THE GENUS HOMO IN THE EARLY PLEISTOCENE OF AFRICA AND EUROPE

DEBORAH DAWN ARGUE

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ABSTRACT

The absence of fossil *Homo* from some periods in the Early Pleistocene (gaps in the fossil record), and the morphological variability between the specimens which we possess, has inhibited attempts to understand human evolution. While some view the variability as representing an ever-increasingly variable species, *H. erectus*, others propose that evolution was, in fact, a branching pattern with species more or less constantly emerging and disappearing. Moreover, for most of the fossils a number of species has been proposed, making it difficult to resolve phylogenetic relationships of *Homo* during this period. Recently, however, new fossil crania and mandibles have been discovered, which provides a good opportunity to seek to resolve these questions.

I used cladistic and morphometric analyses incorporating the Early Pleistocene fossil crania and mandibles from Africa, Eurasia, and Asia to test existing hypotheses about their phylogenetic relationships, and to establish a hypothesis for human evolution during this period. During the course of this study, the discovery of a new species of *Homo*, *Homo floresiensis*, was announced. Its archaic morphology, in parts similar to some of the Early Pleistocene hominins, suggested that it would be worthwhile to retrospectively[1] include it in this study, despite the fact that it is dated to the Holocene.

This study proposes that the variation observable in the fossils from the Early Pleistocene represents a number of species and lineages of which the SK 847 lineage, *H. habilis*, *H. georgicus*, and, somewhat later, *H. erectus* are the earliest; followed by *H. ergaster* and, much later, *H. cepranensis*. A population was present in East Africa 1.8 million years ago until approximately 900,000 years ago, which probably comprises a separate species, *H. louisleakeyi* or *H. rhodesiensis*, that co-existed with *H. ergaster* for at least some of the time.

H. floresiensis, although at present known only from the Holocene, is clearly descended from a very early hominin from the late Pliocene or Early Pleistocene. It challenges a number of paradigms in human evolution: that a species more primitive than *H. georgicus*

[1] Too late to include the Ngandong fossil hominins, which are closer in age to *H. floresiensis* than is my Early Pleistocene sample

was the first to emerge from Africa; that an early species of *Homo* existed at the same time as *H. sapiens* in South East Asia when we had thought that the latter was the sole remaining member of our genus since the demise of *H. neanderthalensis* and *H. erectus*; and it predicts a greater range of hominin variation during the late Pliocene-Early Pleistocene than hitherto had been conceptualized in hypotheses of human evolution.

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1 INTRODUCTION AND BACKGROUND TO HUMAN EVOLUTION IN THE EARLY PLEISTOCENE

1.1 Introduction

While many scholars have focused on the evolution of *Homo* prior to 1.7 million years ago and from 600,000 years ago, the period in between, when *Homo* radiated from Africa, is not well understood. Within the last 12 years, however, new hominin crania and mandibles from the Early Pleistocene have been found in Africa and, for the first time, Europe. In 1997 fossils were discovered at Gran Dolina, Atapuerca, Spain (Bermúdez de Castro et al., 1997) and dated to between 780 Ka and 857 Ka (Falguèrès et al., 1999); a one million-year-old cranium from Buia, Eritrea was reported in 1998 (Abbate et al., 1998); in 1999, two partial crania from Dmanisi, Georgia (Gabunia et al., 2000) were found followed by two more in subsequent years as well as mandibles, some of them associated with the crania, dated to ~ 1.78 Ma (Gabunia et al., 2000; Gabounia et al., 2000; Rightmire et al., 2006); and in 2002, a fossil calvaria ('Daka') dated to more than 800,000 years ago (Asfaw et al. 2002) was found in the Middle Awash, Ethiopia. More recently a cranium KNM-OL 45500 from Olorgesailie, Kenya, has been reported (Potts et al., 2004); and extra facial and cranial bones from Olduvai Hominid 12 have been identified by Antón (2004).

Despite the increased number of hominin fossils available for the Early Pleistocene clarity about phylogenetic relationships between the Early Pleistocene hominins has not emerged. This is because, while studies of each of these hominins typically include comparative analyses with similar fossil material, in most cases this has resulted in considerable controversy as to their affinities and phylogenetic relationships.

Further, variation in the Early Pleistocene, following *Homo habilis,* is explained by some as representing a single species, *H. erectus*, while for others it represents multiple taxa among which *H. erectus* is an exclusively Asian species. Until this controversy is resolved, our understanding of the evolution of *Homo* in the Early Pleistocene will be illusive.

A brief history of issues relating to *H. erectus* demonstrates how this situation evolved and the impact it has on studies of human evolution today. The first material to be found of what was later called *Homo erectus,* Trinil 2 (the type specimen, a calvaria), was discovered by Eugene Dubois (1891) and described as *Anthropopithecus erectus* Dubois 1892; and, two years later, revised to *Pithecanthropus erectus* Dubois 1984 (Meikle and Parker 1994). From 1921, fossil hominins were found at Zhoukoudian in China, and were initially referred to as *Sinanthropus pekinensis* (Weidenreich, 1943). In 1936 and 1938 Von Koenigswald (Weidenreich, 1943) announced the discovery of further fossil skulls of *Pithecanthropus* near Sangiran, Indonesia. Weidenreich and Von Koenigswald (op. cit.) described these, comparing them with *Sinanthropus*, and, although Von Koenigswald noted several differences in the dentition between *Pithecanthropus* and *Sinanthropus*, Weidenreich recognised that they had so many features in common, and were so different from the Neanderthals, that they could be considered representatives of the same stage of human evolution (op. cit.).

In 1950, Ernst Mayr declared that the zoological standards would not permit *Pithecanthropus* and *Sinanthropus* to occupy genera separate from *Homo,* but he believed that the amount of evolution that separates these from *Homo sapiens* is still of a magnitude to allow the recognition of a different species of *Homo.* *Pithecanthropus* and *Sinanthropus,* he advised, should therefore be placed in the genus *Homo* and, according to the Rules of Zoological Nomenclature, the species they jointly represent becomes *Homo erectus.*

In 1964, Le Gros Clark (1964) defined *H. erectus* as distinct from *H. sapiens* and *H. neanderthalensis* and asserted a general consensus of opinion that *H. erectus* is ancestral to *H. sapiens* as the morphological characters of *H. erectus* conformed to a theoretical postulate of an intermediate stage between later species of *Homo* and the presumed common ancestor of Hominidae. This single lineage model of human evolution had earlier been articulated by Dobzhansky (1944) who proposed that 'All the phylogenetic transformations in Hominidae were always taking place within a single genetic system, a species consisting of geographically, but not reproductively, isolated races.' (op. cit. 262). Dobzhansky's model contrasted to the prevailing 'classic' (op cit. 259) view that assumed

the course of human evolution had been steadily divergent, producing a phylogenetic tree with many branches, the sole surviving branch comprising *H. sapiens*.

The tendency to place new hominin fossil finds in *H. erectus*, e.g. KNM-ER 3733 and KNM-ER 3883 (Walker, 1981) and KNM-WT 15000 (Brown et al., 1985) reflected Le Gros Clark's (1964) single lineage model of human evolution, which appears to have become entrenched, apart from some exceptions (eg *H. ergaster*; Groves and Mazák, 1975), as a view that a single, long-existing, polytypic, widely dispersed species preceded *H. sapiens* and its immediate precursors. In the 1980s, however, the lumping of fossil *Homo* into *H. erectus* was explored by Rightmire (1984), Wood (1984), Andrews (1984) and Stringer (1984), who examined the question by comparing the 'African *H. erectus*' KNM-ER 3733 and KNM-ER 3883 with *H. erectus s.s.* Rightmire (1984) concluded from his study of *H. erectus* and KNM-ER 3733 and KNM-ER 3883 that the Asian and African crania are broadly similar, but noted some differences among them; he suggested such variations could be expected over such a wide geographical range. The conundrum arising from his study is whether the variability between the African sample and the differences between the African and Asian fossils affect how *Homo erectus* is defined. Should the definition be modified, or should crania like KNM-ER-3733 and KNM-ER-3883 be excluded from *Homo erectus senso stricto*? Wood (1984) suggested that the morphology of the occipital and frontal regions of KNM-ER-3733 and KNM-ER-3883 are not sufficiently similar to each other or to Asian *H. erectus* to merit their inclusion in *Homo erectus*; to include them in this taxon, the definition of *Homo erectus* would have to be modified to accommodate thinner vaulted crania exhibiting a wider range of frontal, occipital and parietal morphology. In his view, if this were adopted, it would result in a taxon without apomorphic features. In 1991, Wood further developed this concept and suggested that the African fossils should be assigned to a separate taxon, *H. ergaster* (Wood, 1991:58). Although Wood concluded that the frontal morphology and cranial thickness of OH 9 were closer to Asian *Homo erectus* than is the case for KNM-ER 3733 and KNM-ER 3883, he would also exclude it from *Homo erectus*. He contended that *Homo erectus* should be restricted to specimens which share Asian *Homo erectus* derived morphologies (Wood, 1984:58). This conclusion was supported by Stringer (1984), who undertook a cladistic analysis of the characters typifying *Homo erectus*. His sample comprised Trinil, Sambungmacan 2, Sangiran 4, Sangiran 19, Sangiran 12 and Sangiran

17, OH 9, the *H. pekinensis* crania, and some Plio-Pleistocene fossils from Africa. He concluded that the robusticity of the cranial vault, the occipital morphology and facial proportions of *Homo erectus* are highly derived and only the Asian hominins show this assemblage with any consistency and could therefore be referred to as *Homo erectus* 'senso stricto' (op. cit.). *Homo erectus senso stricto*, then, should be restricted to those forms and the African hominins omitted (op cit.137).

Nevertheless, the morphological boundaries of *H. erectus* continued to be stretched. Asfaw et al. (2002) referred the Daka cranium (Middle Awash, Ethiopia dated c.800,000 years ago (op. cit.)) to *H. erectus* despite clear differences in cranial characters from *H. erectus s.s.* such as: strongly arched supraorbitals; relatively steeply sloping frontal; lack of some superstructures (e.g. occipital torus); vertical parietal walls; cranium relatively short compared to *H. erectus s.s.* The Dmanisi hominins were also referred to *H. erectus* (Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Vekua et al., 2002) yet their endocranial volumes (ECV) range from 600cc – 775cc, below the lower margin of the range of *H. erectus s.s.* which is usually cited as 1,000cc (Antón et al., 2007), but in fact ranges from 813cc – 1059cc for the Sangiran crania (Rightmire, 1990). Olduvai Hominid 12 had already been referred to *H. erectus* (Leakey 1971) despite its small ECV of 727cc (Antón, 2004). Ascenzi et al. (1996) referred the Ceprano cranium (Italy) to *H. erectus* while acknowledging differences from *H. erectus s.s.* such as lack of a sagittal keel or parasagittal depression and a larger ECV (1185cc) compared to *H. erectus s.s.* KNM-ER 42700 was referred to *H. erectus* (Spoor et al. 2007) but their *H. erectus* sample comprised KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, OH 9, Dmanisi hominins, Sangiran 17, Ngandong hominins, Ngawi, Sambungmacan 3, and Zhoukoudian III, XI, XII – the affinities of at least half of which are debated; and the effect of which was to almost guarantee that this new hominin would be included within the bounds of the sample. Further, the ECV of KNM-ER 42700 is 691cc – well below the range for *H. erectus s.s.*.

The general augmentation of *H. erectus* and lack of agreement about the morphology of the species hinders any attempt to understand human evolutionary relationships in the Early Pleistocene.

A second issue inhibiting our understanding of human evolution in the Early Pleistocene is that, despite the increased number of fossils available for this period, clarity about phylogenetic relationships has not emerged. This is because, while studies of each of these hominins typically include comparative analyses with similar fossil material, in most cases this has resulted in considerable controversy as to their affinities. While this is clear from the discussion above, it is also apparent in referrals to, and discussions about, the relatively newly discovered hominins that 'fill the gap' in the fossil record for this period. The Dmanisi fossils, representing the earliest known population in Europe, were attributed to *Homo ergaster* when first announced (Gabunia et al 2000). Two years later, Gabounia et al (2002) set Dmanisi apart as a new species *Homo georgicus*, as they considered the size range within the group to be outside the range of *H. erectus* and *H. ergaster*. They believed that this species is close to the roots of the *Homo* clade and that it represents an early diffusion from Africa towards Eurasia between 2 –1.8 million years ago.

Daka was referred to *Homo erectus* by its discoverers and the species *Homo ergaster* rejected (Asfaw, 2002:61). The authors concluded from cladistic analyses that the Daka calvaria is consistent with the hypothesis of a widespread polymorphic and polytypic species existing 1 million years ago representing a single evolving lineage series of *Homo erectus* fossils in Africa. Manzi et al (2003), using a phenetic approach which quantifies overall similarity of single specimens, found that Daka shares the greatest affinities with two fossil specimens from the Koobi Fora region in Africa, KNM-ER 3733 and KNM-ER 3883, which they attributed to *H ergaster*, and that Daka is very different from *H erectus*. They proposed that Daka is best viewed as part of a local African evolutionary lineage spanning 1.8 Mya – about 1Mya.

Ceprano was at first attributed to *H. erectus* (Ascenzi et al. 1996; 2000) but this was challenged by Mallegni et al. (2003). Based on morphometric and cladistic analyses, they claimed that Ceprano is significantly different from all other species, and thus attributed it to a new species, *H. cepranensis*, that did not contribute to the human population of Europe during the Middle and Late Pleistocene.

Other idiosyncratic problems beset our attempts to understand human evolution during the Early Pleistocene: the taxonomic status of SK 847 has been grappled with for 30 years; *H.*

antecessor (Bermúdez de Castro et al., 1997) is based upon a juvenile; the new cranium from Olduvai Gorge, KNM-OL 45500, and KNM-ER 42700 from Koobi Fora stretch the known size range of crania from this period, presenting challenges to our concepts of expected morphological variability within species; the cranium from Buia is not yet fully described nor is it available for study.

Finally, a new and most perplexing species, *H. floresiensis*, living as recently as 100 Kya – c. 12 Kya, has challenged a number of paradigms in human evolution.

1.2 Background to the Early Pleistocene fossil hominins

Below I list the hominins from the Early Pleistocene and briefly describe the controversies for each.

Dmanisi

In late 1991 a well preserved human mandible, D211, was excavated from the site of Dmanisi, Georgia (Gabunia and Vekua, 1995) now dated to 1.76 to 1.77 Mya (van Arsdale 2006:32). This is the earliest evidence for *Homo* outside Africa. It is a relatively small mandible, with a nearly vertical symphysis that curves smoothly into the inferior border of the corpus; the corpus increases in relative thickness from the symphysis distally; molar sizes reduce distally (M_1>M_2>M_3); it has a narrow alveolar arcade; and the ramus commences well anteriorly (Gabunia and Vekua, 1995). Gabunia and Vekua (op. cit.) concluded that the overall size, robustness, symphysis shape, and dental proportions of D211 indicate that it is early *Homo,* most similar to African *H. erectus* (KNM-ER 730 and KNM-ER 992, KNM-WT 15000, OH 22).

Bräuer and Schultz (1996) compared the Dmanisi mandible D211 to a wide range of mandibles of *H. habilis*, *H. erectus* (from Swartkrans, East Rudolf and Olduvai; including mandibles others have referred to *H. ergaster*) and *H. erectus.* They concluded that it represents a 'progressive' (op. cit. 487) form of *H. erectus* or even archaic *H. sapiens* (now generally referred to *H. heidelbergensis*).

In 1999, two crania, D2280 and D2282, were found two meters from D211 in the same level and pit as the latter (Gabunia et al., 2000). Both specimens have small ECVs; for

D2280 it is 775cm^3; for D2282 it is 650cm^3 (op. cit.). They are similar in cranial shape: spheroidal in superior view and relatively low and angular, with greatest cranial breadth at the level of the mastoid processes; both have continuous occipital tori although overall D2280 is more rugose in the nuchal region. Both have marked post-orbital constriction and supraorbital tori, the latter more pronounced in D2282; neither has cranial cresting. Gabunia et al. (2000) referred the Dmanisi hominids to *Homo ex. gr. ergaster*.

In 2000, a second and more complete and robust adult mandible, D2600, was excavated at the Dmanisi site (Gabounia et al., 2002). It is much larger than D211; Gabounia et al. (op cit.) assessed the size range between D211 and D2600 to be outside the range of other species of *Homo*, sufficient, in their view, for the creation of a new species, *H. georgicus sp. nov*. They attributed the differences between the two Dmanisi mandibles to sexual dimorphism within this species.

A third (subadult) cranium, D2700, and an associated mandible, D2735, were discovered in 2002 (Vekua et al., 2002) in the same excavated pit at Dmanisi. D2700 exhibits some differences from D2280 and D2882: for example, there is no supraorbital hollowing behind the brows; and there is faint midline keeling on the frontal. Vekua et al. (op cit.) saw insufficient grounds for assigning the various fossils to more than one taxon (op cit.) and referred them all to *H. ergaster*, adding that they are closely related to *H. habilis s.s.*

In 2005, a fourth cranium (D3444) with associated mandible (D3900) was excavated from the same stratum as the other crania and mandibles (Lordkipanidze et al., 2005). The brief announcement reported that the skull is similar in overall morphology to the Dmanisi crania described earlier (op. cit. 718). This skull is not included in this study – it was announced recently and few morphological details have been provided.

In summary, then, the Dmanisi hominins have been considered to be early *Homo,* most similar to African *H. erectus* (Gabunia and Vekua, 1995); referred to *Homo ex. gr. ergaster* (Gabunia et al., 2000); and to a new species *H. georgicus* (Gabounia et al., 2002).

KNM-ER 992

The adult mandible KNM-ER 992 dated to 1.55 - 1.49 Mya (Feibel et al., 1989) was referred to a new species, *H. ergaster* (Groves and Mazák, 1975), the name *leakeyi* (after the discoverer, which would otherwise have been appropriate), being thought to be preoccupied in the genus *Homo* (op. cit.)[2]. The referral is based upon both comparative metric analyses of dental remains which provide information about statistically different samples, and a measure of taxonomic difference (the Coefficient of Difference; after Mayr, 1978). The hypodigm includes a number of mandibular and maxillary dentitions and fragments, parietal fragments and (probably) the skull KNM-ER 1805 (op. cit.). To this Groves (1989) added the cranium KNM-ER 1813.

