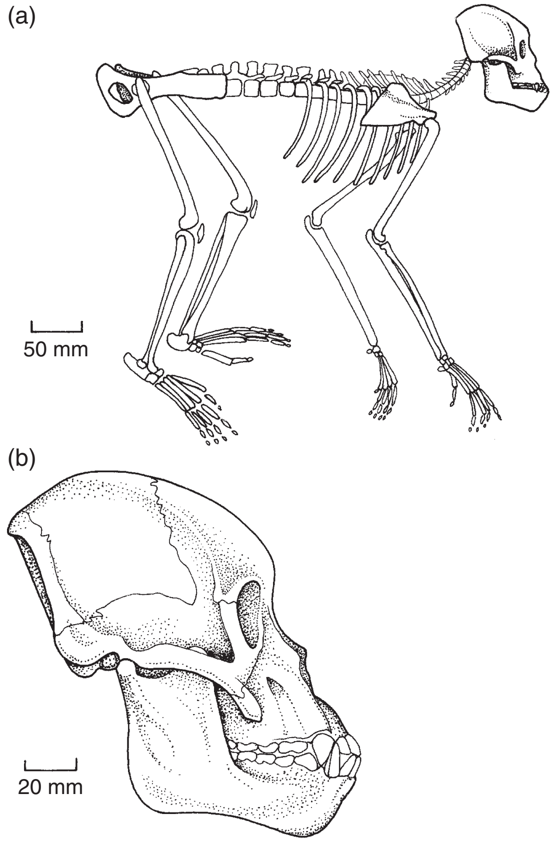


Figure 11.8 Miocene apes: (a,b) *Proconsul* skeleton (a) and skull (b). Source: (a) Adapted from A. Walker in Lewin (2005). (b) Adapted from Walker *et al.* (1983).

Proconsul is regarded as a true ape because it shows a number of derived characters shared with the modern forms, such as the absence of a tail and the relatively large brain size (150 cm^3). In addition, *Proconsul* shows a number of other ape-like characters of the teeth and modifications to strengthen the elbow joint for brachiation.

The story of ape evolution continued in Africa during the mid- and late Miocene (16–5 Myr ago), but some lines branched off and evolved separately in Europe and Asia. The gibbons, 14 species of Hylobatidae, are the most plesiomorphic of living apes, and they appear to have branched off the line to the great apes, the Hominidae, before the late Miocene, when Yuanmoupithecus is known from China, and isolated fossils are known from the Pliocene, Pleistocene, and Holocene of numerous sites across southern China (Jablonski and Chaplin, 2010).

11.4.2 Hominidae: first forms and orang-utan evolution

The living Hominidae fall into two subfamilies, the Ponginae, the two species of orang-utan and its fossil relatives, and the Homininae, five species of chimps, gorillas, and humans and their fossil relatives (see Box 11.3). This split marks a divergence in modes of locomotion from a generalized tree-climbing ancestor: the orang-utans specialized in suspension (brachiation) and slow climbing, whereas the African great apes specialized in terrestrial quadrupedalism (chimps, gorilla) and bipedalism (humans).

The first hominids (Moyà-Sola *et al*., 2009; Begun, 2010; Harrison, 2010) are the Afropithecidae, probably a paraphyletic group, including taxa such as *Kenyapithecus*, *Griphopithecus*, *Equatorius*, *Anoiapithecus* and *Afropithecus*, known mainly from eastern Africa, but also from Turkey, central Europe and perhaps Namibia, from 20 to 14 Myr ago. *Kenyapithecus*, named on the basis of teeth and jaws from Kenya, was a 1-m-tall animal that climbed trees and lived on the ground. The afropithecids were the first hominoids to spread over much of the Old World, and they may have relied on their powerful jaws and teeth to exploit a wide variety of food.

The Ponginae (orang-utans) diverged next, and they have had a long history in south-east Asia from 16 to 13 Myr ago. Close relatives of modern orang-utans include *Lufengpithecus*, known from a few skulls and huge numbers of teeth and jaws from the late Miocene of China (Chaimanee *et al*., 2003), and *Khoratpithecus*, known from a lower jaw from the late Miocene of Thailand (Chaimanee *et al*., 2004).

The Sivapithecinae are a major pongine subclade from the middle and late Miocene. The best known is *Sivapithecus* (Figure 11.9(a)) from Turkey, northern India, Pakistan and China. There were three species, ranging in size from 45 to 95 kg. *Sivapithecus* was rather like the modern orang-utan, with heavy jaws and broad cheek teeth covered with thick enamel, all of which suggest a diet of tough vegetation. There is a specialized pattern of cusps on the molar teeth (Figure 11.9(b)): there are five cusps, separated by deep grooves in a Y-shape, the so-called 'Y-5 molar'. When it was first reported in 1910, *Sivapithecus* was hailed as a 'missing link' between apes and humans, a view confirmed by a superficial comparison of palates (Figure 11.9(c–e)). Apes have a rectangular dental arcade, humans have a rounded tooth row, and the palate of *Sivapithecus* seems to form a perfect intermediate; it is definitively a pongine, based on numerous other anatomical features.

There is disagreement over the modes of locomotion of *Sivapithecus*. Perhaps it was a generalist that moved on all fours both in trees and on the ground, or perhaps some species were adapted for climbing and suspension, and others for quadrupedal locomotion. Some wrist bones even hint at knuckle walking (Begun and Kivell, 2011), which, if it is true, would imply an independent origin of a mode of locomotion seen otherwise only in gorillas and chimps.

The most remarkable sivapithecine is *Gigantopithecus* from the late Miocene of India and the Pleistocene of China. This pongine is known only from its massive heavily worn teeth and some jaw bones (Figure 11.9(f)). Such limited remains have allowed anthropologists free rein in estimating the original body size of *Gigantopithecus*. The teeth suggest it was ten times the size of

BOX 11.3 RELATIONSHIPS OF APES AND HUMANS

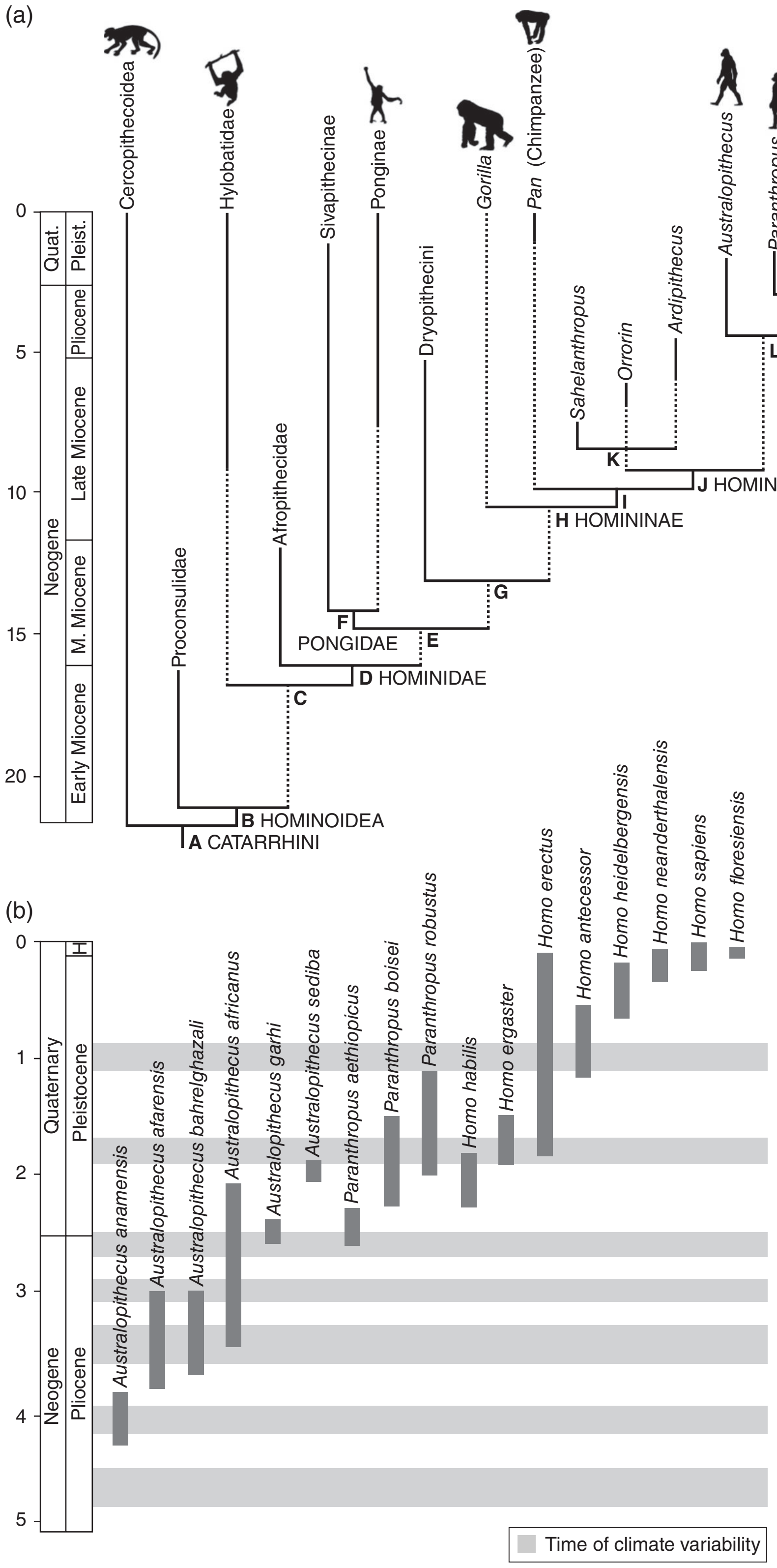
Until about 1980, most anthropologists assumed that humans formed a distinct lineage from the great apes, with forms such as *Sivapithecus* (*Ramapithecus)* being placed on the direct line to humans. The split between apes and humans was dated at 15–25 Myr ago, thus in the late Oligocene or early Miocene.

This view was challenged by the findings of molecular biologists. Early attempts at protein sequencing (see Section 2.5.2) in the 1960s and 1970s showed that humans were much more similar to chimps and gorillas than had been expected, and the branching point was dated at about 5 Myr ago (range of estimates, 9–4 Myr ago). At first, these dates were regarded as gross underestimates by anthropologists, but they were confirmed by later phylogenomic work using DNA sequences. The relatively late split of humans and apes was confirmed in the 1980s and 1990s by restudy of existing ape fossils, and by new specimens of *Proconsul*, *Dryopithecus* and *Sivapithecus* which showed they were side branches from the line to modern apes and humans.

In a cladogram of the apes (figure (a)), most anthropologists accept that Proconsulidae is the basal taxon, followed by the gibbons (Hylobatidae) and then the great apes and humans, Hominidae (Begun, 2010; Harrison, 2010; Williams *et al*., 2010). Within the great ape clade, all evidence confirms that chimps are closest to humans, then gorillas and then the orang-utan. This view is widely accepted, even though there is some morphological support for an African great apes clade: chimps and gorillas share numerous characters that are absent in modern humans, such as thin enamel on the teeth, an enlarged trigonid basin on the lower molars, six sacral vertebrae and ten adaptations for knuckle-walking, but these are presumably convergences or were present in the last common ancestor. Most anthropologists accept that Afropithecidae are basal hominids, perhaps followed by the Pongidae (*Sivapithecus* + orang-utan) and then the dryopithecines, although the latter had also been associated with the Ponginae.

