

## Review

# Human evolution: taxonomy and paleobiology

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### ABSTRACT

This review begins by setting out the context and the scope of human evolution. Several classes of evidence, morphological, molecular, and genetic, support a particularly close relationship between modern humans and the species within the genus *Pan*, the chimpanzee. Thus human evolution is the study of the lineage, or clade, comprising species more closely related to modern humans than to chimpanzees. Its stem species is the so-called ‘common hominin ancestor’, and its only extant member is *Homo sapiens*. This clade contains all the species more closely-related to modern humans than to any other living primate. Until recently, these species were all subsumed into a family, Hominidae, but this group is now more usually recognised as a tribe, the Hominini. The rest of the review sets out the formal nomenclature, history of discovery, and information about the characteristic morphology, and its behavioural implications, of the species presently included in the human clade. The taxa are considered within their assigned genera, beginning with the most primitive and finishing with *Homo*. Within genera, species are presented in order of geological age. The entries conclude with a list of the more important items of fossil evidence, and a summary of relevant taxonomic issues.

*Key words:* Hominins; cladistics; *Homo*.

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### INTRODUCTION

#### *Human evolution: context and scope*

Anatomical, molecular and genetic evidence suggests that the animal most closely related to modern humans is the chimpanzee, *Pan*, with *Gorilla* being more distantly related. Both of these ape genera are decidedly nonhuman in their appearance and behaviour, and until recently their anatomical resemblances had persuaded the majority of commentators to assume that *Pan* and *Gorilla* must be more closely-related to each other, and then to *Pongo*, the orangutan, than to modern humans, but a recent overview of traditional morphology narrowly links *Homo* and *Pan* (Shoshani et al. 1996). Prior to this, analyses of proteins (Zuckerandl et al. 1960; Goodman, 1962, 1963; Zuckerandl, 1963) and, more recently, of both nuclear and mitochondrial DNA of the great apes (Ruvolo, 1997), have shown that the similarities between *Homo sapiens* and *Pan* are very

close. An increasing number of researchers interpret this evidence as supporting the hypothesis that *Homo* and *Pan* share a common ancestry to the exclusion of *Gorilla* (Ruvolo, 1995). However, other scientists continue to maintain that the relationships between *Homo*, *Pan* and *Gorilla* are so close that their details have not yet been satisfactorily resolved, and suggest that the relationship between the 3 taxa is best treated as an unresolved trichotomy (Green & Djian, 1995; Marks, 1995; Rogers & Commuzzie, 1995; Deinard et al. 1998).

Is it possible to determine how long ago a separate human lineage became established? Differences in the amino acid sequences of proteins, and in the base sequences of DNA, can be used to provide an estimate of how long lineages have been independent (Kimura, 1968, 1977). Most naturally-occurring mutations are neutral, conveying no discernible reproductive advantage on the animal. If one makes the reasonable assumption that these neutral mutations have been

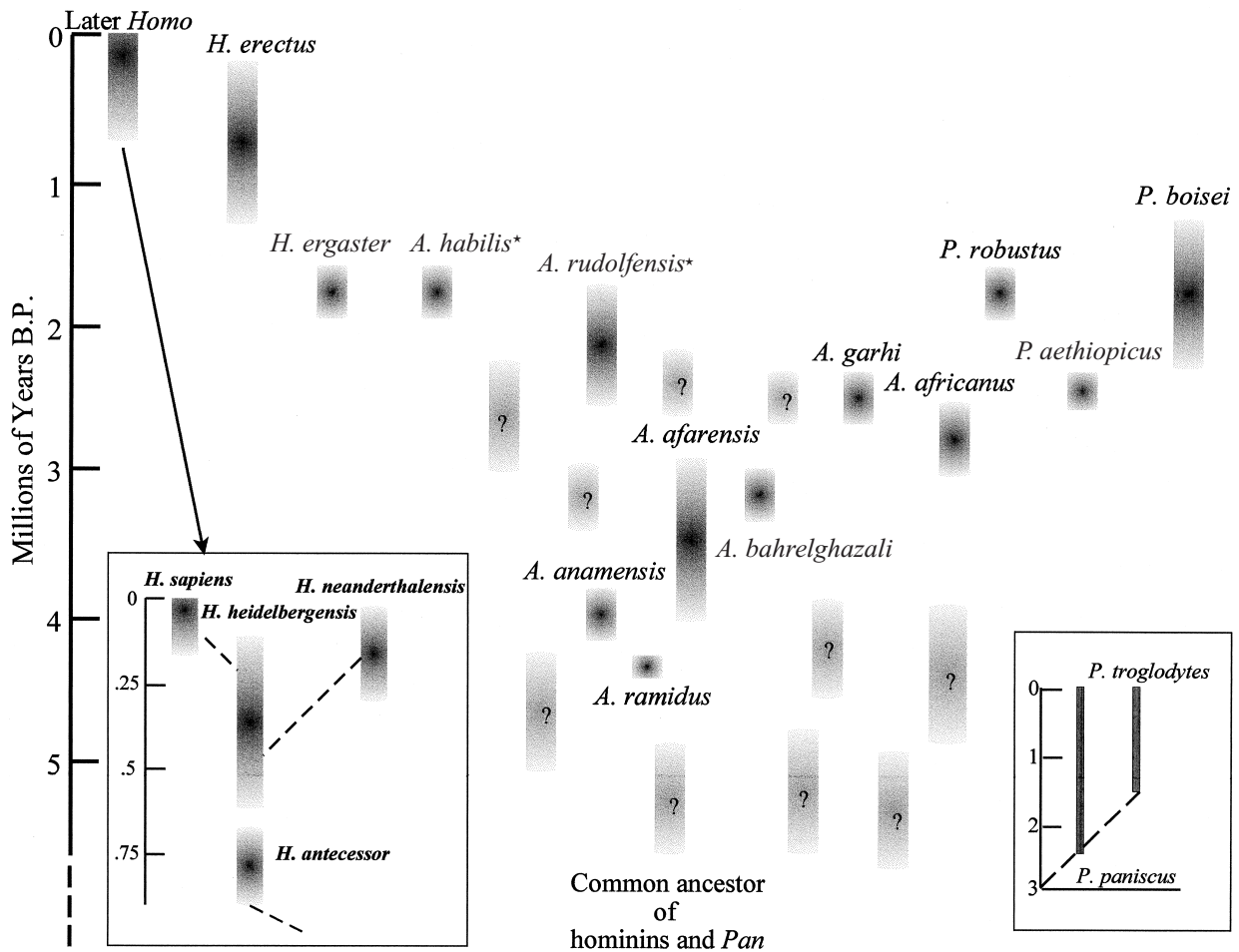


Fig. 1. Hominin phylogram. Species considered to be part of the tribe Hominini, or hominins, as opposed to chimpanzee ancestors, or panins. The horizontal axis spreads the species out according to the relative size of their chewing teeth and brain size. Taxa with large molar and premolar crowns are to the right, and those with smaller postcanine teeth are to the left. Less speciose interpretations of the hominin fossil record do not recognise the taxa that are in bold type. The hypothetical taxa (?) are a reminder that in the relatively unexplored period between 6 and 2 myr ago the number of taxa will probably increase. Although the 2 taxa marked with asterisks are/have conventionally been assigned to *Homo*, it is likely that they are more closely related to *Australopithecus* species.

occurring at the same rate in closely-related lineages, then the degree of molecular difference can be used as a 'clock' to estimate the time elapsed since any 2 lineages separated (Sarich & Wilson, 1967). When this is done for the molecular differences between modern humans and the living African apes, it has been estimated that the human lineage separated from the rest of the hominoids between 5 and 8 myr ago (Ruvolo, 1997).

A traditional classification, together with one that incorporates the taxonomic implications of the molecular evidence, is given in Table 1. The new classification means that the vernacular terms we have been using to describe the human clade are no longer applicable. Thus the clade can no longer be described as containing 'hominids', for the family Hominidae has become more inclusive, and now refers to the common ancestor of the living African apes (i.e. *Homo*, *Pan*, and *Gorilla*) and all of its descendants.

The appropriate vernacular term for a member of the human clade is now 'hominin', for this is the way to refer to members of the tribe Hominini, and its 2 component subtribes, the Australopithecina and the Hominina. Thus, 'hominid evolution' becomes 'hominin evolution'. The vernacular 'hominine' has also taken on a more inclusive meaning, for the subfamily Homininae now includes both 'panins', the vernacular term for members of the tribe Panini containing the chimpanzees, and 'hominins', the vernacular for species in the tribe Hominini. Consequently, the term 'australopithecine', the vernacular for Australopithecinae, the subfamily established by Gregory & Hellman (1939) for the fossils we now allocate to *Ardipithecus*, *Australopithecus* and *Paranthropus*, no longer applies. We use 'australopitths' to refer to members of the subtribe Australopithecina (Table 1a).

Although the molecular data provide powerful

Table 1. *a. A taxonomy of the living higher primates that recognises the close genetic links between Pan and Homo*

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Superfamily Hominoidea ('hominoids')

Family Hylobatidae

    Genus *Hylobates*

Family Hominidae ('hominids')

    Subfamily Ponginae

        Genus *Pongo* ('pongines')

    Subfamily Gorillinae

        Genus *Gorilla* ('gorillines')

    Subfamily Homininae ('hominines')

        Tribe Panini

            Genus *Pan* ('panins')

        Tribe Hominini ('hominins')

**Subtribe Australopithecina ('australopiths')**

**Genus *Ardipithecus***

**Genus *Australopithecus***

**Genus *Paranthropus***

            Subtribe Hominina ('hominans')

                Genus *Homo*

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The fossil-only hominin taxa are included in bold type. The subtribe Australopithecina and the genus *Australopithecus* are almost certainly paraphyletic, but until the relationships of fossil taxa can be resolved more reliably, the present taxonomy should be retained. Note that the uses of 'hominid' and 'hominine' differ from those given in Table 1*b*.

Table 1. *b. A traditional 'pre-molecular' taxonomy of the living higher primates*

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Superfamily Hominoidea ('hominoids')

Family Hylobatidae

    Genus *Hylobates*

Family Pongidae ('pongids')

    Genus *Pongo*

    Genus *Gorilla*

    Genus *Pan*

Family Hominidae ('hominids')

**Subfamily Australopithecinae ('australopithecines')**

**Genus *Ardipithecus***

**Genus *Australopithecus***

**Genus *Paranthropus***

    Subfamily Homininae ('hominines')

        Genus *Homo*

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The fossil-only hominid taxa are included in bold type, and the caveats set out in the legend to Table 1*a* apply.

support for a *Pan/Homo* clade, these data are generally not available within the hominin clade. Thus, apart from *Paranthropus* and later *Homo*, which are probably monophyletic groups (Wood & Collard, 1999; Strait & Grine, 1999), the existing hominin taxa, and in particular *Australopithecus*, are almost certainly paraphyletic. However, until the phylogenetic relationships of early hominin taxa can be resolved with greater confidence, we think it pragmatic to retain the present taxonomy, with the understanding that the subtribe Australopithecina

and the genus *Australopithecus* are probably paraphyletic.

#### *Ape-human differences*

The morphological features that set modern humans apart from the living African apes are found in the dentition, skull, brain, trunk and the limbs. The apes have larger, more pointed, and more sexually-dimorphic canine teeth (Kelley, 1995) than do modern humans, and they are seldom worn down to the level of the occlusal surface of the postcanine teeth. The associated honing mechanism also affects the morphology of the premolars and the spacing of the teeth, the latter producing the marked diastema characteristic of the apes. When related to body mass, the crown areas of the premolar and molar teeth are similar in relative size in chimpanzees and modern humans (Wood et al. 1983), but the jaws of a modern human skull are smaller, more gracile and project less than those of equivalent-sized living apes. The foramen magnum is close to the middle of the cranial base in modern humans, whereas in the apes it is situated more posteriorly (Bolk, 1909; Le Gros Clark, 1950; Luboga & Wood, 1990). There are also differences in the basicranium of modern humans and the living African apes. The modern human cranial base is wider and shorter, with the long axis of the petrous temporal bones oriented coronally rather than sagittally (Dean & Wood, 1981). In the sagittal plane both the internal and external surfaces of the basicranium are flexed in modern humans contrasting with the more open angles in the apes (Lieberman & McCarthy, 1999). Modern human brains are not just absolutely larger than those of the living apes, but they are also larger relative to body mass (Jerison, 1970; Kappelman, 1996).

While the chests of extant apes and modern humans share many features not seen in monkeys, such as a transversely broad thoracic cage, a vertebral column set deeply within the rib cage, a dorsally-placed scapula, and a laterally-facing shoulder joint, there are also marked differences (Schultz, 1961). The thorax of great apes widens towards the base, like an inverted funnel, and it is matched inferiorly by correspondingly-flared ilia (Schultz, 1961) to accommodate a large gut in a short trunk (see below). In contrast, the barrel-shaped modern human thorax is more uniform in width from top to bottom, with the narrower, more curved contour of the lower rib cage and ilia accommodating the relatively small and short modern human gut (Aiello & Wheeler, 1995). With an

average of 12 pairs, humans have fewer ribs than the 13 pairs typically found in African apes, and there are correspondingly fewer thoracic vertebrae (mean 12, range 11–13) in the modern human spine compared to that of African apes (mean 13, range 12–14). The human vertebral column is longer in the lumbar region, with an average of 5 lumbar vertebrae (range 4–6) compared with 3–4 lumbar vertebrae in great apes (range 3–5) (Schultz & Straus, 1945; Schultz, 1961).

Modern humans are more similar to apes in upper limb than in lower limb morphology. Many human upper limb skeletal characteristics can be related to the loss of habitual weight-bearing function. For example, human upper limb bones are generally straighter and less robust than their great ape counterparts, and muscle insertions are typically designed for less power output (Thorpe et al. 1999), but they permit a greater range of motion, or speed. Relative to body size, the human upper limb is shorter than those of apes, but the difference in length occurs in the forearm and hand, not in the upper arm (Aiello & Dean, 1990; Jungers, 1994). Modern humans retain an apelike, mobile, shoulder joint with a few modifications, such as relatively small supraspinous and relatively large infraspinous fossae (Roberts, 1974), less cranially-oriented glenoid fossae and lateral clavicular heads (Ashton & Oxnard, 1964; Stern & Susman, 1983), features that are related to habitual use of the arm in lowered positions. In African apes and humans, the humeral shaft twists from the humeral head, which faces medially, down to the coronally oriented elbow joint (Evans & Krahl, 1945). Differences in elbow morphology between apes and humans are subtle (Robinson, 1972; Aiello et al. 1999). The human distal humerus exhibits an anteriorly oriented (rather than a distally oriented) capitulum, a shallow olecranon fossa, and weak development of the spool shape of the trochlea associated with a relatively modest lateral trochlear ridge. All these characteristics appear to be related to the loss of upper limb weight support in humans (Aiello & Dean, 1990). Great ape radii and ulnae are also more robust and longitudinally curved (Aiello et al. 1999).

The most striking adaptations in the human upper limb occur in the wrist and hand, and they relate to improved manual dexterity. The human wrist is capable of more mobility in extension than those of the African apes, and it has been argued that this is an adaptation for wrist movements involved in tool making and tool use, such as hammering and throwing (Marzke, 1971). The long thumbs and relatively short,

straight fingers of the modern human hand are proportioned so that the thumb and fingers can form a precision grip, in which the broad, fleshy fingertips of the thumb and fingers are opposed in order to hold an object between them (Napier, 1961). The human thumb has a saddle-shaped carpometacarpal joint, a relatively broad metacarpal, and refined motor control based on discrete, well-developed flexor pollicis longus and opponens pollicis muscles that enable independent control of the thumb and full opposability (Susman, 1994); these 2 muscles are smaller, or absent, in African apes. Compared with apes, human manual digits have unusually broad distal phalangeal tufts and fleshy fingertips that provide a large and highly-sensitive frictional surface (Susman, 1998). Humans have shorter and straighter phalanges, unlike the long, curved proximal and middle phalanges of apes, especially the Asian apes, that improve the latter's ability to grasp large arboreal supports and reduce the stresses associated with climbing and suspension (Susman, 1979; Hunt, 1991; Richmond, 2000).

Modern human adult locomotion, unlike that of the living apes, is almost exclusively bipedal, and this is reflected in the morphology of the pelvic girdle and the lower back, knee, ankle and foot, and in the disposition of the muscles connecting the lower limb to the pelvis and trunk. The human pelvis is highly derived compared with that of the apes and other primates. Major changes in skeletal design include a craniocaudally-shortened ilium, which brings the sacroiliac joint in closer proximity to the hip joint, and sagittally-oriented iliac blades, which allows the gluteus medius and gluteus minimus muscles to be used as hip stabilisers during the stance phase of bipedal walking (Stern & Susman, 1981). The human ischium is short, with prominent ischial spines for well-developed sacrospinous ligaments that contribute to pelvic stability when standing, walking, or running.

The modern human birth mechanism is unique. In nonhuman primates the sagittally-elongated pelvic inlet and outlet allow the newborn to emerge with its face ventrally, related to the pubic symphysis (Stoller, 1995). In modern humans, the pelvic inlet is broadest transversely whereas the outlet is widest sagittally. Thus the large head (Schultz, 1941; Jordaan, 1976) of the relatively large-bodied (Sacher & Staffeldt, 1974; Mobb & Wood, 1977) modern human neonate has to rotate during its passage through the birth canal (Rosenberg & Trevathan, 1995).

The substantial differences between the lower limbs of modern humans and apes are largely attributable to the bipedal locomotion of the former. The most

striking difference is the greater absolute and relative length of modern human lower limbs that increases stride length and thus the speed of bipedal walking (Jungers, 1982). Because the lower limbs support the body during bipedal gait, the acetabulum, femoral head and other lower limb joints are relatively larger in humans (Jungers, 1988c). Modern human femora are distinctive in that they show the valgus condition (i.e. they converge towards the knee), thus helping to position the feet closer to the midline (Walmsley, 1933; Tardieu & Trinkaus, 1994). The greater stresses placed on the lateral side of the knee by the valgus orientation of the distal femoral shaft are resisted by larger lateral condyles in modern human distal femora and proximal tibiae (Heiple & Lovejoy, 1971; Ahluwalia, 1997), and by bony buttressing beneath the tibial lateral condyle. Modern human adult femoral condyles are elongated anteroposteriorly (Tardieu, 1986, 1998) with a deep patellar groove, characteristics that increase the moment arm of the quadriceps femoris muscle, and promote the stability of the patella (Heiple & Lovejoy, 1971; Wanner, 1977). Lastly, the human foot shows many adaptive changes in skeletal design for bipedalism, including an adducted hallux, a longitudinal arch, long calcaneal tuberosity with a prominent lateral plantar process, and short straight toes (Susman, 1983; Lewis, 1989).

In addition to the morphological differences between apes and modern humans, there are also contrasts in the rate that their bodies grow and in the order in which structures appear during development (Schultz, 1960). Modern humans reach maturity much more slowly than do apes. They also erupt their teeth in a different order, and the milk, or deciduous, molars wear out before the adult molars have erupted (Smith et al. 1994; Macho & Wood, 1995). The time taken to complete tooth crown development differs between apes and humans, but these differences generally reflect differences in crown height. A major contrast between modern humans and apes is that the former have very extended periods of growth for the final stages of crown formation. It is these differences that are largely responsible for the relatively delayed crown formation, eruption, and root completion of modern humans compared with the African apes (Macho & Wood, 1995).