KNM-ER 3733

In 1976 a nearly complete cranium of an adult was collected from the Upper Member sediments of the Koobi Fora Tuff Complex (Leakey et al., 1976). It is dated to 1.78 Mya (Feibel et al. 1989).

Leakey et al. (1976) pronounced that it was 'strikingly like the Peking cranium' (op. cit. 572) although little morphological information was presented; the attribution of KNM-ER 3733 to *H. erectus* was accepted until some questions about its affinity to the species began to be explored in 1984 when ferment had developed about this taxon. The phylogenetic issue is whether all fossils referred to *H. erectus* represented one species. Wood (1984) suggested that the morphology of the frontals of KNM-ER-3733 and KNM-ER-3883 (see below) are not sufficiently similar to *Homo erectus* to merit their inclusion in that species and that these Turkana hominins, further including KNM-WT 15000, should be assigned to a separate taxon (Wood 1992), *Homo ergaster*. Rightmire (1984), however, came to a different conclusion based upon a detailed morphological comparison of KNM-ER 3733 and KNM-ER 3883 with the *H. erectus* type specimen from Trinil and the hominins from Sangiran. He concluded that the Asian and African crania are broadly similar and represent one species, *H. erectus*. Groves (1989) placed KNM-ER 3733 in *Homo sp. (unnamed)* as it shares derived traits of *H. ergaster*: arched or ridged nasals, broad upper face, endinion lower than ectinion (op. cit 271); as well as sharing derived

[2] In fact, it is not (Groves, 1989:195)

traits with *H. erectus* and *H. sapiens*: mastoid process more than 12mm long, occipital scale shorter than the nuchal scale, and others (op. cit. 276). That is, Groves would not place KNM-ER 3733 in *H. ergaster*.

The attribution of KNM-ER 3733, then, is unclear: it is considered that it is *H. erectus* (Leakey et al., 1976; Rightmire, 1990); *H. ergaster* (Wood, 1992); *Homo sp. (unnamed)* Koobi Fora (Groves, 1989); that it is **not** attributable to *H. ergaster* or *H. erectus* (Schwartz, 2000); and that KNM-ER 3733 and KNM-ER 3883 are not phylogenetically related (Schwartz and Tattersall, 2000).

KNM-ER 3883

A calvaria KNM-ER 3883 was discovered a few years after KNM-ER 3733 and assigned to *H. erectus* (Leakey and Walker, 1976). It is dated to 1.57 ± 0.08 Mya (Feibel et al. 1989), that is, it is about 210 Kya younger than KNM-ER 3733. KNM-ER 3883 and KNM-ER 3733 are often considered conspecific in phylogenetic discussions: the character differences between them have not generally been considered of sufficient scale for placing each in different species (Wood 1992). Schwartz (2000a) and Schwartz and Tattersall (2000), however, proposed the two fossils represent separate species, and that each is significantly different from KNM-WT 15000 (op cit.); for example, KNM-ER 3883 has thickened supraorbital margins that protrude out and slightly down, overhanging the face; the frontal slopes strongly; and it has a large and protrusive mastoid process. Zeitoun (2000) would also separate the two into different species following his cladistic analysis of *Homo*: referring KNM-ER 3733 to a new species, *H. kenyaensis nov. sp.* and KNM-ER 3883 to another new species, *H. okotensis nov. sp.* (op. cit. 147), both of which are acceptable under the International Code of Nomenclature (C. Groves, pers. comm. 2009).

KNM-ER 3883, then, is considered either conspecific with KNM-ER 3733 and referred to *H. erectus* (Leakey and Walker, 1976), or *H. ergaster* (Wood, 1992), or a separate species, unnamed (Schwartz and Tattersall, 2000), or named *H. okotensis nov. sp* (Zeitoun, 2000).

KNM-WT 15000

This comprises an almost complete skeleton discovered at Nariokotome III, west of Lake Turkana, Kenya. It was referred to *H. erectus* when initially announced by Brown et al. (1985) although no comparative analyses were undertaken. The cranium is in relatively good condition, missing only the nasals, ethmoid, lacrimals, central parts of the supraorbital tori, and parts of the sphenoid and vault. There is some distortion of the calvaria. The sutures and all the epiphyses in the postcranium are unfused, indicating that more growth could have been expected; the cranium does not possess strong tori, temporal or nuchal lines, and, along with the degree of root development of the canines, it is presumed to be a male adolescent estimated on human standards to be 12 ±1 years old at death and 1.68m tall (op. cit. 789). It is dated to 1.65 – 1.55 Mya (Feibel et al. 1989:613), and is contemporary with KNM-ER 3883 and younger than KNM-ER 3733.

Although it was initially referred to *H. erectus* (Brown et al., 1985), Wood (1992) proposed that *H. erectus* should be restricted to the Asian morphology and that *H. ergaster* is the proper attribution for KNM-WT 15000, KNM-ER 3733 and KNM-ER 3883. Schwartz and Tattersall (2000) took a systematics approach to the *H. erectus /H. ergaster* issue by comparing KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 to Trinil, the type specimen of *H. erectus*. They found that they differ significantly not only from Trinil, but from each other: that is, they would not include the Koobi Fora hominids in *H. ergaster* or *H. erectus*.

Olduvai Hominid 9 (OH 9)

Discovered in 1959 in Upper Bed II at Olduvai, this calvaria is dated to 1.5-1.4 Mya (Schwartz and Tattersall, 2002). The braincase was originally briefly reported by Leakey (1961) as having a number of superficial similarities to the Pithecanthropines (i.e. *H. erectus* from Java), but differs in having a higher vault. Heberer (1963) conditionally referred OH 9 to *H. leakeyi*, but being conditional this name does not satisfy requirements of the International Code of Zoological Nomenclature (op. cit. 871; Clarke 1994:190). Tobias (1968) named it *H. erectus olduvaiensis* but this name is also unavailable, being again proposed conditionally (Groves 1999; 871). Should it be considered that OH 9 is a separate species, then *H. louisleakeyi*, proposed by Kretzoi (1984), is available.

Groves (1989:279) and Rightmire (1990, 1998) assigned OH 9 to *H. erectus*; Groves (1989) viewing it as the only non-Asian representative of this species.

SK 847

SK 847, a partial cranium, is from the Swartkrans (South Africa) stratigraphic unit Member 1. Curnoe et al. (2001) dated the Hanging Remnant of Member 1 to between 1.63 and 2.1 Mya.

Clarke et al. (1970) discovered that a maxillary fragment, SK 80, and SK 847 joined perfectly. They concluded that SK 847 (now including SK 80) belongs to the genus *Homo*; it would be prudent, they argued, to treat it as *Homo sp. indet.* (op. cit. 1220). A later study by Clarke and Clark Howell (1972) suggested that it may prove conspecific with Olduvai 13, which they referred to *H. habilis*.

Groves and Mazák (1975) regarded the Swartkrans fossils as *Homo incertae sedis* while noting that the dental measurements are most like *H. ergaster spec. nov.*

Olson (1978) assigned the material to *Homo africanus* following Robinson (1972) who had sunk the genus *Australopithecus* into *Homo*.

Clarke (1994) considered that SK 847 is virtually identical to KNM-ER 3733, noting that others had found the same (e.g. Groves 1989; Walker 1981); he further suggested that these are females of the species in which OH 9 is a male, and he argued that, as Groves and Mazák (1975) thought that SK 847 might belong in *H. ergaster* and KNM-ER 3733 is so similar to SK 847, then they should all be assigned to *H. ergaster*.

Curnoe (1999) used cladistic and metric analyses to test the phylogenetic relationships of SK 847/SK 15. He established firstly, that it is *Homo*, and secondly that it formed a sister taxon to *H. habilis* and *H. erectus*; he hypothesised that it shared a common ancestor with these taxa.

Grine et al. (1996) undertook a study of SK 847, Stw 53, OH 24, KNM-ER 1813, KNM-ER 1470, KNM-ER 3733 and KNM-WT 15000 by assessing similarities between pairs of fossils by computation of taxonomic distances (average Euclidean distances) based on

linear measurements and scale-free shape data (to eliminate the effect of size in the analyses). They concluded that all early *Homo* crania - SK 847, Stw 53, OH 24, KNM-ER 1813, KNM-ER 1470 - are differentiated from KNM-ER 3733 and KNM-WT 15000 (*H. ergaster*); and that SK 847 and Stw 53 showed shape differences from OH 24 and KNM-ER 1813. They suggested that there is a taxonomic distinction between the South and East African early *Homo* crania, and that the taxonomic affinities of the early *Homo* fossils from South Africa await a comprehensive comparative analysis.

SK 847, then, has been referred to *H. erectus* (Robinson, 1961); *Homo sp. indet.* (Clarke et al., 1970); possibly *H. habilis* (Clarke and Clark Howell, 1972); *Homo incertae sedis* (Groves and Mazák, 1975); and *Homo africanus* (Olson, 1978). Curnoe (1999) proposed it shared a common ancestor with *H. habilis* and *H. ergaster*; and Clarke (1994) viewed it as identical to KNM-ER 3733, and conspecific with OH 9.

Olduvai Hominid 12 (OH 12)

OH 12 comprises an incomplete small cranium with most of an occipital and both parietals, parts of the left and right temporals including the left mastoid process, part of the right supraorbital torus, and the left part of the palate and maxillary arch. Matrix adhering to the palate indicated that it had been washed down from upper part of Bed IVa, Olduvai, into Bed III (Leakey 1971). These beds lie below the Masak Beds. Tamrat et al. (1995) re-investigated the magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation and provided a date of 1.07 Mya for the base of the Masek Beds. The minimum date for Bed IV, lying below the Masek Beds, is, then, 1.07 Mya but, as Bed IVA is below Bed IVB, which extends some way below the Masek Beds (op. cit.; Fig 6) OH 12 is likely to be somewhat older than 1.07 Mya. It could be surmised, then, that OH12 has a minimum age of > 1.07 Mya (cf Antón's (2004) interpretation of Tamrat's (1995) work, that OH 12 is 0.78 Mya).

OH 12 would seem to be contemporary with Tighenif (if the earlier date for Tighenif is correct; see below). Alternatively, if Antón's (2004) interpretation is correct, it would be roughly contemporary with Gran Dolina, Daka and Ceprano.

Mary Leakey (1971) gave the taxonomic status of OH 12 as 'probably *H. erectus*' (op cit. 230), and Rightmire (1990) argued that its occipital curvature, probable occipital proportions and thickened vault bones justify its assignment to *H. erectus,* its thin supraorbital torus and lack of strong muscle marking on the vault possibly indicating that it is female (and OH 9 a male).

Antón (2004) identified new fragments of OH 12 (held at Kenya National Museum), which enabled her to compare OH 12 with other African and Asian hominins of broadly similar age: OH 16 and 24, KNM-ER 1470 and 1813 (referred to 'non-erectus early *Homo* group'); OH 9, KMN-ER 3733, KNM-ER 3883; Dmanisi D2280, D2282; Zhoukoudian Skulls X, XI. XII and IX; Sangiran 2, 17, 27 originals and casts; and to Daka and Buia (from published descriptions). The supratoral and sulcus morphology, interorbital region, zygomaxillary region and, to a lesser extent, the palate, differ from non-erectus *Homo* (op. cit.). OH 12, she proposed, conforms more to an Early African/Georgian morphological pattern; in particular she observed striking similarities with KNM-ER 3733 in orbital morphology and to OH 9 in posterior cranial morphology. She viewed this shared morphology as existing for one million years, but its morphology differs from Daka and Buia, with which she viewed as coeval. She concluded that only further additions to the fossil record of *H. erectus* will help elucidate whether the variations between African and Asian lineages may be seen as local adaptations/genetic drift within a lineage or more discrete boundaries between lineages (op. cit. 346), but whether 'discrete boundaries between lineages' can be understood to refer to different species is unclear.

Holloway (2000) estimated the endocranial value for OH 12 as 727cc. This is very small compared to the estimated capacity, 1067cc, of the older OH 9, and Holloway questioned the conventional thinking of the time: that hominid evolution involved an increase in cranial capacity through time; he considered that a simple anagenic explanation, of hominins existing as either single lines or types, as extremely speculative and unlikely (op. cit. 99). He posed further questions: are these values extremes of a range? Is OH 12 a remnant of an earlier *H. habilis* taxon? Is it a small female *H. erectus*?

KNM-OL 45500

This is a small adult or subadult cranium recently found at Olorgesaillie, Kenya dated to 970 – 900 Kya (Potts et al 2004). It possesses characters observed in larger *H. erectus* such as midline keeling of the frontal bone, shelf-like morphology of the post-toral sulcus, lack of torsion in the orbital torus and a short temporal squama with flat superior border. It has, however, a double-arched supraorbital torus - more similar to some mid-Pleistocene hominids than *H. erectus*. Although Potts et al. (op. cit.) did not state that KNM-OL 45500 **is** *H. erectus*, they did observe that the Olorgesailie hominid would extend the known range of cranial morphology of *H. erectus*.

Buia (UA31)

A nearly complete adult cranium was recovered from the northern part of the Danakil formation in Eritrea (Abbate et al., 1998; Macchiarelli et al., 2004) and is dated to 992 Kya (Albianelli et al., 2004).

Macchiarelli et al. (2004) viewed the Buia specimen as markedly different from earlier, contemporary, and later specimens in Africa, Europe and Asia, having a unique morphological mix of Early and Middle Pleistocene characters. It has not yet been fully described and is thus unavailable for study (L. Rook, 2004; pers. com.). I cannot, then, perform metric or cladistic analyses, but I will discuss its possible phylogenetic position in Chapter 4.

Daka

A calvaria and postcranial remains from the Dakanihylo member of the Bouri Formation in the middle Awash, Ethiopia, were described in 2002, dated to 800 Kya, and referred to *Homo erectus* (Asfaw et al., 2002) in the context of a chronologically single evolving lineage series of *Homo erectus* fossils in Africa. Manzi et al. (2003), however, propose that Daka has affinities with KNM-ER 3733 and KNM-ER 3883 and that it is far removed from Asian *H. erectus*; while Macchiarelli et al. (2004) viewed it as sharing a common ancestor with Ceprano (below).

Ceprano

Many fragments of a cranium were found near the town of Ceprano, Italy, in 1994 (Ascenzi, 1997). The age for the fossil is estimated at > 700 Kya and probably slightly over 800 Kya (op cit.). It was at first referred to *H. erectus*, particularly to late *H. erectus*, by which Ascenzi et al. (op cit.) were referring to the Middle Pleistocene fossils Arago, Petralona, and contemporaries which, as they acknowledge, some would attribute to *H. heidelbergensis*.

Clarke (2000) undertook a reconstruction of the cranium during 1997 which resulted in a revision of the reported metric values of the calvaria. Although these changes altered a number of characteristics of the cranium, Clarke (op. cit.) retained it in *H. erectus*. Manzi et al. (2001), after declaring their confidence in the new reconstruction, were uncomfortable with the attribution of this cranium to *H. erectus*. They undertook a cladistic analysis and presented unrooted trees which show Ceprano grouped with African mid-Pleistocene *Homo*: Kabwe, Saldhana and Bodo.

Mallegni et al. (2003) went further and proposed a new species for Ceprano based upon their assessment that it possesses a unique suite of characters. Their cladistic analysis included *H. ergaster* (KNM-ER 3733), *H. erectus* (Zhoukoudian and Sangiran specimens), *H. heidelbergensis* (Petralona, Steinheim, Saldhana, Kabwe), two Atapuerca skulls, two Dmanisi crania, and OH 9. A strict-consensus tree placed Ceprano with Daka in a monophyletic group. They named Ceprano *H. cepranensis sp. nov.* (op cit.).

Ceprano, then, has been referred to 'late *H. erectus*' (= *H. heidelbergensis*) (Ascenzi et al., 1994); *H. erectus* and specifically **not** *H. heidelbergensis* (Clarke, 2000); a new species *H. cepranensis sp. nov.* (Mallegni et al., 2003); and, possibly, *H. heidelbergensis* (Manzi et al., 2001).

Tighenif (previously Ternifine)

Three mandibles were excavated from a sand extraction site near Palikao, Algeria (Arambourg, 1955a; 1956). The deposits were laid down during a time of normal polarity and probably belong to either the Brunhes epoch (<780 Kya) or the Jaramillo event (1.1

Mya – 1.0 Mya) (Arambourg, 1955b). The mandibles are different sizes and Arambourg (1956) interpreted the largest, markedly robust mandible as male and the second mandible, a demi-mandible, also robust, as probably female. He concluded that all are very closely related to Pithecanthropus and Sinanthropus (now *H. erectus*) but that they cannot be identified exactly with *Sinanthropus* or *Telanthropus*, and he assigned them to a new species *Atlanthropus mauritanicus* (op. cit.), but he did not list characters that differentiate the Ternifine fossils form *H. erectus* and the name is unavailable under Article 13 of the International Code of Zoological Nomenclature (Clarke 1994:190).

Others have referred to the Tighenif mandibles as *H. erectus* (e.g. Geraads, 1986; Rightmire, 1990).

A parietal from the same site was reported by Arambourg (1955). The curvature of the cranium is like that of Pithecanthropines and maximum cranial width is at a lower level than the temporal-parietal suture. There are no parietal bosses, the temporal lines are marked, and there is an angular torus. Arambourg concluded that it is Pithecanthropine (op. cit.).

Bodo

Hominid material was first found at the site of Bodo d'Ar in 1976 (Conroy et al., 1976). The specimen consists of an almost complete face and partial neurocranium, including most of the frontal bone, nasal bones and the left zygomatic except for the temporal process and parts of the maxilla; much of the basicranium as well as two-thirds of the palate is present. Conroy et al. (2000) estimated the age of the Bodo specimen at 0.64 ± 0.03 Mya. Conroy et al. (1976) refrained from a taxonomic determination. Kalb et al (1982), however, assigned Bodo to *H. sapiens rhodesiensis*.

The robusticity, in terms of keeling, thickness and dimensions for facial breadth and the degree of prognathism, suggested to Stringer (1984) that Bodo has a strong claim to be *H. erectus s.s.* but only if its more *H. sapiens* characters (the large cranial capacity, relatively high vault, and supraorbital torus morphology) are considered to be of less phylogenetic importance than the erectine characters (op. cit. 140-141). He put forward several scenarios for the Bodo morphology: it might represent a late member of an African

lineage in which there is an evolutionary trend for robusticity; the specimen might be a variant of *H. erectus* combining African and Asian *H. erectus* characteristics through gene flow; or the mosaic of characters may indicate a transitional stage between *H. erectus* and *H. sapiens* (Stringer 1984:140).