The 17 or more species of human, divided among the genera *Australopithecus*, *Paranthropus*, and *Homo* (figure (b)), are themselves somewhat unstable as regards their content – palaeoanthropologists debate exactly which skulls and skeletons belong to which species – as well as their phylogenetic placement. The figure shows a temporal succession, with presumed close relatives placed close to each other, but no attempt is made to convert this into a cladogram. As an example of the uncertainty, most palaeoanthropologists accept that *Paranthropus* and *Homo* are clades, whereas *Australopithecus* is probably paraphyletic, but some debate, for example, whether *Homo habilis* and *Homo ergaster* are members of *Homo* or could be australopiths (e.g. Wood and Collard, 1999; Cela-Conde and Ayala, 2003; Tattersall and Schwartz, 2009; Harrison, 2010; Wood and Harrison, 2011; Strait, 2013).

Relationships of the living apes and humans: (a) cladogram showing postulated relationships, based on Begun (2010) Harrison (2010), Williams *et al*. (2010), and others. Animal silhouettes are mostly from the PhyloPic website, and we acknowledge the work of Gareth Monger, T. Michael Keesey, Smokeybjb, Mateus Zica, and Sarah Werning. Synapomorphies: **A CATARRHINI**, two premolars, sexual dimorphism is marked, males have larger canines than females; **B HOMINOIDEA**, relatively large brain size, low-crowned lower premolar 3, tail absent, scapula with elongate vertebral border and robust acromion, humeral head rounded and medially oriented; **C**, enlarged sinuses, palate deep, middle incisors spatulate, lower molars broad with low rounded cusps, clavicle elongated, very long arms relative to legs, broad sternum/broad thorax, short olecranon process and reduced styloid process on ulna, ulna shaft bowed, radial head rounded, hand with long curved proximal phalanges with distally-placed flexor insertions, opposable thumb, femur with asymmetrical condyles, iliac blade broad, calcaneum short and broad; **D HOMINIDAE**, maxillary sinus enlarged, orbits higher than broad, lengthened premaxilla, nasals elongate, narrow incisive foramen, subarcuate fossa in petrosal bone absent, incisors enlarged, upper incisor 2 spatulate, canines robust and long, molars with thick enamel, Y-5 molar, ischial tuberosities absent, hindlimbs reduced in length; **E**, zygomatic arch robust with a rugose top and three foramina; **F PONGIDAE**, narrow interorbital pillar, orbits high and narrow, great size discrepancy between upper incisors, alveolar prognathism; **G**, broad thorax, stiff lower back, powerful grasping hands; **H HOMININAE**, facial klinorhynchy (downward bending of the face on the braincase), enlarged continuous supraorbital torus (eyebrow ridge in skull), frontal sinus, adaptations for knuckle-walking, fusion of os centrale in wrist; **I**, premaxillary suture obliterated in adults, premaxillary alveolar process very elongated, nasal premaxilla very short, upper incisors all similar in shape; **J HOMININI**, bipedal posture, relatively long hindlimbs, basin-like pelvis, foramen magnum located forward in skull, large brain relative to body size, small canine teeth, U-shaped dental arcade; **K**, primitive craniofacial pattern; **L**, incisor/ lower canine step absent, canine size dimorphism reduced, thick enamel, molar row elongated, hallux (big toe) in line with other toes; **M**, enlarged brain, similar cranial base. (b) Time chart of human species, with times of climatic variability (dry-wet) indicated as horizontal shaded bands. Abbreviations: H, Holocene; M, Middle; P, Pleistocene; Quat, Quaternary.



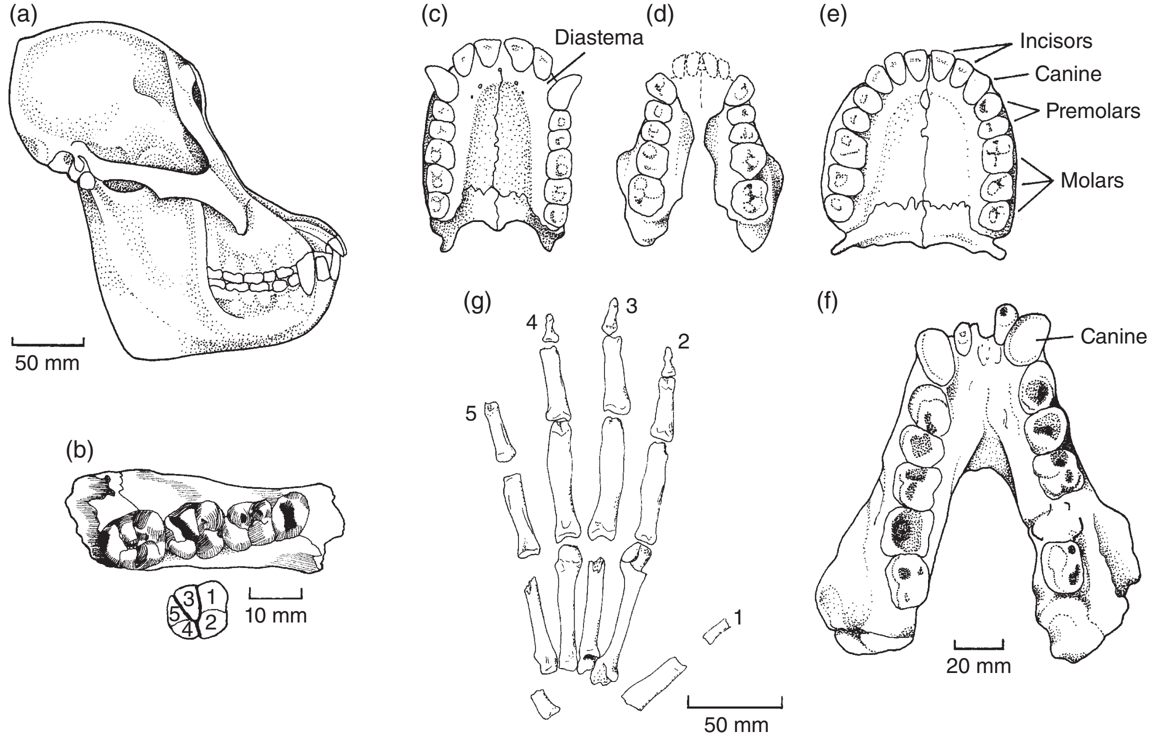


Figure 11.9 Late Miocene apes: (a) skull of *Sivapithecus*; (b) jaw fragment with molar teeth and diagrammatic representation of the Y-5 pattern; palates of (c) the chimpanzee, (d) *Sivapithecus*, and (e) modern human; (f) lower jaw of *Gigantopithecus* in occlusal view; (g) hand of *Dryopithecus*. Source: (a) Adapted from Ward and Pilbeam (1983). (b) Adapted from Gregory and Hellman (1929). (c–e) Adapted from Lewin (2005). (f) Adapted from Simons and Chopra (1969). (g) Adapted from Moyà-Solà and Köhler (1993).

Sivapithecus, and adult males might have reached heights of 2.5 m and weights of 270 kg (others estimate 3 m tall and weighing half a tonne!). This huge animal stalked the forests of south-east Asia from 5 to 0.3 Myr ago and some regard it as the source of stories of yetis in Central Asia and the big foot of North America.

11.4.3 Evolution of European and African hominids

While the pongines were diversifying in south-east Asia, the hominines were evolving in Europe and Africa. The Dryopithecini consist of a number of species of *Dryopithecus* and close relatives that invaded Europe in the middle Miocene. *Dryopithecus* was first reported in 1856 from southern France, the first fossil ape to be found. Since then, further *Dryopithecus* specimens have been found in the late Miocene (12–5 Myr ago) of Europe, from Spain to Hungary (Begun, 2010). *Dryopithecus* was adapted for suspension beneath branches and it probably swung rapidly around the subtropical forests of southern Europe. The arms, and in particular the hands (Figure 11.9(g)), are long, and the thumb and finger bones indicate that there were strong grasping muscles. Other European genera, such as *Pierolapithecus* (13 Myr ago) and *Oreopithecus* (8–6 Myr ago), may be dryopithecines. The Dryopithecini are basal hominines, close to the radiation of African apes and humans (see Box 11.3).

Until recently there was no fossil record for gorillas or chimps, until the report (McBrearty and Jablonski, 2005) of some definitive chimpanzee teeth from the middle Pleistocene of Kenya. These include two spatulate incisors, much thicker antero-posteriorly than human teeth, and a low-crowned molar, all of which have thin enamel, characteristic of *Pan*, and thinner than in *Homo*. The poor fossil record of the African great apes stands in marked contrast to that of their closest relatives, the humans.

11.5 EVOLUTION OF HUMAN CHARACTERISTICS

For centuries, many scientists tried to set humans apart from the animals. There was a heated debate in the 1850s about the features that distinguished *Homo sapiens* from the apes and other mammals, even distinguishing Bimana ('two hands'; humans) from Quadrumana ('four hands'; all other mammals). Even today, many people find it hard to accept the evidence that humans are a very young group that has had a separate evolutionary history for only 5–7 Myr. Two main sets of characters seem to set humans apart from the other apes – bipedalism and large brain size.

11.5.1 Bipedalism: humans as upright apes

Bipedalism, walking upright on the hindlimbs, has led to anatomical changes in all parts of the human body (Figure 11.10). The foot became a flat platform structure with a non-opposable

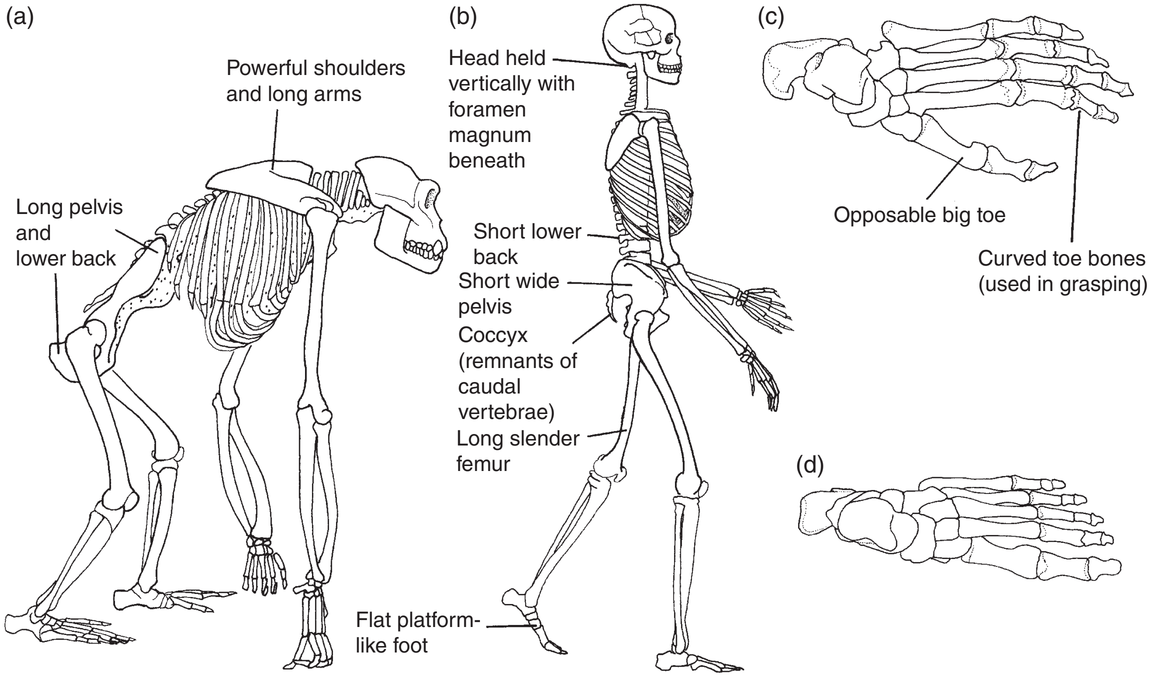


Figure 11.10 Comparison of (a) the skeleton and (c) foot of a gorilla with those (b,d) of a modern human, to show major changes in posture and the anatomical changes associated with bipedalism. Source: Adapted from Lewin (2005).

big toe and straight phalanges in the toes. Apes and monkeys have a grasping foot with curved phalanges and an opposable big toe. The angle of the human knee joint shifts from being slightly splayed to being a straight hinge, and all the leg bones are longer. The hip joint faces downwards and sideways and the femur has a ball-like head that fits into it. The pelvis as a whole is short and bowl-like as it has to support the guts, and the backbone adopts an S-shaped curve. In apes, the pelvis is long and the backbone has a C-shaped curve to brace the weight of the trunk between the arms and legs.