There are many important behavioural differences between modern humans and the living apes, such as the former's elaborate written and spoken language, but most of these behaviours leave little, or no, trace in the hard tissues that make up the hominin fossil record. Thus researchers have turned to other lines of evidence for their reconstruction, and debate is

ongoing about the extent to which these behavioural differences, especially spoken language, can be detected in the paleontological and archaeological records.

#### *Ancestral differences*

Although an impressive number of contrasts exists between the morphology of the living apes and modern humans, the differences between the earliest hominins and the late Miocene ancestors of the living great apes are likely to have been more subtle. Some of the features that distinguish modern humans and the living apes, such as those linked to upright posture and bipedalism, can be traced far into human prehistory. Others, such as the relatively diminutive jaws and chewing teeth of modern humans, were acquired more recently and thus cannot be used to discriminate between early hominins and ape ancestors. At least 2 early hominin genera, *Australopithecus* and *Paranthropus*, had absolutely and relatively larger chewing teeth than later *Homo* (McHenry, 1988; Wood & Collard, 2000). This 'megadontia' may have been an important derived feature of early hominins, but it has been reversed in later hominins. We do not yet have sufficient information about the earliest stages of hominin evolution to determine whether megadontia is confined to hominins, but a preliminary analysis of Miocene hominoids suggests that these are also relatively megadont (P. Andrews & B. A. Wood, unpublished data). How, then, are we to tell a late Miocene/early Pliocene early hominin from the ancestors of *Pan*, or from the lineage that provided the common ancestor of *Pan* and *Homo*?

The presumption is that the common ancestor and the members of the *Pan* lineage would have had a locomotor system that is adapted for orthograde arboreality and climbing, and probably knuckle-walking as well (Washburn, 1967; Pilbeam, 1996; Richmond & Strait, 1999). This would have been combined with projecting faces accommodating elongated jaws bearing relatively small chewing teeth, and large, sexually-dimorphic, canine teeth with a honing system. Early hominins, on the other hand, would have been distinguished by at least some skeletal and other adaptations for a locomotor strategy that includes substantial bouts of bipedalism (Rose, 1991), linked with a masticatory apparatus that combines relatively larger chewing teeth, and more modest-sized canines that do not project as far above the occlusal plane.

These proposed distinctions between hominins,

panins and their common ancestor are ‘working hypotheses’ that need to be reviewed and, if necessary, revised as the relevant fossil evidence is uncovered. Evidence of only one of the possible ‘distinguishing’ features of the hominins and panins set out above may not be sufficient to identify a fossil as being in either the hominin or panin lineages, because there is evidence that primates, like many other groups of mammals, are prone to convergent evolution. This means that we cannot exclude the possibility that some of what many have come to regard as the ‘key’ adaptations of the hominin and the ape lineages (e.g. bipedalism in the former), may have arisen more than once and in more than one group. It is also possible that the first species of hominin was not bipedal. If so, it would be very difficult to distinguish between early members of the hominin and panin lineages in the late Miocene. Lastly, while we know that morphological features we regard as ‘key’ adaptations of the later members of a clade (e.g. small chewing teeth of hominins) are not present in its earlier members, we also have to take into account that, as yet, we have no evidence of the evolutionary history of our closest living relative, the chimpanzee.

Another implication of convergent evolution is that while the simple dichotomy ‘hominins’ and ‘apes’ may be an appropriate and effective way of subdividing the later stages of human and extant higher primate evolution, it may not be applicable to the hominids of the late Miocene and the early Pliocene. It is possible that at this time there were adaptive radiations for which we have no satisfactory extant models. We should expect to find fossil evidence of animals displaying novel combinations of features with which we are familiar, as well as evidence of animals exhibiting novel morphological features (Wood, 1984).

#### *Hominin taxonomy*

It is easy to forget that statements about how many species have been sampled in the hominin fossil record are hypotheses. There is lively debate about the nature of living species, so it is perhaps not surprising that there is a spectrum of opinion about how the species category should be interpreted in the paleontological context (Kimbel & Rak, 1993, and references therein). All species are individuals in the sense that they have a ‘history’ (Hull, 1976; Eldredge, 1993). They have a ‘beginning’, the process of speciation, a ‘middle’, that lasts as long as the species persists, and an ‘end’, which is either extinction, or participation in another speciation event. Living species are ‘caught’, in

geological terms, at an instant in their history, much as a single photograph of a running race is only a partial record of that race. In the hominin fossil record that, albeit imperfectly, samples millions of years of time, the same species may be sampled several times, so, to return to our metaphor, there may be more than one photograph of the same running race. Paleoanthropologists must devise strategies to ensure that the number of species they record in the hominin fossil record is neither a gross under-estimate, nor an extravagant over-estimate, of the actual number. They must also take into account that they are working with fossil evidence that is confined to the remains of the ‘hard tissues’ that make up the bones and teeth. We know from living animals that many ‘good’ species are osteologically and dentally indistinguishable (e.g. *Cercopithecus* species), thus it is likely that an effectively hard tissue-bound fossil record will always underestimate the number of species (Tattersall, 1986, 1992).

When this attitude to estimating the likely number of species in the fossil record is combined with a ‘punctuated equilibrium’ and cladogenetic interpretation of evolution, then a researcher is liable to interpret the fossil record as containing more, rather than fewer, species. Conversely, researchers who favour a more gradualistic, or anagenetic, interpretation of evolution, that sees species as individuals that are long-lived and prone to substantial changes in morphology through time, will tend to resolve the fossil record into fewer species. The taxonomy used below is an explicitly speciose one (see the caption to Fig. 1 for an alternative interpretation). The rules and recommendations specifying how species should be named and referred to, and how the concept of ‘types’ operates, are set out in the new edition of the International Code of Zoological Nomenclature (Ride et al. 1999) and are explained and summarised in Wood & Collard (2000). When referring to a species it is conventional to follow it with the name(s) of the author(s) and the year of publication of the paper that introduced the taxon. If the species has subsequently been referred to a different genus, then the initial citation is placed in parentheses, followed by the citation of the paper that proposed the transfer to the new genus.

#### HOMININ TAXA

Hominin species are set out below by genus, beginning with the oldest in geological age. As far as we can tell from the fossil evidence, it is generally true that the earlier genera and species in the hominin fossil record

Table 2. Key to commonly-used fossil hominin site abbreviations

Site abbreviations	Explanations for the site-specific prefixes used in the text
AL or A.L.	Lower Awash River (Hadar in Afar Depression)
ARA	Aramis Formation
BC	Baringo (Chemeron Formation)
BK	Baringo (Kapthurin)
BOU-VP	Bouri—Vertebrate Paleontology
ER	East Rudolf (now usually called Koobi Fora, or sometimes East Turkana)
GVH	Gladysvale Hominin
HCRP RC	Hominid Corridor Research Project Malema
HCRP UR	Hominid Corridor Research Project Uraha
KB	Kromdraai Site B—Fossils discovered after 1955
KGA	Konso Gardula (now known as Konso)
KNM-	Kenya National Museum (followed by the appropriate site abbreviation e.g. ER, WT etc.)
KP	Kanapoi
KT	Koro Toro, Chad
LH or L.H.	Laetoli Hominin
MAK-VP	Maka—Vertebrate Paleontology
MLD	Makapansgat Limeworks Dumps
OH or O.H.	Olduvai Hominin
Omo	Designation for fossils recovered by the French-led group, from the Shungura Formation, Ethiopia
SE	Sterkfontein 'Extension Site'
SH	Shungura Formation
SK	Swartkrans Hominin (SKW—Swartkrans Wits; SKX—Swartkrans Excavation, refers to specimens recovered by C. K. Brain since 1965)
Sts	Specimens recovered from Sterkfontein Type Site between 1947 and 1949
Stw, StW, Stw/H, or StW/H	Sterkfontein Wits Hominin—specimens recovered from any part and any member of the Sterkfontein Formation after 1968.
TM	Transvaal Museum—the catalogue designation of the following: Sterkfontein—fossils discovered between 1936 and 1938; Kromdraai—fossils discovered between 1938 and 1955
UA	Uadi Aalad site
WT	West Turkana (including Nariokotome)

are also the most primitive (Fig. 1). Within each genus the order of presentation is such that primitive, and generally geologically older, species precede the more derived ones. Each species' entry begins with the history of its discovery, then a list of important sites, a summary of the characteristic morphology, and its behavioural implications, available information about the paleohabitat, a summary of the hypodigm, or fossil record, for that species and, lastly, references to any current taxonomic debates involving that species. Explanations of the letter abbreviations used to identify fossils by site and locality are provided in Table 2.

### *Ardipithecus*

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

The first creature to show at least some rudimentary human specialisations, and currently the most primitive hominin known, is *Ardipithecus ramidus* (White et al. 1994, 1995). The evidence is in the form of

~ 4.5 myr-old fossils recovered in late 1992 and thereafter, from a site called Aramis, in Ethiopia. The remains have some features in common with living species of *Pan*, others that are shared with the African apes in general, and, crucially, several dental and cranial features that are shared with later hominins.

*Sites.* Aramis, Middle Awash, Ethiopia; perhaps also at Tabarin and Lothagam, Kenya.

*Characteristic morphology.* The case White et al. (1994) put forward to justify their taxonomic judgment centres on the cranial evidence. These researchers claimed that compared with *A. afarensis*, *A. ramidus* has relatively larger canines, its first deciduous molars have less complex crowns, the articular eminence is flatter, the enamel thinner, and the upper and lower premolar crowns are more asymmetric, and thus more apelike (White et al. 1994). These workers suggested that *A. ramidus* should be excluded from the apes because it shares a number of derived anatomical features with later hominins, including relatively small upper central incisors, less projecting canines and a poorly-developed canine honing mechanism, broad mandibular molar crowns,

and a foramen magnum that is more anteriorly-situated than in the apes.

*Behavioural implications.* Judging from the size of the shoulder joint, the body mass of *A. ramidus* was in the vicinity of 40 kg. Its chewing teeth were relatively small, and the position of the foramen magnum suggests that the posture and gait of *A. ramidus* were, respectively, more upright and bipedal than in the living apes. The relatively large incisors and the thin enamel covering on the teeth suggest that the diet of *A. ramidus* may have been closer to that of the chimpanzee than is the case for other early hominins. As yet we have no information about the size of the brain, nor any direct evidence from the limbs about the posture and locomotion of *A. ramidus*. The report on the remains of an associated skeleton that has been found (see below) is awaited with considerable interest.

*Paleohabitat.* It has been reported that the remains of the plants and animals, including a large representation of extinct colobines, found with *A. ramidus* suggest that the bones had been buried in a location that was close to, if not actually within, woodland (WoldeGabriel et al. 1994), but the habitat and dietary preferences of fossil *Colobus* may not match those of extant *Colobus*.

*Hypodigm.* Holotype: ARA-VP-6/1, an associated partial set of upper and lower teeth. Paratypes: ARA-VP-1/128, another set of associated teeth; ARA-VP-1/4, a right humeral shaft; ARA-VP-1/500, temporal and occipital remains; ARA-VP-7/2, a fairly complete left humerus, radius, and ulna, as well as a number of teeth and dental fragments (White et al. 1994). Well-preserved specimens: teeth, ARA-VP-6/1 and 1/128; and White et al. (1995) refer to a currently unpublished associated skeleton. With hindsight, the remains from Aramis may not be the first evidence found for this species; the mandibular fragment from Lothagam in Kenya, that has been dated to around 5 myr (Hill & Ward, 1988), may prove to be more similar to *A. ramidus* than to *A. afarensis*.

*Taxonomy.* The new species was initially allocated to *Australopithecus* (White et al. 1994), but has since been assigned to a new genus, *Ardipithecus*, which, the authors suggest, is significantly more primitive than *Australopithecus* (White et al. 1995).

#### *Australopithecus*

*Australopithecus anamensis* Leakey et al. 1995

Fossils dating to between 3.9 and 4.2 myr found by Meave Leakey and her team at Kanapoi and Allia

Bay, in Northern Kenya, have been assigned to a new species of *Australopithecus*, apparently more primitive than *Australopithecus afarensis* (see below) (Leakey et al. 1995, 1998).

*Sites.* Kanapoi and Allia Bay, Kenya.

*Characteristic morphology.* Diagnostic features cited by the authors include the small size and elliptical shape of the external auditory meatus, a narrow mandibular arch with parallel mandible corpora, a sloping mandibular symphysis, long and robust canine roots, upper molar crowns that are broader mesially than distally, and a small humeral medullary cavity. *A. anamensis* displays a number of derived characteristics that distinguish it from *A. ramidus*, including absolutely and relatively thicker enamel similar to that of *A. afarensis*, broader molars, and a tympanic tube that extends only as far as the medial edge of the postglenoid process (Leakey et al. 1995). The main differences between *A. anamensis* and *A. afarensis* relate to mandibular morphology and details of the dentition. The mandibular symphysis of *A. anamensis* is steeply-sloping compared with the more vertical symphysis of later hominids, including *A. afarensis*. In some respects the teeth of *A. anamensis* are more primitive than those of *A. afarensis* (e.g. asymmetry of the premolar crowns, less posteriorly-inclined canine root, and the relatively simple crowns of the deciduous first mandibular molars), but in others (e.g. the low cross-sectional profiles, and bulging sides of the molar crowns) they show similarities to more derived, and temporally much later, *Paranthropus* taxa. Compared with *A. afarensis*, *A. anamensis* also exhibits a primitive, horizontal tympanic plate.

The few known postcranial fossils preserve portions of the upper and lower limb. Contrary to earlier assessments that it is humanlike, the distal humerus of *A. anamensis* does not closely resemble extant humans or African apes, and instead resembles other fossil hominins, including *A. afarensis*, *P. robustus*, and *Homo* sp. in overall morphology (Lague & Jungers, 1996). The radius is apelike in several features, including its considerable overall length, the length of a distinct radial neck, and the well-developed brachioradialis insertion, but it lacks the pronounced shaft curvature typical of African apes (Heinrich et al. 1993). The distal end shows a mosaic of Asian ape and African ape features, resembling the former in exhibiting a relatively large articular surface for the lunate, but sharing with African apes a distally-projecting dorsal ridge, relatively coplanar scaphoid and lunate facets, and a large, dorsally-oriented scaphoid notch. The manual proximal phalanx is



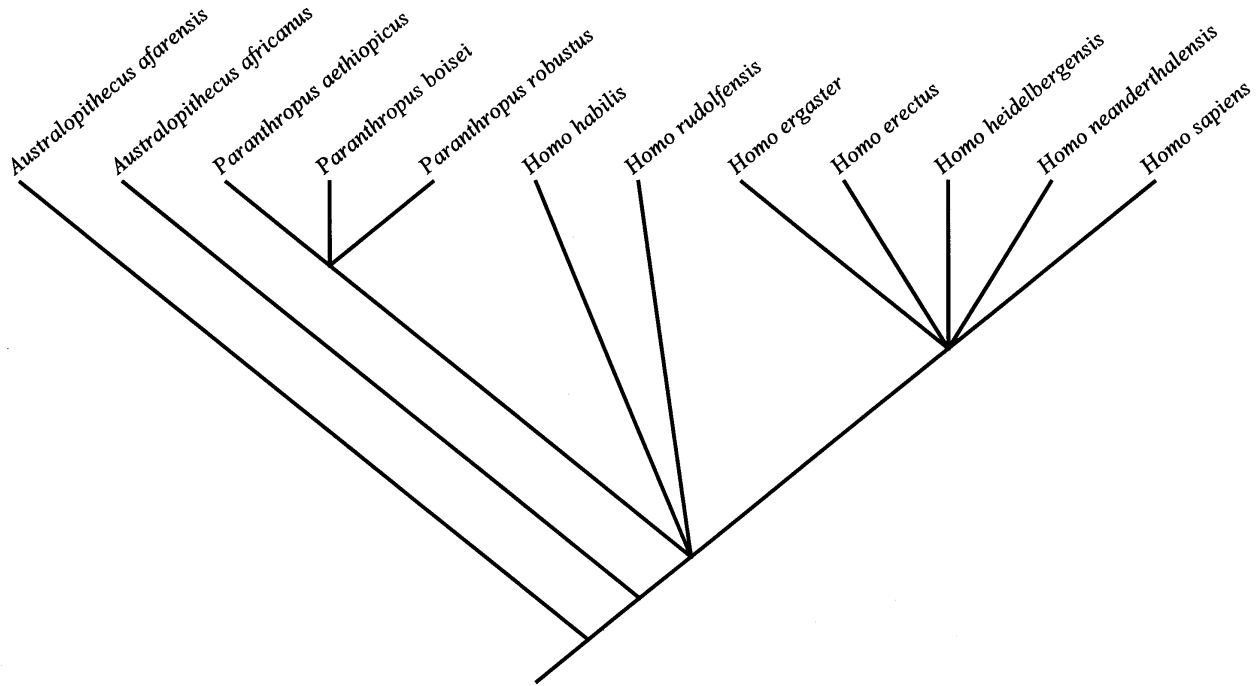


Fig. 2. Hominin cladogram. Consensus cladogram of hominin taxa for which there is sufficient evidence to provide scores for a substantial number of craniodental character states. This cladogram includes no postcranial character states. It is based upon bootstrap analysis of the character states provided in Stringer et al. (1987) and Strait et al. (1997). Adapted from Wood & Collard (1999).

longitudinally-curved like those of *Pan* and *A. afarensis* (Ward et al. 1999). In the lower limb, the tibia of *A. anamensis* is derived in a number of ways related to erect walking. The condyles are approximately perpendicular to the shaft and are concave and subequal in size (Leakey et al. 1995), unlike the ape condition in which they are posteriorly tilted and the lateral condyle is much smaller than the medial one. The proximal shaft expands to buttress the lateral condyle and, on the distal end, the main tibiotalar articular surface is also approximately at right angles to the tibial shaft (Ward et al. 1999).

**Behavioural implications.** The body mass of at least one individual of *A. anamensis* is ~ 50 kg, based on estimates from the proximal tibia (~ 55 kg) and distal tibia (~ 47 kg) (Leakey et al. 1995). The morphology of the tibia described above includes what is currently the earliest undisputed evidence of habitual bipedalism in hominins (Leakey et al. 1995). However, *A. anamensis* also retained primitive features, such as curved fingers (Ward et al. 1999) and a long radius with evidence of a powerful brachioradialis muscle and a long lever arm for the biceps brachii muscle (Heinrich et al. 1993), that suggest capabilities for arboreal activity. Primitive features of the distal radius, including the distally-projecting dorsal ridge and large scaphoid notch, also suggest that wrist extension was limited in this early hominin taxon, much as it is in knuckle-walkers.

The relatively large incisors of *A. anamensis* suggest that it was frugivorous. However, *A. anamensis* is the earliest hominin known to have thick enamel, suggesting that among the derived adaptations of this species is a dental apparatus mechanically-suited to deliver high bite forces and which is also resistant to wear, attributes that would enable it to process nuts, grains, or hard fruit.

**Paleohabitat.** The mammalian macro- and micro-fauna recovered along with the hominins at Kanapoi suggest a fairly dry, perhaps open woodland or bushland, habitat. However, along the river that transported the sediments, there is evidence of a gallery forest extensive enough to support a variety of primates, including galagos and colobines (Leakey et al. 1995). *A. anamensis* appears to have had access to a variety of habitats.