Rightmire (1996) undertook a detailed description and comparative analysis of the Bodo cranium with *H. erectus* (Asia and Africa) and later Middle Pleistocene fossils (Kabwe, Ndutu, Omo 2, and Petralona). Like Stringer (1984), the impression Rightmire (1996) gained from the cranium is that it is 'intermediate' in its anatomy (op. cit. 32). It shares both primitive and derived characters with *H. erectus*: the cranium is low (cf Stringer who views the cranium as relatively high), cranial bones are thick, the supraorbital torus projects and is heavily constructed; there is a supratoral hollowing; and the frontal profile is flattened, and there is midline keeling and a bregmatic eminence. Its wide facial proportions, however, differ from both *H. erectus* and the later Middle Pleistocene fossils to which it is compared. Further, the ECV for Bodo is large relative to *H. erectus* (1300cc compared to a maximum of 1100cc for *H. erectus*) - a character that links Bodo with generally more advanced humans. Rightmire (op cit.) concluded that it seems most reasonable to group Bodo with Kabwe and similar specimens from the Middle Pleistocene sites in Africa and Europe.

Gran Dolina (ATD 6-15 + 6-69).

Human fossils recovered from the excavation TD6 level at Gran Dolina in the Sierra de Atapuerca in Spain, dated to between 780 – 857 Kya (Falguèrès et al., 1999), comprise neurocranial, mandibular, facial and dental material and many postcranial bones that represent six individuals (Bermudez de Castro, 1997). The remains were referred to a new species, *H. antecessor* (Bermudez de Castro et al., 1997), based upon a unique combination of cranial, mandibular, dental and postcranial traits, all of which they viewed as different from *Homo erectus* and *Homo ergaster*. The name of the new species, *H. antecessor*, was chosen to reflect that the authors considered it to be the common ancestor of *Homo neanderthalensis* and modern humans, although they reviewed the phylogenetic position of Gran Dolina when the dates for its purported descendants, the nearby Sima de los Huesos (HS) fossils, were revised to an earlier time frame of 400-500 Kya (Bischoff et al., 2003).

Cranial capacity, derived from a comparison of the minimum frontal breadth and bistephanic breadth of ATD6-15 and other hominins, is estimated to be 1000cc (Bermudez de Castro et al., 1997). The ATD6-15 dimensions are well above those of KNM-ER 3733, KNM-ER 3883, Sangiran 2, and Trinil - all skulls with cranial capacities below 1000 cm^3 (op. cit.)

In 2007 the symphyseal region of a hominin mandible (ATE9-1) and an isolated molar belonging to the same individual were recovered from the Sima del Elphante cave in the proximity of the Gran Dolina site (Bermúdez de Castro et al., 2009). The mandible has a well-developed anterior marginal tubercle, and a distinct mental trigone; it lacks a superior transverse torus, mental fossae and mental tubercles. Bermúdez de Castro et al. (2009) provisionally attribute it to *H. antecessor* based upon morphological analyses of the mandible and dentition, although they point out that a symphysis for *H. antecessor* is not represented. As this has only been recently reported, there has been no opportunity for me to study it and it is not included in my analyses.

Kabwe

An isolated cranium was found during mining operations in the basal wall of a steeply sloping cleft emanated from a cave within a small hillock at Broken Hill (now called Kabwe), Zambia (then Northern Rhodesia). It has not been dated, and, as it seems to have rolled down the cleft at an unknown time, it is not possible to reliably estimate its age, and the hillock no longer exists.

Smith Woodward (1921) announced the discovery of the skull, stating that (erroneously: Hrdlicka 1930) a fragment of upper jaw, a sacrum, tibia, and two ends of a femur had been extracted with the skull. It appeared to Smith Woodward (1921) that the skull was Neanderthal-like while recalling Pithecanthropus in many ways, although possessing a much larger cranial capacity than the latter, with a more human-like vault shape than the Neanderthals. The large ECV, the position of foramen magnum, and the essentially modern postcranial bones he viewed as so different from *H. neanderthalensis* that he named the material *H. rhodesiensis* (op. cit.). That is, the attribution of the species is based partly upon unassociated postcranial material.

Pycraft (1928) also based his analyses upon the supposed association of the skull and postcranial remains and concluded that Rhodesian man differs from any other fossil hominid yet described, and because these differences are so far-reaching, he proposed a new genus, *Cyphanthropus gen. nov.* (stooping man) as he interpreted the remains to have belonged to a member of a genus that habitually stooped.

Rightmire (1976) compared the Broken Hill skull to those of *H. neanderthalensis*, Omo I and II, Hopefield, and OH 9. Based on a morphological comparison of the differences observed, he gave Kabwe a subspecific designation *H. sapiens rhodesiensis*. The similarities he observed with OH 9 suggested to him that *H. sapiens rhodesiensis* can be regarded as an expanded, higher version of the latter and that the populations sampled at Broken Hill and Omo are probably evolved from local groups of *H. erectus* (op. cit.).

Bräuer (1984) assigned Kabwe to 'early archaic *H. sapiens'* (op. cit. 387). This group would include Bodo, Hopefield, Eyasi, Ndutu and other African crania, as their cranial vaults are more expanded than *H. erectus*, and they would therefore possess affinities with *H. sapiens*. The term 'early archaic *H. sapiens'* is now considered unsatisfactory, being a descriptive category rather than a taxonomic term, and has been replaced with *H. heidelbergensis;* the taxon is usually considered to comprise similar fossils from Africa and Europe.

Groves (1989) placed Kabwe in a subspecies of *H. sapiens, H. sapiens heidelbergensis*, that includes the African and European Middle Pleistocene fossils; Kabwe, Bodo, Tighenif and later fossils from Europe and Africa.

Further remains were discovered at the site, including a maxilla (Kabwe 2), femora, tibia, sacrum, two innominates, and a humerus but it is unlikely that any are associated with the skull (see Chapter 4).

Homo floresiensis

The hominin bones from Liang Bua cave on the island of Flores in Indonesia (Brown et al., 2004) are in stratigraphic levels dated to between 13.4-10.2 Kya and about 100 Kya

(Roberts et al., 2009); that is, they represent a population that existed for a period of approximately 86,000 – 90,000 years. *H. floresiensis*, then, is not known from the Early Pleistocene, but preliminary investigations I undertook in response to the archaic characters described by Brown et al. (2004), and work undertaken by Cameron (pers. comm.) and Donlon (pers. comm.), led me to investigate whether there could be any phylogenetic relationship between this species and those from the Early Pleistocene (Argue et al., 2006). The results showed phenetic similarities of *H. floresiensis* to Early Pleistocene hominins and I now want to test these using a different analytical approach: cladistic analyses. For this purpose, Professor Mike Morwood and Dr Tony Djubiantono kindly offered me the opportunity to study the original cranial and mandibular remains in Jakarta, Indonesia.

1.3 Summary and Aims

In summary, until recently we have not been in a favourable position to formulate hypotheses about human evolution in the Early Pleistocene. With the relatively new discoveries of fossil *Homo* from the period 1.7 – c.800,000 years ago, what had once been poorly represented in terms of fossils – a gap in the fossil record – now provides an opportunity to incorporate this much expanded record for Early Pleistocene *Homo* into one comprehensive study to establish hypotheses about their phylogenetic relationships.

The aim of this thesis, therefore, is to include these crania and mandibles in cladistic and morphometric analyses to test the hypotheses for each, and to make predictions about their phylogenetic relationships. My strategy is to firstly assess whether Early Pleistocene hominins from East Africa attributed to *H. erectus* do indeed belong in that species. The process to be followed comprises:

1. Establish if KNM-ER 3733, KNM-ER 3883, KNM-WT 15000 are distinct or not from *H. erectus*.
2. If they are distinct from *H. erectus*, establish whether or not they comprise a single homogeneous group.
3. Establish whether or not they represent *H. ergaster*. This cannot be done directly from cranial comparisons, as the hypodigm for *H ergaster* is the mandible KNM-ER 992. Of the three crania generally attributed to *H. ergaster*, only KNM-WT 15000 has an associated mandible, so it is this that needs to be compared to KNM-ER 992 in the

first instance. This will test the attribution of one of the specimens in question, KNM-WT 15000, to that species. The same process will also test the hypothesis that KNM-ER 992 could share a common ancestor with *H. erectus*, as Sangiran 9 is included in the mandibular analyses.

4. Should it be determined that KNM-WT 15000 represents *H. ergaster*, test whether KNM-ER 3733 and KNM-ER 3883, usually attributed to *H. ergaster*, also belong in that species.

Following this, I assess the other Early Pleistocene OTUs against whichever species survive these tests, and test specific hypotheses proposed for each of the OTUs.

The results of these analyses enable me to develop an hypothesis for the phylogenetic relationships of the Early Pleistocene fossil hominins.

The materials and methods used are reported upon in Chapter 2; the results of the analyses are presented in Chapter 3, and discussed in Chapter 4. Chapter 5 formulates a hypothesis for human evolution in the Early Pleistocene.

2 MATERIALS AND METHODS

To gain insight into the meaning of variability in *Homo* during the Early Pleistocene I undertake two kinds of analyses: multivariate analysis, which uses measurements taken between landmarks on the cranium; and cladistic analysis, which assesses which hominins may have shared a common ancestor, for which I compile a list of cranial characters and a list of mandibular characters and record the states for each Operational Taxonomic Unit (OTU). I also report my observations on each hominin to assist in the discussion of the phylogenetic relationships of the OTUs in Chapter 4.

2.1 Cranial and Mandibular Sample

Metric data, and information about cranial and mandibular states, were obtained from original fossil material and casts of Early Pleistocene *Homo* (Table 2). The cranial sample comprises:

- Sangiran 2, 4, 9, 17 and Trinil (*H. erectus*);
- *Homo habilis* KNM-ER 1813, OH 24;
- KNM-ER 3733;
- KNM-ER 3883;
- KNM-WT 15000 (*H. ergaster* or *H. erectus*);
- Dmanisi (D2282, D2280, D2700);
- SK 847;
- Olduvai Hominid 9 (OH 9);
- KNM-OL 45500;
- Daka;
- Ceprano;
- Bodo;
- Kabwe (*H. rhodesiensis*); and
- LB1.

Data for Olduvai Hominid 9 (OH 9) and D2282, D2280, and D2700 (the Dmanisi group) are from casts. The Buia skull from Eritrea is not available for study until it has been fully

published (pers. comm. Lorenzo Rook, 10/7/2004) and my discussions about its affinities rely on published information.

Mandibular data are obtained from KNM-ER 992, KNM-WT 15000 (*H. ergaster*); Dmanisi group. i.e. D211 (data from Gabunia et al., 1995), D2600 (data from Swartz and Tattersall 2002), D2735 (Rightmire, 2006); three mandibles from Tighenif (1954-3-825 (Tighenif 1), 1955-13-1001 (Tighenif 3), 1954-7-2c (Tighenif 2)); LB1/2 and LB6/1 (*H. floresiensis*), Zhoukoudian P695, P696, and two *H. sapiens*. The two *H. sapiens* and three *G. gorilla* mandibles are included in the mandibular analyses for comparative purposes (Table 2; Table 3). There are too few comparative metric data for the mandibles (Appendix 1) to enable a mandibular PCA to be performed.

H. floresiensis is included in this study. Although dated to the late Pleistocene[3], it is hypothesised to be a remnant population of little-changed very early *Homo* (Brown et al., 2004, Morwood et al., 2004, Argue et al., 2006; Argue et al., 2009). The publication of *H. floresiensis* occurred several months after I had completed my fieldwork study of the early Pleistocene material, yet it is important to compare *H. floresiensis* with *H. habilis* and the Australopithecines, which I had not originally intended to include in my study. I therefore did not have an opportunity to obtain data from the original specimens of *H. habilis* or Australopithecine fossils for this study, I obtained data from casts of *H. habilis,* (KNM-ER 1813 and OH24) and *Australopithecus africanus* (Stw 505, Sts 71 Sts 5), the only ones available to me; *A. africanus* is a proxy for the diverse genus *Australopithecus* as these are the only specimens available to me, and it serves to provide polarity for the *Homo* sample. That is, Australopithecine and *H. habilis* skulls were included retrospectively; and it was not the intention in this study to resolve questions relating to the phylogeny of these species.

D2700 and KNM-ER 15000 are subadults (Rightmire et al., 2006; Smith, 1993), and Gran Dolina is a juvenile. They therefore might not represent the true adult form. Nevertheless I include them for exploratory purposes. Sangiran 2, SK 847 and ATD6-69 are not included

[3] LB1 is dated to 18 Kya by Accelerator Mass Spectrometry (AMS) and bracketed by luminescence dates of 34 ± 4 Kya and 14 ± 2 Kya (Brown et al., 2004); the minimum age for *H. floresiensis* is 13.4-10.2 Kya (Roberts et al., 2009).

in the morphometric analyses as they are too fragmented to enable a reasonable number of measurements to be taken.

To identify ancestral, or pleisiomorphic, states for *Homo* in the cladistic analyses four skulls of *Pan paniscus,* three *Gorilla gorilla* and one *Gorilla beringei* are included as outgroups. This is a relatively small sample, but it is all that was available to me in Australia. 11 combined male and female *H. sapiens* are also included for comparative purposes. Data for these were obtained from original material held at ANU and the Australian Museum. *H. sapiens* is also included in the morphometric analyses to provide perspective.

There are some limitations to this study. It is possible that some of the assumptions in cladistic analyses (discussed below, Chapter 2) are not met; specifically, it may be that some of the characters are not genetically independent of each other. We do not have a way of assessing genetic independence of characters, but I have attempted to minimise the possible effects of this by avoiding over-emphasis on any given morphological feature.

The Australopithecine sample, included retrospectively to compare to *H. floresiensis*, is also small, limited by the availability of fossil casts, and the availability of descriptions from the literature.

H. floresiensis was included retrospectively, and it would have been useful to include the Ngandong hominins, from the same region, and closer in age to *H. floresiensis* than most of the hominins in my sample, to test for any possible close phylogenetic relationship between these two species. Unfortunately, however, *H. floresiensis* was included after the completion of my fieldwork studies, and it was too late to study, and include, the Ngandong hominins.

I include sub-adults Dmanisi D2700, KNM-WT 15000, and KNM-OL 45500, although the latter might represent a small adult (Potts et al., 2004). Sub-adults may not represent the adult form, and an argument can be made that conclusions about their phylogenetic

relationships may not be sound. This is a limitation for phylogenetic studies, but I make some attempt to deal with it, while noting that my conclusions may be controversial. Further, I note that sub-adult D2700 forms a supported clade with adult hominins from Dmanisi which suggests that at least some subadults reflect the adult form of the species.

Finally, there remains the problem of overlap of morphological variation in inferring taxonomic classification. This is a problem faced by palaeoanthropologists and I am not attempting to resolve it in this study.

The results of the analyses are presented in the next Chapter.

Table 1. Cranial specimens used in the study

Specimen	Original/ cast	Curatorial institution	Original site	Date	Species
Sts 5 Sts 7 Stw 505	casts	ANU, Canberra, Australia	South Africa	2.8 – 2.3 Mya	*A. africanus*
Trinil	original	National Museum of Natural History, Leiden, Holland	Indonesia	> 700 Kya and < 1 Mya	*H. erectus*
Sangiran 2	original	Forschungsinstitut Senckenberg, Frankfurt, Germany	Indonesia	unknown	*H. erectus*
Sangiran 4	original	As above	Indonesia	> ?1.51 ± 0.08 Mya (Grenzbank Formation)	*H. erectus*
Sangiran 17	original	Geological Museum, Bandung, Indonesia	Indonesia	c. 1 Mya (Bapang-AG Formation)	*H. erectus*
SK 847	original	Transvaal Museum of Natural History, Pretoria, South Africa	South Africa	Between 2.1 and 1.63 Mya	*Homo sp.*
KNM-ER 3733	original	Kenya National Museum, Nairobi, Kenya	East Africa	1.8 Mya	*H. ergaster*; *H. erectus*
Dmanisi D2280	cast	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
Dmanisi D2282	cast	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
Dmanisi D2700	cast	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
KNM-ER 1813 OH24	casts	Australian National University (ANU), Canberra, Australia	East Africa	1.7 - 1.88 Mya	*H. habilis*
KNM-ER 3883	original	Kenya National Museum, Nairobi, Kenya	East Africa	1.55 – 1.6 Mya	*H. ergaster*; *H. erectus*
KNM-WT 15000	original	Kenya National Museum, Nairobi, Kenya	East Africa	1.65 – 1.55 Mya	*H. ergaster*; *H. erectus*
KNM-ER 42700	Spoor et al., 2007	Kenya National Museum, Nairobi, Kenya	East Africa	1.53 – 1.61 Mya	*H. erectus*
OH9	cast	Kenya National Museum, Nairobi, Kenya	East Africa	1.52 -1.48 Mya	*H. erectus H. louisleakey*

OH12	Schwartz and Tattersall, 2003; Anton, 2003	Kenya National Museum, Nairobi, Kenya	East Africa	> 1.07 Mya	*H. erectus?*
Tighenif parietal	original	Museum National Histoire Naturelle, Paris, France	North Africa	1.1 mya – 1.0mya or 780 Kya	*H. erectus*
KNM-OL 45500	original	Kenya National Museum, Nairobi, Kenya	East Africa	970-900 Kya	*H. erectus?*
Gran Dolina	original	Museo Burgos, Burgos, Spain;	Spain	780 – 857 Kya	*H. antecessor*
Daka	original	Ethiopian Museum, Addis Ababa, Ethiopia	Ethiopia	Estimate: 800 Kya	*H. erectus Homo erectus ergaster H. ergaster*
Ceprano	original	Universitá di Roma Rome, Italy	Italy	estimate: > 700 Kya and probably slightly over 800 Kya	*H. cepranensis sp. nov*; *H. heidelbergensis*
Bodo	original	Ethiopian Museum, Addis Ababa, Ethiopia	Ethiopia	0.64 ± 0.04 – 0.55 ± 0.03 Mya	'archaic' *H. sapiens* (= *H. heidelbergensis*)
Kabwe	original	Natural History Museum, London, U.K.	Zimbabwe	unknown	*H. heidelbergensis; H. rhodesiensis*
Liang Bua 1 (LB1)	original	National Archaeological Research Centre, Jakarta, Indonesia	Flores, Indonesia	18 kyr (luminescence dates of 35 ±4 kyr and 14 ± 2 kyr)	*H. floresiensis*

Homo sapiens (6 males; 5 females)	original	ANU, Canberra, Australia	Indonesia (2) India (1) African (1) Egyptian (1)) 'Caucasoid' (1) New Guinea (3) Polynesia (1) Japan (Ainu) (1)	modern	*H. sapiens*
P. troglodytes (2 males, 2 females)	original	Australian Museum, Sydney, Australia			
G. gorilla *G. beringei* (2 males, 2 females)	original	ANU, Canberra; Australian Museum Sydney, Australia			

Table 2. Mandibular specimens used in the study

Specimen	Original/ cast	Curatorial institution	Original site	Date	Species
Sangiran 9	Schwartz and Tattersall (2002)	Geological Museum, Bandung, Indonesia	Indonesia	>0.99 Kya or < 1.51 ± 0.08 Mya	*H. erectus*
Dmanisi D2735	Rightmire (2006)	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
Dmanisi D2600	Gabounia et al. (2002)	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
Dmanisi D211	Gabunia and Vekua (1995)	Georgian State Museum, Tblisi, Georgia	Rep. of Georgia	1.8 Mya	*H. erectus, H. georgicus H. ergaster*
Tighenif	original	Museum National du Histoire Naturelle, Paris, France	North Africa	1.1 mya – 1.0mya or 780 Kya	*H. erectus*
KNM-WT 15000	original	Kenya National Museum, Nairobi, Kenya	East Africa	1.5 - 1.6 Mya	*H. ergaster*
KNM-ER 992 (mandible)	original	Kenya National Museum, Nairobi, Kenya	East Africa	1.49 Mya	*H. ergaster*
Liang Bua (LB6/2; LB 6/1)	original	National Archaeological Research Centre, Jakarta, Indonesia	Flores, Indonesia		*H. floresiensis*
H. pekinensis	Weidenreich 1943		Zhoukoudian, China	< 620 Kya	*H. pekinensis*
Homo sapiens	original	ANU, Canberra, Australia		modern	*H. sapiens*
G. gorilla G. beringei	original	ANU, Canberra; Australian Museum Sydney, Australia		modern	

2.2 Principal Component Analyses (PCA)

Measurements were taken between landmarks on each cranium and mandible. The cranial measurements follow those of Martin and Saller (1957) and Howells (1996); mandibular landmarks are from Bass (1995). See Table 1.