Bipedalism also introduced changes in the skull, as it now sat on top of the vertebral column, instead of at the front. The occipital condyles and the **foramen magnum**, the skull opening through which the spinal cord passes, are placed beneath, rather than behind, the skull roof. This makes it possible for a palaeoanthropologist to identify a bipedal hominid even from a small skull fragment in the region of the foramen magnum.

The evidence for the evolution of bipedalism includes the oldest hominin skeletons, dated as 6–4 Myr old (see Section 11.6.1), and a trackway of footprints in volcanic ash dated as 3.75 Myr old. Bipedalism probably arose 8–5 Myr ago in the hominin line, when it split from the African apes. According to one theory, the forest-dwelling Miocene apes became restricted to the west of Africa, where they gave rise to the gorillas and chimps, after the Great Rift Valley began to open up, and the apes that remained in the east had to adapt to life on the open grasslands.

A key adaptation to life in the open habitats was to stand upright in order to spot dangerous predators. Bipedal movement allowed these apes to carry food and other objects with them. The great majority of early human fossils, remains of this East African ape lineage, come from the eastern region of Africa, in a strip from southern Ethiopia, through Kenya and Tanzania, to Malawi and South Africa. This classic 'savanna hypothesis' for the origin of humans has been very actively debated; many recent authors have pointed out that early human fossils often occur in wooded habitats. However, a reanalysis of the evidence (Dominguez-Rodrigo, 2014) suggests that the rejection was wrong. Savanna habitats were not simply open grassland, but mosaic habits comprising patches of grassland and woodland, and he concludes that this is a highly plausible setting for the early evolution of bipedalism.

11.5.2 Increased brain size

The second key human character was the increase in relative brain size that occurred much later, only about 2 Myr ago with the origin of the genus *Homo*. The early bipedal humans still had rather ape-like heads with brain sizes of 400–550 cm^3, similar to apes, and by no means comparable with modern humans, who have a brain size of 1000–2000 cm^3 (mean, 1360 cm^3), a value approached by some examples of 500,000-year-old fossil *Homo*.

Various anatomical characters changed as a result of the increase in brain size. The back of the head became enlarged to accommodate it, the face became less projecting and placed largely beneath the front of the brain, rather than in front of it. Thus, the projecting face of the apes was lost with increasing brain size in the human line and this led to a shortening of the tooth rows. The rounded tooth row with a continuous arc of teeth and no gap (diastema) between the incisors and canines (see Figure 11.5(d)) is a human character.

Present fossil evidence then suggests that human evolution followed a 'locomotion-first' pattern, with bipedalism arising before 6 Myr ago and the enlarged brain less than 2 Myr ago. During of the first half of the twentieth century, though, many experts held to the more comforting 'brain-first' theory, and the fossil evidence seemed to confirm their view.

11.5.3 'Brain-first' theories of human evolution

The first fossil human specimen was a Neanderthal child's skull found in Belgium in 1828, but its importance was not realized. The first partial skeleton was found in 1856 in Germany, an injured specimen, named Neanderthal man after the Neander Valley where it was found. This poor individual became the type 'cave man', our brutish forebear, coarse of limb, hairy of body and small of brain. He grunted at his fellows, tore raw meat from the bones of prey animals, dragged his wife along by her hair and huddled miserably in caves to keep warm.

Older human remains, found in 1891 in Java, were hailed as the 'missing link' and named *Pithecanthropus erectus* (now *Homo erectus*), a primitive form. Key evidence for the 'brain-first' theory came in 1912 when a remarkable skull was found by an amateur, Charles Dawson, in southern England, at the village of Piltdown. The skull (Figure 11.11(a)) showed a large brain size of modern proportions, but the jaw was primitive, with ape-like teeth. This specimen was a godsend to the leading anthropologists of the day, the true 'missing link', clearly ancient, and yet a brainy forebear. Not only that, he was English!

In 1925, Raymond Dart announced an even more ancient skull from southern Africa, which he named *Australopithecus africanus*. It was a child's skull (Figure 11.11(b)), with a small ape-like braincase. Dart's new fossil was greeted widely with scepticism. Surely it was only a fossil ape, with nothing to do with our ancestry? Piltdown man proved the 'brain-first' model.

During the 1950s, two important chains of events overthrew the received wisdom on our ancestry. First, Piltdown man was shown to be a forgery – a recent human braincase with a modern orang-utan's jaw. The great champions of Piltdown man, the anatomists Elliot Smith and Arthur Keith, and the palaeontologists Arthur Smith Woodward and W. P. Pycraft, had died.

The second set of events took place in southern Africa, where many specimens of *Australopithecus* had been coming to light, and the weight of new material was proving harder to discount by the supporters of Piltdown. The unmasking of Piltdown in 1953 passed without any major public dispute, and scientific attention from that time onwards has focused on African fossils of early, small-brained bipedal humans.

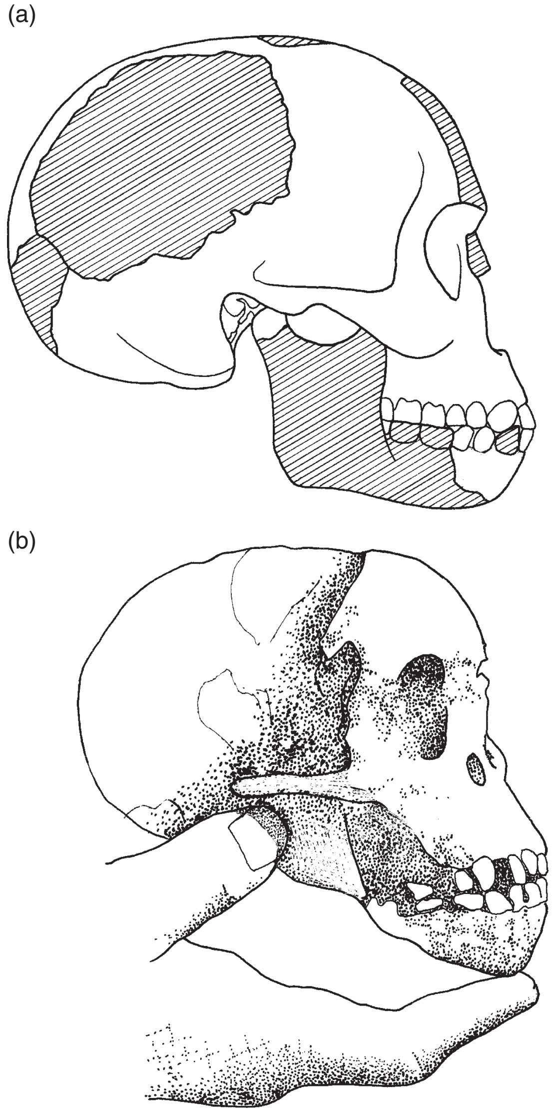


Figure 11.11 Two controversial hominid skulls of the early twentieth century: (a) Piltdown man, found in 1912, and subsequently shown to be a hoax; (b) the first skull of *Australopithecus africanus*, the Taung child, reported in 1925. Source: Adapted from various photographs.

11.6 THE EARLY STAGES OF HUMAN EVOLUTION

The line to modern humans includes as many as 22 species, four species of pre-australopiths, nine species of australopiths and nine of *Homo* (Wood and Harrison, 2011; Strait, 2013). Until 1990, the australopiths were generally all assigned to one genus, *Australopithecus*, but new finds suggest that as many as six genera is a more appropriate division: *Orrorin* and *Sahelanthropus* from the late Miocene, *Ardipithecus* and early species of *Australopithecus* from the Pliocene, and later species of *Australopithecus* and *Paranthropus* from the Plio-Pleistocene. Similarly, after a century of ever more subdivision, most anthropologists had lumped all specimens of *Homo* into three species, but current views indicate perhaps seven, or up to ten by some counts.

11.6.1 The pre-australopiths: *Orrorin*, *Sahelanthropus*, *Ardipithecus*

Until 2000, the oldest humans were Pliocene in age, 4 Myr or younger, but then a series of fossils from different parts of Africa pushed that fossil record back to 6 and 7 Myr ago. These early dates are within the range of molecular estimates for the split of humans from chimps (8–5 Myr ago), but they exceed the favoured estimate of 5 Myr ago derived from genetic analyses.

There are two ancient contenders, both announced in rapid succession by rival teams, and both from the late Miocene of Africa. First is *Sahelanthropus* from 7 Myr-old old sediments in Chad, named by Brunet *et al.* (2002) on the basis of a distorted, but nearly complete cranium (Figure 11.12) and fragmentary lower jaws. The skull shows a mixture of primitive and advanced characters: the brain size, at 320–380 cm^3, is comparable to that of chimpanzees, but the canine teeth are small, more like those of a human, and the prominent brow ridges are of the kind seen only in *Homo*. There has been some dispute about the location of the foramen magnum, whether it lies below the skull (indicating bipedality) or towards the back (ape-like quadrupedality). *Sahelanthropus* has generally been accepted, however, as a basal hominid (Cela-Conde and Ayala, 2003; Strait, 2013), perhaps the closest we will find to the common ancestor of chimps and humans.

Slightly younger is *Orrorin tugenensis*, named by Senut *et al.* (2001) from teeth, jaw fragments and broken limb bones from sediments in Kenya dated at about 6 Myr old. The teeth are rather ape-like, the arm bones indicate some ability to brachiate, but the femora suggest that *Orrorin* was an upright biped. The limited remains led to considerable controversy about the posture and affinities of *Orrorin* (e.g. Cela-Conde and Ayala, 2003), and doubts about the initial claims that it was more closely related to humans than the younger australopiths. Re-study of the *Orrorin* femurs (Richmond and Jungers, 2008) confirm they come from a biped, but not more closely related to *Homo* than to *Australopithecus*.

Equally controversial is *Ardipithecus ramidus* from Ethiopia, dating from 4.4 Myr ago and the older species *Ar. kadabba* from 5.8 to 5.2 Myr ago. *Ar. ramidus* is especially thoroughly known (White *et al.*, 2009; Suwa *et al.*, 2009; Simpson, 2013), being represented by 110 fossils, including a partial female skeleton from an individual that probably weighed about 50 kg and stood about 1.2 m tall (Figure 11.13). Brain size (300–350 cm^3) was no larger than in a modern chimpanzee of the same body mass. The numerous teeth and a largely complete skull show that *Ar. ramidus* had a small face and a reduced canine/premolar complex, suggesting minimal social aggression (modern chimpanzees and gorillas use their long canines in open-mouth threat displays). *Ardipithecus* has relatively large canine teeth, narrow molars, thin enamel and other primitive features, but these teeth are more hominine than in any of the great apes. They indicate a diet mainly of fruit and leaves.