**Hypodigm.** Holotype: KNM-KP 29281, an adult mandible with complete dentition, and a temporal that probably belong to the same individual (Leakey et al. 1995). Paratypes: 21 specimens—18 cranial and 3 postcranial—as listed in Leakey et al. (1995, table 1, p. 567). Well-preserved specimens: Skull (Juvenile)—KNM-KP 34725; Maxilla—KNM-KP 29283; Mandible—KNM-KP 29281; Lower limb—KNM-KP 29285. The associated juvenile dental and cranial remains, KNM-KP 34725, are among the fossils found since the initial description (Leakey et al. 1998).

*Australopithecus afarensis* Johanson et al. 1978

Some half a million years after the present evidence for *A. ramidus*, and perhaps contemporaneous with fossils of *A. anamensis*, there is evidence in East Africa of another relatively primitive hominin, *Australopithecus afarensis*. This was the name given to hominin fossils recovered from Laetoli, in Tanzania, and from the Ethiopian site of Hadar (Johanson et al. 1978). When the classification of the material was first considered it was natural that researchers contemplated its relationship to *Australopithecus africanus* Dart 1925, evidence of which had been recovered half a century earlier from a cave site in southern Africa (see below). The results of morphological analyses suggest that there are significant differences between the 2 hypodigms (White et al. 1981; Kimbel et al. 1984; Johanson, 1985). Support for this assessment comes from the results of cladistic analyses (e.g. Skelton & McHenry, 1992; Strait et al. 1997) in which they are rarely related as sister taxa (Fig. 2). Comparisons have also emphasised that in nearly all the cranial characters examined, *A. afarensis* displays a more primitive character state than does *A. africanus* (e.g. White et al. 1981; Kimbel et al. 1984).

The fossil record of *A. afarensis* is best known from 3.4 to 3.0 myr-old sediments at Hadar, older remains are known from Laetoli in Tanzania (3.7 myr) and Fejej in Ethiopia (as old as 4.2 myr; Kappelman et al. 1996). Thus *A. afarensis* is presently much better sampled than *A. ramidus* or *A. anamensis*, for it includes a skull, (Kimbel et al. 1994), substantial fragments of several skulls, many lower jaws and sufficient limb bones which allow for a reliable estimate of the stature and body mass of *A. afarensis*. The collection also includes a specimen that preserves just less than half of the skeleton of an adult female, whose field number is A.L.-288, but which is better known as 'Lucy'.

*Sites.* Laetolil Beds at Laetoli (originally 'Laetolil'), Tanzania; Hadar ~ Sidi Hakoma, Denen Dora and Kadar Hadar Members; Middle Awash ~ Maka and Belohdelie; Fejej, and Lower Omo Valley ~ White Sands, all in Ethiopia. Hominin fossils from Koobi Fora, Allia Bay, and South Turkwell, all in Kenya, may also belong to *A. afarensis*. The taxonomy of the Tabarin mandible needs to be reassessed in the light of the discovery of *A. ramidus* (see above).

*Characteristic morphology.* All systematic assessments of *A. afarensis* have stressed the primitive nature of the cranium and dentition. Indeed, in their cladistic analysis of 60 cranial and dental characters, Strait et al. (1997) list just 10, the smallest number for

any of the hominins they consider, that distinguish *A. afarensis* from their *Pan/Gorilla* outgroup, and they list only 2 *A. afarensis* autapomorphies (Strait et al. table 4). The features that distinguish the cranium of *A. afarensis* from that of *Pan* are mainly related to the smaller canine and larger postcanine teeth of the former, and the influence the smaller canines has on the face of *A. afarensis*, including the reduced snout and the presence of a canine fossa. Otherwise, apart from the frontals lacking the type of supratoral sulcus seen in *Pan* (Kimbel et al. 1994), the pattern of ectocranial creasing in *A. afarensis* is *Pan*-like, as is the smooth transition between the nasoalveolar clivus and the floor of the nose, the shallow palate, the I<sup>2</sup>/C diastema (modest though it is), the exaggerated mastoid pneumatization, and the weakly flexed cranial base (White et al. 1981; Kimbel et al. 1984). Most crania show osseous evidence of the type of occipito-marginal sinus venous drainage pattern that also occurs at a high incidence in *Paranthropus* (Falk & Conroy, 1983). The fossa for the mandibular condyle is apelike; it is shallow, with little, or no, development of the articular eminence. Apart from their relatively small canines, the mandibles share with the African apes straight postcanine tooth-rows, and tall and narrow corpora with substantial hollowing on the lateral surface.

Turning to the dentition, the crowns of the dm<sub>1</sub>s are intermediate between the simple cusp arrangements seen in *Pan*, and the more complex cusp patterns of *A. africanus* and *Paranthropus* sp. (White et al. 1994). The upper canines show the oblique wear seen in living great apes, the majority of the P<sub>3</sub> crowns are unicuspid, and the P<sub>4</sub> crowns are more asymmetric than in more recent australopith taxa. The incisors are smaller than those of the apes, and the thick-enameled cheek teeth have larger crowns. The subocclusal morphology of the mandibular postcanine teeth is, at least among the hominins studied, distinctive in having narrow root canals and distal root components that project towards the buccal surface of the mandibular corpus, giving a serrated appearance when viewed from the lingual side (Ward & Hill, 1987).

Postcranially, *A. afarensis* provides the first evidence that, with the exception of lower limb features related to bipedalism, australopiths retained a generally apelike skeletal design and body shape (McHenry, 1991). Evidence from fossil rib fragments, including the apelike rounded cross-section and absence of flattening in the middle section of the body of the ribs, suggests that the rib cage of *A. afarensis* was capacious and retained the inverted funnel shape

typical of great apes (Schmid, 1983). A derived trait shared with humans is the single articular facet on the first rib in *A. afarensis*, a feature that appears to be related to habitual orthograde posture (Stern & Jungers, 1990). The vertebrae tend to have long, apelike spinous and transverse processes, and the vertebral bodies are intermediate in size compared with the ape and human conditions. Lumbar vertebrae are wedged such that the anterior length of the body is greater than the posterior length. The upper limb of *A. afarensis* is shorter than a great ape of comparable mass, but long relative to humans. These differences are driven by variation in radius and ulna length, because the relative humerus length of *A. afarensis* is comparable to that of African apes and humans (Jungers, 1994). In the shoulder, the scapula retains a primitive cranially-oriented glenoid fossa (Stern & Susman, 1983), and the humeral head is less spherical than in apes, and resembles humans in having a relatively large lesser tubercle (Robinson, 1972). The humeral shaft may exhibit less marked torsion than in *Pan* or *Homo* (Larson, 1996), and the distal end exhibits a well-developed, *Pan*-like, lateral trochlear ridge, but lacks the steep lateral margin of the olecranon fossa typical of African apes. The distal humerus resembles *Paranthropus* humeri in exhibiting a well-developed, superiorly-positioned, lateral epicondyle. Like *A. anamensis* and African apes, the distal radius of *A. afarensis* has a distally-projecting dorsal ridge, relatively coplanar scaphoid and lunate articular surfaces, and a large, dorsally-situated scaphoid notch (Richmond & Strait, 1999). In the hand, the pisiform is long and the fingers are intermediate in length between the long fingers of extant apes and the short ones in modern humans (Latimer, 1991), but they are longitudinally-curved as in chimpanzees and *A. anamensis*. The tufts on the distal phalanges are relatively narrow (Bush et al. 1982), suggesting that *A. afarensis* did not possess broad, fleshy fingertips. Like most apes (except *Gorilla*), the pollical metacarpal is not robust (Susman, 1994).

The pelvis shows a mixture of primitive and derived features. Apelike morphology includes the coronal orientation of the iliac blades, a somewhat long ischium without a raised tuberosity, a reduced acetabular anterior horn, and evidence of weakly-developed sacroiliac ligaments. However, the pelvis shares with humans a short, wide ilium, a well-developed sciatic notch and anterior inferior iliac spine, and wide sacrum. The femoral head and acetabulum, as well as sacroiliac and lower intervertebral joints, are small relative to humans of

comparable size (Jungers, 1988*a*). The femoral neck is long, and the cortical bone is thick inferiorly as in modern humans (Ohman et al. 1997). Although longer than that of apes, the femur is shorter than a human of similar stature (Jungers, 1982). The femur has a bicondylar angle that is even more valgus than in humans, owing to the wide pelvis and short femoral length. The feet also exhibit a mosaic morphology, including a derived adducted hallux, robust calcaneal tuberosity with a lateral plantar process, relatively short toes (compared with apes), and dorsally-oriented metatarsophalangeal joints, combined with primitive features, such as the shape of the talar trochlea, and the curvature and length (greater than humans) of the pedal proximal phalanges (Stern & Susman, 1983; Latimer & Lovejoy, 1989, 1990*a, b*).

*Behavioural implications.* To judge from the size of the postcranial remains, the species ranged in body mass from ~ 25 kg, for a small female, to ~ 50 kg for a large presumed male (Jungers, 1988*b*; McHenry, 1992). The suggestion that A.L. 288-1, one of the smallest *A. afarensis* individuals, may be a male (Häusler & Schmid, 1995), which would strengthen the case for taxonomic heterogeneity, has been effectively refuted (Wood & Quinney, 1996; Tague & Lovejoy, 1998). Stature estimates suggest a range of ~ 1.0–1.5 m. The estimated brain volume of *A. afarensis* is between 375 and 540 cm<sup>3</sup>, with a mean of c. 470 cm<sup>3</sup>. This is larger than the average brain size of a chimpanzee, but, if the estimates of the body size of *A. afarensis* are anything like correct, then, relative to estimated body mass, the relative brain size of *A. afarensis* is not much greater than that of *Pan*. It has incisors that are smaller than those of extant chimpanzees, but the chewing teeth—the premolars and molars—of *A. afarensis* are relatively larger than those of *Pan* (McHenry, 1988). The thick enamel of the *A. afarensis* cheek teeth suggest that nuts, seeds, and hard fruit may have been an important component of the diet of this species.

The shape of the pelvis and the lower limb suggests that *A. afarensis* was adapted to bipedal walking. This indirect evidence for the locomotion of *A. afarensis* is complemented by the discovery, at Laetoli, of several trails of fossil footprints (Leakey & Hay, 1979). These provide very graphic, direct, evidence that *A. afarensis*, or another contemporary hominin, was capable of bipedal locomotion. The size of the footprints, and the length of the stride, are consistent with stature estimates based on information from the limb bones of *A. afarensis*. These suggest that the standing height of the individuals in this early hominin species was between 1 m and 1.5 m (Jungers, 1988*a*).

Debate continues as to whether bipedal gait in *A. afarensis* was humanlike or not (Stern & Susman, 1983; Lovejoy, 1988; Crompton et al. 1998; Stern, 1999). Stern & Susman (1983) have argued that the coronal orientation of the iliac blades indicates an absence in *A. afarensis* of the anterior gluteal muscle fibres that, in humans, control hip movements during late support phase. Based on this and other evidence (e.g. acetabular morphology), they suggest that in *A. afarensis* the mechanism for lateral hip balance was apelike, in essence a 'bent-knee, bent-hip' gait (Stern & Susman, 1983; Stern, 1999). Expansion of the articular surface of the anterior aspect of the femoral head may be consistent with a bent-hip gait (MacLatchy, 1996). This manner of walking is probably less efficient than that practiced by modern humans (Crompton et al. 1998), perhaps to the degree that chimpanzee terrestrial quadrupedalism is more costly than that of most other mammals (Taylor & Rowntree, 1973; Stern, 1999). Whatever the manner of gait, the relatively small size of many weight-bearing joints, including the femoral head and acetabulum, and sacroiliac and intervertebral joints, suggest that *A. afarensis* was not adapted for long-range bipedalism (Stern & Susman, 1983; Jungers, 1988c; Hunt, 1996). Furthermore, the relative short lower limbs in *A. afarensis* indicate that stride length and speed were lower, and thus energetic expenditure higher during bipedal locomotion than in equivalent-sized modern humans (Jungers, 1982).

There is disagreement about whether or not arboreality played a significant role in the behavioural repertoire of *A. afarensis*. Underlying the debate is disagreement about the extent to which primitive retentions should be used to infer behaviour (Latimer, 1991; Susman & Stern, 1991; Duncan et al. 1994; Gebo, 1996; Richmond, 1998). Those who believe that arboreality continued to play a significant role in the locomotor repertoire of *A. afarensis* cite numerous primitive traits, such as curved and relatively long manual and pedal proximal phalanges and a cranially-oriented glenoid fossa. Others argue that, as primitive retentions, these traits do not provide meaningful information about function (Latimer, 1991; Gebo, 1996).

Other aspects of behaviour may also be inferred from the skeleton. Primitive features of the hand, including the narrow apical tufts of the distal phalanges and gracile pollical metacarpal, indicate that *A. afarensis* lacked the refined manual dexterity characteristic of later hominins, including modern humans. Evidence from the pelvis, especially its extreme width, suggests that the birth process in *A.*

*afarensis* involved a transversely-oriented head rather than the sagittal orientation of chimpanzees, or the rotation that occurs in humans (Tague & Lovejoy, 1986). The substantial sexual dimorphism in *A. afarensis* suggests that male–male competition was intense, and in living taxa such levels are associated with polygyny (i.e. males mating with more than one female). However, the reduced canine dimorphism compared to the living great apes suggests that the use of morphological proxies to predict social behaviour in the early hominins may not be simple (Plavcan & van Schaik, 1997).

*Paleohabitat.* Paleoenvironmental reconstructions suggest that *A. afarensis* inhabited a mosaic environment. Evidence from Hadar suggests a mixture of dry bushland, riparian woodland, probably with seasonal floodplains, and riverine forest habitats (Johanson et al. 1982; Reed & Eck, 1997). One reconstruction of Laetoli suggests open grassland, with closed-woodland nearby (Harris, 1987), but others interpret the same evidence as indicating a much more wooded environment (Andrews, 1989).

*Hypodigm.* Holotype: L.H.—4, adult mandible. Paratypes: numerous paratypes from the Laetolil Beds, Tanzania, and the Hadar Formation, Ethiopia are listed in Johanson et al. (1978). Well-preserved specimens: skulls—A.L. 444-2; crania—A.L. 58-22, 162-28, 333-45, and 333-105; mandibles—A.L. 266-1, and 400-1a; upper limb—A.L. 438-1, MAK-VP 1/3; associated skeleton—A.L. 288-1.

*Taxonomy.* There is substantial size range within the hypodigm relative to the absolute body mass of *A. afarensis*, and some workers have suggested that the hypodigm of *A. afarensis* may consist of the remains of more than one species of early hominin (e.g. Olson, 1981, 1985; Senut & Tardieu, 1985). However, bootstrap analyses indicate that the size dimorphism is consistent with that observed in the living great apes (Lockwood et al. 1996), being greater than that in *Pan*, but only slightly less than in *Gorilla* and *Pongo*.

*Nomenclature.* The cladistic study of Strait et al. (1997) concluded that the retention of *A. afarensis* within *Australopithecus* almost certainly made the latter a paraphyletic group. On these grounds, they suggested that the hypodigm of *A. afarensis* should be referred to *Praeanthropus africanus* (Weinert, 1950), the taxonomic solution considered by Day et al. (1980). However, this meant that there would be 2 identical species names in use, 'africanus Dart 1925' and 'africanus Weinert 1950'. To avoid confusions such as this, as early as 1995 an application was made to the International Commission of Zoological Nomenclature (ICZN) to have the specific name

'*africanus* Weinert 1950' suppressed. The results of the deliberations were published as 'Opinion 1941' in the Bulletin of Zoological Nomenclature (ICZN, 1999). In it the ICZN confirmed that '*africanus* Weinert 1950' be suppressed so that if it is to be removed from *Australopithecus*, the *A. afarensis* hypodigm should be referred to as *Praeanthropus afarensis*.

*Australopithecus bahrelghazali* Brunet et al. 1996

Hominin fossils collected in Chad, in North-central Africa, and faunally-dated to ~ 3.5 myr (Brunet et al. 1995), have been assigned to *A. bahrelghazali*. They extend the known geographical range of fossil hominins far beyond East and southern Africa (Wood, 1995). The discovery of these fossils underscores how little we currently know about the ranges of extinct hominin species and the biogeographical history of hominin evolution (Foley, 1999; Strait & Wood, 1999).

*Site.* Bahr el ghazal region, Chad, North-central Africa.

*Characteristic morphology.* The published evidence, a mandible and a maxillary premolar tooth, has been interpreted as being sufficiently distinct from *A. ramidus*, *A. afarensis* and *A. anamensis* to justify its allocation to a new species. Brunet et al. (1996) claim that the thickness of its enamel distinguishes the Chad remains from *A. ramidus*, and that the more vertical orientation and reduced buttressing of the mandibular symphysis, together with the more symmetric crowns of the P<sub>3</sub>, separates it from *A. anamensis*. The complexity of the mandibular premolar roots is the main feature that distinguishes *A. bahrelghazali* from *A. afarensis* (but see below), and its more slender corpus, larger incisors and canines and more complex mandibular premolar root system separate it from *A. africanus*.

*Behavioural implications.* At present little can be said about the behaviour of *A. bahrelghazali* other than that its similarity to *A. afarensis* in terms of enamel thickness and dental morphology suggests that the 2 taxa shared a similar diet (e.g. fruit, nuts, and seeds).

*Paleohabitat.* Associated fauna reflect both open and wooded habitats. The remains of some aquatic taxa indicate the presence of a river, or riparian woodland. Thus the paleohabitat of *A. bahrelghazali* is consistent with that of australopiths from East and southern Africa.

*Hypodigm.* Holotype: KT 12/H1, anterior mandible. Paratype: KT 12/H2, right P<sub>3</sub>.

*Taxonomy.* In a recent paper White et al. (2000)

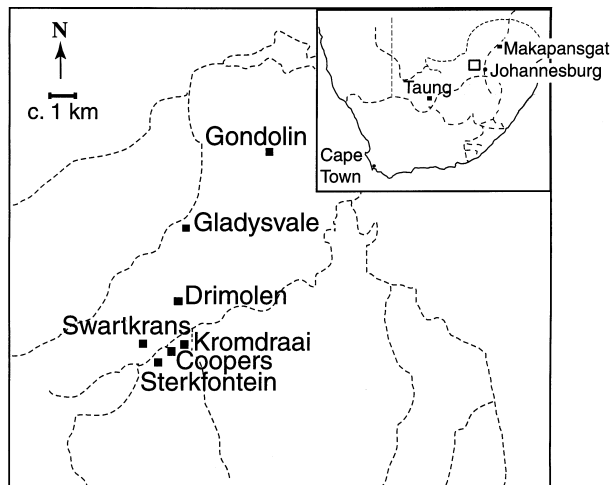
claimed that a complex P<sub>3</sub> root system is also seen in a percentage of *A. afarensis* specimens, and thus it cannot be used to distinguish *A. bahrelghazali*.