Multivariate statistical techniques summarise and describe morphometric data so that biological parameters underlying morphological relationships among individuals may be more readily discovered (Albrecht, 1979). It is a descriptive, data-analytic approach which represents the quantitative version of comparative anatomy, and is applicable to problems in which multidimensional data are used to characterise morphological relationships among populations with proper concern for the effects of individual variation within the various populations. Nearness, or distance, in the multivariate space, must be translated directly as similarity, or difference, in morphology. There may, of course, be significant differences in the interpretations when different investigators view the analyses. As well, different or additional measurements may change the metric estimates of morphological relationships that could impact upon the biological inferences made (Albrecht, 1980).

I perform cranial morphometric analyses using the PCA function of the SPSS Statistics 17 data analysing program. PCA, based in this case upon a correlation matrix, synthesises data from all variables into a set of axes by fitting a regression line to represent the best summary of the linear relationship between the variables; that is, it reduces variables to a number of Factors (axes) - the 'new' factor is a linear combination of the variables[4]. The first Factor, or axis, usually explains most variation between specimens and the second axis explains the next most variation. The process may be continued to third, fourth, and further components if most of the variation is not accounted for in the first two axes (which, in most cases, it is). A table of the variation expressed by each axis is generated (Total Variance Explained); while inspection of the weightings for each axis (Component Matrix table) will show which variables contribute most to the variation (Dytham, 2005).

I do not use Discriminant Function analysis as, although it works in much the same way as PCA, it requires individuals to be divided into groups prior to performing analyses so that a set of weightings are generated that allow the groups to be distinguished. Weightings may then be used on individuals to assess the probability that they belong to a group (op cit.). I, however, aim to *identify* groups, rather than pre-determining them, and therefore Discriminant Function analysis is an inappropriate tool for my purposes.

The goal of my analyses is to assess similarities and differences in crania after the effect of size is removed. I sought a technique that would separate, as far as possible, the effects of size and shape in the analyses. I, therefore, use log-transformed data; this minimizes though it does not fully alleviate, size effects. The issue of size in these kinds of analyses is vexed; and even after methods to exclude size, for example by the use of Geometric Mean, allometric shape differences will remain.

Differential preservation of fossil material means that not all variables are available for all fossils. Several multivariate analyses are performed to ensure that each specimen may be accommodated in at least one of the analyses.

[4] Source: Electronic Textbook 'Statistica'; produced by StatSoft, Inc. http://www.statsoft.com/textbook/stfacan.html#basic

Table 3. Cranial measurements taken for the study.

Martin and Saller (1957) reference number		Notes (after Howells, 1973).
1	**GOL**	Maximum cranial length (from glabella)
1d	**NOL**	Greatest length in median sagittal plane, measured from nasion to opisthocranion
8	**XCB**	Max cranial breadth (mid-sagittal plane)
17	**BBH**	Basion – lowest point on rim of anterior foramen magnum
10	**XFB**	Maximum frontal breadth at coronal suture
9	**Min Frontal (ft-ft)**	Fronto-temporal to fronto-temporal. Minimum distance between the temporal lines on the frontal.
14	**WCB;**	Minimum cranial breadth (at fronto-sphenoid suture)
45	**ZYB (bizygomatic)**	Bizygomatic breadth. Direct distance between most lateral points on zygomatic.
5	**BNL**	Basion-nasion. Direct distance from the lowest point on the anterior margin of foramen magnum to nasion
40	**BPL**	Basion-prosthion length
12	**ASB (biasterionic)**	Asterion – asterion (where squamous, lambdoid and occipital sutures meet)
11b	**AUB (biauricular)**	Least exterior breadth across roots of zygomatica wherever found. With skull resting on occiput and base towards observer (palate away from observer)
48	**NPH or NPL**	Upper facial height. Direct distance prosthion-nasion (nasion-prosthion length)
43	**Upper Facial Breadth**	Direct distance fmt-fmt.
10b	**STB**	Bistephanic breadth: between where temporal lines cross with coronal suture; use the superior temporal line
	FMB	Bifrontal breadth; breadth across frontal bone between frontomalare anterior on each side i.e. the most anterior point on the fronto-malar suture.

55	**NLH**	Nasion to midpoint of a line connecting the lowest points of inferior margin of the nasal notches; nasion to lowest point on border of nasal aperture on either side. Measure to both sides and average them. If this not possible, measure to (inferior) nasal spine.
54	**NLB**	Maximum nasal breadth.
52	**OBH**	Orbital height (left orbit if possible). Perpendicular to orbital breadth line.
51 or 51a	**Orbital breadth**	From dacyron (dacryon is at junction of frontal, lacrimal and nasal sutures) to entoconchion.
49(a)	**DKB**	Dacyron to dacryon.
45(1)	**JUB**	Bijugal breadth; external breadth across the malars at jugalia i.e. the deepest points in the curvature between the frontal and temporal processes of the malars.
	WMH	Cheek height: maximum distance from lower border of orbit to lower margin of maxilla, mesial to the masseter attachment on the left side
29	**FRC**	Nasion-bregma chord.
	FRA	Nasion-bregma arc (note how affected by glabella).
30	**PAC**	Bregma-lambda chord.
31	**OCC**	Lambda – opisthion chord (midpoint of posterior margin of foramen magnum)
	Lambda-Opisthion arc	
31(1)	**Lambda -Inion chord**	
	Lambda - Inion arc	
31(2)	**Inion -Opisthion chord**	
	Inion -Opisthion arc	
	Supraorbital torus	Central, medial, lateral measurements

	Maximum supraorbital breadth	
	Palate length	
61	**MAB (palate breadth)**	Maxillo-alveolar breadth. Max. breadth at lateral surfaces of 2nd molars.
n/a	**MDH (mastoid ht)**	Length of mastoid process below, and perpendicular to, the eye-ear plane, in the vertical plane
n/a	**MDB (mastoid width)**	From digrastic groove to corresponding level on external surface; width of mastoid at its base through its transverse axis
	ZMB	Breadth across the maxillae, from one zygomaxillare to the other
	FOL (foramen magnum length)	Basion to opisthion

2.3 Cladistic analyses

Cladistic analysis is widely used in the biological sciences as a methodological approach to phylogenetic reconstruction and has been applied to hominin taxa since the 1970s. It assumes that shared features observed among taxa can be explained by hypotheses of common ancestry that are represented by sets of characters in a hierarchical pattern of taxa (Faith and Cranston,1991) and is based upon Hennig's (1966) approach to systematics, specifically his approach to descent with modification. Descendants acquire traits transmitted genetically from their ancestors and these are passed on to subsequent descendants (Humphries, 2002). The aim of cladistic analysis is to identify taxa that share a common ancestor by finding, or distinguishing, shared derived character states (synapomorphic) from among the characters in the data set; taxa sharing synapomorphies are called sister taxa, and they represent branching of an evolutionary lineage (Groves, 2001). The point of branching is the theoretical separation of the sister species from their ancestor; this point is referred to as a node. Each of the individual taxa within the sister groups may have uniquely derived states, called autapomorphies, which, although they could have some intrinsic interest, are not evidence for relationship hypotheses.

Cladistic analysis makes no assumptions regarding ancestors and descendants; it does not take absolute time into account although nodes near the root of the tree are obviously earlier than those at the tip of the tree.

The basis of cladistic analysis, then, is data on the character states in the OTUs. I compiled 89 cranial character states (Appendix 2) from Zeitoun (2000) who used a combination of states for *H. erectus* and later hominids derived from Weidenreich (1943), MacIntosh and Larnach (1972), Sartono and Grimald (1983), Grimaud (1982), and Hublin (1978). Zeitoun (op. cit.) did not list the facial characters he used (if any) so I incorporated those described by Weidenreich (1943) for *H. erectus* and Lahr's (1996) coding scheme for human facial characters. For the mandible I developed a list of 34 character states following Schwartz and Tattersall's (2002) description protocol (Appendix 3). The cranial and mandibular analyses are undertaken separately as too few of the mandibles are associated with the crania.

Characters were scored on originals and casts (Table 2). Scores for casts were crosschecked in the literature where there was any doubt about the expression of the character. For this purpose I referred to Rak (1983), Schwartz and Tattersall (2002), Tobias (1991) and Wood (1991).

Fossil hominin crania and mandibles are rarely discovered intact. It is therefore inevitable that some character states will not be known for some specimens. These are coded '?' in the data matrix and are not used by the PAUP* program to choose between trees. If a character is absent from the specimen it is also coded as '?', but I include a corresponding 'present/absent' state for that character to ensure that the information (that the character is not expressed on the fossil) is included in the analysis.

Of the 89 characters, 6 are treated as ordered (5, 6, 22, 24, 52, 72); all other characters have only two possible states, or are not clearly directional in evolutionary terms and any state can transform directly into another. All characters are equally weighted. Where a character presents more than one state in any given taxon, all observed states are included for that character in that taxon; I set PAUP* to treat such characters as polymorphisms. The data are at Appendix 4.

Assumptions in cladistic analysis

1. That any taxa included as OTUs are real. This is tested in the initial PAUP* analysis, although I use crania Sts 5, Sts 71 and Stw 505 (*A. africanus)* as a proxy for the diverse taxon *Australopithecus*, as this taxon is not being tested in these analyses.

2. Changes in characters occur in lineages over time. This is one of the Darwinian principles but can confound cladistics in cases where a continuous variation is observed within populations. In many cases, I coded for multiple states of a character, when 'present' or 'absent' was too restrictive. For example, while I code for the shape of the occipital as 'convex' or 'linear', and for the external occipital crest, there are four possible states. If more than one of these character states was observed within an OTU, I coded that character for all the states it presents (usually termed 'multistate' or 'polymorphic for that character').

3. Any group of hominin is related by descent from a single common ancestor.
Cladistics assumes a branching pattern of lineage splitting, preferably into two groups although an unresolvable polytomy may result. Alternatively, branches that were once separated might well come together again (reticulation of populations); cladistics is not designed to deal with this situation.

4. Characters are genetically independent of each other. We do not have a way of assessing genetic independence of characters, but bias may be minimised in an analysis by avoiding over-emphasis on any given morphological feature.

The small number of fossil specimens poses a problem for cladists in that we cannot be certain that the full range of cranial morphological states is expressed in the sample. This is of particular importance when a putative species is represented by only one cranium, as, for example, is the case for *H. floresiensis*, because it is unlikely that the full expression of character states is represented. In fact, all of the fossil hominin samples are small because the fossil record is relatively scant and it is unlikely that the full range of variation for each is expressed in any of these samples. The problem of limited sample populations is a problem faced by all palaeoanthropologists seeking to understand hominin phylogenetic

relationships. Cladistic analysis is flexible and testable, however, and should further specimens be found or new or different characters identified, the analyses can be repeated and the hypotheses may be corroborated or reformulated.

Cladistic analysis produces cladograms, which are branching diagrams that depict species divergence from common ancestors. The cladogram groups OTUs that share common ancestors into clusters called clades and these represent hypotheses about relationships among them. Cladistic analysis is based upon the total number of character changes necessary to support the relationship of OTUs in a tree. The shortest trees are those that account for the observed differences among taxa in the smallest number of evolutionary steps. They are the most parsimonious trees and present the best working hypotheses.

I use two cladistic programs to perform the cranial, and mandibular, analyses. In the first instance, I use PAUP* (Phylogenetic Analysis Using Parsimony) Version 4.0b10 for Macintosh (Swofford, 2002) to perform a heuristic search of the cranial data to find the most parsimonious tree. Where there is more than one tree of the same length, I generate a Majority Rule consensus, which contains all clades appearing in 50% or more of the trees. The Majority Rule consensus tree is then transposed into MacClade and each OTU is tested against whatever groups survive the first test from the initial cladistic analysis. I then perform cladistic analyses of the mandibular data.

The cladograms require further evaluation of the degree of support before hypotheses of phylogenetic relationships are made (Faith and Cranston, 1991). I therefore perform tests to ascertain the degree of confidence I have in the analyses.

The Bootstrap technique (Felsenstein, 1985) is the most commonly used method for assessing nodal support and has been used to estimate the statistical confidence of phylogenetic analyses since its introduction in 1985 (Li and Zharkikh, 1994). I use the Bootstrap technique to test the stability of the clades found in the initial analysis. It involves random sampling of a set of characters with replacement until a replicate data set of the same size as the original data set is constructed. This replicate data set is subsequently analysed and a tree is reconstructed according to a specified search strategy. This process is repeated a number of times (usually 1000 or more).

The frequency at which each clade is recovered is termed the bootstrap support (Mort et al., 2000). If a group shows up 95% of the time in the bootstrap analyses, then that group is considered to be statistically significant (Felsenstein, 1985), although Hillis and Bull (1993) have argued that bootstrap proportions of more than 70% indicate a strong probability that the clade is real and may, in fact, represent a probability of >90% support for the clade. There may be problems with the bootstrapping technique, including the assumption that the characters in the data matrix represent a random sampling of all possible characters (Strait and Grine, 2004) and the fact that some of the original characters may not be sampled and are thus omitted, whereas other characters may be sampled more than once, which, in effect, simulates weighting procedures (Trueman, 1993), but it is nevertheless widely used in cladistics and I use it in this study. It also assumes a large number of internally consistent characters so that the same clades will be appear in most of the runs, but clades may well disappear if there are only a few synapomorphies supporting them. In fact, Hillis and Bull (1993) contend that bootstrap proportions are highly imprecise, except where the parametric values are near 0 and 1 Bootstrapping is not, then, an assessment of clade accuracy, or a determination that clades are real. I use it in this analysis because it does give an estimate of number of characters supporting a given clade. 10,000 Bootstrap replicates are performed using the Heuristic search option and retention of groups of >50% frequency.

As well as producing a cladogram, PAUP* produces a list of character states for each node and indicates the direction of change, but it does not readily identify which are plesiomorphic and which are derived, or exclusive, to given OTUs. To obtain this information I transfer the shortest tree to MacClade (Maddison and Maddison, 1992) and examine each shared character identified in PAUP* for the OTUs to ascertain whether or not it is shared by any other taxon or is derived for that OTU.

MacClade provides an interactive environment for exploring phylogeny and was developed to help biologists explore relationships between data and hypotheses in phylogenetic biology (op. cit.). In MacClade's tree window, phylogenetic trees (cladograms) can be manipulated and alternative hypotheses for an individual taxon, or

groups of taxa, may be explored. I, therefore, reproduce the Majority Rule tree produced in the initial analysis (that used PAUP*) into MacClade so that I can:

i) identify the most parsimonious phylogenetic solution for each target OTU, and

ii) test hypotheses that have been presented for each OTU.

Clades identified in this way are then tested using a topology-dependent permutation tail probability test (T-PTP); this tests the support for clades, or sister taxa, shown in the cladogram (Faith and Cranston, 1991; Faith, 1991). The test is defined as the estimate of the proportion of times that a given clade can be found, generated from permuted data that are as short as, or shorter, than the original tree. That is, it compares the degree of corroboration for the observed data to that expected by chance alone, so is a test of monophyly of selected nodes. I reject the null hypothesis, that the data have no cladistic structure beyond that produced by chance, at the 0.05 level if fewer than 5 out of 100 of the trees have a length as short, or shorter, than the cladogram, that is, if the T-PTP result is ≥ 0.05.

3 ANALYSES

A. CRANIAL ANALYSES

Background

Cladistic and morphometric analyses of the Early Pleistocene fossil hominin crania are undertaken to test the various hypotheses for the hominins and species discussed in Chapter 1. The aim of cladistic analysis (as described in Chapter 2) is to depict sister group relationships between OTUs using non-metric cranial and mandibular character states.

Principal Component analyses supplement the cladistic analyses. Morphometric data comprising cranial measurements are used to distinguish between crania. Nearness, or distance, in the multivariate space, may be translated directly as similarity, or difference, in morphology as discussed in Chapter 2.

Cladistic and morphometric analyses of the mandibles will be presented in Section B.