The limb bones of *Ardipithecus* show that it could clamber about in trees, grasping branches and trunks with its hands and feet, but there were no adaptations for brachiation, vertical climbing, or knuckle walking. The limbs and forwardly placed foramen magnum show that *Ardipithecus* was a biped, but less accomplished than *Australopithecus* and *Homo*. In particular, the foot has a stiffened midfoot region and the toe joints were capable of bending upward at the end of a pace. However, the big toe is divergent, as in a modern chimp or gorilla. The foot bones also indicate that *Ardipithecus* placed its weight asymmetrically along the outer margin of the sole of the foot, as chimps do today, rather than evenly across the entire width of the foot sole, as modern humans do.

Figure 11.12 The near-complete skull of *Sahelanthropus*, possibly the oldest human ancestor, from the upper Miocene of Chad. Source: M. Brunet, Université de Poitiers, Poitiers, France. Reproduced with permission.

Figure 11.13 The early hominin *Ardipithecus ramidus*, reconstructed CT-scanned skull in anterior view. Source: © T. Michael Keesey/CC BY 2.0.

In sum, *Ardipithecus* shows that the common ancestor of chimps and humans was like neither of the modern forms, and chimps have evolved as many specializations since that point as have modern humans.

11.6.2 Early *Australopithecus*: Lucy and her relations

Basal hominins flourished in the Pliocene. Several species have been named, some of them sometimes assigned to *Praeanthropus*, a genus that had been named in 1948 for a jaw fragment from the Pliocene of Kenya (Cela-Conde and Ayala, 2003). This assignment has not been widely accepted, and most palaeoanthropologists assign these very early hominins to *Australopithecus*, which is then a long-ranging genus, known from 4.2 to 1.4 Myr ago.

Leakey *et al.* (1995) reported an ancient hominin, *Australopithecus anamensis*, from sediments 4.1–3.9 Myr old near Lake Turkana in Kenya, which appears to be an intermediate between *Ardipithecus* and later species. The remains include jaws, a humerus, a tibia and isolated teeth. It has a primitive jaw with a shallow palate and large canines. The tibia shows, however, that *Au. anamensis* was a biped. A further find of *Au. anamensis* from Ethiopia (White *et al.*, 2006) extends the age range back to 4.2 Myr ago, and includes teeth and a femur that confirm assignment to this genus and species.

The most complete, and famous skeleton of a Pliocene hominin, *Australopithecus afarensis*, was discovered by Donald Johanson and colleagues in Ethiopia in 1974. The skeleton was from a young female, nicknamed Lucy, which consisted of 40% of the bones, unusually complete by usual standards (Figure 11.14(a)). Some 240 specimens were found at Hadar in the 1970s, and since then dozens of additional specimens have been found at several localities in Ethiopia, Kenya, Tanzania, and Chad (Kimbel and Delezene, 2009). Lucy is dated as 3.2 Myr old and *Au. afarensis* specimens range from 3.7 to 3.0 Myr in age. Further specimens from Laetoli in Tanzania are dated as 3.7–3.5 Myr old. These include some bones and the famous trackway of bipedal footprints.

Australopithecus afarensis individuals are 1–1.2 m tall, with a brain size of only 415 cm^3 and a generally ape-like face. Other plesiomorphic characters include a small diastema (Figure 11.14(b)), long arms and rather short legs and curved finger and toe bones (Figure 11.14(c–e)). These curved bones imply that Lucy still

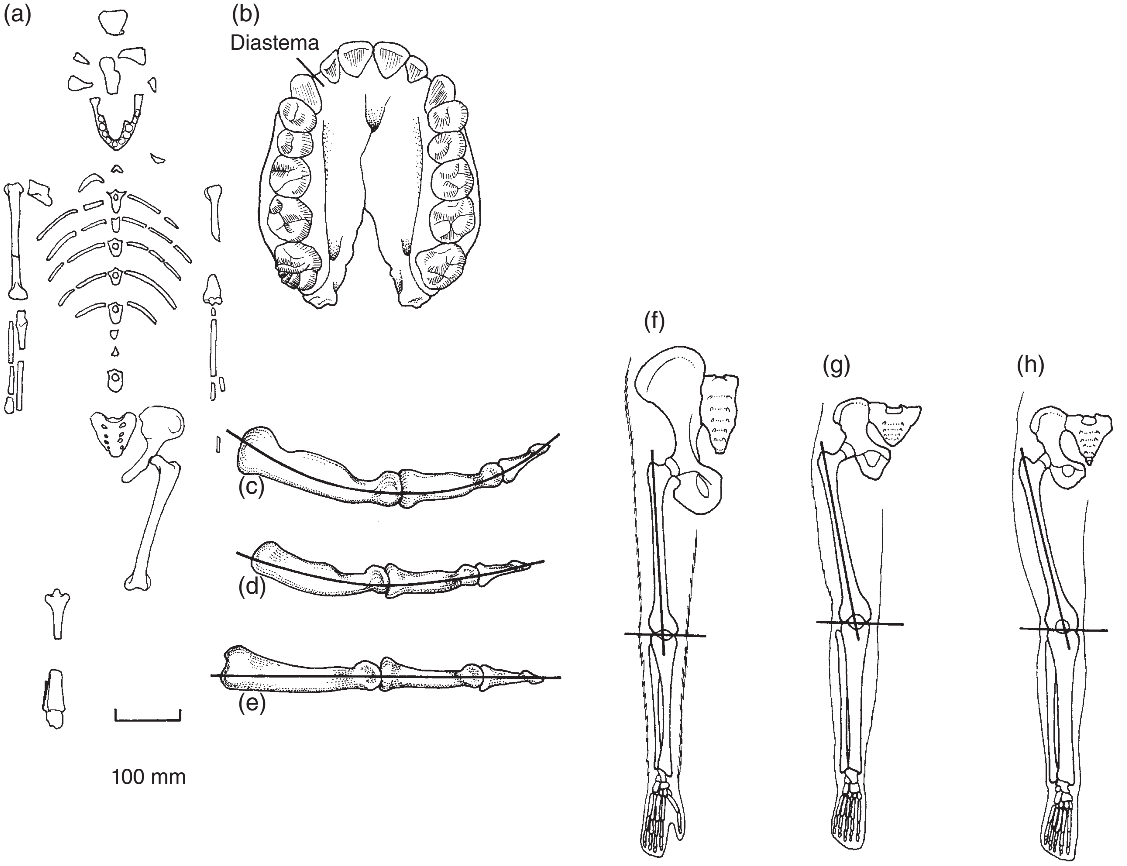


Figure 11.14 The australopiths: (a) skeleton of 'Lucy', the oldest reasonably complete hominid, *Au. afarensis*; (b) palate of 'Lucy'; fingers of (c) an ape, (d) *Australopithecus* and (e) a modern human, showing the loss of curvature, used for grasping branches; the hindlimbs of (f) an ape, (g) *Au. afarensis* and (h) a modern human, showing changes in pelvic shape, limb bone length and angle. Source: (a) Adapted from various photographs. (b,f–h) Adapted from Lewin (2005). (c–e) Adapted from Napier (1962).

used her hands and feet in grasping branches, as apes do. *Au. afarensis* is more human, though, in some significant ways: the tooth row is somewhat rounded (Figure 11.14(b)) and hindlimbs and pelvis are fully adapted for a type of bipedal locomotion (Figure 11.14(f–h)), although there is some dispute over just how 'modern' Lucy's bipedalism was (Kimbel and Delezene, 2009). The fuller collections now available show that *Au. afarensis* was a sexually dimorphic species, with males having jaws 30% larger than females.

The likely diet of *Au. afarensis* has been hotly debated, with evidence coming from tooth shape, enamel thickness, microwear patterns, and palaeoecological analysis of the surrounding sediments, but with little agreement (Kimbel and Delezene, 2009). Stable carbon isotopic analyses of 20 *Au. afarensis* samples from different localities in Ethiopia shows that these individuals had eaten considerable quantities of C_4/crassulacean acid metabolism foods, that is foods derived from grasses, sedges, and succulents, all of which are common in tropical savannas and deserts (Wynn *et al.*, 2013). This marks a major step in hominid evolution. Earlier hominins had fed on leaves, fruits and nuts from trees. With the expansion of grasslands at least 1 Myr earlier, massive new plant food resources had become available, but had not yet been exploited by early humans. In this sense, *Au afarensis* was the first human to take advantage of the richest food resources in its new savanna home.

A further hominin fossil is *Kenyanthropus platyops* from 3.5-Myr-old rocks in Kenya (Leakey *et al.*, 2001), based on a relatively complete cranium. The face is flatter than in *Au. afarensis* and the skull differs in further details, although White (2013) suggests this is most likely a distorted specimen of *Au. afarensis*.

11.6.3 The later australopiths

The australopiths lived on in Africa through the late Pliocene and earliest Pleistocene, from about 3.6 to 1.1 Myr ago, and there were as many as seven species; *Australopithecus africanus*, *Au. sediba*, and *Paranthropus robustus* from southern Africa, *Au. garhi*, *P. boisei* and *P. aethiopicus* from eastern Africa (Ethiopia, Kenya, Malawi) and *Au. bahrelghazali* from Chad (Roberts, 2011; Reed *et al.*, 2013). There were two size classes of australopiths living in Africa at the same time (Figure 11.15), the lightly built, or gracile, *Au. africanus*, which was typically 1.3 m tall, 45 kg in body weight and had a brain capacity of 445 cm^3, and the heavier *P. aethiopicus*, *P. robustus* and *P. boisei*, which were 1.75 m tall, 50 kg in body weight and had a brain capacity of 520 cm^3.

These australopiths show advances over *Australopithecus afarensis* in the flattening of the face, the loss of the diastema and the small canine teeth. They show some specializations that place them off the line to modern humans. For example, the molars and premolars are more massive than in *Au. afarensis* or *Homo*, and they are covered with layers of thick enamel, adaptations in this lineage to a diet of tough plant food. After many years of collecting new remains of *Au. africanus*, ever since 1925 (see Section 11.5.3), palaeontologists have now added new australopithecines to the roster, including *Au. sediba* (see Box 11.4).

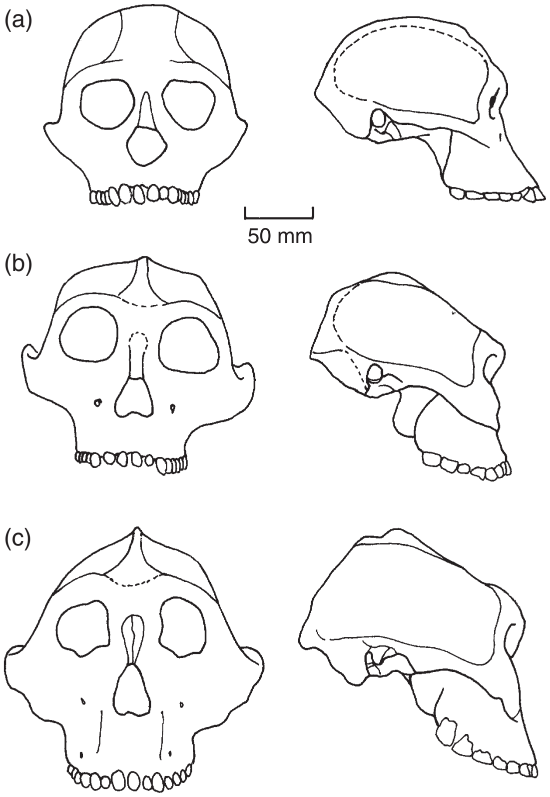


Figure 11.15 Skull proportions of the australopiths: skulls of (a) *Australopithecus africanus*, (b) *Paranthropus robustus* and (c) *P. boisei* in anterior (top) and lateral (bottom) views. Source: Adapted from Tobias (1967).