*Australopithecus africanus* Dart, 1925

In 1924, nearly 50 years before the discovery of the East African remains belonging to *A. afarensis*, an early hominin child's skull was found among the contents of a small cave exposed during mining at the Buxton Limeworks at Taungs (the name was changed later to Taung) in southern Africa. To judge from the fossil mammals found with it, the Taung hominin was more ancient than any of the hominin remains that had been recovered in Europe, Java or China (see below). The new hominin was described by Raymond Dart, who referred it to a new genus and species, *Australopithecus africanus*, literally the 'southern ape of Africa' (Dart, 1925). Dart referred to postcranial remains in his description of the material, but only the skull survives. No other australopiths have been recovered from the Buxton Limeworks.

Given the difficulties of assessing a juvenile specimen, Dart's analysis of the Taung was remarkably perceptive, for he claimed it was an example of an 'extinct race of apes intermediate between living anthropoids and man' (ibid, p. 195). This judgment depended heavily on Dart's interpretation of the relative size of the face, and his conclusion, based on the height of the canine crown and the small size of the gap, or 'diastema', between the incisors and canine, that the dentition 'is humanoid rather than anthropoid' (ibid, p. 196). He also cited the relatively robust mandibular corpus and the vertical and unbuttressed symphysis as further evidence of the Taung child's human affinities. It is noteworthy that Dart explicitly contrasted the humanoid nature of the Taung symphysis with that of the Piltdown jaw, noting that the symphysis of '*Eoanthropus dawsoni* scarcely differs from the anthropoids' (ibid, p. 197). Dart related the foramen magnum to prosthion, anteriorly, and inion, posteriorly, in a '... head-balancing index ...'. The value for Taung, 60.7, was intermediate between the value for an 'adult chimpanzee', 41.3, and 'Rhodesian man', 83.7 (ibid, p. 197). Lastly, Dart interpreted the relatively posterior location of the lunatic sulcus as evidence of expansion of the 'parietal region' of the brain (ibid, p. 198).

Since the discovery at Taung, the remains of hominins we now classify as *A. africanus* have been found at 3 other cave sites in southern Africa. At all these cave sites, as at Taung, early hominin fossils are mixed in with other animal bones in rock and bone-laden, hardened, cave fillings, or breccias. The cave at



□ Location of Locality Map Shown on Insert Map

■ Fossil Hominin Locality

--- River

Fig. 3. Location of cave sites in and around the Blauwbank Valley, South Africa.

Sterkfontein (Fig. 3) yielded its first hominin fossils in 1936, with further specimens being recovered in 1937 and 1938. When Robert Broom announced the discovery of the cranium TM 1511 in 1936, he expressed the opinion that the new cranium ‘probably agrees fairly closely with the Taungs ape’, but he went on to state that ‘... it is advisable to place the new form in a distinct species, ...’ (Broom, 1936*b*). He subsequently gave it the name *Australopithecus transvaalensis* (Broom, 1936*a*), but transferred it to a new genus, as *Plesianthropus transvaalensis*, some 2 years later (Broom, 1938), by which time mandibular (e.g. TM 1515) and postcranial (e.g. TM 1513) evidence had come to light. Excavations at Sterkfontein were held in abeyance until 1947, when Broom and John Robinson restarted them. To date, Sterkfontein has yielded a collection of more than 600 *Australopithecus* remains, most of them coming from Member 4 (but see below).

The first evidence of fossil hominins from Makapansgat, another southern African cave site, was the calvarium MLD 1, found in 1947. Raymond Dart allocated it to a new species, and gave it the name *Australopithecus prometheus* (Dart, 1948) because he believed that the Makapansgat hominin was capable of making fire. Hominin fossils continued to be recovered from Makapansgat until the early 1960s. In 1951 Sherwood Washburn, a primatologist, and Bryan Patterson, a paleontologist, wrote a joint letter to ‘Nature’ suggesting that the taxonomy of the Taung, Sterkfontein and Makapansgat hominins be rationalised, and their proposal received influential support from Sir Wilfrid Le Gros Clark (1955) in his

monograph ‘The Fossil Evidence for Human Evolution’. Thereafter it became conventional to refer all the ‘gracile’ remains from southern Africa to a single genus, *Australopithecus*, and it was not long before researchers and commentators carried the process of rationalisation a stage further by subsuming *A. transvaalensis* and *A. prometheus* into the species of *Australopithecus* with taxonomic priority, namely *A. africanus* Dart, 1925. The third site to yield the remains of *A. africanus* is Gladysvale (Fig. 3). Broom collected fossils there in 1936, but the first hominins, 2 teeth (referred to as GVH 1 and 2 in Berger et al. 1993, but as GVH-7 in Berger & Tobias, 1994) and a phalanx (GVH-8) were recovered nearly 60 years later, in 1991.

Until recently (see Partridge et al. 1999), the cave sites in southern Africa could only be dated by comparing the remains of the mammals found in the caves with the mammalian fossils found at the better-dated sites in East Africa. In this, and in other ways, the ages of the *A. africanus*-bearing breccias have been estimated to be between 2.4 and 3 myr. Claims for a substantially earlier age for Member 2 (Clarke & Tobias, 1995; Clarke, 1998; Partridge et al. 1999) have been challenged (McKee, 1996).

*Sites.* Taung (D-C), Sterkfontein (Member 4, and probably Member 2, but see below), Makapansgat (Member 3), Gladysvale, all in South Africa.

*Characteristic morphology.* The differences between *A. africanus* and *A. afarensis* are set out in detail in White et al. (1981) and Johanson (1985). Cranially the main contrasts are in the *A. africanus* face, which is broader and less prognathic than in *A. afarensis*. The mandibles of *A. africanus* have more robust corpora than those of *A. afarensis*. The main difference in the teeth is that, relative to *A. afarensis*, the anterior teeth are reduced in size and the postcanine teeth enlarged in *A. africanus*. Aside from these differences the crown of the  $dm_1$  is more complex in *A. africanus* than in *A. afarensis*.

In most respects, the postcranial skeleton of *A. africanus* resembles *A. afarensis* (McHenry, 1986), but there are a few important differences. First, the limb proportions of *A. africanus* may be less modern humanlike than those of *A. afarensis* and *A. anamensis* (McHenry & Berger, 1998). The lower vertebral column known for *A. africanus* shows that it possessed 6 functionally-defined lumbar vertebrae, more than the 5 typical of modern humans and 3–4 characteristic of great apes. In this way, it resembles *Homo ergaster*, and suggests that 6 lumbar vertebrae is the primitive condition for hominins. The suggestion that the *A. africanus* tibia is more chimpanzee-like (Berger &

Tobias, 1996) and the hallux more abducted than in *A. afarensis* and early *Homo* (Clarke & Tobias, 1995) is consistent with the apelike limb proportions. However, the tibial and pedal fossils of *A. africanus* and *A. afarensis* have not yet been directly compared. Although the hand of *A. africanus* retains apelike features such as longitudinal curvature and pronounced flexor ridges of the proximal phalanges, the pollical distal phalanx shows the derived morphology of having a large insertion for a flexor pollicis longus muscle and broad apical tuft (Ricklan, 1987). The wrist is also derived relative to extant African apes, *A. anamensis*, and *A. afarensis*, and is similar to modern humans, in lacking a distally-projecting dorsal ridge. Other postcranial differences between *A. africanus* and *A. afarensis* are more subtle, such as the tall glenoid fossa in *A. africanus* (McHenry, 1986).

*Behavioural implications.* The Sterkfontein evidence suggests that males and females of *A. africanus* differ substantially in body size, to a degree probably not unlike that in *A. afarensis* (Lockwood & Kimbel, 1999). The picture of *A. africanus* that is emerging from morphological and functional analyses suggests that its physique was much like that of *A. afarensis*, but its chewing teeth are larger (McHenry, 1988) and its skull is not as apelike. Its brain is larger than that of *A. afarensis*, but not substantially so. The postcranial skeleton (e.g. the pelvis) suggests that gait in *A. africanus* was similar to that in *A. afarensis*. The long lower back, more mobile and abductable hallux, and curved lateral tibial condyle are thought to have contributed to a pattern of bipedal gait unlike that of modern humans. This conclusion has recently received support from new data showing that the trabecular bone in the pelvis, which is highly responsive to loading patterns during life, is not arranged in the distinctive human pattern and, thus, it is likely to have experienced a biomechanical loading pattern unlike that seen during modern human bipedal gait (Macchiarelli et al. 1999). The more mobile hallux and curved tibial condyle, in addition to primitive traits such as curved phalanges shared with *A. afarensis*, suggest that *A. africanus* was a capable arboreal climber (McHenry, 1986; Ricklan, 1987; Clarke & Tobias, 1995; McHenry & Berger, 1998). However, the morphology of the pollical distal phalanx suggests that *A. africanus* had a thumb that was both powerful and equipped with a broad, fleshy fingertip useful in precision pinch and power grasping (Ricklan, 1987; Marzke, 1997). Furthermore, *A. africanus* has a flat distal radius designed to permit considerable extension at the wrist, possibly associated with tool-related manipulation (Marzke, 1971). The similarities in

pelvic anatomy between *A. afarensis* and *A. africanus* suggest that they shared a similar birth mechanism, namely that the birth process may have involved a transverse neonatal head position (but see Stoller, 1995). Stable isotope analysis of teeth from Makapansgat suggests that *A. africanus* ate  $^{13}\text{C}$ -enriched foods; that is, it either consumed plants such as grasses, or the flesh of animals, or insects, whose diet was  $^{13}\text{C}$ -rich (Sponheimer & Lee-Thorp, 1999).

*Paleohabitat.* The other animal fossils and the plant remains found with *A. africanus* suggest that the immediate habitat was dry woodland, with grassland beyond (Reed, 1997). One reconstruction of the habitat sampled at Makapansgat suggested that it was a subtropical forest environment (Rayner et al. 1993). The bones of the medium and large mammals found in the breccias of all the southern African hominin cave sites, as well as the hominins themselves, were either accumulated by predators, or they are there because the animals fell into, and were then trapped within, the caves.

*Hypodigm.* Holotype: Taung 1, a juvenile skull with partial endocast, Taung (formerly Taungs), South Africa, 1924. Paratypes: none. Well-preserved specimens: skulls—Taung 1; crania—Sts 5 and 71, Stw 505; mandibles—Sts 52; Stw 327, 384, 404 and 498; teeth—Stw 73, 151 and 252; axial skeleton—Stw/H 8; associated skeletons—Sts 14, Stw 431 and 573.

*Taxonomy.* Some researchers suggest that the fossil hominins recovered from Member 4 at Sterkfontein may sample more than one hominin species (e.g. Clarke, 1988; Kimbel & White, 1988; Moggi-Cecchi et al. 1998), with the cranium Sts 19 and the fragmented juvenile skull Stw 151 cited as possible examples of an 'early *Homo*'. More recently Clarke (1994) has suggested that the Member 4 hominin sample may include evidence of a 'proto' *Paranthropus robustus* (see below). It remains to be seen whether the foot bones, identified recently among fossils recovered in 1980 from Dump 20, Member 2 (Clarke & Tobias, 1995), and the Stw 573 skeleton of which they are part (Clarke, 1998), belong to *A. africanus*, or to a more primitive taxon. However, the case for taxonomic heterogeneity is currently not convincing enough to abandon the existing 'single-species' hypothesis as an explanation for the variation that is seen in the Member 4 sample (e.g. Ahern, 1998; Lockwood & Tobias, 1999).

*Australopithecus garhi* Asfaw et al. 1999

The Middle Awash sites of Aramis and Maka have, respectively, contributed all of the fossil evidence for

*Ardipithecus ramidus*, and an important component of the hypodigm of *A. afarensis* (see above). However, it was 2.5 myr-old hominin fossils (Asfaw et al. 1999) recovered from localities within the Hatayae (abbreviated to 'Hata') Member of the Bouri Formation (de Heinzelin et al. 1999), ~ 30 km to the south of the aforementioned sites, that prompted the recognition of another new australopith taxon. The new species is based on cranial fossils of which the best-preserved is the holotype, BOU-VP-12, from Locality 12.

*Sites.* Bouri, Middle Awash, Ethiopia.

*Characteristic morphology.* The taxon combines a relatively primitive cranium with canines larger than those of *A. afarensis*, and large-crowned postcanine teeth, especially premolars, that, despite the small size of the Bouri cranium, are as large as those of *Paranthropus boisei* (see below). However, unlike any *Paranthropus* species *A. garhi* possesses a relatively large anterior dentition and its postcanine teeth lack the extreme enamel thickness seen in *Paranthropus*. The authors of the paper announcing the new species claim that the cranium lacks the derived features of *Paranthropus*, and suggest that its face, palate and subnasal morphology are more primitive than that of *A. africanus* and *Homo*. The essentially primitive nature of *A. garhi* is suggested by the results of a recent cladistic analysis (Strait & Grine, 1999).

Although an associated skeleton, BOU-VP-12/1 A-G, has been recovered from an equivalent horizon, at a nearby locality, the discoverers of both this and the type specimen of *A. garhi* have resisted making the assumption that the skeleton and the cranium belong to the same species. The skeleton represents the first evidence of femur elongation in the hominin fossil record. However, this individual also exhibits a forearm that is as long or longer, relative to its humerus, as the upper limbs of *Pan*, *A. afarensis* and probably *A. africanus*, and contrasts with that of *Homo ergaster* (see below).

*Behavioural implications.* Behavioural implications have not yet been discussed in the literature, but the elongated femur suggests anatomical refinements related to bipedalism. However, the retention of long arms and a very high brachial index suggests that arboreality was also a significant component of the locomotor repertoire of whatever taxon is represented by the associated skeleton. Cut-marks on animal bones found at nearby localities suggest that *A. garhi*, or another contemporary hominin not yet found in the Bouri region (e.g., *H.* [or *A.*] *rudolfensis* or *P. aethiopicus*), was exploiting mammalian carcasses as a source of meat.

*Paleohabitat.* The fossil cranium was recovered

from sediments laid down on a floodplain crossed by channels making their way to a lake that fluctuated in size. The antelopes and pigs found from horizons similar to those yielding the hominins suggest a mixed, open woodland, paleohabitat (de Heinzelin et al. 1999).

*Hypodigm.* Holotype: BOU-VP-12/130, a cranium (N.B. the field number given in the formal description [Asfaw et al. 1999] of the holotype, ARA-VP-12/130, is a misprint; see erratum note in *Science*, **284**, p. 1623), Bouri, Middle Awash, Ethiopia; Paratypes: none.

*Taxonomy.* The announcement of *A. garhi* implied that it is the ancestor of *Homo*, but its morphology is consistent with other interpretations. For example, it could represent the sister-taxon of a clade comprising *A. africanus*, *Paranthropus*, and *Homo* (Strait & Grine, 1999). At present, the relationships of *A. garhi* are unresolved, and will remain so until researchers can determine which aspects of its morphology are synapomorphic and which are homoplastic.

### *Paranthropus*

Just as there are East and southern African variants of the so-called 'gracile' australopiths, there are also regional variants of another type of hominin that many now assign to a separate genus, *Paranthropus*. They are often referred to as 'robust' australopiths because of their relatively massive faces and lower jaws.

*Paranthropus robustus* Broom, 1938 and  
*Paranthropus crassidens* Broom, 1949

Remains of *Paranthropus robustus* come from southern African cave sites, and are dated to between ~ 1.9 and ~ 1.5 myr. The type specimen, an adult, presumably male, cranium, TM 1517, was recovered in June, 1938, at Site B of a cave called Kromdraai, and was announced and described in the same year (Broom, 1938). Kromdraai, like the caves of Swartkrans, Drimolen (see below), and Sterkfontein (see above), is in the Blaaubank Valley (Fig. 3). Subsequent discoveries were made at Kromdraai in 1941 (TM 1536), 1944 (TM 1603) and then again in the middle 1950s. Fossils found in excavations carried out in the 1970s have brought the number of hominin fossils recovered from Kromdraai to close to 20, sampling a minimum of 6 individuals (Vrba, 1981). Recent excavations in the cave have recovered a deciduous molar, KB 5503 (Thackeray, pers. comm.).

The first hominin, SK 6, was recovered from



Swartkrans in 1948 and was reported a year later (Broom, 1949). Three years of intensive excavation of Member 1 resulted in a rich collection of hominin remains. Hominins attributed to *P. robustus* have since been recovered not only from Member 1, but also from the Member 1/2 interface and from Members 2 and 3 (Brain, 1993, 1994). Nearly all of the research on the interpretation of how the various types of breccia entered the Swartkrans cave has been carried out by C. K. (Bob) Brain. It was also due to his efforts that the role played by predators in the accumulation of the fossil bones in the southern African cave sites was established (Brain, 1993). More recently, *P. robustus*-like hominins have been recovered from the sites of Drimolen and Gondolin (Fig. 3). The Drimolen site was discovered in 1992 and has already yielded 49 fossil hominins, the vast majority of which are referable to *P. robustus*. Gondolin was excavated by Vrba in 1979 (Watson, 1993), and the faunal remains now include 2 *Paranthropus* teeth, GDA 1 and 2 (Menter et al. 1999). Clarke (1994) reported the discovery of 3 *P. robustus*-like teeth, including a lower molar (StW 566) and an upper incisor and canine, during recent excavations in Member 5 at Sterkfontein.

*Sites.* Kromdraai B, Swartkrans (Members 1–3), Drimolen, Gondolin, and possibly Sterkfontein (Member 5), all in South Africa.

*Characteristic morphology.* The brain, face and chewing teeth of *P. robustus* are larger than those of *A. africanus*, yet the incisor and canine teeth are smaller. The postcanine teeth, like those of *P. aethiopicus* and *P. boisei*, have thick enamel. The cranium has ectocranial crests, and the cranial base is more flexed than in *A. africanus*. The cranial capacity has recently been reassessed to  $\sim 475 \text{ cm}^3$  (Falk et al. 2000). It also shares with *P. boisei* (see below) and *A. afarensis* a tendency for the intracranial venous blood to drain through a supplementary occipitomarginal system of dural sinuses. Some authors treat this evidence as strong support for a *Paranthropus* clade (Falk & Conroy, 1983), but others are less inclined to treat it as a phylogenetically-valent trait (Kimbel, 1984).

There are quite a few postcranial fossils from Kromdraai and, especially, Swartkrans that probably belong to *P. robustus*. The uncertainty stems from the fact that craniodental remains of both *Paranthropus* and *Homo cf. erectus* have been recovered from the lower members of Swartkrans (Susman, 1988b; Trinkaus & Long, 1990). However, because over 95% of the craniodental fossils are attributable to *P. robustus*, it is inferred that most of the postcranial

remains probably belong to this taxon (Susman, 1988b). With this caveat in mind, the postcranial skeleton of *P. robustus* retains some primitive features, but in many ways it is remarkably modern humanlike. The distal humerus resembles modern humans in its articular morphology, and the dorsal margin of the distal radius does not project distally as in the knuckle-walking African apes (Susman, 1988b; Grine & Susman, 1991). Hand fossils from Swartkrans show a number of derived humanlike features, including a broad pollical metacarpal head, straight-shafted manual proximal phalanges with relatively weak flexor sheath markings, and a pollical distal phalanx with a broad apical tuft with spines, and large insertion for a strong flexor pollicis longus muscle. The pelvis and hip joint resembles the morphology of *A. afarensis* and *A. africanus*, but the iliac blade is wider and the acetabulum, femoral head and sacral articular surface are smaller (McHenry, 1975). The femur shares with *P. boisei* and *H. habilis* femora an anteroposteriorly-flattened neck, and the cortical bone of the proximal femoral shaft of *P. robustus* is thick, and lacks the mediolateral buttressing seen in *H. erectus* (Ruff et al. 1999). In the foot, the hallucal metatarsal is strikingly humanlike, with an expanded inferior base, and dorsally-extended distal articular surface (Susman, 1988b).