3.1 Methodology

Cladistic analyses

The first stage of the cladistic analyses is to test the homogeneity of the putative taxa: *H. habilis* (KNM-ER 1813 and OH 24), *H. erectus* (Sangiran 2, 4, 9, 17, Trinil), the Dmanisi group (D2282, D2282, D2700), and the Turkana group (KNM-ER 3733, KNM-ER 3883, KNM-WT 15000; *H. ergaster*). If any individual within one of the traditionally accepted taxa diverges from the group or cannot be unequivocally included within it, the specimen is treated as a separate OTU. It is assumed that *H. sapiens* comprises a single species and thus is not subjected here to testing; data for 6 males and 5 female *H. sapiens* are combined to form a single polymorphic OTU that is used in all the cladistic analyses.

The most parsimonious tree or trees found using PAUP* are then transposed into MacClade. In these next analyses, *H. rhodesiensis* (represented by Kabwe) is included as a proxy for later African hominins, and *Pan* and *Gorilla* are outgroups. The objective of the analyses is to see if there may be evidence that any of the target fossil crania (OTUs) are sister taxa to any other OTUs. T-PTP and Bootstrap analyses are used as appropriate.

Morphometric analyses

I perform cranial morphometric analyses using Principal Components Analysis (PCA). As the goal of the cranial metric analyses is to assess similarities and differences in crania after the effect of size is removed or reduced, I use log-transformed data. Because fossil crania are in different states of preservation, not all data for each cranium is available. As explained in Chapter 2, I perform a number of analyses, using the maximum number of variables that enables each relevant cranium to be included.

This chapter reports the results of the cranial analyses; discussion about the results is in Chapter 4.

3.2 RESULTS

3.3 Homo habilis, Sangiran, Dmanisi and Turkana crania

3.4 Cladistic analyses

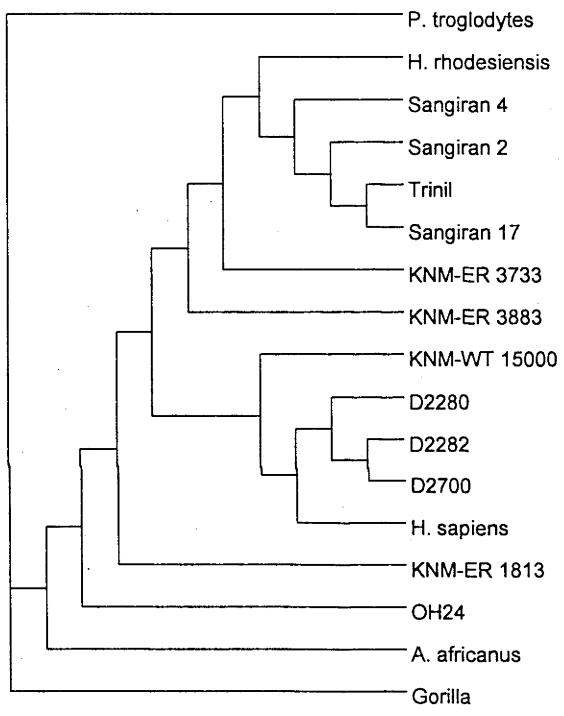
The first analyses undertaken are to test whether the taxa or other groupings to which individual crania are to be compared are indeed homogeneous. The subjects of this analysis are *H. habilis* (OH 24, KNM-ER 1813), the Dmanisi group (D2282, D2282, and the sub-adult D2700), *H. ergaster*, or African *H. erectus* (KNM-ER 3733, KNM-ER 3883, and the sub-adult male KNM-WT 15000), Kabwe (*H. rhodesiensis*) and the Sangiran group or Javanese *H. erectus* (Sangiran 2, 4, 9, 17 and Trinil). The data set is at Appendix 5.

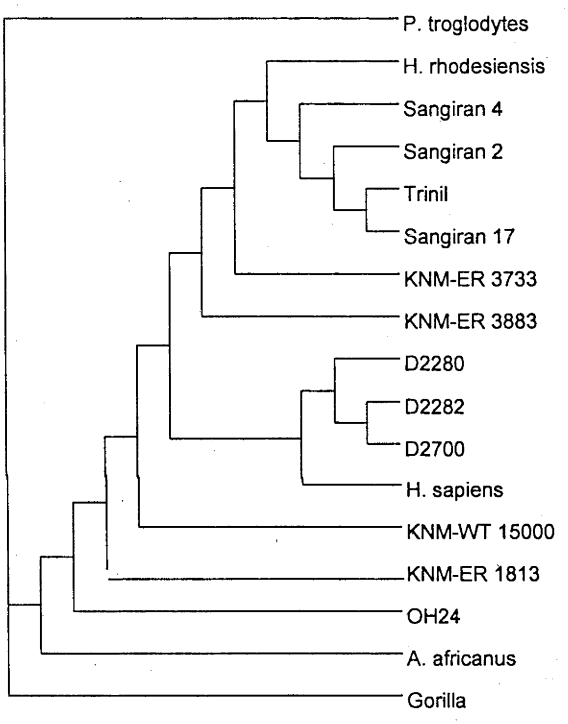
Results

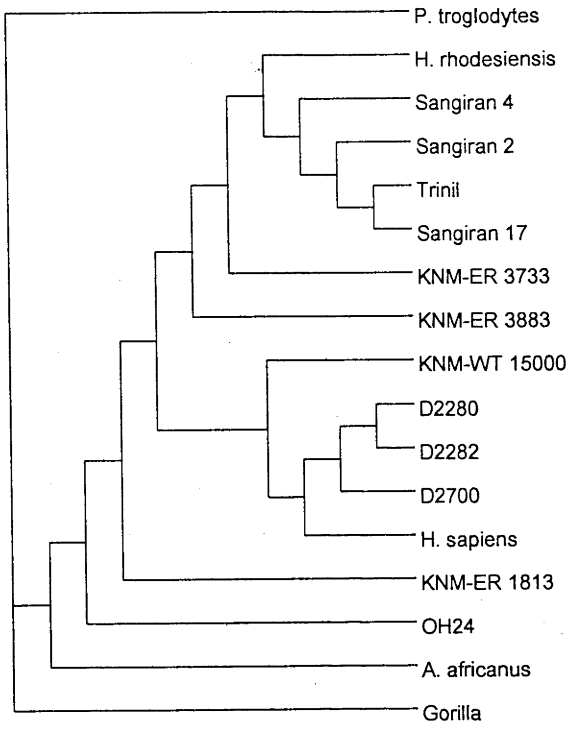
i) Cladistic analysis

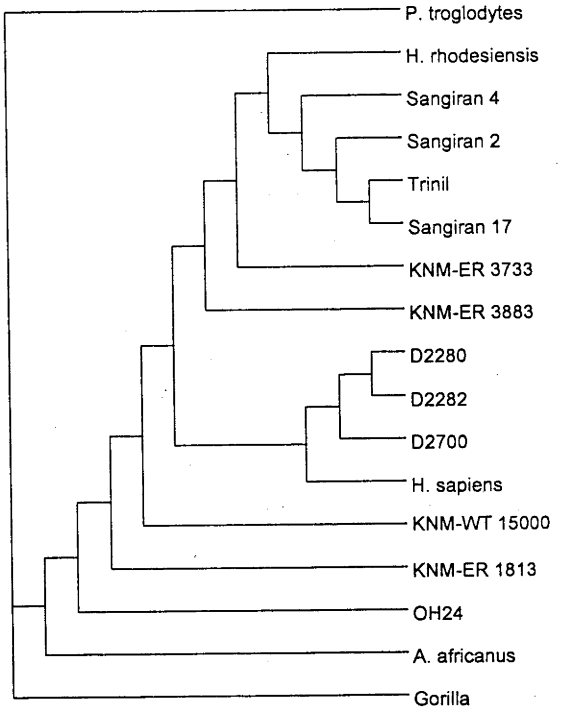
Four trees of equal length (343 steps) were found using the heuristic algorithm in PAUP*. These are shown below, along with the Majority Rule consensus and Bootstrap trees.

3.4.1 Figure 3-1 Four trees of equal length; Majority Rule Consensus; Bootstrap

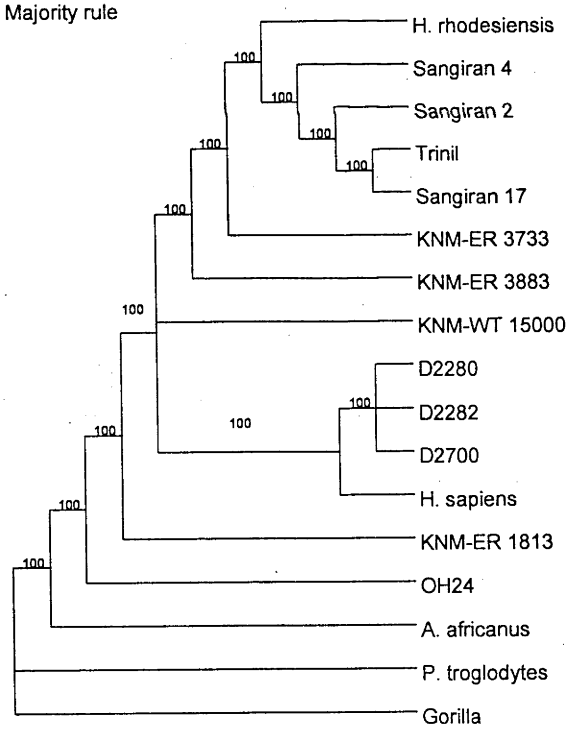




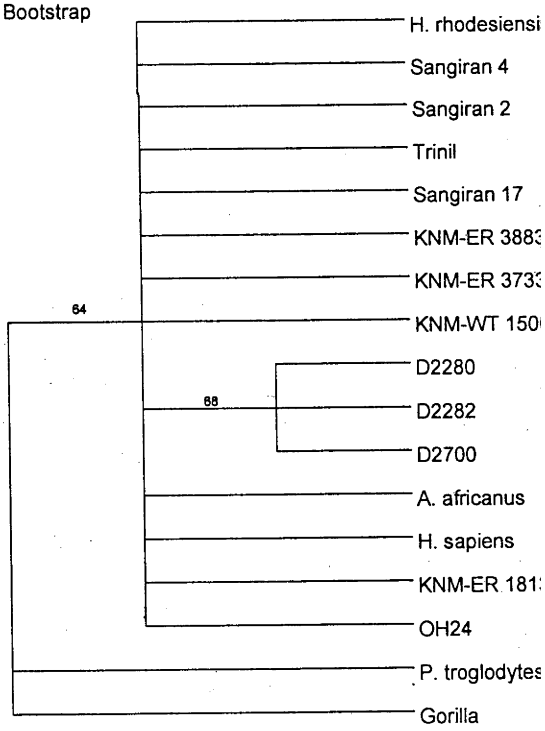




Majority rule



Bootstrap



Homo erectus

The earliest hominins in Asia are commonly included in *H. erectus* and dated to 1.8 Mya (Swisher et al., 1994); 1.51 ± 0.08 – 1.02 ± 0.06 (Larick et al., 2001) or 1.1 Mya (Watanabe and Kadar, 1985; Pope, 1988; see also Kaifu, 2005). The background to *H. erectus* is discussed in Chapter 1.

In the PAUP* analyses Trinil and Sangiran 17 form a clade to which Sangiran 2 is sister. Although this group does not form a branch in the bootstrap analysis, the T-PTP for the Sangiran group is p = 0.01. The null hypothesis that the group came together by chance, therefore, is rejected. The group includes the type specimen for *H. erectus*, Trinil, and shares the following possible[5] synapomorphies:

- Horizontal posttoral plane from which the squama rises posteriorly (condition for Sangiran 4 not known)
- Weak temporal band on the frontal
- Metopic keeling
- Triangular shape of temporal squama (parallel with KNM-WT 15000)
- Supramastoid crest in the region of porion is weak (parallel with KNM-ER 3733, KNM-WT 15000, *H. sapiens*)
- Mastoid and supramastoid crests diverge anteriorly (parallel with KNM-ER 3733, Dmanisi, *H. sapiens*)
- A pre-glenoid plane precedes the mandibular fossa (parallel with *H. sapiens*, Dmanisi, *A. africanus*).
- Crest on lateral edge of mandibular fossa (Trinil, Sangiran 2 condition unknown)
- Postglenoid does not extend out beyond the tympanic plate (parallel with KNM-WT 15000; condition for Trinil unknown)
- Sagittal keeling on the first half of parietal (parallel with Dmanisi)

As the group shares synapomorphies, has a T-PTP of p = 0.01 and includes the type specimen for *H. erectus*, I conclude that the group comprises *H. erectus*. In all future

[5] A particular character state might occur in taxa that are not included in this analysis, so we cannot say categorically that a given state is uniquely synapomorphic for the sister taxa in this study.

analyses, then, the data for these crania will be combined into one polymorphic species, *H. erectus*. Note, however, that Sangiran 4, the oldest of these (Kaifu et al., 2006), is sister to the rest.

The T-PTP for Sangiran and *H. rhodesiensis* is also p = 0.01 but *H. rhodesiensis* shares only two possible synapomorphies with *H. erectus*:

- Horizontal posttoral plane from which the squama rises posteriorly (conditions for Sangiran 2 and Sangiran 4 not known)
- Strength of supramastoid crest in the region of porion is weak (parallel with KNM-ER 3733, KNM-WT 15000, *H. sapiens*)

H. rhodesiensis will therefore be left ungrouped in all analyses, to further explore its affinities.

3.4.2 Dmanisi

The Dmanisi hominins are referred to *H. erectus* (Gabunia and Vekua, 1995; Brauer and Schultz, 1996; Vekua et al., 2002); *H. georgicus* (Gabounia et al., 2002); and *H. ergaster* (Vekua et al., 2002). Each of these hypotheses is tested below.

The Dmanisi crania and mandibles included in this study (after Martinón-Torres et al., 2008).

Skull	Mandible	Age
D2280	-	**Adult**
D2282	**D211**	**Young adult**
-	**D2600**	**Adult**
D2700	**D2735**	**Subadult**

Cranial cladistic analyses

In all trees, the Dmanisi crania form a clade; this has a Bootstrap value of only 68. The clade forms a sister clade with *H. sapiens*, which shares 4 possible synapomorphies:

- convex frontal edge (parallel with KNM-ER 1813)
- main axis of tympanic in norma lateralis is vertical

- posterior part of tympanal joins anterior of mastoid process (D2282 unknown; *H. sapiens* polymorphic)
- zygomaticoalveolar crest forms an arc (parallel with KNM-ER 3733)

Although *H. sapiens* and Dmanisi form a clade in all the most parsimonious trees, the T-PTP for {Dmanisi, *H. sapiens*} is p = 0.12. The null hypothesis that Dmanisi and *H. sapiens* came together by chance is not refuted; they are not clearly sister taxa. *H. sapiens* will be included in the following analyses as a separate OTU.

The Dmanisi crania share the following possible synapomorphies:

- zygomaticoalveolar crest forms an arch
- sharp high line divides the floor of the orbit from the facial portion of the malar
- shallow digastric fossa
- frontal edge in norma verticalis is linear (parallel with *H. sapiens*, KNM-ER 1813)
- supraorbital form is a>b, b<c and a>c (where 'a' is central, 'b' is middle and 'c' is lateral; parallel with *A. africanus*)
- bregmatic eminence (*H. erectus* polymorphic)
- strong occipital torus (parallel with *H. erectus*)
- main axis of tympanal in norma lateralis is vertical (parallel with *H. sapiens*)
- postglenoid process is strongly involved in the wall of the mandibular fossa (parallel with *A. africanus*)
- posterior part of tympanal joins anterior part of mastoid process (D2282 n/a)
- the *jugum alveolar* forms a broad and prominent ridge (D2280 n/a)
- glasserian fissure

Although there is no indication in the cladistic analyses that Dmanisi and any of the Turkana crania shared a common ancestor, in view of Gabunia et al.'s (2000) referral of the Dmanisi crania to *H ergaster* it is necessary to test for any probability of a close phylogenetic relationship. I therefore performed a number of T-PTP tests:

Dmanisi	Turkana	T-PTP
Dmanisi	KNM-ER 3733, KNM-ER 3883, KNM-WT 15000	0.37
Dmanisi	KNM-WT 15000	0.66
Dmanisi	KNM-ER 3733	0.69
Dmanisi	KNM-ER 3883	0.95
D2280	KNM-ER 3733, KNM-ER 3883	0.43

All T-PTP results indicate that the Dmanisi group and Turkana crania would form a clade by chance alone.

Subadult crania are often omitted from phylogenetic and morphometric analyses. Such seems to be the case for KNM-WT 15000 (see, for example, Manzi et al. 2001; Mallegni et al. 2003; Villmoare 2005; Bruner and Manzi 2005, who all use KNM-ER 3733 and 3883 in their analyses but omit KNM-WT 15000). The omission is probably based upon the assumption that the subadult form does not represent the adult of the taxon. Yet in the case of the Dmanisi crania, D2700 forms a highly supported clade with the adults of this group, despite its sub-adult status.