The robust australopiths, species of *Paranthropus*, have broad faces, huge molar and premolar teeth and a heavy sagittal crest over the top of the skull in presumed males (Figure 11.15(b)). These are all adaptations for powerful chewing of tough plant food. The sagittal crest supports this interpretation because it marks the upper limit of jaw muscles that were much larger than in *Au. africanus* or in *Homo*. The robust australopiths may have fed on tough roots and tubers, and the gracile *A. africanus* perhaps specialized on soft fruits and leaves in the wooded areas.

11.6.4 *Homo habilis* and *H. rudolfensis*: the first of our line?

A lower jaw and other skull and skeletal remains found in 1960 and 1963 in the Olduvai Gorge, Kenya by Louis Leakey and others, could be the oldest species of our own genus, *Homo*. This hominid had a large brain, in the range of 630–700 cm^3, and its hands had the manipulative ability to make tools, hence its name *Homo habilis* (literally 'handy man'). A more complete skull (Figure 11.16) found ten years later near Lake Turkana (formerly Lake Rudolf) in Kenya, by Richard Leakey, was also

BOX 11.4 *AUSTRALOPITHECUS SEDIBA*: TRANSITIONAL FOSSIL

A new australopithecine, *Au. sediba* (Berger *et al*., 2010; Berger, 2013), from the Malapa site in South Africa, dated at just under 2 Myr ago, appears to be in some way intermediate between other gracile australopithecines and *Homo*. The first fossil was found in August 2008, by Matthew Berger, son of Lee Berger, a palaeoanthropologist at the University of the Witwatersrand, Johannesburg, South Africa. Matthew had found a hominid clavicle, and when his father Lee turned over the rock, he reported, ‘sticking out of the back of the rock was a mandible with a tooth, a canine, sticking out. And I almost died.’

After several subsequent field seasons, Berger and his team extracted remains of six skeletons, an adult male, an adult female, a juvenile male, and three infants. These six early humans were all found together at the bottom of Malapa Cave, where they had apparently all fallen to their death. Because their skeletons lay where they had fallen, the scientists were able to extract a great deal of information about how they had lived. For example, there were tiny plant remains trapped in the dental plaque of some individuals, which pointed to specific parts of their diet.

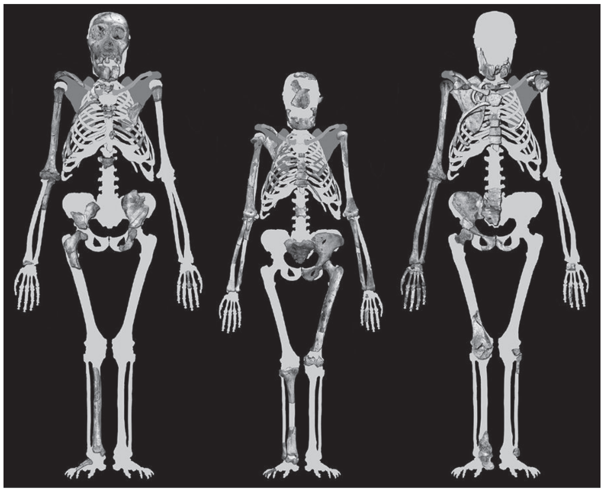
The *Au. sediba* remains show a mosaic of australopithecine and *Homo* characters (Berger, 2013). For example, the teeth are similar to *Au. africanus*, but the mandibular remains differ in size and shape from that species, and approach *Homo* in some aspects. The arm is more primitive, however, sharing with other australopiths adaptations for arboreal climbing and possibly suspension. The rib cage is rather ape-like in being narrow, quite unlike the broad cylindrical chest of humans, and the shoulders were narrow and high, giving something like the ‘shrugged’ shoulder appearance of standing African apes. On the other hand, the vertebrae of the lumbar region indicate a long and flexible back as in *Homo erectus,* and unlike *Au. africanus*.

The *Au. sediba* hindlimb is particularly odd. The detailed anatomy of the heel, foot, knee, hip, and back differ from all other hominins, but in combination they suggest bipedal walking, but perhaps with a mode that differs from other species of *Australopithecus* and *Homo*. In detail, perhaps *Au. sediba* walked with a fully extended leg and with an inverted foot during the swing phase of bipedal walking. It probably did not place the foot flat on the ground, as we do, but the lateral side of the foot touched the ground first, and then as the rest of the foot touched down, there was a substantial rotation around the joints of the foot. In particular, there was extreme transfer of the weight of the body in a medial (inwards) direction, termed hyperpronation.

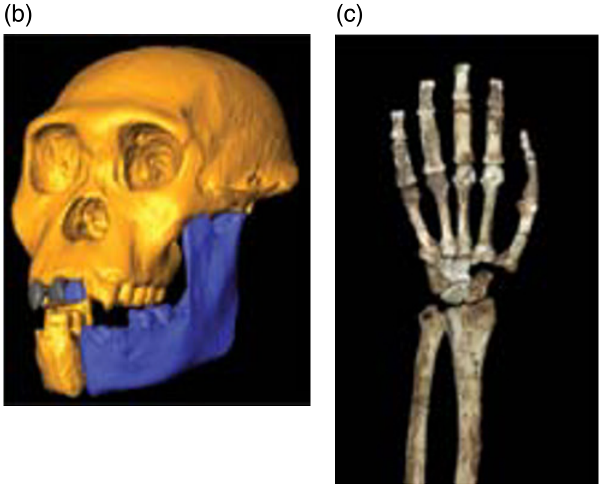
Au. sediba lived on the South African savannah of 2 Myr ago, side-by-side with several other early hominin species, feeding on grasses, as well as fruits and nuts. Its brain size of 420 cm^3 is at the high end of the range for *Au. africanus*, but much less than any *Homo*. Whether this species is truly intermediate between *Australopithecus* and *Homo* is debated, but the six skeletons have offered a remarkable opportunity for highly detailed studies of the anatomy of an early hominin, comparing males, females, and infants.

The detailed descriptions of *Australopithecus sediba* are available as a series of papers in the online edition of *Science*, at: http://www.sciencemag.org/site/extra/sediba/index.xhtml.

(a)



Skeleton and skull of *Australopithecus sediba*: (a) the juvenile male, Malapa hominin 1 (MH1) left, Lucy (AL 288-1) centre, and the adult female, Malapa hominin 2 (MH2) right;



(b) reconstruction of the MH1 skull; (c) hand and forearm. See Colour plate 11.4. Source: L.R. Berger, University of the Witwatersrand, Johannesburg, South Africa. Reproduced with permission. (a,c) Image created by P. Schmid, Anthropological Institute, University of Zurich, Switzerland. (b) Reconstruction by K. Carlson, University of the Witwatersrand, Johannesburg, South Africa.

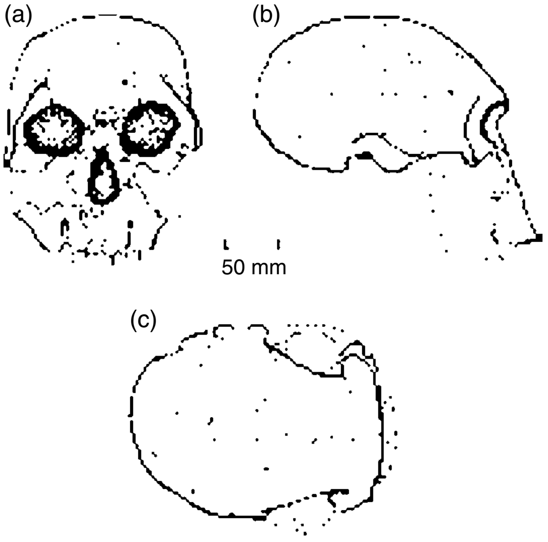


Figure 11.16 The skull of *Homo rudolfensis* in (a) anterior, (b) lateral and (c) dorsal views. Source: Adapted from Day *et al.* (1974).

assigned to *H. habilis*. This specimen showed a brain size of about 700 cm^3.

The identity of these early *Homo* specimens from Olduvai and Lake Turkana has been much debated, whether there were two or more *Homo* species living side-by-side in East Africa, *H. habilis* at Olduvai and Lake Turkana specimens, and *H. rudolfensis* also at Lake Turkana specimens (Leakey *et al.*, 2012), or whether there is serious over-inflation of species names (White, 2013). *H. habilis* and *H. rudolfensis* (Figure 11.16) are distinguished on the basis of a number of characters. *H. rudolfensis* has a larger mean brain size, but appears to be primitive in other skull features (smaller 'eyebrow ridge', palate large). Many palaeoanthropologists question whether these two species are really members of the genus *Homo*, and they emphasize their many australopith characters (e.g. Wood and Collard, 1999; Tattersall and Schwartz, 2009).

The remains of *H. habilis* and *H. rudolfensis* are dated as 2.4–1.5 Myr old and they have been found in association with the remains of various species of australopith. This conjures up the striking notion of four or five different human species living side by side and presumably interacting in various ways.

11.7 THE PAST TWO MILLION YEARS OF HUMAN EVOLUTION

Human beings spread out of eastern and southern Africa perhaps as long ago as 1.9 Myr, seemingly for the first time. Until then, all known phases of evolution of the australopiths and *Homo* seem to have taken place in the part of Africa between Ethiopia and South Africa.

11.7.1 *Homo erectus* – the first widespread human

A new hominin species arose in Africa about 1.9 Myr ago that showed advances over *H. habilis*. The best specimen, and one of the most complete fossil hominid skeletons yet found (Figure 11.17(a)), was collected in 1984 by Richard Leakey and colleagues on the west side of Lake Turkana, Kenya. The pelvic shape shows that the individual is a male and his teeth show that he was about 12 years old when he died. He stood about 1.6 m tall and had a brain size of 830 cm^3. The skull (Figure 11.17(b)) is more primitive than *H. sapiens* because it still has large eyebrow ridges and a heavy jaw with no clear chin. The skeleton seems largely modern and fully bipedal in adaptations.