*Behavioural implications.* Average body size estimates for *P. robustus* males ( $\sim 40 \text{ kg}$ ) and females ( $\sim 32 \text{ kg}$ ) suggest substantial sexual dimorphism. Cranial and dental differences between the taxa have led to the suggestion that the diet of *P. robustus* differed from that of *A. africanus*. Evidence from studies of dental microwear indicate that *P. robustus* ate foods that were substantially harder (Grine, 1986), but which considering the small size of their incisors, coupled with the relatively low microwear feature density (Ungar & Grine, 1991), may have required less incisal preparation. Stable isotope analysis of *P. robustus* tooth enamel suggests that its diet included substantial components of C-4 foods (Lee-Thorp et al. 1994), including grasses, sedges, some tubers, and the animals that eat these plants (Koch et al. 1994). Brain (1994) interprets these data as indicating that *P. robustus* 'were generalized rather than specialized feeders' (ibid, p. 222). Wear on bone tools found in the same breccia is consistent with digging, possibly for buried food items such as roots and tubers (Brain, 1988).

The similarities in hip and pelvic morphology with *A. afarensis* and *A. africanus* suggest that the gait of *P. robustus* probably resembled that of the 'gracile' australopiths (Macchiarelli et al. 1999). These simi-

Table 3. Differences between southern African 'gracile' (e.g. Sterkfontein) and 'robust' (e.g. Swartkrans) australopiths (taken from Robinson 1954b<sup>1</sup> and 1968<sup>2</sup>)

	'Gracile'	'Robust'
Cranial		
1. Overall shape <sup>1</sup>	Narrow, with 'unmistakable' forehead; higher value for supraorbital height index (Le Gros Clark, 1950)	Broad across the ears; lacking a forehead; low supraorbital height index
2. Sagittal crest <sup>2</sup>	Normally absent	Normally present
3. Face <sup>1</sup>	Weak supraorbital torus; variable degree of prognathism, sometimes as little as 'robust' form	Supraorbital torus well developed medially to form a flattened 'platform' at glabella; face flat and broad, with little prognathism
4. Floor of nasal cavity <sup>1</sup>	More marked transition from the facial surface of the maxilla into the floor of the pyriform aperture; sloping posterior border to the anterior nasal spine and lower insertion of the vomer	Smooth transition from facial surface of maxilla into the floor of the pyriform aperture; small anterior nasal spine that articulates at its tip with the vomer
5. Shape of the dental arcade and palate <sup>2</sup>	Rounded anteriorly and even in depth	Straight line between canines, deeper posteriorly
6. Pterygoid region <sup>2</sup>	Slender lateral pterygoid plate	Robust lateral pterygoid plate
Dental		
7. Relative size of teeth <sup>2</sup>	Anterior and posterior teeth in 'proportion'	Anterior teeth proportionally small; posterior teeth proportionally large
8. dm <sub>1</sub> <sup>1</sup>	Small, with relatively larger mesial cusps. Lingually situated anterior fovea; large protoconid with long, sloping buccal surface	Large, molariform, with deeply incised buccal groove and relatively large distal cusps
9. P <sup>3</sup> -roots <sup>1</sup>	Single buccal root	Double buccal root
10. $\bar{c}$ <sup>1</sup>	Large, robust and symmetric crown with slender marginal ridges and parallel lingual grooves	Small, <i>Homo</i> -like, with thick marginal ridges and lingual grooves converging on the gingival eminence
11. $\bar{c}$ <sup>1</sup>	Asymmetric crown with marked cusplet on the distal marginal ridge and marked central ridge on the lingual surface	More symmetric crown with parallel lingual grooves, weak lingual ridge and featureless distal enamel ridge

larities also suggest that *P. robustus* may have been obstetrically similar to the gracile australopiths. The expanded base of the hallucal metatarsal provides evidence that the foot of *P. robustus* possessed a well-developed plantar aponeurosis, and the dorsal expansion of the distal articular surface indicates humanlike extension of the hallux at toe-off of the gait cycle, both characteristics of modern human walking (Susman, 1988b). Unlike the 'gracile' australopiths, evidence is lacking for arboreal locomotion and posture; for example, the proximal manual phalanges are straight and lack pronounced muscle markings (Susman, 1988b). Instead, adaptations in the hand, such as a broad pollical metacarpal head, strong flexor pollicis longus insertion, and broad distal phalangeal tufts, suggest that *P. robustus* possessed the anatomical capabilities for powerful thumb use, and the refined manipulatory control involved in tool-making and tool-use (Susman, 1988a, 1994). Thus, *P. robustus* may have been responsible for the manufacture of the bone and stone artifacts found at Swartkrans (Brain, 1994).

*Paleohabitat.* Open, or bush/wooded, grassland seems to have been the context for the collections

recovered at Swartkrans and Kromdraai Site B (Reed, 1997).

*Hypodigm.* *Paranthropus robustus*. Holotype: TM 1517, adult cranium and associated skeleton, 'Phase II breccia', now Member 3. Kromdraai Site B, South Africa. Paratypes: none. *Paranthropus crassidens*. Holotype: SK 6, adolescent mandible, Member 1, Swartkrans, South Africa. Paratypes: none. Well-preserved specimens: crania—SK 48; mandibles—SK 12, 23, 34, 63; axial skeleton—SK 50.

*Taxonomy.* For a time some researchers insisted that *Australopithecus* and *Paranthropus* from southern Africa belonged to the same species (Wolpoff, 1971), but the 'single species' hypothesis, as it was called, has long since been refuted (e.g. Leakey & Walker, 1976). Details of the cranial and dental differences between the hominins recovered from Sterkfontein and Swartkrans cited by Robinson (1954a, b, 1968) as justification for their taxonomic separation are given in Table 3. Some workers consider that the differences between the hominins recovered from Swartkrans and Kromdraai are such that they advocate allocating the former to a separate species, *Paranthropus crassidens* Broom, 1949 (Howell, 1978; Grine, 1988).

*Paranthropus boisei* (Leakey, 1959) Robinson, 1960

The first evidence of an East African species of hominin resembling *P. robustus*, 2 deciduous lower teeth, OH 3, a canine and a molar, was found in 1955 at Olduvai Gorge, in Tanzania (Leakey, 1958). The type specimen of the new species, OH 5, a magnificent, undistorted, cranium with a well-preserved dentition, was recovered in July, 1959 (Leakey, 1959). The open sutures, the partially-erupted M<sup>3</sup>s, and the well-developed sagittal crests point to the cranium being that of an immature male. The new species was initially included in a new genus, *Zinjanthropus* (Leakey, 1959), but subsequent taxonomic reviews resulted in it being relegated to a subgenus (Leakey et al. 1964), and 3 years later it was proposed that any generic distinction between *Zinjanthropus* and *Australopithecus* should be abandoned (Tobias, 1967). It is now usual to refer to the taxon as *Australopithecus boisei*, or *Paranthropus boisei* (see also Robinson, 1960); the latter implies a sister group relationship between the 'robust' australopiths from East and southern Africa (see below). A fragmented cranium (OH 30) and several isolated teeth (OH 3, 26, 32, 38, 46 and 60) from Olduvai have been assigned to the same species. An ulna (OH 36) may also belong to *P. boisei* (Aiello et al. 1999).

Further evidence of *P. boisei* emerged with the discovery in 1964 of a mandible with a large, robust body, large premolar and molar crowns and small incisors and canines, at the Peninj River, on the shores of Lake Natron, in Tanzania (Leakey & Leakey, 1964; Tobias, 1965). Thereafter, some cranial, mandibular, but mostly dental, remains were recovered from the Shungura Formation in Ethiopia (Howell & Coppens, 1976; Coppens, 1980); an incomplete cranium (Carney et al. 1971), and cranial and tooth fragments (summarized in Wood, 1999b) were found at Chesowanja, in the Chemoigut basin, to the East of Lake Baringo, in Kenya; and the first skull (KGA 10-525), and 8 other ~1.4 myr-old specimens of *P. boisei*, were recovered from the site of Konso, in Ethiopia (Suwa et al. 1997). More details of all but the Konso specimens are given in Wood (1991, p. 27 and thereafter). Most recently a poorly-preserved maxillary fragment (HCRP RC 911) was recovered from the Chiwondo Beds, at Malema, Malawi (Kullmer et al. 1999). However, the site collection that provides the most comprehensive evidence about *P. boisei* is that from Koobi Fora, which is on the north-eastern shore of Lake Turkana. The Koobi Fora evidence includes crania, partial crania, many mandibles and

isolated teeth, and is described in detail in Wood (1991).

*Sites.* Olduvai Gorge and Peninj/Natron, in Tanzania; Shungura Formation, Omo Region and Konso Gardula, in Ethiopia; Koobi Fora, Baringo Region, and West Turkana, in Kenya; and Malema, in Malawi.

*Characteristic morphology.* The features that set *P. boisei* apart are to be found in the cranium, mandible and dentition. Cranially, it is the only hominin that combines a massive, wide, flat, face with a modest-sized neurocranium (~450 cm<sup>3</sup>). The face of *P. boisei* is larger and wider than that of *P. robustus*, yet its brain volume is the same, or smaller. Some features are apparently unique to *P. boisei*, such as the complex, overlapping parietotemporal suture, and others, such as the dominance of the occipitomarginal venous sinus system for draining blood from the base of the brain, are shared with other taxa. The flexed cranial base seems to be uniquely organised, with the foramen magnum situated relatively far forward for a hominin with a modest brain size. The articular region of the temporal bone combines a relatively deep, laterally-extensive fossa for the condyle of the mandible, a pronounced articular eminence and virtually no pregenoid planum (this morphology contrasts with the more primitive mandibular fossa of *P. aethiopicus*, see below). The mandibles have a larger and wider corpus, than any other hominin. The dentition combines very large-crowned, broad-based and thick-enamelled premolar and molar teeth (Wood et al. 1983) with small anterior (i.e. incisor and canine) teeth. The tooth crowns apparently grow at a faster rate than in any other early hominin (Beynon & Wood, 1987). The morphological differences between the southern and the East African forms of *Paranthropus* are listed in Wood (1991, pp. 258–268, Tables 2.8 and 2.9).

Despite the richness of the cranial evidence for *P. boisei*, there are no postcranial remains that can, with certainty, be ascribed to that taxon. Individual postcranial bones and a partial skeleton from Koobi Fora have been linked with the taxon (Grausz et al. 1988; Walker et al. 1989), but the evidence for doing so is far from conclusive (Wood, 1991, p. 182). The partial skeleton is characterised by limb proportions that resemble *A. afarensis* (Grausz et al. 1988), and are less apelike than those of *A. africanus*.

*Behavioural implications.* The picture that emerges from the fossil evidence is that *P. boisei* was a markedly sexually-dimorphic hominin, with the estimated average body mass of presumed males (~50 kg) being much greater than the mass of females

(~ 34 kg) (McHenry, 1992). The absolutely and relatively small canines mean that if there was intrasexual competition for females, then the males used other means to signal threats. The estimated cross-sectional areas of the mandibular corpora are between 2 and 3 times larger than expected for a hominoid of that body size. The large-crowned, thick-enameled, chewing teeth and the large mandibles with wide bodies, have conventionally been interpreted as evidence that the diet of *P. boisei* was a highly specialised one, devoted to eating seeds or fruits with hard outer coverings. It may be that this is entirely wrong, and *P. boisei* might have been the higher primate equivalent of a bushpig. In other words although its morphology is specialised, its large teeth and mandibles probably enabled it to cope with a wide range of dietary items, except that its jaws and teeth would have been ill-equipped to slice, or tear, raw meat.

If the partial skeleton, KNM-ER 1500, belongs to *P. boisei*, the limb proportions show that this hominid possessed hindlimb elongation indicative of bipedalism, like that in *A. afarensis* (Grausz et al. 1988). However, like *A. afarensis*, the relatively long forelimbs suggest that the locomotor behaviour of *P. boisei* included an arboreal component.

*Paleohabitat.* Shipman & Harris (1988) suggested that *P. boisei* specimens were more likely to be found in closed habitats, but a more recent analysis found that *P. boisei* remains are most commonly associated with relatively open habitats associated with grassland, including open woodland and scrub woodland, close to a water source (Reed, 1997).

*Hypodigm.* Holotype: OH 5, adolescent cranium found at site FLK, Bed I, Olduvai Gorge, Tanzania. Well-preserved specimens: skulls—KGA 10-525; crania—KNM-ER 406, 407, 732, 13750, 23000, KNM-WT 17400; mandibles—Peninj 1, KNM-ER 729, 3230, 15930.

*Taxonomy.* Researchers have suggested that the hypodigm of *P. boisei* may display more variation than can be accommodated within one species (Dean, 1988). However, some of the apparently excessive variation in size is due to taphonomic factors, and the residue does not exceed the variation observed in living higher primate taxa (Silverman et al. unpublished).

*Paranthropus aethiopicus* (Arambourg & Coppens, 1968) Chamberlain & Wood, 1985

The earliest East African fossil evidence for 'robust' australopiths is interpreted by some researchers as

being taxonomically distinct from the main *P. boisei* hypodigm. One of the oldest of the 'robust' mandibles recovered from the Shungura Formation was made the holotype of a novel species and genus, *Paraustralopithecus aethiopicus* (Arambourg & Coppens, 1968), and when a distinctive 2.5 myr-old cranium (Walker et al. 1986) was recovered from sediments at West Turkana it was natural to consider whether it should be assigned to the same taxon. Suwa (1988) has pointed out that the pre-2.3 myr-old dental remains are not as derived as the bulk of the *P. boisei* sample that is younger than 2.3 myr, and he has suggested that these differences might warrant separate taxonomic recognition. Wood et al. (1994) found that several features of the mandible and the mandibular dentition of the East African *Paranthropus* lineage change around 2.3 myr-ago, and they supported the interpretation that the 'early' and the 'late' stages of the robust lineage in East Africa should be recognised as different taxa, with the former being referred to as *Paranthropus aethiopicus*.

*Sites.* Shungura Formation, Omo Region, in Ethiopia; Nachukui Formation, West Turkana, Kenya.

*Characteristic morphology.* *P. aethiopicus* has a more primitive cranial vault and base, including a shallow articular fossa, and a low articular eminence continuous with a flat pregenoid planum, along with a more prognathic face, larger incisors and a less-flexed cranial base than *P. boisei*. No postcranial remains are currently known for this taxon.

*Behavioural implications.* The larger incisors suggest that these teeth played more of a role in feeding and food processing than is the case for *P. robustus* and *P. boisei*.

*Paleohabitat.* Associated faunas suggest that the habitat of *P. aethiopicus* was 'more closed' than that of *P. boisei* (Reed, 1997).

*Hypodigm.* Holotype: Omo 18.18 (or 18.1967.18), edentulous adult mandible, locality Omo 18, Section 7, Member C, Shungura Formation, Omo Region, Ethiopia. Well-preserved specimens: cranium—KNM-WT 17000; mandible—KNM-WT 16005.

*Taxonomy.* (See above.)

### *Homo*

*Homo habilis* Leakey et al. 1964

In 1960, a year after the discovery of the type specimen of *P. boisei*, OH 5, from Bed I at Olduvai Gorge, Louis and Mary Leakey recovered substantial parts of both parietal bones, 'a large part of a left

foot', and 6 hand bones making up the specimens that became known as OH 7 and 8 (Leakey, 1960). In the next year, or so, further evidence of a 'non-robust' hominin was unearthed in both Beds I (OH 4 and 6—skull fragments and teeth; OH 7—a juvenile mandible and more hand bones; OH 14—juvenile cranial fragments, and OH 16—a fragmented cranial vault and maxillary dentition of a young adult), and Bed II (OH 13—the incomplete skull of an adolescent) of Olduvai Gorge (Leakey, 1961*a, b*; Leakey & Leakey, 1964). The parietal bones of OH 7 showed no sign of *P. boisei*-like bony crests, and the premolar and molar teeth were too small for *Paranthropus*. In 1964, Louis Leakey, Phillip Tobias and John Napier set out the case for recognising a new species for the nonrobust hominin from Olduvai, and for accommodating it within the genus *Homo* (Leakey et al. 1964). This necessitated amending Le Gros Clark's 1955 diagnosis of *Homo*. It involved relaxing some criteria, such as brain size, so that the relatively small-brained ( $\sim 600\text{--}700\text{ cm}^3$ ) crania from Olduvai Gorge (OH 7, 13 and 16) could be included. Leakey and his colleagues argued that the Olduvai evidence for *H. habilis* complied with the functional criteria for assigning species to *Homo*, namely dexterity, an upright posture and a bipedal gait. The proposal to erect a new species, and then to incorporate it within *Homo*, was received with some skepticism. Some critics suggested that the new material was not sufficiently different from *A. africanus* to justify creating a new species (e.g. Le Gros Clark, 1964*a*; Holloway, 1965). Others took the view that the *Homo habilis* hypodigm was a mixture of *A. africanus*-like material from Bed I, and *Homo erectus*-like remains from Bed II (e.g. Robinson, 1965).

In due course additional specimens from Olduvai were added to the hypodigm of *H. habilis*, the most significant being the cranium OH 24 (Leakey, 1969; Leakey et al. 1971), and the fragmentary associated skeleton, OH 62 (Johanson et al. 1987). The discovery of OH 24 was important because it resembled OH 13, but was found not in Bed II, but near the base of Bed I, making it the oldest of the specimens from Olduvai Gorge allocated to *H. habilis*. This meant that it was no longer possible to argue that there was a temporal cline in the morphology of the *H. habilis* remains, from more 'primitive' specimens at the base of Bed I, to morphologically 'more advanced' fossils in Bed II (see below). The implications of the OH 62 associated skeleton were rather different. Its limb proportions were evidently more primitive than those of any other *Homo* species, indeed it has been claimed that they were more primitive than those of *A. afarensis*

(Hartwig-Scherer & Martin, 1991). If OH 62 belonged to *H. habilis*, then the locomotor adaptations of *H. habilis* were no more later *Homo*-like than those of early australopiths.

The most significant contribution to the collection of fossils attributed to *H. habilis sensu lato* came from the site of Koobi Fora. The Koobi Fora evidence includes well-preserved crania (e.g. KNM-ER 1470, 1805, 1813), mandibles (e.g. KNM-ER 1802) and isolated teeth; all this material was found either in the 1972 field season, or thereafter (Wood, 1991). Initially these specimens were not allocated to a species, but given the informal name 'early *Homo*'. Some of the hominin fossils recovered from Members G and H of the Shungura Formation have been assigned to *H. habilis*, including a fragmented cranium, L894-1 (Boaz & Howell, 1977), 2 mandibles and isolated teeth (Coppens, 1980; Suwa et al. 1996). A fragmentary cranium and some isolated teeth from Member 5 at Sterkfontein are said to resemble *H. habilis* (Hughes & Tobias, 1977), and the same proposal has been made with respect to the so-called 'composite' cranium, SK 847, from Member 1 at Swartkrans (Grine et al. 1993), and a maxilla from Hadar (Kimbel et al. 1997). Suggestions that *H. habilis* remains have been recovered from sites beyond Africa (Tobias & von Koenigswald, 1964) have not received wide acceptance. The youngest of the specimens allocated, or likened, to *H. habilis* is OH 13 which is dated to  $\sim 1.6$  myr; the oldest would be the  $\sim 2.3$  myr A.L. 666-1 maxilla from the Kadar Hadar Member at Hadar (Kimbel et al. 1997).