Mandibular cladistic analyses

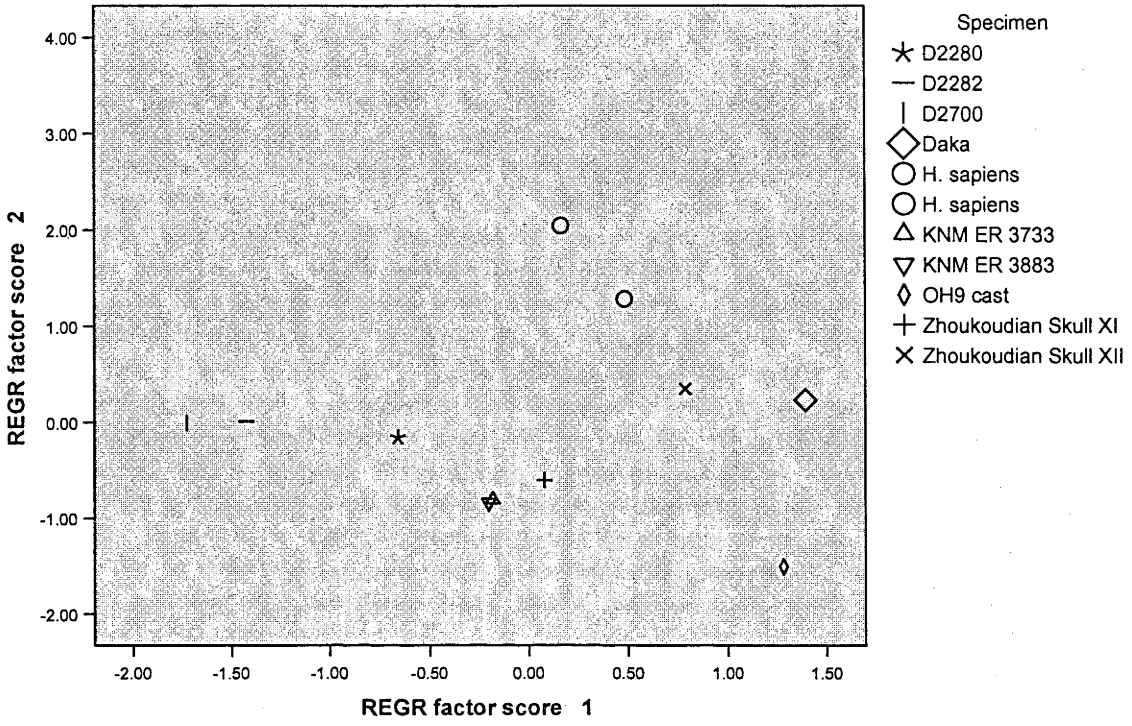
In the cladistic analyses performed for this study, the largest mandible (D2600) and smallest (D2735, associated with cranium of sub-adult D2700) formed a clade in 78% of the most parsimonious trees (see Majority Rule consensus tree, below; Figure 3.51) and the clade has a T-PTP value of p = 0.01. The third Dmanisi mandible, D211, formed a clade with Tighenif 3 or with KNM-WT 15000 in the most parsimonious trees, but, as discussed below (Part B; Mandibles), neither of these clades is supported. I therefore tested whether D211 could form a supported clade with the other Dmanisi mandibles. When they were thus constrained, the tree was only one step longer than the shortest tree and the T-PTP for the clade was p = 0 .065. The three mandibles share two possible synapomorphic states: the digastric fossa is shallow (Parallel with LB6/1, *H. sapiens*

polymorphic); and the symphyseal region is uniformly thick inferiorly (parallel with *H. pekinensis*).

I tested for other possible phylogenetic relationships for the three mandibles. The Dmanisi group has been attributed to *H. erectus* as possibly a subspecies, by Rightmire et al. (2006). When they are constrained with *H. erectus* (Figure 3.54), however, the tree was 3 steps longer than the most parsimonious and the T-PTP was p = 0.71; this strongly suggests that Dmanisi did not share a common ancestor with *H. erectus*. When Dmanisi is constrained with *H. pekinensis* (Figure 3.55), the shortest tree is only one step longer than the most parsimonious but the T-PTP is p = 0.19, again, this phylogeny is unsupported.

Principle Component Analyses

There are three Principle Component analyses that include the Dmanisi crania. In the analysis below, D2282 and D2700 cluster on both axes; D2280 is somewhat larger, but nevertheless clusters with the other two crania on Function 2. That is, the three crania are similar in overall shape in this analysis. Further, the spread for the group is no broader than that for *H. pekinensis* (the Zhoukoudian crania). In Analysis 2a (Figure 3.9), however, D2280 clusters with the Turkana crania KNM-ER 3733 and KNM-ER 3883, and differs from D2700 in that the latter has a smaller frontal arc and narrower vault. D2800 also clusters with KNM-ER 3733 and KNM-ER 3883 and differs from D2700 in Figure 3.22 (refer to OH 9 analyses, below). D2280 has a relatively wider and somewhat longer cranium that is relatively wider in the biauricular and upper facial region than D2700 (Figure 3.9) and the latter has a shorter bregma-lambda chord and arc (Analysis 1; Figure 3.2).



Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.261	71.018	71.018	4.261	71.018	71.018
2	1.047	17.451	88.469	1.047	17.451	88.469
3	.316	5.267	93.736	.316	5.267	93.736
4	.175	2.922	96.658			
5	.144	2.401	99.059			
6	.056	.941	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logXFB	.865	.070	-.487
logMIN_FRONTAL_ BREADTH	.958	-.031	.122
logASB	.707	-.644	.115
logSTB	.590	.772	.114
logFRC	.924	.107	.192
logna_br_arc	.945	-.137	-.023

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

Figure 3-2 PCA Analysis 1: Dmanisi

The three Dmanisi crania vary in size, assuming Function 1 represents primarily size differences (all variables on PC 1 show positive values, though not equally strongly). The Dmanisi group does not separate from the other early hominins on Function 2, although OH 9 has a narrower biasterionic breadth in relation to its bistephanic breadth than the others. The results are discussed more fully above.

I conclude the Dmanisi group represent a single polymorphic OUT. This group will be further discussed in Chapter 4.

3.4.3 Homo habilis

H. habilis is one of the species to which the unknown specimens are being compared. The sample in this analysis comprises KNM-ER 1813 and OH 24. These did not, however, form sister taxa in the PAUP* cladistic analysis, as would have been expected as they are both usually attributed to this species; rather, OH 24 forms a sister taxon to all other *Homo* OTUs.

KNM-ER 1813 and OH 24, then, were included as separate OTUs in the subsequent analyses to further assess their affinities. In each of these they formed a clade. The T-PTP value for the clade is $p = 0.01$ and it shares three possible synapomorphies: no preglenoid plane precedes the glenoid cavity (parallel with KNM-ER 3733, KNM-ER 3883; KNM-WT 15000); the *facies anterior* and alveolar process forms a flat surface (parallel with *A. africanus*); and a sharp high line divides the floor of the orbit from the facial part of the malar (parallel with Dmanisi).

3.4.4 The Turkana group

KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 are usually referred to the same species, *H. ergaster* (or African *H. erectus*), although Schwartz and Tattersall (2002:139) described KNM-WT 15000 as sharing a morphology that places it within a group comprising KNM-ER 1813 (normally attributed to *H. habilis*), KNM-ER 1482a and KNM-ER 1805, and they also described a 'KNM-ER 3883 morph' (op. cit. 136-138) that does not include KNM-ER 3733. Zeitoun (2000), too, separated KNM-ER 3733 and KNM-ER 3883, attributing KNM-ER 3733 to a new species *H. kenyaensis* and KNM-ER 3883 to another species *H. okotensis*, based upon his cladistic analysis of *H. erectus*.
KNM-ER 3733 is dated from 1.78 Mya; KNM-ER 3883 to 1.65 – 1.50 Mya (Feibel et al. 1989); and KNM-WT 15000 to 1.56 Mya (Brown and McDougall, 1993).

Observations

KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 are curated at the National Museum of Kenya. To maximise the safe handling of the specimens, the museum policy is that only one cranium at a time may be examined. I was therefore unable to directly compare the morphological variation between the three, although on one occasion I could make observations on KNM-ER 3733 and KNM-ER 3883, keeping one in its box while observing the other. In other words, direct comparisons were not easy to make. The number of measurements, character states, and photographs I have taken, however, ensures I have more than adequate comparative data.

KNM-ER 3733 and KNM-ER 3883

In lateral profile, the crania KNM-ER 3733 and KNM-ER 3883 have relatively low profiles that form a rounded curve to a relatively flat occipital region. They differ in that KNM-ER 3733 has some metopic swelling on the frontal, a more marked supraorbital sulcus, and a steep frontal slope, and the supraorbital sulcus and metopic keeling give the frontal a somewhat foreshortened appearance compared to KNM-ER 3883. They are similar in occipital view, with slightly curved temporals that slope inward towards the vault; and the crania are widest at the mastoid region. There are some differences in frontal view: the KNM-ER 3883 supraorbitals are only moderately developed and are thickest centrally, while on KNM-ER 3733 they are marked and of uniform thickness. The

frontal on KNM-ER 3883 rises gently from just posterior to glabella, while on KNM-ER 3733 it rises relatively steeply from a more posterior position (after the posttoral sulcus). Both have prominent temporal lines, and where the remains of the fronto-maxillary regions can be detected they are similar. KNM-ER 3733 has an oval depression behind glabella (~100 x 125mm) that is incised into the postorbital sulcus.

In both crania the supraorbital margin forms an edged crest demarcated from the roof of the orbit; and the infraorbital margin is relatively rounded, but raised in relation to the floor of the orbit.

The nasofrontal suture takes an inverted 'V' course on KNM-ER 3733 and a horizontal course on KNM-ER 3883. Bone thickness adjacent the nasal aperture region on KNM-ER 3733 is 0.97mm but this region is thinner on KNM-ER 3883 (0.39mm) (taken 1cm in from nasal edge and 0.33mm below nasion). Much of the rest of the facial region is missing from KNM-ER 3883; on KNM-ER 3733 nasospinale lies in front of rhinion and the *margo limitans* includes a pre-nasal groove; from what is available for the maxillary region, it would appear that the *facies anterior* and alveolar process is well filled out. There is no jugum alveolare, and no malar notch.

There is a precoronal depression on KNM-ER 3733 but this is absent on KNM-ER 3883; both lack a postcoronal depression. The temporal bands on KNM-ER 3733 are more marked than those of KNM-ER 3883. As the skull is broken in the bregmatic region, it is unclear if there was a bregmatic eminence in KNM-ER 3733; there is none on KNM-ER 3883; and neither has an obelionic depression.

The KNM-ER 3733 temporal squama is low in relation to the vault, whereas KNM-ER 3883 has a relatively high squama; nevertheless their temporal bone shapes are similar, comprising a rounded anterior margin and a linear superior margin. There is no asterionic process, parietal bossing, or angular tuberosity on KNM-ER 3733.

KNM-ER 3733 and KNM-ER 3883 are quite different in their digastric fossa configuration: KNM-ER 3883 has a well defined U-shaped fossa and juxtamastoid

eminence, whereas KNM-ER 3733 has no identifiable digastric fossa or juxtamastoid eminence, rather, it is composed of a relatively flat plane in this region.

There is no evidence in KNM-ER 3733 for postglenoid processes, unless they have been broken off; KNM-ER 3883 has this process, although the tympanic makes up most of the posterior wall of the mandibular fossa. Both crania have vaginal processes with styloid pits; the styloid process is available for, but no longer attached to, KNM-ER 3733. Both KNM-ER 3733 and KNM-ER 3883 have a space between the entoglenoid formation and tympanic plate (as opposed to this region being fused or grooved). Both KNM-ER 3733 and KNM-ER 3883 have a sigmoid shape to the base of the mandibular fossa (similar to OH 9 but not as marked), and for both, the entoglenoid process is of similar size to the opposing sphenoid edge.

The occipital torus is strong in KNM-ER 3733; it is not, however, linked with the supramastoid or mastoid crest, nor with the temporal line. There is no occipital sulcus although there is a depressed area above the occipital torus on the left and right side. A retromastoid process (tubercle) is at each end of, and somewhat separated from, the occipital torus. KNM-ER 3883 has no occipital torus or occipital sulcus, although there is a small horizontal raised oval area left of centre; on the right is a horizontal ridge of bone, rather than a true torus. In lateral view, the occipital is superiorly-inferiorly flat and below this the nuchal is flat to slightly concave.

The *tuberculum linearum* is strong on KNM-ER 3733 and only moderately so on KNM-ER 3883. The external occipital crest is present for the whole of the nuchal region of KNM-ER 3733 (i.e. to the anterior edge of foramen magnum); on KNM-ER 3883 it is present only below the inferior nuchal line to the anterior edge of the foramen.

KNM-ER 3733 has strong supramastoid and mastoid crests; whereas those of KNM-ER 3883 are weak. The supramastoid sulcus on KNM-ER 3733 is narrow; it is wide on KNM-ER 3883. The mastoid and supramastoid crests are divergent anteriorly on KNM-ER 3733; on KNM-ER 3883 they are parallel. Neither cranium has a direct link between the supramastoid crest and inferior temporal line or a continuity between the mastoid crest and superior temporal line; nor do they have an angular tuberosity.

The development of the mastoid processes cannot be assessed on KNM-ER 3733 as they are either eroded or damaged; on KNM-ER 3883 the process is relatively large and, in lateral view, projects below the base of the cranium.

KNM-WT 15000

This comprises a nearly complete skeleton, attributed to *H. erectus* when initially described by Brown et al. (1985), discovered at Nariokotome III, west Lake Turkana, Kenya, and excavated *in situ.* The cranium is in relatively good condition, missing only the nasals, ethmoid, lacrimals, central parts of the supraorbital tori, and parts of the sphenoid and vault. There is some distortion of the calvaria with the upper part slightly skewed to the left. The sutures and all the epiphyses in the post cranium are unfused, indicating that more growth could have been expected; the cranium does not possess strong tori, temporal or nuchal lines and it is therefore a presumed male adolescent estimated on human standards to be 12 ±1 years old at death and 1.68m tall (op. cit. 789).

It was excavated from between Okote Tuff and Black Pumice tuff and thus dated to 1.65 – 1.55 (Feibel et al. 1989:613), making it contemporary with KNM-ER 3883 and younger than KNM-ER 3733, with both of which it is often grouped as *H. ergaster* or *H. erectus*.

Walker and Leakey (1993) presented a detailed description of KNM-WT 15000 and assigned it to *H. erectus* (op. cit 420), but suggest testable alternative affinities based upon models of human evolution: if there has been no split in the lineage leading to *H. sapiens* since the early Pleistocene, the specimen would be *H. sapiens.* If there are sufficient differences found between the African specimens and Asian *H. erectus*, then KNM-WT 15000 might be accommodated in the new (African) species, which they would then name *H. ergaster* because when they compared the mandible of KNM-WT 15000 to the type specimen of *H. ergaster*, and making allowances for its juvenile state, they find the similarities striking, 'even down to the subocclusal morphology as revealed by X-ray' (op. cit. 421). This perceived similarity of KNM-WT 15000 and KNM-ER 992 may not be supported by Schwartz and Tattersall (1999:246) who note differences in the premolars and molars of the lower jaw of KNM-WT 15000 and those of KNM-ER 992 (op cit. p. 144).

Observations

In lateral view, the cranium is rounded from the frontal to the nuchal region; and the facial region is prognathic. The frontal rises from a very slight, or narrow, upward sloping shelf (similar to KNM-ER 1813). The cranium appears relatively short compared to, for example, KNM-ER 3733 and KNM-ER 3883. In occipital view, the cranium is relatively low and globular, with the widest part at, or just above, the mastoids.

The temporal bands are weak; there is no keeling of any kind, with no bosses, or notable depressions, no asterionic process, or angular tuber. The temporal squama is low in relation to vault height, and is triangular in shape, with straight upper and frontal edges.

There is an occipital torus comprising a slight swelling following the superior nuchal line, but no occipital sulcus. The external occipital protrusion extends inferiorly. There is a moderate tuberculum linearum with a depression above the meeting of the nuchal lines. The external occipital crest is a low mound flanked by a depression at each side.

The mastoid process is large, orientated inwards, and projects below the base of the cranium; there is a wide space between the tympanic and the anterior of the mastoid process. The supramastoid crest forms an angle with the zygomatic process; it does not meet with the temporal line. The mastoid crest and supramastoid sulcus are weak; the mastoid crest does not link with the superior temporal line. The digastric fossa is a short, deep and wide U-shaped furrow; the juxtamastoid eminence is weak.

There is no postglenoid process; the tympanic makes up the mandibular fossa wall. The mandibular fossa is of simple construction; the shape of the posterior edge of the tuberculum articulare in *norma basilaris* is flat and transversely straight. There is a gap between the entoglenoid formation and sphenoid edge adjacent. The articular eminence is lower than the posterior part of the mandibular fossa

The tympanic is thick (>2mm), oval-shaped, and slopes down anteriorly. It has a 'tympanic trough', a fissure-like feature that extends along the midsection of the tympanic in basal view. This feature also occurs to varying degrees on D2700 (Dmanisi group) and Zhoukoudian Skull III (Weidenreich 1943:54). Tobias described it for *Zinjanthropus*

boisei (Olduvai Hominid 5), suggesting that it results from a poor or incomplete fusion between the two moieties of the tympanic bone (Tobias 1967:31); he later described the same feature for Olduvai Hominin 24 (Tobias 1991:96), and it may occur on *A. afarensis* AL 444-2 (Kimbel et al. 2004). It is evident on the *H. floresiensis* cranium (Liang Bua 1).

The *facies anterior* and alveolar process has a sunken appearance, as opposed to being flat, or inflated. There is no *jugum alveolare;* the infraorbital sulcus is wide and relatively long; there is no malar notch and no zygomaxillary pillar.

The naso-alveolar clivus is relatively flat, although there are two slight superior-inferior troughs above each incisor. Between these, from nasospinale to prosthion, is a deep fissure between two very narrow rows of raised bone.

The zygomatic arch runs at the level of the Frankfurt Horizontal.

The orbits are almost square-shaped although the lower orbital border extends inferiorly towards the outer rim.

Results: Turkana group

Cladistic analysis

The three Turkana crania are separate in the PAUP* Consensus tree: they do not form a clade. In the four equally parsimonious trees, KNM-ER 3733 forms a sister taxon to the Sangiran group and KNM-ER 3883 is sister to this group. KNM-WT 15000 forms a clade with the Dmanisi crania in two of the trees. In the remaining two trees it branches off immediately after KNM-ER 1813. The T-PTP for {Dmanisi, KNM-WT 15000}, however, is $p = 0.33$, indicating that the null hypothesis, that clade came together by chance, is not rejected.

The somewhat unexpected separation of KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 is tested by transferring the consensus tree to MacClade so that alternative configurations for these OTUs may be explored.

In these trees, *H. sapiens* is constrained as the most derived OTU and the Dmanisi crania and *H. erectus* crania are each combined as polymorphic OTUs, as discussed above.