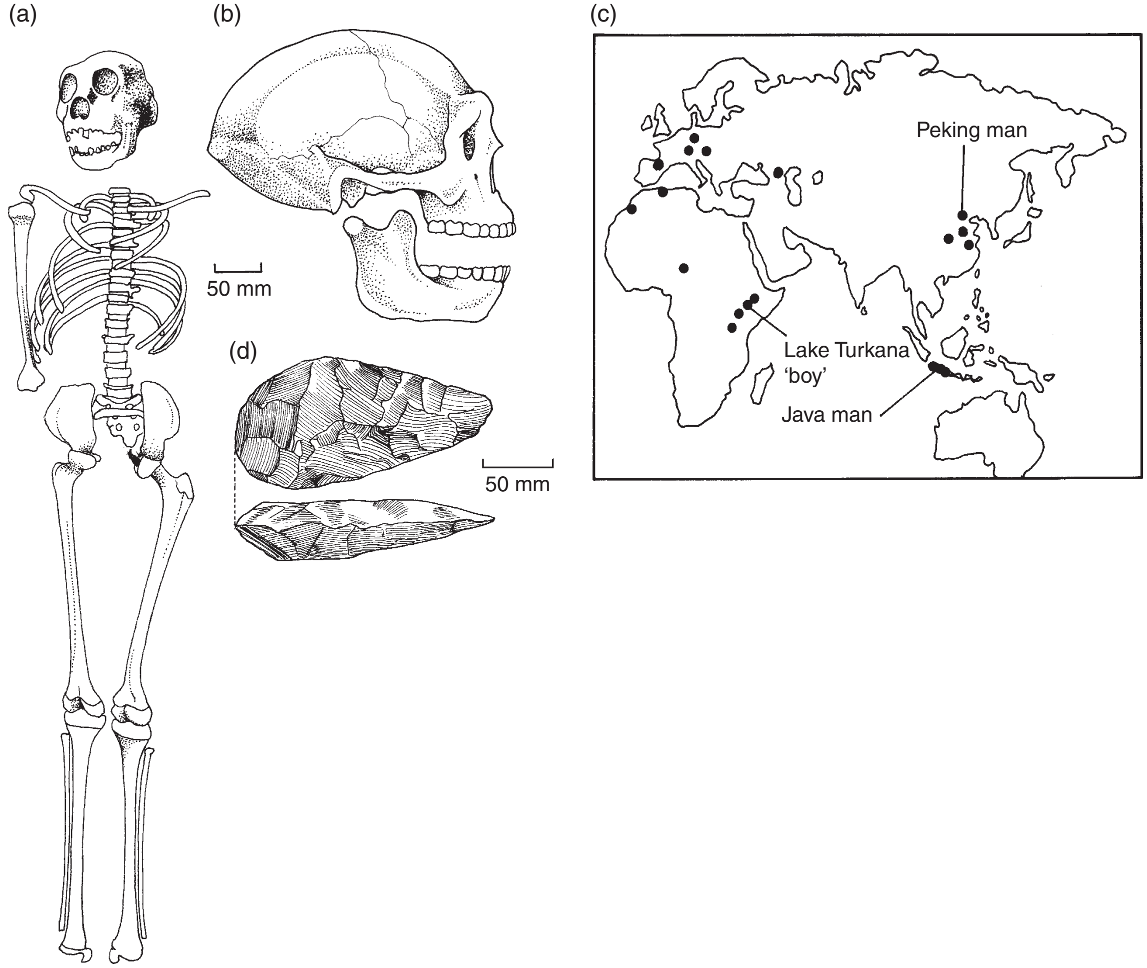


Figure 11.17 Finds of *Homo ergaster* (a) and *H. erectus* (b): (a) the skeleton of a youth from Lake Turkana, Kenya; (b) skull of Peking man; (c) map showing the distribution of finds of *H. erectus* and *H. ergaster*; (d) Acheulean hand axe. Source: (a) Adapted from a photograph. (b) Adapted from Black (1934). (c) Adapted from Delson (1985). (d) Adapted from Savage and Long (1986).

This remarkable early find from Africa was assigned to *Homo erectus*, but it might more appropriately be retained in a separate primitive species, *H. ergaster* (Klein, 2009; Wood, 2012), and the name *H. erectus* is used only for younger and more specialized material. This includes fossils from eastern and southern Africa dating from 1.6 to 0.6 Myr ago, as well as specimens from other parts of the world.

But when did *Homo* first leave Africa? Until recently, the oldest fossils of *H. erectus* from outside Africa were dated at about 1.25 Myr ago, and dates from 1.25 to 0.5 Myr ago were assigned to numerous localities in North Africa, Asia and Europe (Figure 11.17(c)). Then, discoveries from Dmanisi in Georgia, in the Caucasus area east of Turkey, overturned this idea: they were dated at 1.8–1.7 Myr ago. The remains include partial skeletons of females, males, and juveniles, with males 1.5 m tall and with a brain volume of 610–775 cm^3. They were initially assigned to the new species *Homo georgicus* (Vekua *et al.*, 2002), but were later recognized as a subspecies, or even local variant of *Homo erectus* (Lordkipanidze *et al.*, 2005; Tattersall and Schwartz, 2009; Hublin, 2014).

Homo erectus evidently spread across Europe and Asia at about this time. Some Chinese materials are dated at 1.9 Myr, and they comprise isolated teeth and jaw fragments from cave deposits. Re-dating of the famous specimens of Java man have also yielded more ancient dates, in the range 1.6–1.8 Myr ago. If these ages are confirmed, it is evident that *H. erectus* set out from Africa much nearer 2 Myr ago, than 1 Myr ago. Further, the Java *H. erectus* may have survived until very recently, perhaps 50,000 years ago, hence probably overlapping with the first *Homo sapiens* to reach the area (Baba *et al.*, 2003).

One of the richest sites for *H. erectus* is the Zhoukoudian Cave near Beijing in China, the source of over 40 individuals of 'Peking Man' (Figure 11.17(b)). They were found in cave deposits dating from 0.8 to 0.2 Myr ago and seem to show an increase in mean brain size from 900 to 1100 cm^3 during that time. The cave was thought to have provided evidence for a number of major cultural advances, including the use of fire, but the evidence has since been shown to be unreliable. Older evidence for the use of fire by *H. erectus* is reported from a cave site in South Africa dated as 1.5–1.0 Myr ago.

Homo erectus sites elsewhere show that these peoples manufactured advanced tools and that they foraged and perhaps hunted in a cooperative way. *Homo erectus* in East Africa perhaps made the Acheulean tools, which date from 1.5 Myr ago. These show significant control in their execution with continuous cutting edges all round (Figure 11.17(d)). The older Oldowan tools of East Africa, dated from 2.6 to 1.5 Myr ago and generally ascribed to *H. habilis*, *H. ergaster* and *H. rudolfensis*, are simple and rough, consisting of rounded pebbles with usually only one cutting edge. The Oldowan and Acheulean industries were often classed together as early Palaeolithic ('Old Stone Age').

11.7.2 Middle Pleistocene hominins

Palaeoanthropologists have long been puzzled over a series of large-brained humans that lived in the Middle Pleistocene of Africa and Europe, side by side with *Homo erectus*. These forms differ substantially from *H. erectus* and must be assigned to the roots of modern *H. sapiens*, but currently there is little agreement about what to call them or their placement in the phylogeny (Rightmire, 2013).

The first of these to be named was *Homo heidelbergensis*, for a jawbone found in Germany in 1907. Since then, further similar, advanced human remains have been recovered from the middle Pleistocene of Africa and Europe in rocks dated from 0.6 to 0.2 Myr ago. English remains consist of a tibia and some teeth, associated with Acheulean tools. These perhaps indicate a unique radiation of humans in the mid-Pleistocene of Europe that were more derived than *H. erectus*, but ancestral to the Neanderthals. The African specimens, skulls and postcranial remains from Ethiopia, Zambia and South Africa, used to be termed 'archaic *Homo sapiens*'. They date from 0.6 to 0.4 Myr ago. These forms, showing apparently intermediate characters between *H. erectus* and *H. sapiens*, may also belong to *H. heidelbergensis*.

Recent finds from Spain have been interpreted in different ways. The famous Atapuerca sites have yielded jaws and partial skulls from an ancient cave dated as 0.8–1.2 Myr old (Blain *et al.*, 2013). Tools associated with the Spanish fossils indicate a pre-Acheulean industry. These peoples have been named *Homo antecessor*, members of a species that is claimed to include the common ancestors of Neanderthals and modern *Homo sapiens*. However, it is still debated which of the Spanish materials belong to *H. heidelbergensis* or *H. antecessor*, and whether some of the younger (0.4–0.6 Myr) specimens might even represent early populations of *H. neanderthalensis* (Tattersall and Schwartz, 2009; Stringer, 2012b).

11.7.3 The Neanderthal peoples

The first Neanderthal was reported from Germany in 1856 (see Section 11.5.3) and originally regarded as a dim-witted slouching brute, but actually had a larger brain capacity (mean 1450 cm^3) than many modern humans (mean 1360 cm^3). The heavy eyebrow ridges, massive jaws and large teeth compared with modern *H. sapiens* (Figure 11.18(a, b)) could mean little more than that Neanderthals were merely a coarsely-built race of *Homo sapiens*. Indeed, it has been remarked that if a Neanderthal man were shaved and dressed in modern clothes, he would pass unnoticed on a busy city street (Figure 11.18(c))! However, the morphological distinctiveness of Neanderthals suggests they are a distinct

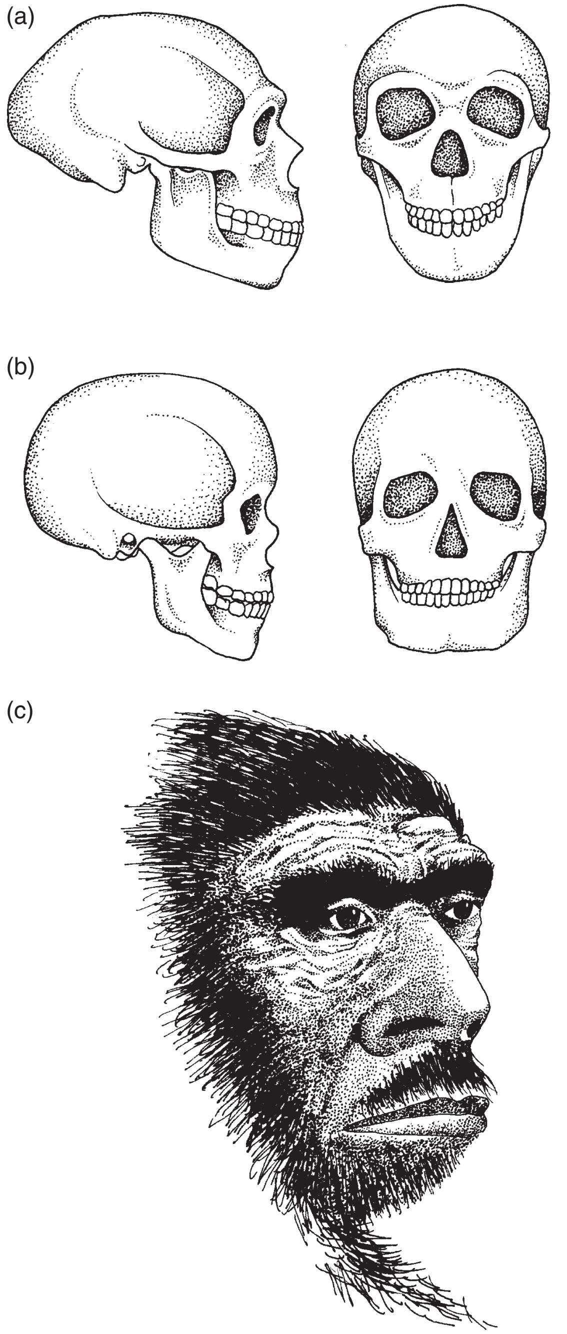


Figure 11.18 Comparing *Homo neanderthalensis* and *Homo sapiens*: skulls of (a) Neanderthal and (b) modern humans, in lateral and anterior views; (c) restoration of the head of a Neanderthal man. Source: (a,b) Adapted from Lewin (2005). (c) Adapted from Savage and Long (1986).

species (Wood and Collard, 1999; Tattersall and Schwartz, 2009; Stringer, 2012b; Wood, 2012), and this was confirmed by an early study of Neanderthal DNA (Krings *et al*., 1997), which showed that Neanderthals separated from modern humans some 0.6 Myr ago. Since 1997, there have been remarkable advances in understanding of the Neanderthal genome (see Box 11.5), and these help resolve the question of how Neanderthals relate to modern humans, and how many Neanderthals lived at any time.

Neanderthals have been found in Europe and Asia as far east as Uzbekistan, and in the Middle East, in sites dated as 200,000–27,000 years old (Tattersall and Schwartz, 2009). The most abundant remains come from France and central Europe and, in their most extreme form, they are associated with phases of the later Ice Ages that covered much of the area. A robust compact body is better able to resist the cold than our generally more slender form.