*Sites.* Olduvai Gorge, Tanzania; Shungura Formation, Omo Region, and Hadar Formation, in Ethiopia; Koobi Fora, Kenya.

*Characteristic morphology.* The material allocated to what some refer to as 'early *Homo*', and others as *H. habilis sensu lato*, has a relatively wide-range of cranial morphology. The endocranial volume ranges from just less than  $500\text{ cm}^3$  to  $\sim 800\text{ cm}^3$ , and all the crania in this group are wider at the base than across the vault. The facial morphology varies, with KNM-ER 1470 having its greatest width across the mid-face and little nasal projection, compared with KNM-ER 1813 which is broadest across the upper face. The mandibles vary in size and robusticity, with those from the larger individuals having robust bodies and premolar teeth with complex crowns and roots. Knowledge of the postcranial skeleton has traditionally come from the remains from Bed I at Olduvai Gorge, but although these were allocated to *H. habilis* it is by no means certain that one can exclude their allocation to *P. boisei* (Wood, 1974, 1991). The only

postcranial evidence from Olduvai Gorge that can, with confidence, be allocated to *H. habilis* is the associated skeleton OH 62, and some of the postcranial bones associated with the OH 7 type specimen. Very little of the morphology of OH 62 is preserved, but it is possible to estimate the relative lengths of the segments of the upper and lower limbs and these show that the skeleton probably had longer arms relative to leg length than any other species within *Homo*, and possibly also *A. afarensis* and *A. garhi* (Hartwig-Scherer & Martin, 1991; Asfaw et al. 1999). If estimates for OH 62 are accurate (Korey, 1990), only *A. africanus* matches, or exceeds, its upper limb size (McHenry & Berger, 1998). Other characteristics of the OH 62 postcranium are also primitive, such as the relatively large radial tuberosity, the *A. afarensis*-like ulna, and the small, gracile femur with a long neck and low neck-shaft angle (Johanson et al. 1987). The femur resembles those of *Paranthropus* in having an anteroposteriorly-narrow neck. The femora KNM-ER 1472 and KNM-ER 1481 are much larger and more modern than the OH 62 femur, and almost certainly do not represent *Homo habilis sensu lato*, despite suggestions to the contrary (Wood, 1992).

Of the 21 bones described as comprising the OH 7 hand of *H. habilis*, only 15 are hominid and, of those, only 2 are adult (Napier, 1962). The remaining 13 bones include seven that are clearly subadult and 6 of uncertain age, as well as carpals from the left and right sides (Day, 1976). These 13 bones, together comprising the OH 7 hand(s), display a mosaic of primitive and derived traits (Susman & Creel, 1979). Apelike features shared with *Australopithecus*, but not *P. robustus*, include robust and curved middle and proximal phalanges, with well-developed markings for the flexor digitorum superficialis muscle and flexor sheaths, respectively. Modern humanlike features, also present in the Swartkrans fossils (see above), include the morphology of pollical carpometacarpal joint of the trapezium, and the broad apical tufts of the distal phalanges (Napier, 1962; Susman & Creel, 1979). The foot is characterised by a humanlike adaptations to stabilise the lateral side and the calcaneocuboid joint, but has a relatively mobile talonavicular joint, and a robust, but slightly less adducted, hallux than that seen in modern humans (Kidd et al. 1996). In sum, there is little to distinguish the postcranial skeleton of *H. habilis* from that of *Australopithecus* and *Paranthropus*.

*Behavioural implications.* Few, if any, of the initial interpretations of *H. habilis* have survived closer scrutiny, or have been supported by subsequent additions to the hypodigm. Estimates of body mass on

probable female specimens suggest that the range for *H. habilis* was in the order of 25–37 kg based on orbital dimensions (Aiello & Wood, 1994); these estimates are consistent with those of 30–33 kg based on limited postcranial evidence (McHenry, 1992). When these estimates are used to scale brain and postcanine tooth size, *H. habilis* is more similar to the australopiths than to later *Homo* (Wood & Collard, 1999).

Similar conclusions apply to the locomotor and language abilities of *H. habilis*. If OH 62 is representative of *H. habilis*, the skeletal evidence suggests that its bipedalism was not unlike that in australopiths, and the curved proximal phalanges and well-developed muscle markings on the phalanges of OH 7 indicate a hand used for more powerful grasping than is evident in any other species of *Homo*. Such features are most likely to be related to arboreal activities (Susman & Creel, 1979; Susman & Stern, 1982). Evidence for mobility in some regions of the foot is consistent with this interpretation. Conclusions to the effect that *H. habilis* was capable of spoken language (Tobias, 1987) were based on inferences about the links between endocranial morphology and language comprehension and production that are no longer valid (Gannon et al. 1998). Adaptations in the hand (see above) indicate that *H. habilis* was capable of the manual dexterity involved in the manufacture and use of tools, including the tool-types of the Oldowan Industry. Despite the small absolute size of the teeth and jaws, when these are scaled using estimated body mass, *H. habilis* has a larger mandible than would a living hominoid of the same body mass (Wood & Aiello, 1998), and it is relatively megadont (Wood & Collard, 1999). This indicates that its diet was much like that of the australopiths.

*Paleohabitat.* There is no indication that *H. habilis sensu lato* remains were restricted to a particular habitat and the taxon persists at Olduvai Gorge, and elsewhere, even when habitats became more open.

*Hypodigm.* Holotype: OH 7—partial calotte and hand bones, FLKNN 1, Bed 1, Olduvai Gorge, Tanzania. Paratypes: OH 4, MK I; OH 6, FLK I; OH 8, FLKNN I; OH 13, MNK II, all at Olduvai Gorge, Tanzania; Hadar Formation, Ethiopia. Well-preserved specimens of *H. habilis sensu stricto*: skulls—OH 13, KNM-ER 1805; crania—OH 24, KNM-ER 1813; teeth—OH 16; lower limb—OH 8.

*Taxonomy.* From the outset researchers have questioned the integrity of *H. habilis*. Initially, the main criticism was that, within the linear, anagenetic, model of evolution prevailing at the time, there was insufficient ‘morphological space’ between *A.*

*africanus* and *H. erectus* for another taxon. Critics claimed that *H. habilis* was in effect an amalgam of geologically older ‘advanced’ *A. africanus* fossils, and geologically younger ‘primitive’ *Homo erectus* remains. This criticism was countered by the demonstration that at Olduvai Gorge one of the most morphologically ‘advanced’ (OH 24) specimens was also geologically the oldest. Researchers have also shown that the distinguishing features of *H. habilis* are not simply an admixture of the characteristics of *A. africanus* and *H. erectus*, but are a distinctive combination of morphological features (Wood, 1991, 1992). The third objection to *H. habilis* has been the claim that it had begun to subsume fossils whose morphology was so different that the variability within the taxon had become excessive. It was simply too variable to make a plausible species. Views on this are polarised, with some researchers supporting the retention of a single taxon, *H. habilis sensu lato*, for this material (Miller, 1991; Tobias, 1991; Suwa et al. 1996), and others supporting a ‘two-taxon’ solution (e.g. Wood, 1985; Stringer 1986; Lieberman et al. 1988; Kramer et al. 1995; Grine et al. 1996). This debate is explored in more detail below in the next section on *Homo rudolfensis*. A recent reassessment of cladistic and functional evidence concluded that there are few, if any, grounds for retaining *H. habilis* in *Homo*, and recommended that the material be transferred (or, for some, returned) to *Australopithecus* (Wood & Collard, 1999), as *Australopithecus habilis* (Leakey et al. 1964) as *Australopithecus habilis* (Leakey et al. 1964, Wood & Collard, 1999).

*Homo rudolfensis* (Alexeev, 1986) *sensu* Wood, 1992

In a presentation of the fossil evidence for human evolution, published in English in 1986, the Russian anthropologist Valery Alexeev (1986) suggested that the differences between the cranium KNM-ER 1470 and the fossils from Olduvai Gorge allocated to *Homo habilis* justified referring the former to a new species, *Pithecantropus rudolfensis*, within a genus others had long ago sunk into *Homo* (see *H. erectus* section below). Some workers have claimed that Alexeev either violated, or ignored, the rules laid down within The International Code of Zoological Nomenclature (Kennedy, 1999). However, there are no grounds for concluding that Alexeev’s proposal did not comply with the rules of the Code, even if he did not follow all of its recommendations (Wood, 1999*a*). Thus, if *Homo habilis sensu lato* does subsume more variability than is consistent with it being a single species, and if

KNM-ER 1470 is judged to belong to a different species group than the type specimen of *Homo habilis sensu stricto*, then *Homo rudolfensis* (Alexeev, 1986) would be available as the name of a second early *Homo* taxon.

This does seem to be the case, for several independent studies have shown that the degree of variation within *Homo habilis sensu lato* is greater than that which would be expected in a single species (Lieberman et al. 1988; Wood, 1991; Rightmire, 1993; Kramer et al. 1995; Grine et al. 1996). Several researchers have recommended that the material be split into 2 species. The scheme that has received most support sorts the material into *H. habilis sensu stricto* (hereafter referred to as *H. habilis*), whose hypodigm consists of all the material attributed to the original taxon from Olduvai Gorge, together with a subset of the material attributed to *H. habilis sensu lato* from Koobi Fora (Wood, 1991, 1993). The distinguishing features of the second taxon, *Homo rudolfensis* (Alexeev, 1986) *sensu* Wood, 1992, are described below.

*Sites.* Olduvai Gorge, Tanzania; Koobi Fora, Kenya; Uraha, Malawi, and perhaps also the Shungura Formation, Ethiopia.

*Characteristic morphology.* The main ways that *H. rudolfensis* departs from *H. habilis* are their different mixtures of primitive and derived, or specialised, features. For example, although the absolute size of the brain case is greater in *H. rudolfensis*, its face is widest in its mid-part, whereas the face of *H. habilis* is widest superiorly. Despite the absolute size of its brain (~ 750–800 cm<sup>3</sup>), when it is related to estimates of body mass the brain of *H. rudolfensis* is not significantly larger than those of the australopiths (Kappelman, 1996). Similarly, *H. rudolfensis* also shows the postcanine megadontia that characterizes all australopiths, except the earliest hominin *Ardipithecus*. The more primitive face of *H. rudolfensis* is combined with a robust mandible and postcanine teeth with larger crowns and more complex premolar root systems than those of *H. habilis*. There are no postcranial bones associated with *H. rudolfensis*, despite the implication that the femora KNM-ER 1472 and KNM-ER 1481 should be assigned to *H. rudolfensis* (Wood, 1992).

*Behavioural implications.* Orbital dimensions based on a probable male fossil predict a body mass of ~ 45 kg (Kappelman, 1996). The mandible and postcanine teeth are larger than one would predict for a generalised hominoid of the same estimated body mass (Wood & Aiello, 1998), suggesting that its dietary niche made similar mechanical demands to

that of the australopiths. There is no associated postcranial evidence, thus no reconstructions of locomotion and dexterity can be made.

*Paleohabitat.* No information available.

*Hypodigm.* Lectotype: KNM-ER 1470—Area 131, Upper Burgi Member, Koobi Fora Formation, Koobi Fora, Kenya. Well-preserved specimens: crania—KNM-ER 1470, 1590 and 3732; mandibles—KNM-ER 1802, UR 501.

*Taxonomy.* The case for a separate species has been set out above. A recent review of the cladistic and functional evidence for *H. rudolfensis* has concluded that there are few grounds for its retention in *Homo*, and recommended that it be transferred to *Australopithecus* as *Australopithecus rudolfensis* (Alexeev, 1986) Wood & Collard, 1999.

#### *Homo ergaster* Groves and Mazák, 1975

This taxon was introduced in the wake of a review of the fossils from Koobi Fora allocated to 'early *Homo*' (Groves & Mazák, 1975). The type specimen is KNM-ER 992, an adult mandible that had been compared with, and by some workers, referred to, *Homo erectus*. The paratypes include the skull KNM-ER 1805, but the only detailed analysis of KNM-ER 1805 concluded that it should be referred to *H. habilis* (Wood, 1991). Thus, in these circumstances, decisions about whether *Homo ergaster* is a good taxon depend on researchers demonstrating that the type specimen, KNM-ER 992, can be distinguished from *H. erectus* (see below). Similarities between the Koobi Fora component of the *H. ergaster* hypodigm and the juvenile skeleton, KNM-WT 15000, from West Turkana, suggest that the latter should be included in *H. ergaster*. Remains attributed to *H. ergaster* span the time between ~ 1.9 myr and ~ 1.5 myr.

*Characteristic morphology.* The features that have been claimed to distinguish *H. ergaster* from *H. erectus* fall into 2 groups (Wood, 1984, 1994). The first consists of the ways in which *H. ergaster* is more primitive than *H. erectus*. The best evidence in this category comes from details of the mandibular dentition, and in particular the mandibular premolars. It is claimed that the crowns and the roots of these teeth in *H. ergaster* are more like those of the hypothetical common ancestor of the hominins than are those of *H. erectus*. The second category consists of the ways that *H. ergaster* is less specialised, or derived, in its cranial vault and cranial base morphology, than is *H. erectus*. For example, it is argued that *H. ergaster* lacks some of the more derived features of *H. erectus* cranial morphology, such as

thickened inner and outer tables, and prominent sagittal and angular tori (Wood, 1984, 1991), but others dispute the distinctiveness of this material (see below).

Characterisation of the postcranial skeleton is largely based on the associated juvenile KNM-WT 15000 skeleton that in many respects resembles modern humanlike morphology more than any hominins discussed up to this point. First, the body size, with an estimated stature at adulthood of 185 cm, and an adult body mass of ~ 70 kg (Ruff & Walker, 1993), is larger than any earlier hominin. It has a humanlike rib cage that does not diverge inferiorly, and a pelvis that is relatively narrow compared with australopiths, but substantially broader with more flaring ilia than modern human pelves (Ruff, 1995). KNM-WT 15000 retains a long back with 18 thoracolumbar segments, comprised of 12 thoracic and 6 lumbar vertebrae (Latimer & Ward, 1993). The lower limb is as long as would be expected for a modern human of the same stature, giving *H. ergaster* modern human-like intermembral proportions. KNM-WT 15000 provides the earliest evidence of modern human-like brachial proportions, and they compare best with modern humans from hot, arid regions (Ruff, 1995). The upper limb bones generally lack the curvature, length, and robusticity characteristic of australopiths and *H. habilis*. The long femoral neck is set at a relatively low angle to the shaft, but the femoral head is as large as an equivalent-sized modern human (Brown et al. 1985).

*Behavioural implications.* Wood & Collard (1999) suggest that *H. ergaster* is the first large-bodied hominin taxon with a body shape that was closer to that of modern humans than to the australopiths (see also Ruff & Walker, 1993). It was also the first to combine modern human-sized chewing teeth with a postcranial skeleton (e.g. long legs, large femoral head) committed to long-range bipedalism. It is also the first hominin that appears to lack features associated with arboreal locomotor and postural behaviours. The relatively small size of the thoracic vertebral canal has been taken as evidence that fine control of breathing necessary for sophisticated speech is lacking (MacLarnon & Hewitt, 1999), but the link is a tenuous one, and skeletal dysplasia may have contributed to the narrow canal (Ohman et al. 1998).

The mandible and postcanine tooth crowns of *H. ergaster*, when scaled to a surrogate for body mass, are no larger than those of modern humans, in comparison with the australopiths. This suggests that either *H. ergaster* was ingesting different foodstuffs, or



that the same foodstuffs were being prepared outside the mouth, perhaps by cooking (Collard & Wood, 1999; Wood & Brooks, 1999).

*Paleohabitat.* There are insufficient specimens to establish whether the paleohabitat of East African *H. ergaster* was significantly different from that of its australopith precursors and contemporaries. Claims for the presence of *H. ergaster* in Asia (Wanpo et al. 1995) and the Caucasus (Gabunia & Vekua, 1995; Bermúdez de Castro et al. 1998), implying that *H. ergaster* was capable of flourishing in temperate climates, rest, in the former case, on relatively tenuous morphological evidence.

*Hypodigm.* Holotype: KNM-ER 992, Area 3, Okote Member, Koobi Fora Formation, Koobi Fora, Kenya. Paratypes: KNM-ER 730, 731, 734, 803, 806, 807, 808, 809, 820, 1480, 1805. Well-preserved specimens: skeleton—KNM-WT 15000; crania—KNM-ER 3733, 3883; mandibles—KNM-ER 820, 992.

*Taxonomy.* It should be pointed out that the majority of researchers do not regard the *H. ergaster* hypodigm as worthy of a separate species. They have either disputed that there are any consistent, or significant, morphological differences between the ‘early African’ part of *H. erectus* (i.e. *H. ergaster*) and the main *H. erectus* hypodigm (e.g. Bräuer & Mbua, 1992; Bräuer, 1994), or they acknowledge that there are differences, but suggest that they do not merit recognition at the level of the species (e.g. Turner & Chamberlain, 1989; Harrison, 1993; Kramer, 1993; Rightmire, 1998).

*Homo erectus* (Dubois, 1892) Mayr, 1944

In 1890 Eugene Dubois found a mandible fragment in Java at a site called Kedung Brubus. Less than a year later, in 1891, at excavations on the banks of the Solo river at Trinil, workers unearthed a skullcap that became the type specimen of a new, and what was at the time a significantly more primitive, species of fossil hominin. In his initial, 1892, publication of the Trinil remains Dubois placed the skull cap in the genus *Anthropopithecus*, but 2 years later, in 1894, he transferred the new species to *Pithecanthropus*. What made the discovery of the Trinil braincase so significant was its small cranial capacity relative to that of modern humans,  $\sim 850 \text{ cm}^3$ , and its primitive shape with its low brain case and quite sharply-angulated occipital region; these were the same features that caused Dubois to think initially that he had recovered the remains of an ape. The search for hominins at Trinil continued for a decade; the last hominin fragment to be recovered from the site was

found in 1900. The focus for the next phase of the search for hominin remains in Java was upstream of Trinil, where the Solo River cuts through the Plio-Pleistocene sediments of what is called the Sangiran Dome. It was here in 1936 that a German paleontologist, Ralph von Koenigswald, began his search for evidence for hominin evolution. He recovered a cranium that resembled the distinctive shape of the Trinil skullcap, but the brain size,  $\sim 750 \text{ cm}^3$ , was even smaller than that of the Trinil calotte. More remains were recovered until WWII curtailed research.

Meanwhile, a Swedish paleontologist, Gunnar Andersson, and a junior colleague from Austria, Otto Zdansky, had excavated for 2 seasons, 1921 and 1923, at the Zhoukoudian (formerly spelled Choukoutien) Cave, near Beijing, in China, recovering only quartz artifacts and what were apparently nonhominin fossils. However, in 1926, in the course of reviewing the excavated material that had been shipped to Uppsala, Zdansky realized that 2 of the ‘ape’ teeth were hominin. The teeth, an upper molar and a lower premolar, were described by the anatomist Davidson Black in 1926, and together with a well-preserved left permanent first lower molar tooth (Ckn. A.1.1) found in 1927, they were assigned to *Sinanthropus pekinensis* (Black, 1927). In the same year Black, together with a Chinese colleague, Weng Wanhao, and Anders Bohlin, resumed the excavations at Zhoukoudian. The first cranium was found in 1929 and excavations continued until they were interrupted by WWII. The fossils recovered from Locality 1 were consistent in their morphology, which resembled that of *Pithecanthropus erectus* recovered in the previous century from Java.