Two shortest trees of length (L) = 317 are found in MacClade (Figure 3.3). In the first of these (below), KNM-WT 15000 is a separate taxon branching off between *H. erectus* and Dmanisi; in the second it forms a clade with *H. erectus*:

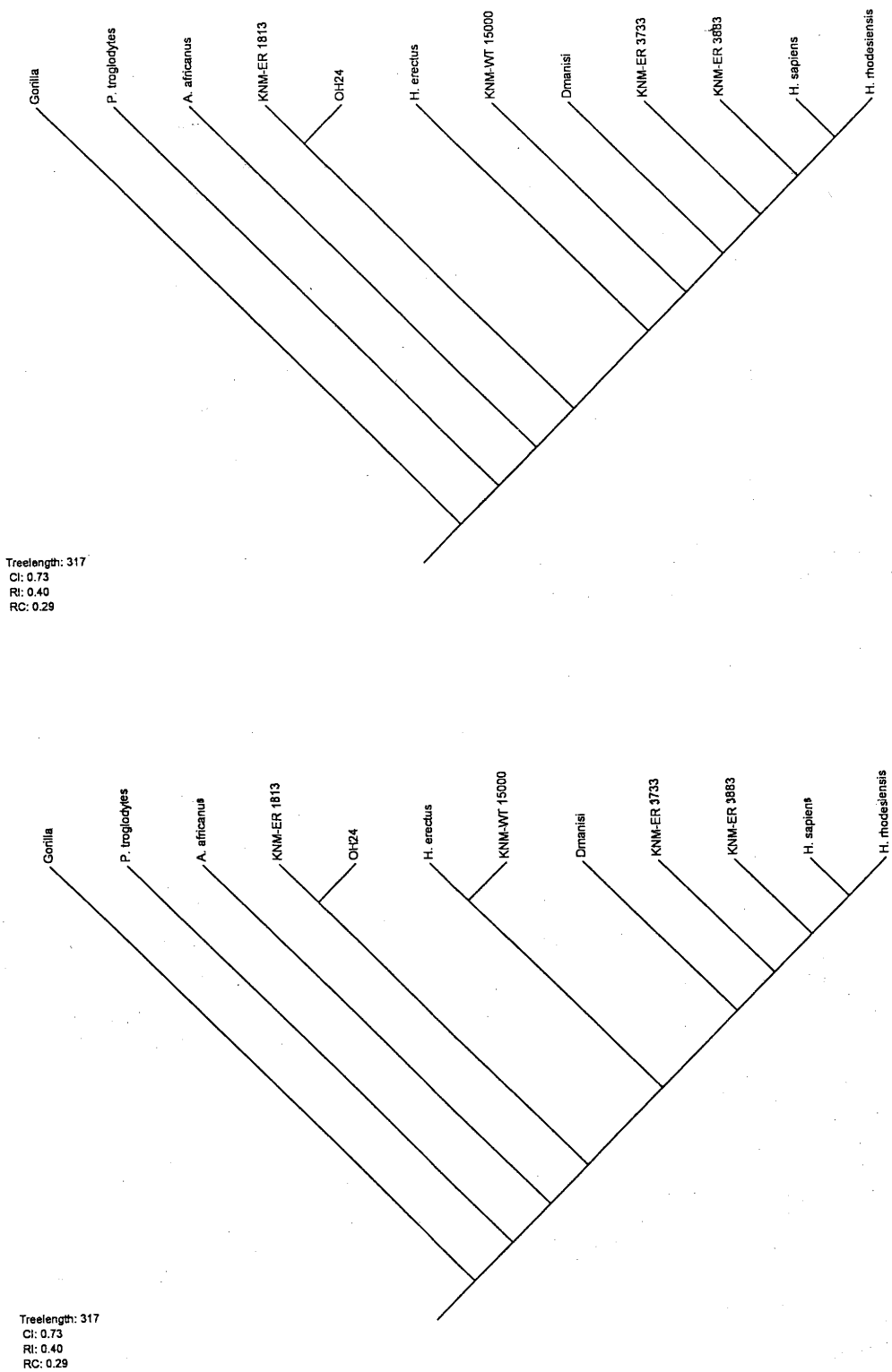


Figure 3-3 Shortest trees

The T-PTP for {KNM-WT 15000, *H. erectus*}, however, is 0.21; the null hypothesis that these OTUs would come together by chance is not rejected and it is unlikely that KNM-WT 15000 and *H. erectus* shared a unique common ancestor. Tree 1 (above) therefore represents the more parsimonious solution for KNM-WT 15000.

When the OTUs KNM-WT 15000, KNM-ER 3733 and KNM-ER 3883 are manoeuvred to form a clade (Figure 3.4), there are two trees of equal length (L = 320) - 3 steps longer than the shortest trees (L = 317):

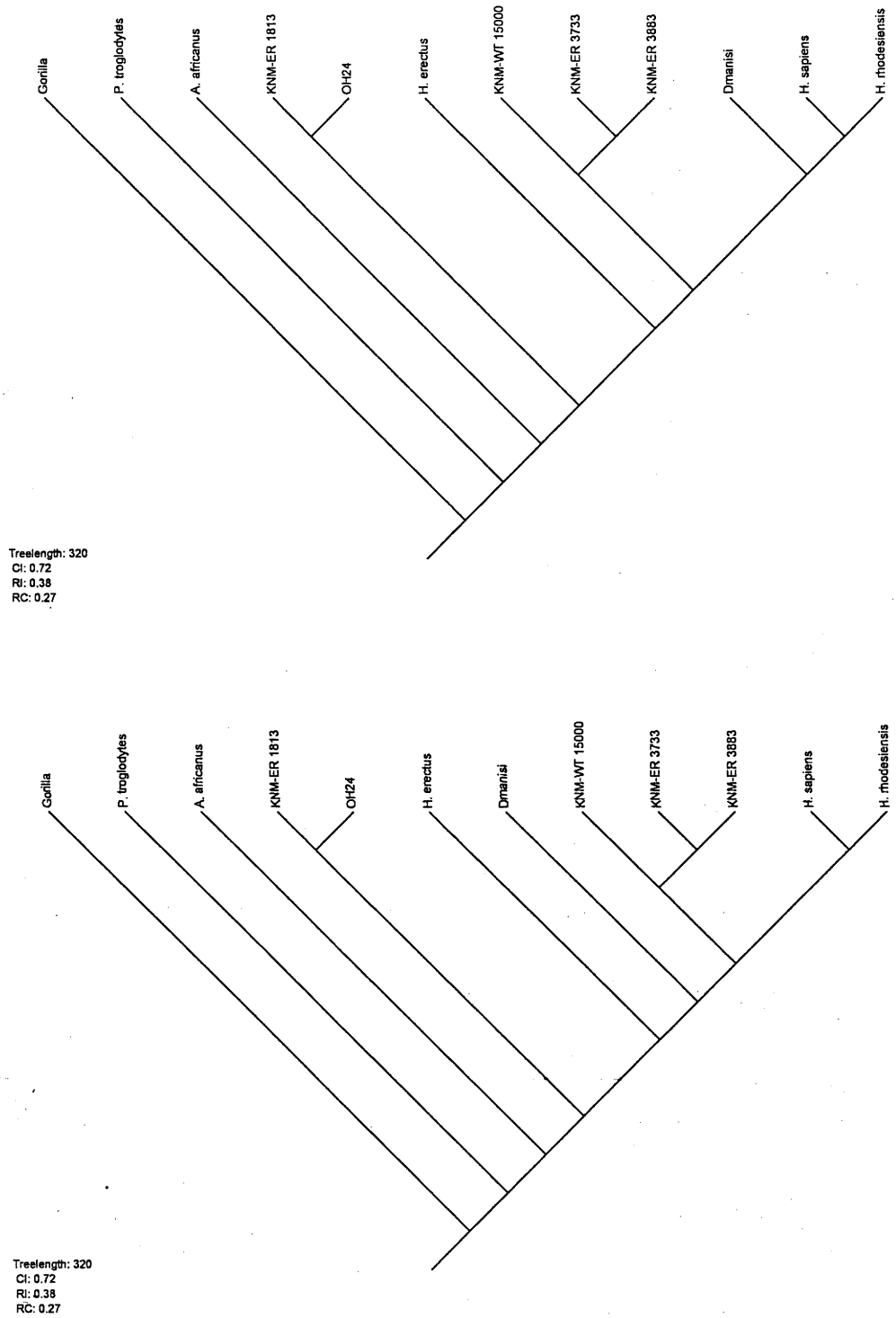
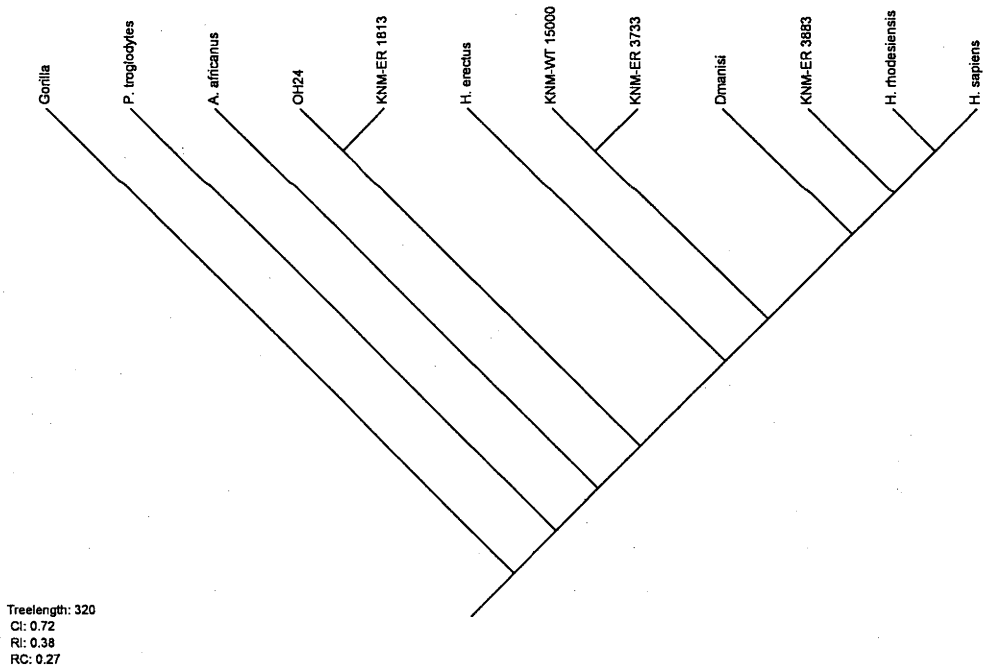


Figure 3-4 KNM-WT 15000, KNM-ER 3733, KNM-ER 3883.

The T-PTP for {KNM-WT 15000, KNM-ER 3733, KNM-ER 3883} is p = 0.25; the null hypothesis that these would come together by chance is not refuted. That is, the clade is unsupported: the trees are longer than the shortest and the T-PTPs suggest that such a clade would form by chance alone.

I also tested for possible clades {KNM-WT 15000, KNM-ER 3733} and {KNM-WT 15000, KNM-ER 3883}. When KNM-WT 15000 and KNM-ER 3733 were constrained (Figure 3.5; first tree), the tree was 3 steps (L = 320) longer than the shortest (L = 317) and the T-PTP is p = 0.40. For KNM-WT 15000 and KNM-ER 3883 the tree was 5 steps longer (Figure 3.5; second tree) and the T-PTP for the constrained clade was p = 0.45. It is, then, unlikely that there is a close phylogenetic relationship between KNM-WT 15000 and either of these OTUs.



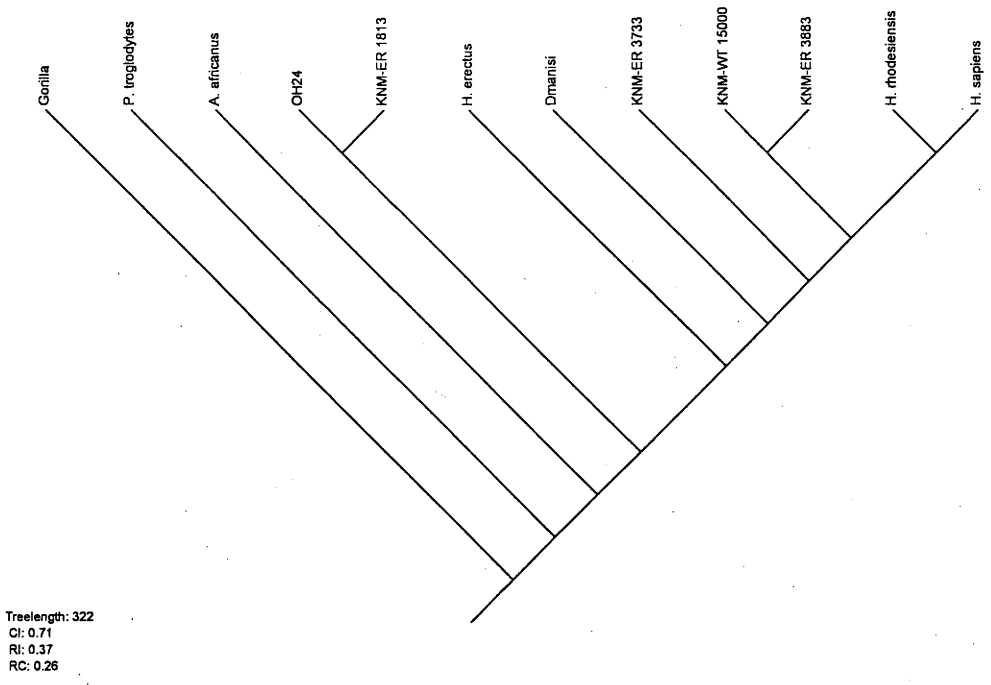
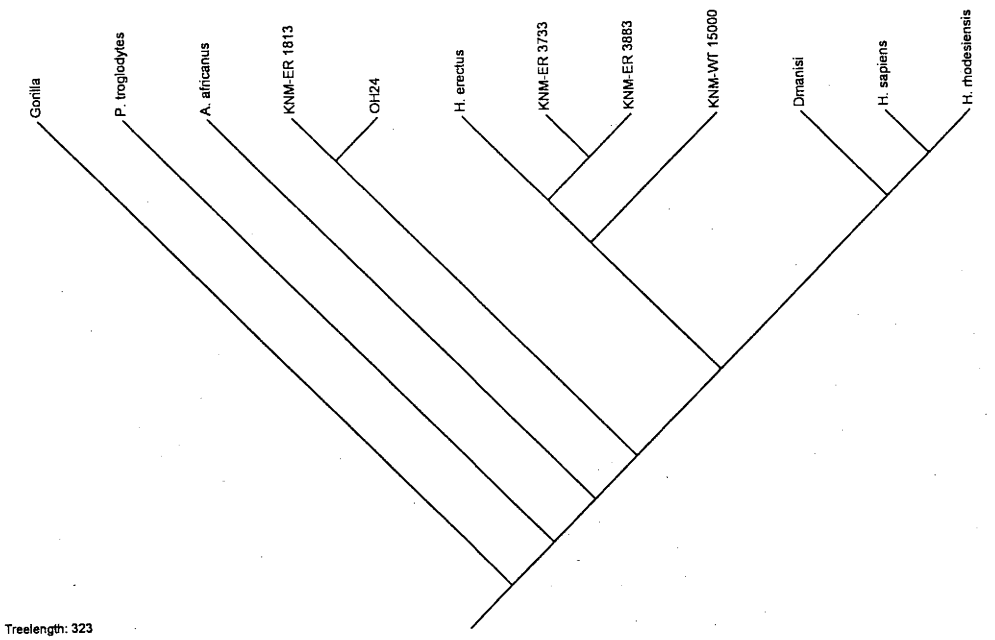
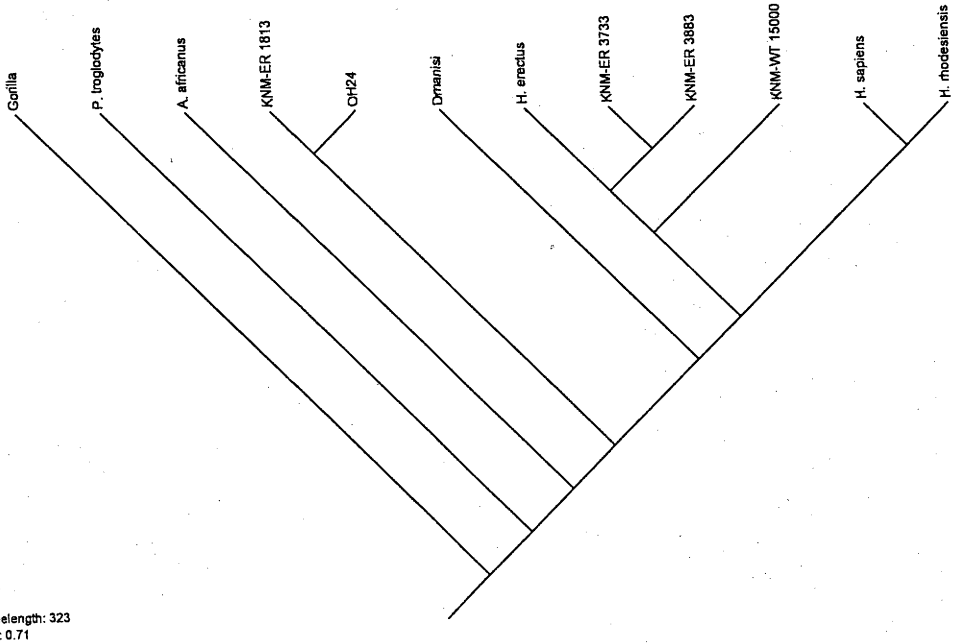


Figure 3-5 KNM-WT 15000 and KNM-ER 3733; KNM-WT 15000 and KNM-ER 3883

The Turkana crania have also been attributed to *H. erectus* (e.g. Rightmire 1984; Walker and Leakey and 1993) but they do not form a clade with *H. erectus* in the initial (PAUP*) cladistic analysis (above). This outcome can be tested in MacClade. When KNM-WT 15000, KNM-ER 3733, KNM-ER 3883 are placed on a branch that also comprises *H. erectus,* the shortest configurations are L = 323, 6 steps longer than the shortest tree (L = 317, above):



Treelength: 323
CI: 0.71
RI: 0.36
RC: 0.26



Treelength: 323
CI: 0.71
RI: 0.36
RC: 0.26

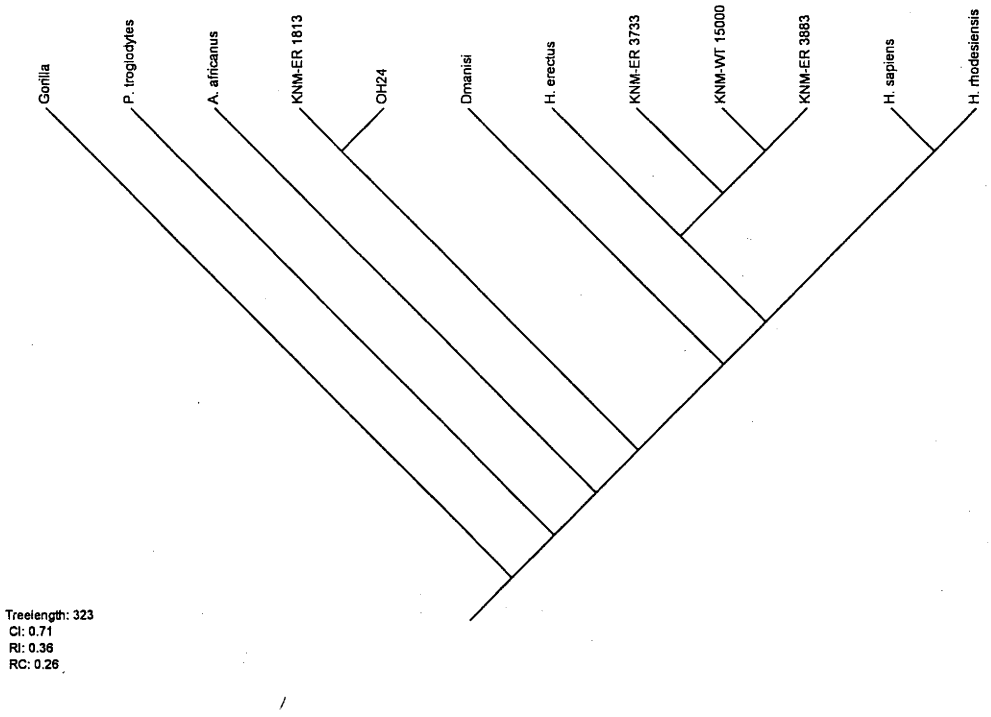


Figure 3-6 *H. erectus*, KNM-ER 3733, KNM-ER 3883, KNM-WT 15000.