Neanderthals were culturally advanced in many ways (Finlayson, 2010; Gamble, 2011; Monnier, 2012; Papagianni and Morse, 2013). For example, they made a variety of tools and weapons from wood, bone and stone, the Mousterian (Middle Stone Age, Middle Palaeolithic) culture of Europe. These include delicate spearheads, hand axes, scrapers for removing fat from animal skins and pointed tools for making holes in skins and for engraving designs on bone and stone, a total of 60 or so tool types. Neanderthals also made clothes from animal skins, used fire extensively, lived in caves or bone and skin shelters and perhaps even had ritual. At Le Moustier in France, a teenage boy was buried with a pile of flints for a pillow and a well-made axe beside his hand. Ox bones were nearby, which suggests that he was buried with joints of meat as food for his journey to another world. It is hotly debated whether Neanderthals could have formed words or made language-like sounds.

The Neanderthals disappeared about 27,000 years ago; their last refuge may have been in northern Spain and southwest

BOX 11.5 NEANDERTHAL AND DENISOVAN GENOMICS

At one time it would have seemed an impossible dream, to sequence the entire genome of a fossil species. And yet, since the initial work in 1997, knowledge of the Neanderthal genome has grown exponentially (Hawks, 2013). In that first study, Krings *et al*. (1997) sequenced a 360-base-pair (bp) section of the mitochondrial DNA (mtDNA) of the original 1856 Neanderthal specimen. Thirteen years later, Green *et al*. (2010) reported 5.5 billion bp of nuclear DNA sequence data from six Neanderthals, and partial or complete mtDNA sequences from more than 20 other specimens.

Mitochondrial DNA occurs in the mitochondria of cells, and hence mtDNA is passed down only in the female line. Nuclear DNA (nDNA) is transmitted through the egg and the sperm to any offpsring, but sperm do not transfer mitochondria. Initial studies focused on sequencing mtDNA because the scale is more manageable (human mtDNA contains 16,600 bp and codes for 37 genes, whereas human nDNA comprises 3 billion bp and codes for 20,000 genes) and rates of change are slower, so the analysis is not confused by numerous small population-scale mutations. However, nDNA is the stuff of evolution, and newer work has reported Neanderthal nDNA, the genome of this extinct species (Green *et al*., 2006, 2010; Noonan *et al*., 2006).

Sequencing ancient DNA has always been technically very difficult. In some early efforts, analysts confidently announced DNA from Mesozoic insects, plants, and even dinosaurs. However, all those early studies from the 1990s were flawed by massive contamination. Even a microscopic droplet of sweat, a sneeze, a particle of a modern organism can be multiplied by the polymerase chain reaction (PCR) equipment and entirely invalidate the analysis. There are only a small number of reliable ancient DNA laboratories in the world, and these must carry out no PCR work on modern genomes. The labs are sterilized every night. In fact, ancient DNA can be recovered from specimens only up to a few hundred thousand years, not millions of years, because the DNA rapidly breaks into tiny fragments (Dabney *et al*., 2014).

The new genomic work shows that Neanderthal and modern human genomes are about 0.15% different from each other, and so about 99.85% genetically similar (Green *et al*., 2010; Sankararaman *et al*., 2014). To put this in context, any randomly selected pair of modern human genomes are about 0.1% different, whereas humans and chimpanzees are about 2% different. Among living humans, non-Africans are more similar than Africans to Neanderthals, but overall, the Neanderthal genome is always more different from modern human genomes than the differences between genomes of any modern humans. This all suggests that Neanderthals share some common ancestry with Europeans and Asians, but less with Africans.

Comparison of genomes of contemporary humans can suggest the actual population sizes. Whereas there are 7 billion humans today, all *Homo sapiens*, the genomic variation of Neanderthals suggests population sizes as low as a few hundred corresponding to the Mousterian culture in France, with as few as 10,000 Neanderthals across Europe for most of their existence, and at most 40,000 in the late Palaeolithic across Europe and western Asia (Hawks, 2013).

Ancient human genomes include another, unusual, example, from Denisova Cave in the Altai Mountains in central Siberia, where samples were taken from teeth and isolated finger bones of a juvenile female who lived 41,000 years ago. The genome differs from the Neanderthal and modern human sufficiently to provide evidence for a whole population of 'Denisovans', which differ as much genomically from modern humans as do the Neanderthals (Krause *et al*., 2010; Reich *et al*., 2010; Hawks, 2013). The Denisovans show closest relationship to modern indigenous peoples of Australia and New Guinea. These studies have highlighted that genomic data can reveal whole human populations – even species – represented by minimal skeletal material. The Denisovans are fast becoming as much talked about as the Neanderthals, and yet they have no face.

France. It is not clear whether they were seen off by the loss of cold-weather habitat as the ice sheets retreated, or whether they were slaughtered by more modern *H. sapiens* of our own type (Klein, 2003). Although the initial molecular evidence (Krings *et al.*, 1997) suggested that Neanderthals did not interbreed with the interlopers, more recent studies (Green *et al.*, 2010; Pääbo, 2014) have shown that modern European and Asian DNA contains 1–4% Neanderthal genes. Indeed, some of those Neanderthal genes are associated with keratin formation, and so may have survived in Europeans and Asians in cold climates as a means of maintaining hair growth (Sankararaman *et al.*, 2014). This suggests that before Neanderthals became extinct, some, at least, interbred with modern humans.

11.7.4 Modern *Homo sapiens*

When did our own species originate? Undisputed modern *Homo sapiens* fossils were known from several sites in Africa and Israel dated as 195,000–100,000 years old (Figure 11.19). The earliest possible example of *H. sapiens* is the partial cranium Omo 1 from southern Ethiopia (Figure 11.19(d)), dated at 195,000 years ago, although it lacks critical characters of the brow and chin that distinguish *H. sapiens* from other hominin species (Tattersall and Schwartz, 2009). Slightly younger is the 160,000-year-old Herto skull, also from Ethiopia, which shows some very modern features (White *et al.*, 2003), but others are uncertain (Tattersall and Schwartz, 2009). Other skulls from

Figure 11.19 Diverse later Pleistocene Homo crania, in anterior view: (a) Guattari 1, Monte Circeo, Italy; (b) Skull 5, Simo de los Huesos, Atapuerca, Spain; (c) Cro-Magnon 1, Les Eyzies-de-Tayac, France; (d) Cast of Omo 1, Omo Kibish, Ethiopia. See Colour plate 11.5. Source: Tattersall and Schwartz (2009). Reproduced with permission.

Jebel Qafzeh in Israel, include the definitively *H. sapiens* Qafzeh 9 skeleton, dated at 93,000 years. In all such cases, it can be hard to distinguish primate species from limited remains of the skull and skeleton.

Modern *H. sapiens* spread into Europe from 40,000 to 30,000 years ago. The early European forms, often known as the Cro-Magnon peoples (Figure 11.19(c)), brought their advanced Upper Palaeolithic tools and filled the caves of France and northern Spain with paintings and carved objects. They must have seen Neanderthals and much has been made of such possible encounters. A child's skeleton from Lagar Velho in Portugal has been put forward as evidence for hybridization, and DNA evidence (see Box 11.5) suggests that modern Europeans and Asians share some genetic heritage at least with Neanderthals, showing evidence of interbreeding.

Modern *H. sapiens* then spread truly worldwide from about 40,000 years ago (Figure 11.20), reaching Russia and travelling across Asia to the southeast Asian islands and Australia (Diamond and Bellwood, 2003). How these relate to the unique, dwarfed Flores hominins (see Box 11.6) is still much debated. The date of arrival of modern humans in Australia was often reckoned to be 40,000–30,000 years ago, but the Malakunanja

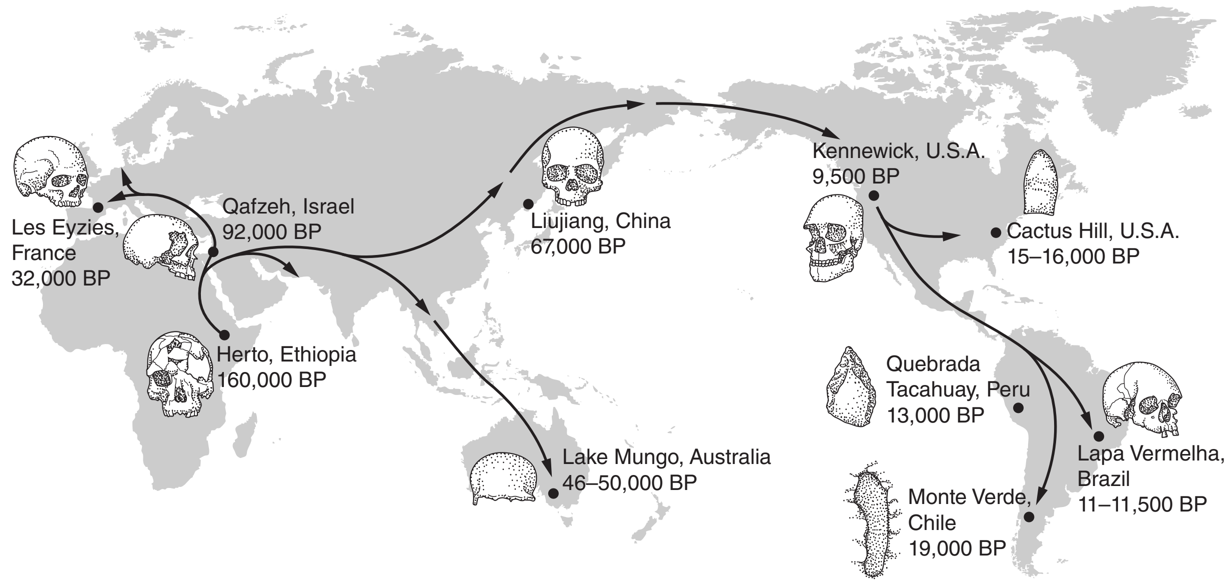


Figure 11.20 The spread of modern *Homo sapiens* out of Africa in the past 100,000 years. Key finds and oldest dates are shown. Source: Adapted from various sources.

BOX 11.6 THE FLORES HOBBIT

One of the most sensational human fossil finds has been Flores man, or the 'hobbit', a population of tiny modern humans from Flores Island, in Indonesia. The first fossils were collected in 2003 by a joint Australian-Indonesian team (Brown *et al*., 2004), and they have proved controversial ever since: are these the remains of a tiny, but distinct human species that lived alongside *Homo sapiens*, or are they a local variant or even diseased population of *Homo sapiens*?