Since then similar material has been found at other sites in China (e.g. *Sinanthropus lantianensis* (Woo, 1964), at Lantian, 1963–4); southern Africa (*Telanthropus capensis* Broom & Robinson, 1949, at Swartkrans, 1949 and thereafter); East Africa (*Homo leakeyi* Heberer, 1963, at Olduvai Gorge, 1960 and thereafter); early African *H. erectus/ergaster* (Groves & Mazák, 1975), at West and East Turkana, 1970 and thereafter; *Homo* sp. at Melka Kunture, 1973 and thereafter, and *Homo* sp. at Buia, Eritrea, 1995 and 1997; and in North Africa (*Atlantropus mauritanicus* Arambourg, 1954 at Tighenif, 1954–5). Many researchers also include the remains from Ngandong, Indonesia (*Homo (Javanthropus) soloensis* Oppenoorth, 1932) in this group (Santa Luca, 1980; Rightmire, 1990).

Despite the relatively large numbers of crania from Java, China and elsewhere, little was known about the

postcranial morphology of what was to become *H. erectus*, and it was discoveries from East African sites that provided the crucial evidence. This came in the form of a pelvis and femur from Olduvai Gorge (OH 28), 2 fragmentary partial skeletons from East Turkana (KNM-ER 803 and 1800), and an especially rich source of evidence was the unusually well-preserved skeleton from West Turkana (KNM-WT 15000). However, see the discussion in the previous section for an alternative classification of the East and West Turkana components of this ‘early African’ evidence from Koobi Fora that some refer to *H. ergaster*. Recent proposals have extended the temporal range of *H. erectus sensu stricto* from ~ 1.8 myr to ~ 50 kyr if suggestions for the extreme antiquity for Modjokerto/Perning (Swisher et al. 1994) and the very recent date for Ngandong (Swisher et al. 1996) are confirmed.

*Sites.* Africa (e.g. Olduvai Gorge, Tanzania; Melka Kunture, Ethiopia); Asia (e.g. Zhoukoudian, China; Sangiran and Sambungmachan, Indonesia).

*Characteristic morphology.* The crania of *H. erectus* all have a low vault, the greatest width of which is low down on the cranium. There is a substantial, essentially continuous, torus above the orbits, a post-toral sulcus, a sagittal torus, and an angular torus that runs towards the mastoid process. The occipital region is sharply-angulated, with a well-marked supratotal sulcus. The inner and outer tables of the cranial vault are thick. Cranial capacity varies from ~ 725 cm<sup>3</sup> for OH 12, to ~ 1250 cm<sup>3</sup> for the Solo V calotte. The greatest width of the face is in the upper part. The palate has similar proportions to those of modern humans, but the buttressing is more substantial. The body of the mandible is more robust than that of modern humans and the subvertical symphysis lacks a well-marked chin. The tooth crowns are generally larger than those of modern humans, the third molar usually being smaller, or the same size, as the second. The roots of the premolar teeth tend to be more complicated than those of modern humans. The cortical bone of the postcranial skeleton is generally thicker than is the case for modern humans. The limb bones are modern humanlike in their proportions and have robust shafts, with the femoral shaft flattened from front to back (platymeria) and the tibial shaft flattened from side to side (platycnemia) relative to those of modern humans. Like other fossil *Homo* taxa, the pelvis has a large acetabulum and exhibits a characteristic ‘iliac pillar’, a thickened region of the iliac blade superior to the acetabulum (Day, 1971), and the pelvic inlet appears to be relatively wide transversely and shallow anteroposteriorly (Ruff,

1995). Some of the hypodigm displays morphology which is later *Homo*-like, e.g. Ngandong (Santa Luca, 1980) and Buia (Abbate et al. 1998), but these tend to be isolated characters in otherwise *H. erectus*-like crania or calottes. More details of the characteristic morphology of *H. erectus* are given in Wood (1984, 1991) and Rightmire (1990).

*Behavioural implications.* There are morphological differences between this material and *H. sapiens*, but all the dental and cranial evidence points to a more modern human-like diet than that of the australopiths, and the postcranial elements are consistent with a habitually upright posture and obligate, long-range bipedalism. The shape of the true pelvis suggests that, during birth, the neonatal head was oriented transversely and did not involve rotation (Ruff, 1995). There is no direct fossil evidence relevant to assessing the dexterity of *H. erectus*, but if *H. erectus* manufactured Acheulean artefacts then a high degree of dexterity would be implicit.

*Paleohabitat.* *H. erectus* (or perhaps *H. ergaster*—see above) is the first hominin to be found ‘out of Africa’ in regions that were more seasonal and temperate than East and southern Africa.

*Hypodigm.* Holotype: Trinil 2, adult calotte found at Trinil, near Ngawi, Java in 1891. Well-preserved specimens: crania—‘*Sinanthropus*’ Skulls II, III, X, XI, and XII; Sangiran 2 (Pith II), 4 (Pith IV), 17 (Pith VIII); OH 9; mandibles—‘*Sinanthropus*’ B 1, G 1; Sangiran 9; Tighenif 1–3.

*Taxonomy.* Until the taxonomy was rationalised, the 2 main regional subsets of this material were attributed to 3 different genera, *Pithecanthropus* and *Meganthropus* in Java, and *Sinanthropus* in China, with a fourth genus, *Atlanthropus*, being used for the North African material. In 1940 Le Gros Clark suggested that *Sinanthropus* be subsumed into *Pithecanthropus*, and in 1943 Franz Weidenreich made a formal proposal to this effect. Mayr (1944) sank *Pithecanthropus*, *Meganthropus*, and *Telanthropus* into *Homo*, and finally, Le Gros Clark (1964*b*) proposed that *Atlanthropus* be transferred to *Homo*. Over the years several authors have suggested that morphological continuity between *H. erectus* and later *Homo sapiens* effectively invalidates the specific status of the former, resulting in the proposition that *H. erectus* be sunk into *Homo sapiens*, Linnaeus, 1758. Recent advocates of this course of action include Wolpoff et al. (1994) and Tobias (1995).

*Homo heidelbergensis* Schoetensack, 1908

This species was introduced for a hominin mandible found in 1907 at Mauer, near Heidelberg, Germany,

dating from ~ 400 kyr. The mandible has no chin and the body is a good deal larger than those of the mandibles of modern humans living in Europe today. Cranial evidence from Zuttiyeh (Israel, 1925) may belong to this group. The next evidence within Europe of fossil remains that showed equivalently archaic features came from Petralona (Greece), where in 1959 a cranium was recovered from a cave. Because of the lack of any sedimentary context its proposed age of ~ 350–400 kyr can only be approximate. A similar date is likely for comparable evidence from Arago (France, 1964–9), whereas the more fragmentary, but similarly morphologically archaic, material from Montmaurin (France, 1949), Vértesszöllös (Hungary, 1965; ~ 185 kyr) and Bilzingsleben (Germany, 1972–7, 1983 and thereafter) are apparently more recent (~ 250 kyr). Nearly all of these remains have at one time, or another, been regarded as subspecies of *H. erectus*, but although these remains are consistently more archaic than modern humans, and even though they share some of these archaic features with *H. erectus*, they lack the full suite of distinctive features that characterise *H. erectus* (see above). Researchers responsible for the discovery and analysis of the hominids from Sima de los Huesos, Sierra de Atapuerca, Spain, assign that collection to *H. heidelbergensis* (e.g. Pérez-Pérez et al. 1999), but other researchers are more inclined to treat this evidence as an early form of *Homo neanderthalensis* (see below).

The first African evidence for what we now call *H. heidelbergensis* came in 1921 with the recovery of a cranium from a cave in the Broken Hill Mine at Kabwe, in Zambia. It was initially placed in a new species, *Homo rhodesiensis* Woodward, 1921, and dates from ~ 250–300 kyr. Other morphologically-comparable remains have been found from the same, or earlier, time period in southern Africa (*Homo saldanensis* Drennan, 1953 at Hopefield/Elandsfontein, 1953 and thereafter, and Berg Aukas, Namibia, 1965), East Africa (*Paleoanthropus njarensis* Kohl-Larsen & Reck, 1936, at Eyasi, 1935–8), and North Africa (e.g. Rabat, 1933). The earliest evidence of this African ‘archaic’ group comes from Bodo (Ethiopia, 1976), at ~ 600 kyr, and specimens intermediate in age (~ 400 kyr) include crania from southern (Hopefield/Elandsfontein, 1953), East (Ndutu, 1973) and North Africa (Sale, 1971; Thomas Quarry, 1969/72). The Asian evidence for an ‘archaic’ form of *Homo* comes from China (Dali, 1978; Jinniushan, 1984; Xujiayao, 1976/7, 1979; Yunxian, 1989/90) and possibly India (Hathnora, 1982). These fossils are generally not reliably dated, and their ages range from ~ 100 to 200 kyr.

*Sites.* Europe (e.g. Mauer, Petralona); Africa (e.g. Kabwe); Asia (e.g. Dali).

*Characteristic morphology* What sets this material apart from *H. sapiens* is the morphology of the cranium and the robusticity of the postcranial skeleton. Some brain cases are as large as those of modern humans, but they are always more robustly built, with a thickened occipital region and a projecting face, and with large, separate ridges above the orbits unlike the more continuous browridge of *H. erectus*. Compared with *H. erectus*, the parietals are expanded, the occipital rounded, and the frontal broader. Postcranially the shapes of the limb bones are much like those of *H. sapiens*, except that the shafts of the long bones are typically more robust.

*Behavioural implications.* *H. heidelbergensis* is the earliest hominin to have a brain as large as anatomically-modern *H. sapiens* (Leigh, 1992; Wood & Collard, 1999), and its postcranial skeleton exhibits robust long bones and large lower limb joints well-suited to long-distance bipedal walking. Its body mass was large and its shape was ‘cold-adapted’ (Stringer et al. 1998; Trinkaus et al. 1999), despite a range that apparently included central and southern Africa.

*Paleohabitat.* There is no consistent paleohabitat preference other than the obvious implication that *H. heidelbergensis* was adapted for a temperate climate.

*Hypodigm.* Holotype: Mauer 1—adult mandible, Mauer, Heidelberg, Germany. Well-preserved specimens: crania—Kabwe, Ndutu, Jinniushan; mandible—Mauer.

*Taxonomy.* A wide range of taxonomic devices have been used to accommodate the *H. heidelbergensis* hypodigm remains, ranging from the erection of new genera (e.g. *Paleoanthropus njarensis* (Kohl-Larsen & Reck, 1936) for Eyasi, and *Cyphanthropus rhodesiensis* Pycraft et al. 1928 for Kabwe (Broken Hill)), and species (e.g. *Homo saldanensis* Drennan, 1953 for Hopefield), to their inclusion in existing taxa, (e.g. *Homo sapiens* for Hathnora). For many years it was conventional to label this material as ‘archaic’ *Homo sapiens*, but there is now overwhelming evidence that this group of specimens, in terms of its overall cranial, dental and postcranial morphology, is distinct from that of *Homo sapiens* (Howell, 1994). Thus it is reasonable to place it in a separate species. There are currently, however, different views about the scope and phylogenetic relationships of *H. heidelbergensis*. Some interpret the taxon to include all non-Neanderthal ‘archaic’ *Homo* fossils. Others interpret it as being confined to the European Middle Pleistocene fossil evidence, and would retain the name ‘to denote a Middle Pleistocene chronospecies of the

European-neanderthal lineage' (Rosas & Bermúdez de Castro, 1998*a*, p. 696). Stringer (1996) entertains an even stronger link between *H. heidelbergensis* and *H. neanderthalensis*, so strong that he suggests sinking *H. heidelbergensis* into *H. neanderthalensis*. If there is to be a single species name to cover the archaic material from Europe, Africa and Asia then the species name should be *Homo heidelbergensis* Schoetensack, 1908. However, if there were evidence that the non-European subset of the hypodigm sampled an equally good species, then the species name that would have priority is *Homo rhodesiensis* Woodward, 1921.

*Homo antecessor* Bermúdez de Castro et al. 1997

The same cave complex that provided the fossils from the Sima de los Huesos site (see above) has also yielded remains from level 6 of the Gran Dolina (TD) site; this material is most likely at least 500 kyr, and perhaps ~ 750 kyr, old. The authors of the initial report (Bermúdez de Castro et al. 1997) claim that the material shows a combination of morphology not seen in any other hominin species. They contrast the remarkably modern humanlike morphology of the face, with the relatively primitive crowns and roots of the teeth. The authors consider that because *H. heidelbergensis* shares some derived traits with *Homo neanderthalensis*, and because these derived features are not seen in the Gran Dolina material (except for the double-arched browridge), then there are grounds for not allocating the TD collection to *H. heidelbergensis*. It is the apparent lack of these derived features, combined with differences from *H. ergaster*, that led the researchers involved to propose that the Gran Dolina fossils should be assigned to a new hominin species (Bermúdez de Castro et al. 1999). They also propose that *H. antecessor* is probably the last common ancestor of Neanderthals and *H. sapiens*, and according to their taxonomy *H. heidelbergensis* is an exclusively European taxon (Arsuaga et al. 1997*b*; Rosas & Bermúdez de Castro, 1998).

*Site.* Gran Dolina, Spain.

*Characteristic morphology.* The TD6 craniodental remains exhibit a mosaic of primitive and derived traits. Primitive traits shared with *H. ergaster* and *H. erectus* include the presence of cingula in the mandibular canines and premolars, and asymmetry in the crowns of mandibular third premolars, as well as other dental symplesiomorphies (Bermúdez de Castro et al. 1997). However, according to the original describers (Bermúdez de Castro et al. 1997), the cranial remains share derived features, such as brain

enlargement and an arched supraorbital torus, with modern humans and Neanderthals. What is especially remarkable about the TD6 remains is the modern humanlike morphology of the midfacial region, with only slight midfacial prognathism, a well-developed canine fossa, and a sharp inferior nasal margin (Arsuaga et al. 1999*a*). The authors (Bermúdez de Castro et al. 1997, 1999) argue that the peculiar midfacial and mandibular specialisations of Neanderthals (see below) were derived from the more generalised morphology seen in *H. antecessor*.

In general, the postcranial remains more closely resemble the morphology seen in modern humans than that of Middle and Upper Paleolithic humans and Neanderthals (Carretero et al. 1999; Lorenzo et al. 1999). The radii are long, and the long bones generally lack the extreme robusticity of the Neanderthals. From various skeletal elements, stature is estimated at ~ 170 cm. The capitate is intermediate in form between early australopiths on one hand, and *H. sapiens* and *H. neanderthalensis* on the other. Only the clavicle appears to be more Neanderthal-like than modern humanlike (Carretero et al. 1999). The manual and pedal phalanges are short, and lack the extreme muscle markings seen in the phalanges of *H. habilis* and gracile australopiths (Lorenzo et al. 1999).

*Behavioural implications.* The long, relatively gracile radii suggest a fairly high brachial index, allowing us to rule out adaptation to extremely cold climate. The modern humanlike morphology of the hand points to well-developed dexterity in *H. antecessor*. Similarly, the pedal remains point to a fully modern pattern of bipedal gait. For the size of the face the teeth are relatively large, but given its likely body mass *H. antecessor* was unlikely to have been as megadont as the australopiths.

One of the most striking signs of behaviour is the frequent occurrence of cut marks on the human skeletal remains that show evidence of deliberate defleshing and possible cannibalism (Fernández-Jalvo et al. 1999).

*Paleohabitat.* The cave contains representatives of temperate fauna.

*Hypodigm.* Holotype: ATD 6-5—mandible and associated teeth found at Gran Dolina, Spain in 1994. Paratypes: the 35 paratypes are listed in Carbonell et al. (1995, table 1, p. 827). Well-preserved specimens: crania—ATD 6-69; mandible—ATD 6-5.

*Homo neanderthalensis* King, 1864

The type specimen of *Homo neanderthalensis* consists of an adult skeleton recovered in 1856 from the

Feldhofer Cave in the Neander Valley, in Germany. With hindsight this was not the first evidence of Neanderthals to come to light, for a child's skull found in 1829, at a site in Belgium called Engis, and a cranium recovered in 1848, from Forbes' Quarry in Gibraltar (*Homo calpicus*, Keith, 1911), also display the distinctive Neanderthal morphology. The next Neanderthal discovery was from Moravia (*Homo primigenius* Schaaffhausen, 1880, at Šipka, 1880). Thereafter came discoveries in Belgium (Spy, 1886), Croatia (Krapina, 1899–1906), Germany (Ehringsdorf, 1908–1925) and France (*Homo transprimigenius* Forrer, 1908), at Le Moustier, 1908 and 1914; La Chapelle-aux-Saints, 1908; La Ferrassie, 1909, 1910 and 1912, and at La Quina, 1911, and in the Channel Islands (*Homo breladensis* Marett, 1911 at St Brellade). However, it was not until 1924–26 that finds were made outside western Europe at Kiiik Koba in the Crimea. Thereafter came discoveries at Tabun cave on Mount Carmel, in the Levant, in 1929, and then in central Asia, at Teshik-Tash (but see Weidenreich, 1945), in 1938. In the meantime 2 more sites in Italy, Saccopastore (1929–35) and Guattari/Circeo (1939), had yielded the remains of Neanderthals. Further evidence was added after the 1939–45 war, first from Iraq (Shanidar, 1953, 1957–60), then from more sites in Israel (Amud, 1961, 1964 and thereafter; Kebara, 1964 and thereafter) and Syria (Dederiyeh, 1993), and more recently still from sites in France and Spain (e.g. St Cesaire, 1979; Zaffaraya, 1983, 1992, and Moula-Guercy, 1991). Thus, Neanderthal remains have been found throughout Europe, with the exception of Scandinavia, as well as in the Near East, the Levant and Western Asia. Many elements of the characteristic morphology of the Neanderthals can be seen in remains recovered from sites such as Steinheim and Reilingen (Germany) and Swanscombe (England) that date from ~200–300 kyr. They are also said to be evident in precursor form in the remains that have been found in the Sima de los Huesos, a cave in Sierra de Atapuerca, Spain (Arsuaga et al. 1993, 1997b), and if so this would extend the time of origin of the Neanderthals back to beyond ~300 kyr. The geologically most recent evidence of Neanderthals, from Zaffaraya, in Spain, dates to just less than 30 kyr.

*Sites.* (See above for examples, and Stringer & Gamble, 1993, for an exhaustive list.)