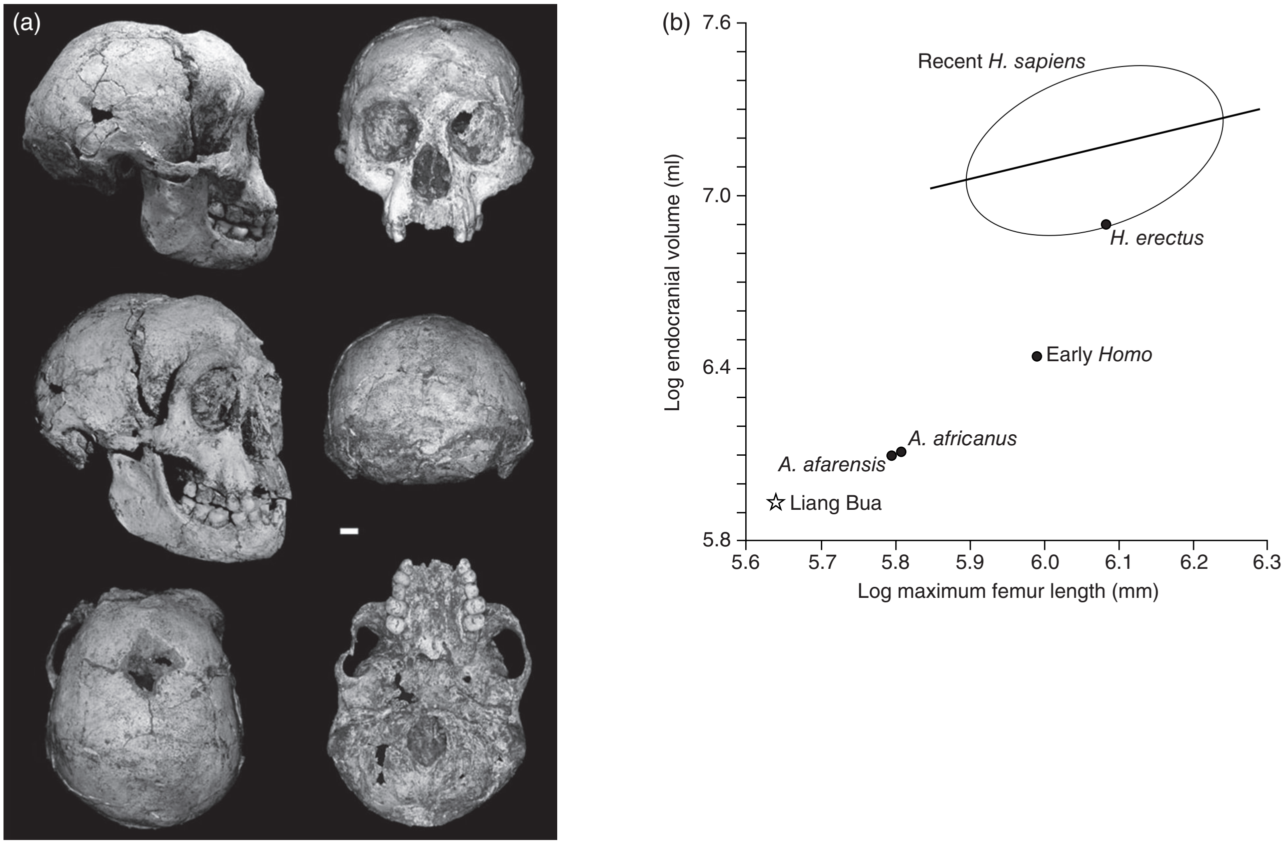
The fossils were found deep below the floor of the Ling Bua cave, comprising remains of eight skeletons, dating from 38,000 to 13,000 years ago. Adult individuals measured 0.9-1.1 m tall, just over half the height of *Homo sapiens* individuals. The skeletons were found associated with sophisticated (but small) stone tools, as well as remains of the elephant *Stegodon*, as well as giant rats, Komodo monitors, and other large extinct lizard species. Other localities show that *Homo sapiens* reached Indonesia 45,000 years ago, so our own species must have encountered their smaller, forest-dwelling relatives for many thousands of years.

In the original description, the hobbit was named *Homo floresiensis*, a definite new species, distinguished from *H. sapiens* by the smaller size, smaller brain capacity, aspects of the teeth, absence of a chin, and differences in the head of the humerus. The body size range of 0.9–1.1 m is definitively less than even the smallest of modern races of *Homo sapiens* (1.4–1.5 m), and body mass estimates suggest an even greater distinction, with *H. floresiensis* estimated at 25 kg adult weight, much smaller than *H. sapiens* (60–80 kg) and even than *H. erectus* (50–60 kg). The brain size of *H. floresiensis* was remarkably small, at 426 cm^3, much less than the modern human range (mean, 1360 cm^3), placing the hobbit in the range of chimpanzees and australopiths, and well below the measure in any other example of the genus *Homo*. Proportional to body size, the relative brain size is just human, but primitive, lying between that of *H. erectus* and the great apes.

Since 2004, there have been scandals about damage to the original specimens and about difficulties of access (once described, fossils should be publicly available for all researchers). More significant though has been the debate about whether the Flores population really represents a distinct species or not. There have been claims that these were in some way an unusual human population, where all individuals were microcephalics (a condition in modern humans where the head size is reduced), or suffered from Laron's syndrome (a genetic disorder that reduces head size), or were endemic cretins perhaps suffering from hypothyroidism caused by a lack of iodine in their diet. All such claims of genetic disorders, diseases, and disordered growth seem unlikely in that all individuals share the morphological features, but also the specific osteological indications of the different diseases have been refuted (Brown, 2012).

The Flores humans have been the subject of lively debate (Aiello, 2010; Montgomery, 2013), and these debates are likely to continue for a while. The stakes are high; this could be the only human species to have survived until relatively recently side-by-side with our own species.

Follow the unfolding story of the discovery and subsequent disputes about *Homo floresiensis* on the *Nature* news pages, here: http://www.nature.com/news/specials/flores/index.html.



Skull and relative size of *Homo floresiensis*: (a) The LB1 skull and mandible, the first-found specimen from an adult female, in lateral and three-quarter views, and the cranium in dorsal, anterior, posterior, and ventral views; (b) Comparison of the relative body size (x-axis) and brain volume (y-axis) for the Flores cranium ('Ling Bua') and various hominins, including modern humans. Source: Brown *et al*. (2004). Reproduced with permission from Nature Publishing Group.

site, in the northwest, source of stone tools and evidence of pigment use, dates back to 60,000 years ago (Bird *et al*., 2013).

The timing of the peopling of North America is highly controversial (Meltzer, 2009). Ice sheets retreated from the area of Beringia (Siberia and Alaska) and there was an ice-free land bridge from Siberia to Alaska from 18,000 to 10,200 years ago. Hundreds of North American archaeological sites with tools of the Clovis industry date from 11,500 years ago, but a human occupation site at Monte Verde in southern Chile dates back to 14,600 years ago, suggesting rapid migration down the length of the Americas long before the makers of the Clovis points. Human faeces from the Paisley Caves, Oregon date to 14,200–14,000 years ago, and other human remains of this age have now been reported (Curry, 2012). Ancient DNA evidence also confirms these dates, showing that humans entered North America after the end of the last glacial maximum, whether they island hopped from Asia to North America, or used boats to work down the coast.

The palaeontological and archaeological evidence then suggests that modern *H. sapiens* has populated the world, from a birthplace in Africa or the Middle East, in the last 60,000 years or so. This would imply that the modern human races have differentiated in this very short time. Confirming evidence has come from molecular studies, which find that there are only minute inter-racial genetic differences. Several studies of human DNA have also suggested an African origin for all human races 200,000–100,000 years ago. In the original study, Cann *et al.* (1987) analysed the mitochondrial DNA (mtDNA) of 147 people from different parts of the world. They found that there was only 0.3–0.4% variation among the mtDNAs of these individuals, regardless of their racial origin, and this low level of variation calibrates to the figure of 200,000 years for the origin of modern *Homo sapiens*. Such studies of mtDNA necessarily concern only the female line of descent, which is why the common ancestor of all modern humans is sometimes called, rather picturesquely, African Eve.

Models for modern human origins have been in constant flux, not least because of the paucity of data. At one time, for example, the modern races were traced back to different geographic variants of *Homo erectus*, so positing an independent history of 1 Myr for modern Africans, Europeans, and Asiatic peoples. However, the combination of fossil, genomic, and cultural evidence has convinced most that modern humans diverged some 200,000 years ago from an African ancestral population, and began their long trek round the globe about 100,000 years ago – termed the 'single, recent origin' or 'Out of Africa' model (Stringer and Andrews, 1988). There is still much uncertainty about the various ancestral *Homo sapiens* fossils from Africa and the Middle East, about the role of interbreeding with Neanderthals and the mysterious Denisovans (see Box 11.5), and the timing of movements of human populations round the world, and how these geographically isolated human populations relate to modern genomic 'clans' (Stewart and Stringer, 2012).

The record of human evolution seems to show an ever-quickening pace of change. Major innovations have occurred ever more rapidly: bipedalism (10–5 Myr ago), enlarged brain (3–2 Myr ago), stone tools (2.6 Myr ago), wide geographical distribution (2–1.5 Myr ago), fire (1.5 Myr ago), art (35,000 years ago), agriculture and the beginning of global population increase (10,000 years ago). The rate of population increase was about 0.1% per annum at that time, rising to 0.3% per annum in the eighteenth century and about 2.0% per annum today. In other words, the total global human population will more than double during the lifetime of individuals born today. In numerical terms at least, *Homo sapiens* has been a spectacularly successful species!

11.8 FURTHER READING

Fuller accounts of modern primate biology and anatomy include Ankel-Simons (2007), Campbell *et al.* (2010), Setchell and Curtis (2011), and Fleagle (2013), and modern primates are surveyed by Redmond (2010) and Petter (2013). Hartwig (2008) gives a detailed survey of fossil primates. Basic texts on human evolution include Lewin and Foley (2003), Lewin (2005), Wood (2005), Klein (2009), Roberts (2011), Stringer and Andrews (2011), Boyd and Silk (2012), Conroy and Pontzer (2012), Stringer (2012a), and Tattersall (2013), and Gibbons (2007) and Reader (2011) tell the often highly colourful stories of the palaeoanthropologists in search of our ancestors, and glory. Two excellent encyclopedias of human evolution, with contributions by the world's leading palaeoanthropologists, are Delson *et al.* (2002) and Begun (2013). Reed *et al.* (2013) explore aspects of the palaeobiology of *Australopithecus*, and an array of recent books deals with Neanderthals (e.g. Finlayson, 2010; Papagianni and Morse, 2013; Pääbo, 2014) and the origins of modern human races (Oppenheimer, 2004; Stringer, 2012a). The definitive account of all hominid fossils is Schwartz *et al.* (2005).

An excellent introduction to everything concerning modern primates is at: http://www.alltheworldsprimates.org/Home.aspx. There are many portals that provide reports and summary diagrams about human evolution, such as: http://www.bbc.co.uk/sn/prehistoric_life/human/human_evolution/, http://www.becominghuman.org/, and http://www.newscientist.com/topic/human-evolution. Some museum offerings on human evolution include: http://www.nhm.ac.uk/nature-online/life/human-origins/ and http://humanorigins.si.edu/resources/intro-human-evolution. See a video about the investigation of the early hominin *Ardipithecus* here: http://www.sciencemag.org/content/326/5949/60.2.full. Digital images of hominid fossils may be accessed at: http://paleo.eva.mpg.de/, http://peabody2.ad.fas.harvard.edu/skhul/, http://www.virtual-anthropology.com/3d_data/3d-archive/3d_data/free_data, and https://www.nespos.org/display/openspace/Home.

QUESTIONS FOR FUTURE RESEARCH

1 Are plesiadapiforms primates or relatives of dermopterans or scandentians?
2 How rapidly did Primates diverge in the Palaeocene and early Eocene?
3 What were the relationships and ecological roles of the diverse Eocene primates, including the adapiforms and omomyids?
4 When did lemurs reach Madagascar, and how did these early primates diversify their ecological roles to take over modes of life not normally occupied by primates?
5 What is the early history of anthropoids, including the origins of Old World and New World monkeys?
6 How and when did the platyrrhines reach South America? Was it a single migration, or more, and when did modern forms diversify?
7 Why were apes so diverse in the Miocene, how did they divide up their different ecological roles, and how do they relate to modern hominoids?
8 How did pongids evolve, especially the exctinct sivapithecines and the enigmatic *Gigantopithecus*?
9 Were the major steps in hominid evolution in Africa driven by changes in climate and vegetation?
10 Where do Neanderthals fit into the pattern of evolution of modern humans?
11 How and when did modern human populations reach different parts of the world, and how did these modern forms interact with Neanderthals, Flores persons, and other hominin species they encountered?

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