*Characteristic morphology.* The characteristic Neanderthal morphology is seen throughout the cranial and postcranial skeleton. In the cranium it includes thick, double-arched brow ridges, a face that projects anteriorly in the midline, a large nose,

laterally-projecting and rounded parietal bones, a rounded, posteriorly-projecting, occipital bone (i.e., an occipital 'bun'), an additional bony crest medial to their small mastoid process, large incisor teeth, and postcanine teeth with large root canals (Patte, 1955; Vleck, 1969; Stringer & Trinkaus, 1981, Stringer 1993; Heim, 1982; Trinkaus, 1986; Hublin & Tillier, 1992; Tyrell & Chamberlain, 1998). The mandible is characterised by a 'retromolar' gap behind the third molar, a weak chin, and a mental foramen typically underneath the first molar. Estimates of Neanderthal brain size suggest that their brains were as large, if not larger, than the brains of living *Homo sapiens*, but perhaps slightly smaller relative to body mass (Ruff et al. 1997). The Neanderthal body is remarkably stout, including a broad rib cage, long clavicle, and wide pelvis, and the limb bones are generally robust with well-developed muscle insertions (Trinkaus, 1986; Stringer & Gamble, 1993). The distal extremities tend to be short, making the brachial and crural indices low compared to *H. ergaster* and most modern *H. sapiens*. Like modern humans, Neanderthals had a long, stout thumb relative to finger length. Anatomical specialisations include, but are not limited to, a long pubic ramus and anteriorly-placed sacrum, especially well-marked muscle attachment areas along the scapula, a long pollical distal phalanx, flat pollical carpometacarpal joint, robust hands and feet, and unusually-bowed femora (Trinkaus, 1986; Arsuaga et al. 1999b).

*Behavioural implications.* Aside from the inferences about climatic adaptation that can be drawn from the skeletal remains of the Neanderthals, the relative size of the anterior teeth, the generally well-marked muscle attachments, and the relative thickness of long bone shafts provide some guide to the lifestyle of the Neanderthals. The size and wear on the incisors suggest that the Neanderthals regularly used their anterior teeth as 'tools', either for food preparation, or to grip hide, or similar material. Microwear on the buccal surface of the postcanine teeth from Sima de los Huesos has been interpreted as the result of a 'highly abrasive' diet (Pérez-Pérez et al. 1999, p. 433). Hutchinson et al. (1997) scrutinised the Krapina teeth for hypoplasia, but although they found an unexplained high incidence in the molars, they concluded that, at least in the Krapina Neanderthals, 'nutritional stress was not especially elevated compared with that affecting several other world populations' (ibid, p. 913). Variation in body size suggests that, by the Middle Pleistocene, sexual size dimorphism was comparable to that of modern humans (Arsuaga et al. 1997a; Quinney & Collard, 1997). Churchill (1994,

1996) has suggested that the pronounced upper limb robusticity indicates more intensive and extensive use of the upper limbs for foraging. The functional anatomy of the lower limb indicates that they were long-range, obligate bipeds. The muscularity and the large joint surfaces suggest that the Neanderthals possessed considerable physical strength and perhaps elevated activity levels, but the fact that greater muscularity and robusticity develop in Neanderthal children at a young age suggest that these features were primarily inherited (Tillier, 1989; Rak & Kimbel, 1996). Although the pubis is extremely long, and was thought to indicate an enlarged birth canal and long gestation time in Neanderthals (Trinkaus, 1984), the discovery of the more complete Kebara pelvis revealed that the birth canal was no larger than expected for, and of similar shape to, a comparable-sized modern human (Rak & Arensburg, 1987). Thus, the gestation time and birth mechanism for Neanderthals were probably not unlike those in modern humans. Proportions and muscularity of the hand, in combination with other features, indicate that the Neanderthal hand was both powerful and capable of fine manipulation. It is clear that the Neanderthals possessed the cognitive and manipulative abilities to create a sophisticated, versatile tool kit, and possibly objects of symbolic value (Stringer & Gamble, 1993). Whether or not Neanderthals were capable of complex speech typical of modern humans remains unknown, largely because the neural adaptations that make speech possible do not preserve in the fossil record. There is currently no agreement among researchers on whether anatomical evidence from the size of the hypoglossal and vertebral canals are reliable indications of whether they had sufficient innervation of the tongue and breathing to control movements related to speech (Kay et al. 1998; DeGusta et al. 1999; MacLarnon & Hewitt, 1999). What may be of more importance is the shape of the vocal tract, which in modern humans is a dynamic 'two-tube' filter with equally long horizontal and vertical portions whose cross-sectional dimensions can be modified independently by the tongue (Lieberman et al. 1992). Some reconstructions (e.g. Lieberman, 1984) suggest that the Neanderthal vocal tract had a less optimal configuration which would have been capable of fewer differentiable vowel sounds than that of modern humans, but this hypothesis remains difficult to test (Lieberman & McCarthy, 1999).

Although there is some skepticism (Gargett, 1989, 1999), most researchers (e.g. Frayer & Montet-White, 1989; Trinkaus, 1989; Belfer-Cohen & Hovers, 1992) interpret the evidence as indicative of intentional

burial by the Neanderthals. Researchers have also drawn attention to compelling evidence for deliberate defleshing ('cannibalism') in ~100 kyr-old Neanderthals from Moula-Guercy (Defleur et al. 1999).

*Paleohabitat.* Paleoenvironmental and anatomical data indicate that Neanderthals typically occupied cold, marginal habitats that would have been extreme for 'archaic' *H. sapiens*, and for modern human populations with relatively-recent African origins (Bar-Yosef, 1992; Mellars, 1996), and their physiognomy suggests that their trunk, limbs and crania were cold-adapted (see above).

*Hypodigm.* Holotype: Neanderthal 1—adult calotte and partial skeleton, found in the Feldhofer Cave, Elberfeld, Germany, in 1856. Paratype(s): none. The size and quality of preservation of the Neanderthal hypodigm exceeds that of any of the hominin species considered thus far.

*Taxonomy.* Although the species *Homo neanderthalensis* was established in 1864, debate has continued over whether the evidence was strong enough to support the claim that the material should be placed in a separate species. In the past decade or so there has been an increasing acceptance that the Neanderthals are morphologically distinctive, so much so that many consider it unlikely that such a specialised form could have given rise to the morphology seen in modern humans (e.g. Stringer, 1996; Tattersall, 1986; Schwartz & Tattersall, 1996). There is, however, another school of researchers who point to, and stress, the morphological continuity between the fossil evidence for *H. sapiens* and the remains others would attribute to *H. neanderthalensis* (e.g. Wolpoff, 1989; Frayer et al. 1993). Some have argued that morphologically intermediate specimens are evidence of 'admixture' between Neanderthals and modern humans (Duarte et al. 1999), but this interpretation is highly questionable and has been challenged (Tattersall & Schwartz, 1999).

Recently researchers have recovered short fragments of mitochondrial DNA from the humerus of the type specimen (Kriings et al. 1997, 1999). They were able to show that the fossil sequence falls well outside the range of variation of a diverse sample of modern humans, and they suggest that Neanderthals would have been unlikely to have made any contribution to the modern human gene pool. In fact, the differences compared with modern humans suggest ~550–690 kyr of separation. The fragment of mtDNA that has been studied is a very short one, but if these findings were to be repeated for other parts of the genome, then the case for placing Neanderthals in

a separate species from modern humans on the basis of their skeletal peculiarities would be greatly strengthened, and arguments for significant admixture (Duarte et al. 1999) would be further weakened (Tattersall & Schwartz, 1999).

#### *Homo sapiens* Linnaeus, 1758

The first evidence that modern humans were ancient enough to have fossilised representatives came when a series of skeletal remains were discovered by workmen at the Cro-Magnon rock shelter at Les Eyzies de Tayac, France, in 1868. A male skeleton, Cro-Magnon 1, was made the type specimen of a novel species, *Homo spelaeus* Lapouge, 1899, but it was not long before it was realised that it was not appropriate to discriminate between this material and modern *Homo sapiens* (Topinard, 1890; Keith, 1912). Thereafter, other early discoveries were made at sites such as Mladec (1881–1922), Predmostí (1884–1928), and Brno (1885) in Czechoslovakia. The first African fossil evidence of populations that are difficult to distinguish from anatomically-modern humans came in 1924, from Singa, in the Sudan. Thereafter comparable evidence came from Dire-Dawa, Ethiopia (1933); Dar es-Soltan, Morocco (1937–8); Border Cave, Natal, (1941–2, 1974); Omo (Omo 1—Kibish Formation), Ethiopia, (1967) and from Klasies River Mouth, Cape Province (1967–8). None of these sites are more than 150 kyr-old, and most date from less than 100 kyr. In the Near East comparable fossil evidence has been recovered from sites such as Mugharet Es-Skhul (1931–2) and Djebel Qafzeh (1933; 1965–1975). In Asia and Australasia anatomically-modern human fossils have been recovered from sites that include Wadjak, Indonesia (1889–90), the Upper Cave at Zhoukoudian, China (1930), Niah Cave, Borneo (1958), Tabon, Philippines (1962) and the Willandra Lakes, Australia (1968 and thereafter). All this material has been judged to be within, or close to, the range of variation of living regional samples of modern human populations, and thus it is not appropriate to distinguish it taxonomically from *Homo sapiens*.

*Sites.* See above for examples.

*Characteristic morphology.* Paradoxically, it has proved easier to assemble information about the characteristic morphology of extinct hominin taxa than the only hominin species with living representatives, *H. sapiens*. Just what features of the cranium, jaws, dentition and the postcranial skeleton are specific to *H. sapiens*? For each morphological region, what are the ‘boundaries’ of living *H. sapiens*

variation? How far beyond these boundaries, if at all, should we be prepared to go and still refer the fossil evidence to *H. sapiens*? These are simple questions, to which one would have thought there would be ready answers. However, the concept of ‘modern humanness’ has proved to be complex and difficult to express. Some researchers have made explicit suggestions that *H. sapiens* should be much more inclusive than just being limited to living and recent modern humans. For example, because they can see no obvious morphological discontinuity between *H. sapiens* and *H. erectus*, Wolpoff et al. (1994) have recommended that the boundary of *H. sapiens* be lowered to incorporate *H. erectus*, thus echoing a proposal made some time ago by Mayr (1950). This taxonomy has received little support, but at least the authors made an explicit statement about the scope of the morphology they were prepared to subsume into *H. sapiens*. Those who advocate a less inclusive definition for that taxon have generally not published the criteria that must be met before fossil evidence can be included in *H. sapiens*. Attempts have been made to specify acceptable ranges of morphometric variation for the cranium (e.g. Stringer et al. 1984; Day & Stringer, 1991), but the former authors admit that these criteria must be relaxed such that any given population of *H. sapiens* need only meet ~ 75% of the defining characteristics. In a review of variation in regional samples of modern humans, Lahr (1996) emphasises that regional peculiarities must not be translated into general species criteria. Lieberman (1998) distilled existing cranial definitions of *H. sapiens*, and suggested that to be regarded as ‘anatomically modern human,’ skulls need to have ‘... a globular braincase, a vertical forehead, a diminutive browridge, a canine fossa and a pronounced chin.’ (ibid, p. 158), features that may be related to a reduction in facial projection (Spoor et al. 1999).

Howells (1973, 1989) has carried out the most comprehensive sampling (n = 28 groups) of modern human cranial measurements and so presumably has, as well as anybody, captured the essence of modern human cranial variation. His results show that the totality of modern human variation, as measured in Mahalanobis D<sup>2</sup> distances, is comparable to the distance that separates all modern human crania from a small sample of Neanderthal crania. Small-bodied modern humans tend to have smaller crania, but overall there is very little between-sample difference in the overall size of the modern human cranium. Howells comments that modern human crania share a ‘... universal loss of robustness ...’, and goes on to

write that ‘variation in shape seems to be largely located in the upper face, and particularly the upper nose and the borders of the orbits’ (Howells, 1989, p. 83).

Modern human postcanine teeth are notable for the absolutely, and relative to body mass, small size of their crowns, and for the related tendency to reduce the number of cusps and roots (Kraus et al. 1969; Hillson, 1996), and presumably this would be the same for fossil representatives of *H. sapiens*. Postcranially, anatomically-modern humans show clear contrasts with Neanderthals. These include, in *H. sapiens*, more elongated distal limb bones (Trinkaus, 1981), limbs that are long relative to the trunk (Holliday, 1995), a narrow trunk and pelvis, and low body mass relative to stature (Ruff et al. 1997). Many of these traits cause the earliest modern humans (e.g. those from Skhul and Qafzeh) to resemble extant people from hot, arid climates, and the clarity of postcranial contrasts between modern humans and Neanderthals has more to do with the uniqueness of Neanderthal morphology than with the ability to adequately define the characteristic features of *H. sapiens* (Pearson, 2000). Thus, the features of the skeleton that make extant human populations ‘modern’ are described in general terms in order to encompass the entire range of climatic and altitudinal adaptations exhibited by living humans. Compared with their archaic immediate precursors, modern humans can be characterised postcranially by their reduced body mass (Kappelman, 1996; Ruff et al. 1997), linear physique, and unique pelvic shape including a short, stout pubic ramus, and relatively large pelvic inlet (Pearson, 2000).

*Behavioural implications.* Conventional wisdom maintains that the appearance of anatomically modern *H. sapiens* in Europe coincided with the advances in behaviour subsumed in the phrase the ‘Upper Paleolithic Revolution’ (Mellars, 1996). This combines elaborate speech with the conceptual and manipulative skills necessary to design and manufacture fine stone and bone tools, such as needles and fish-hooks, as well as symbolic objects and art. How far this interpretation is correct is the subject of spirited debate, for there is little doubt that in Africa ‘modern morphology’ and ‘modern human behaviour’ did not appear at the same time, and appeared earlier in Africa than in Europe (Brooks, 1996).

*Paleohabitat.* Fossil evidence of anatomically modern *H. sapiens* has been found in a wide range of habitats, including sites at high altitude, and ranging from sites in dry-cold to those in hot-arid regions. The body proportions of fossilised modern humans re-

semble those of living human populations from warm regions of the world.

*Hypodigm.* No specimen has been formally designated as the holotype, or lectotype, of *H. sapiens*. The standard of preservation and completeness of remains attributed to *H. sapiens* is generally much higher than that of earlier hominins.

*Taxonomy/precursors.* The origin of *H. sapiens* has been the subject of considerable debate. Two lines of evidence, fossil and molecular, will be briefly addressed here. The burden of the fossil evidence is that the earliest evidence of anatomically modern human morphology comes from sites in Africa or the Levant, some of which are listed above. It is also in Africa that there is evidence for a likely morphological precursor of anatomically modern human morphology (Bräuer, 1984; Rightmire, 1984; Stringer et al. 1984; Stringer 1993). This takes the form of crania that are generally more robust and archaic-looking than those of anatomically-modern humans, yet which are not archaic enough to justify their allocation to *H. heidelbergensis*. Specimens in this category include Florisbad, Orange Free State (1932); Jebel Irhoud, Morocco (1961, 1963); Omo 2 (Kibish Formation), Ethiopia (1967); Laetoli 18, Tanzania (1976); Eliye Springs (KNM-ES 11693), Kenya (1985) and Ileret (KNM-ER 999 and 3884), Kenya (1971 and 1976 respectively). There is undoubtedly a gradation in morphology that makes it difficult to set the boundaries between anatomically-modern humans, the subset of ‘archaic’ *Homo sapiens* presented above, and the hypodigm of *H. heidelbergensis*. However, it is clear that unless at least one boundary is set then morphological variation within *H. sapiens sensu lato* is so great that it strains credulity (Bräuer, 1992; Bräuer et al. 1997). Some researchers (e.g. Lahr & Foley, 1994) have suggested that this African subset of late ‘archaic’ *H. sapiens* deserves taxonomic recognition, in which case *Homo (Africanthropus) helmei* Dreyer, 1935 for the Florisbad hominin, is the species name that has priority.

A detailed discussion of the molecular evidence for the origin of modern humans is beyond the scope of this contribution, but the early debate is well summarised in Stoneking (1993) and Relethford (1995), and the discussion is updated, and put in context, in Mountain (1998).

### Conclusions

Most attempts to reconstruct human phylogeny suggest that the monophyletic group, or clade, containing modern humans separated from the chim-



panzee clade between 8 and 5 myr ago. The hominin fossil record currently samples taxa that between them span the period between  $\sim 4.5$  myr and the present day. Thus, depending on whether the earlier or later date for the hominin/panin common ancestor is the correct one for the origin of the hominin clade, the fossil evidence provides evidence about more than half, or almost all, of the human clade's independent history (Fig. 1).

Advances in absolute dating methods have enabled geochronologists to provide more precise estimates of the ages of much of the East African fossil hominin evidence. These new data have confirmed that during several periods in the past  $\sim 4.5$  myr (Fig. 1) distinctly different hominin taxa have coexisted, at least in terms of geological time, in the same region, if not in the same locality. This suggests that at these times there was more than one evolutionary lineage within the human clade. Support for this interpretation comes from the results of cladistic analyses of the hominin fossil record. Although the reliability of these analyses has been questioned, there is substantial support for 2 subclades within the main human clade (Fig. 3). One includes *Homo sapiens*, *Homo neanderthalensis*, *Homo heidelbergensis*, *Homo erectus* and *Homo ergaster*, and the other *Paranthropus robustus*, *Paranthropus boisei*, and *Paranthropus aethiopicus*. These realities mean that earlier interpretations of human evolution, that likened it to a ladder leading from an apelike creature on the bottom rung, through a succession of less apelike and more modern human-like forms, to modern humans on the top rung of the ladder, are no longer appropriate. Human evolution is more like a bush, with many stems, some of them leading up through most of the height of the bush, others passing through only its uppermost part (Fig. 1). Only one stem, that containing *Homo sapiens*, reaches the top of the bush.

The genus is a category containing taxa that should be both monophyletic and adaptively coherent. Thus the species within a genus must satisfy two criteria. They must belong to the same clade, and they should share a common adaptive regime. When these criteria are applied to the genera presently included the hominin fossil record, not all genera satisfy them. *Australopithecus* fails to do so because, as currently constituted, it is most likely to be a paraphyletic group. When the two tests are applied to current interpretations of *Homo*, it fails both of them. A *Homo* clade that includes *Homo habilis* and *Homo rudolfensis* is not well-supported, for cladograms that include these 2 basal *Homo* species are barely more parsimonious than clades that exclude them (Fig. 3).

Similarly, indicators sensitive to diet are expressed differently in these 2 taxa than they are in the geologically later, and more derived, taxa within the *Homo* clade. Furthermore, locomotor behaviour in *H. habilis* contrasts with that inferred for later *Homo* species. This is the nub of the recent proposal that the genus *Homo* be restricted to taxa that share with modern humans a reduction in the size of the postcanine tooth row, an upright posture, and an obligate bipedal gait. Even within this more restrictive definition of *Homo* one could make a case that the appearance of complex language marks an adaptive shift that merits recognition above the species level. However, this presupposes that the acquisition of language can be detected via the paleontological and archeological records. The lack of published evidence about *Ardipithecus* makes it difficult to assess the latter's place in the spectrum of hominin adaptations.

The 'bushiness' of hominin phylogeny has profound implications for assumptions about the evolutionary history of important aspects of human adaptations and competencies. For example, we can no longer be sure that stone tool manufacture was a behaviour exclusive to members of the genus *Homo*, and there is evidence that, in more than one hominin clade, the locomotor repertoire shifted from one that included a significant arboreal component to one in which bipedalism dominated. Although it is likely that bipedalism originated only once in the hominin clade, subsequent adaptations to locomotion and diet appear to have evolved in a complex fashion in the course of human evolutionary history. Deducing a functional repertoire from a mixture of retained primitive and newly-derived morphologies is going to require new and more sophisticated analytical strategies than are presently applied to these problems. Such strategies are critical for obtaining accurate reconstructions of the relationships and adaptive histories of members of the hominin clade.

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