The difference between the trees is the location of the Turkana/*H. erectus* branch, and the configuration of the Turkana OTUs.

To further explore for any possible phylogenetic relationship between these Turkana OTUs and *H. erectus*, KNM-ER 3733 and KNM-ER 3883 are separately tested as possible sister taxa to *H. erectus* (the likelihood that KNM-WT 15000 and *H. erectus* did not share a unique common ancestor is demonstrated above).

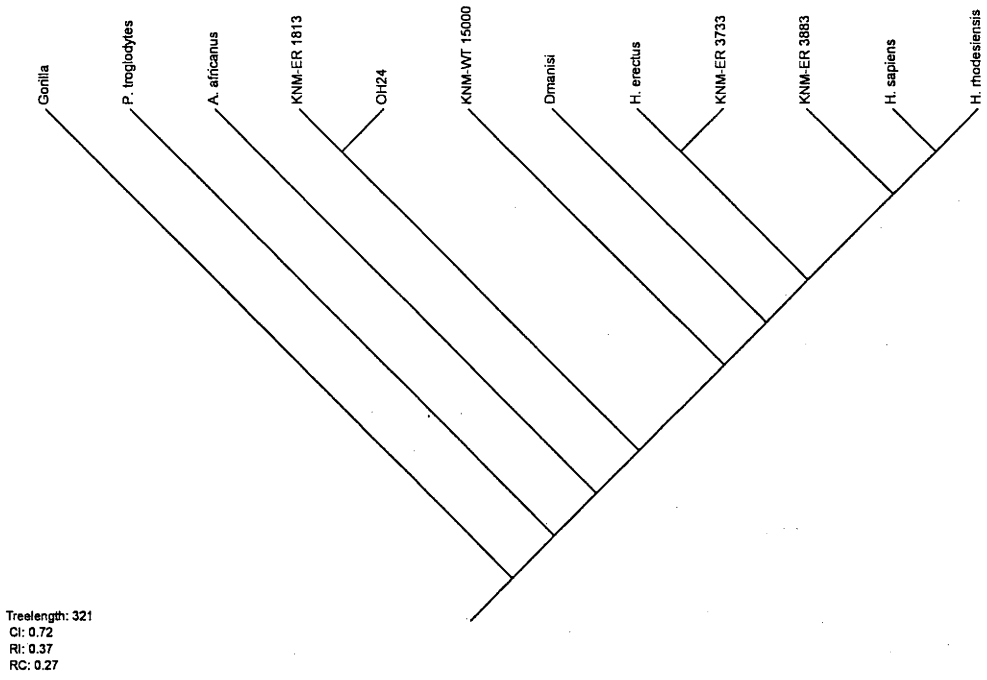


Figure 3-7 *H. erectus* and KNM-ER 3733.

The tree that includes the clade {*H. erectus*, KNM-ER 3733} length is 321 steps, 4 steps longer than the shortest tree.

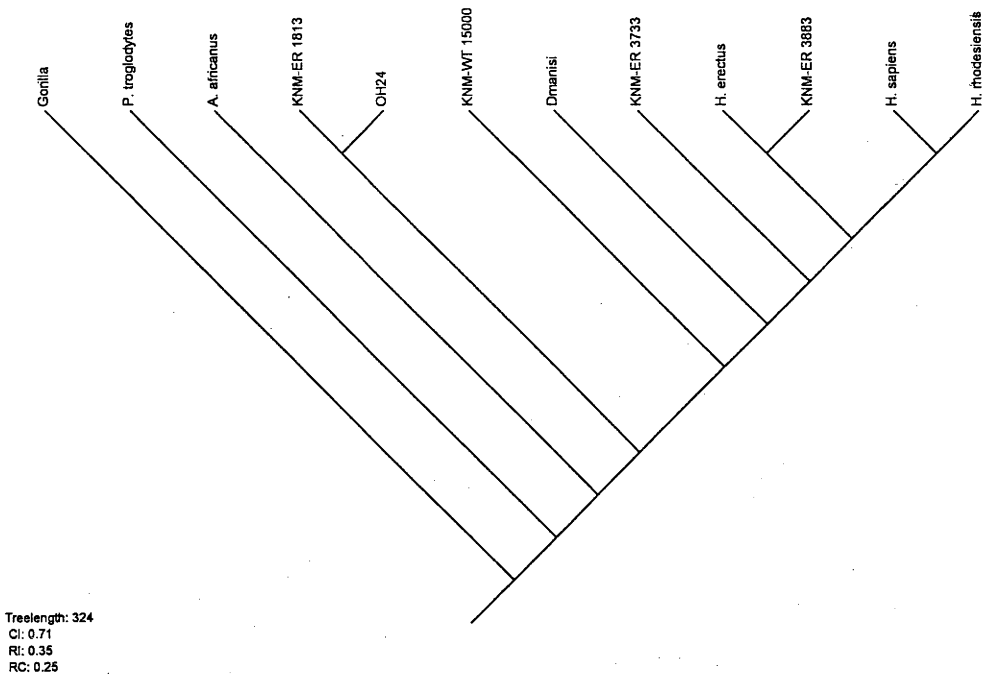


Figure 3-8 *H. erectus* and KNM-ER 3883.

The shortest length for a tree that includes a clade {*H. erectus*, KNM-ER 3883} is 324 steps, 7 steps longer than the shortest tree. The T-PTP for {KNM-ER 3733, *H. erectus*} is p = 0.70; for {KNM-ER 3883, *H. erectus*} it is p = 0.82. The null hypothesis that each clade would come together by chance is not rejected.

As these trees are longer than the shortest tree, and the T-PTPs do not support either a {*H. erectus*, KNM-ER 3733} or {*H. erectus*, KNM-ER 3883} clade, it is unlikely either shared a common ancestor with *H. erectus*.

Nevertheless, KNM-ER 3733 and KNM-ER 3883 share 8 possible synapomorphies (below) so I will continue to test their possible phylogenetic relationships whilst examining the other OTUs in the study.

Table 4. KNM-ER 3733 and KNM-ER 3883 possible synapomorphies.

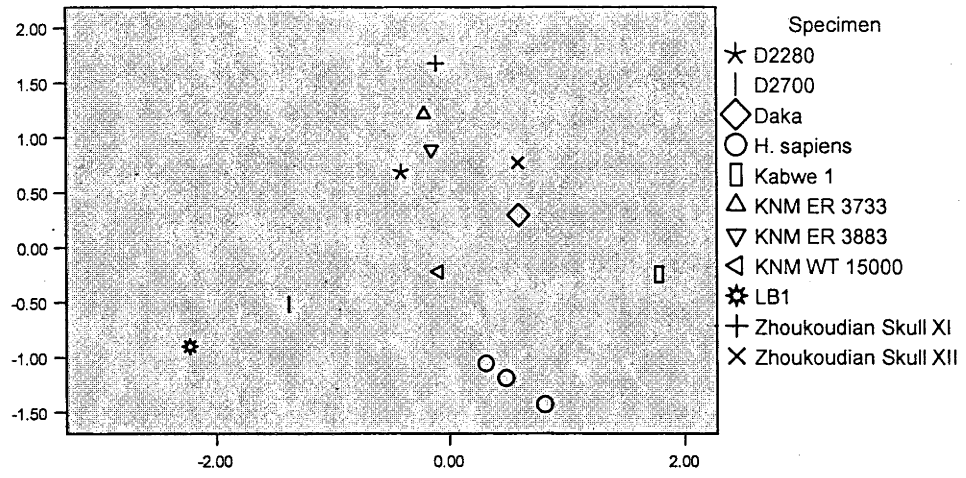
KNM-ER 3733 KNM-ER 3883	Character	State	Synapomorphies for the clade	Notes
	7	2	There is a sulcus between the posterior aspect of elevated supraorbital rim and frontal squama	Parallel with Dmanisi.
	9	1	Prominent temporal band on the frontal	Parallel with *H. sapiens*, Dmanisi
	55	2	Entoglenoid is similar in size to tuberculum zygomaticum anterior	Parallel with KNM-WT 15000, *H. sapiens*
	56	2	Entoglenoid formation is very posterior to the tuberculum zygomaticum	Parallel with *H. rhodesiensis,* Sangiran 17
	59	2	Posterior edge of the tuberculum articulare in norma basilaris is a sigmoid shape	
	64	1	Entoglenoid marginally extended posteriorly	Dmanisi polymorphic
	66	2	Profile of nasal saddle and nasal roof: nasals slightly raised, forming a curve	Parallel with *H. sapiens*, *H. rhodesiensis*
	78	2	Relatively rounded orbital margin but raised in relation to floor of orbit	Parallel with *H. erectus*, *A. africanus*

3.5 Morphometric analyses

Principal Components analyses are performed for the Turkana crania.

3.5.1 The Turkana group

As discussed above (Chapter 1) KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 are normally attributed to either *H. ergaster* or *H. erectus,* but the cladistic analyses suggest that they may not share a unique common ancestor. Morphometric analyses are now performed to further examine this. Note that LB1 is included too.



Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	5.268	75.258	75.258	5.268	75.258	75.258
2	1.108	15.832	91.090	1.108	15.832	91.090
3	.276	3.939	95.029	.276	3.939	95.029
4	.233	3.334	98.363			
5	.056	.807	99.169			
6	.048	.680	99.849			
7	.011	.151	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logGOL	.891	.413	-.050
logXCB	.800	.540	-.106
logXFB	.862	.236	.439
logMIN_FRONTAL_ BREADTH	.939	.115	-.246
logSTB	.874	-.342	-.021
logPAC	.868	-.451	-.064
logbr_la_arc	.832	-.507	.066

Extraction Method: Principal Component Analysis.

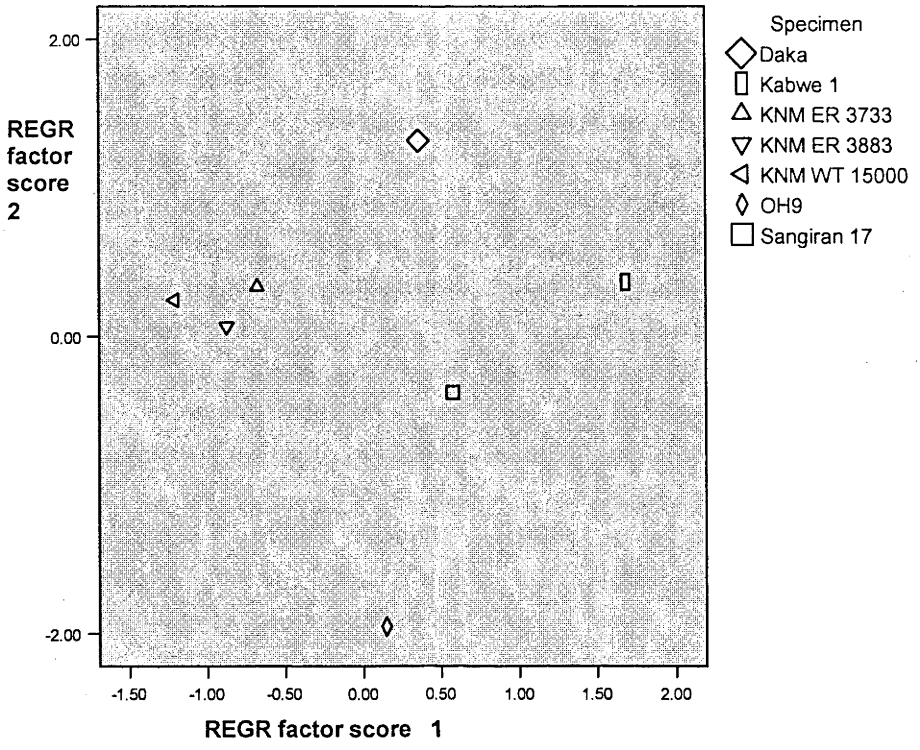
a. 3 components extracted.

Figure 3-9. PCA Analysis 2a: Turkana group. Y axis represents Regression Factor 2.

Factor 1 (75.2% of the variance) returns only positive values, and these are very evenly weighted, so may reflect primarily size differences between crania. KNM-WT 15000 is separated from the other two Turkana crania on Factor 2 (15.8% of the variance), having a relatively rounder occipital (bregma-lambda arc; refers to 'br_la_arc' in the analysis) in relation to cranial width than the other Turkana crania. It is similar to D2700, Kabwe and LB1 in this respect, although Kabwe is at the extreme positive (end) of the Factor 1 axis, being a much larger cranium, and the small LB1 cranium is at the opposite end of this axis. KNM-WT 15000 is well separated from *H. erectus* (*H. pekinensis* group).

KNM-ER 3883 and KNM-ER 3733 cluster together and Dmanisi D2280 is relatively close to KNM-ER 3883.

The following analysis uses characters that enable the three Turkana crania to be compared to Sangiran 17, the only *H. erectus* cranium that has enough metric data to be included in a morphometric analysis.



Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.510	75.170	75.170	4.510	75.170	75.170
2	.958	15.960	91.129	.958	15.960	91.129
3	.241	4.012	95.142	.241	4.012	95.142
4	.217	3.614	98.755			
5	.052	.862	99.617			
6	.023	.383	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logGOL	.788	-.566	.101
logXCB	.900	.113	.398
logSTB	.850	.461	-.118
logBBH	.785	.529	-.028
logMIN_FRONTAL_ BREADTH	.957	-.186	-.184
logMax_supra_br	.910	-.313	-.153

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

Figure 3-10 PCA Analysis 2b: Turkana group

The three Turkana crania cluster and they are separate from *H. erectus* (Sangiran 17) on both axes. They are relatively smaller than Sangiran 17 (Function 1; 75.1% of the variance, returns only positive values reflecting primarily size differences, but the values are unevenly weighted, and Function 1 might also represent some shape variation. The Turkana crania differ from Sangiran 17 on Function 2 (15.9% of the variance); Sangiran 17 has a relatively longer cranium and supraorbital breadth in relation to vault height, although the difference between Sangiran 17 and the Turkana crania, particularly KNM-ER 3883, is not marked.

3.6 SK 847

3.6.1 Background and Observations

This was originally assigned to *Telanthropus capensis* (Broom and Robinson 1949), but Robinson (1961) later synonymised *Telanthropus* with *Homo*, and sunk *T. capensis* into *H. erectus*. It is dated to between 1.63 and 2.1 Mya (after Curnoe et al., 2001). It has been referred to a number of species; as *Homo sp. indet.* (Clarke et al., 1970); *Homo incertae sedis* (Groves and Mazák, 1975); *Homo africanus* (Olson, 1978); possibly *H. habilis* (Clarke and Howell, 1972); while Clarke (1994) considered that SK 847 is virtually identical to KNM-ER 3733; and Curnoe (1991) that it formed a sister taxon to *H. habilis* and *H. erectus*. (Also refer to Chapter 2).

Observations

SK 847 comprises a partial cranium and a number of fragments. The cranium has been assembled such that prosthion is on the same vertical plane as the internal lower medial extremity of the orbit, rather than aligned centrally; that is, the upper portion of the cranium is offset from the lower portion, with the naso-alveolar clivus and palate too far to the left. This differs from photos of the cranium taken in 1998 (observations from images taken by C. Groves). The nasal bones have been placed centrally but below the level of the inferior orbital margin.

Although laterally broken, it appears to me that the supraorbital arches are likely to have been fused medially. Posterior to the supraorbitals is a sulcus from which the frontal rises relatively steeply. Glabella is not available but enough remains of the supraorbitals in this

region to reasonably assume that they were joined at glabella. The supraorbitals are thickest medially, as they approach glabella. The temporal lines commence at the lateral extremities of the supraorbital region but sweep across the sulcus to rise at about the medial region posterior to the torus. There is a very narrow sulcus between each set of temporal lines.

The inferior-temporal *planum* is of similar configuration to a cast of KNM-ER 3733 to which I was able to compare characteristics. The mandibular fossa is very wide. The sphenoid edge is a pointed crest, as is the entoglenoid formation, although the latter does not extend as far inferiorly as the sphenoid edge.

Enough remains of the facial region to suggest that it is relatively flat, with a rounded canine fossa medial to a superior/inferior inflated region that extends from the inferior lateral border of the orbit and disappears at the level of the rounded canine fossa; the facial region projects forward slightly. The malar notch forms an arch with a sharp angular and downward projecting tubercle anterior to the malar-zygomatic suture. If it has been reconstructed correctly, the zygomatic forms a straight line after turning sharply, without any flaring, from the maxilla.

The nasal bones are wider inferiorly and are raised to form a central superior/inferior ridgeline.

The orbit forms a square shape with a sharp lateral edge and a slightly rounded inferior lip; the inferior orbital bone is on more or less the same level as the orbital rim.

The palate appears very long and narrow, squared off anteriorly.

In the following analyses SK 847 is considered in its relationship to the following: KNM-ER 3733; OH 9 (as a potential male of the same species) (Clarke 1994); *Australopithecus africanus*; as a common ancestor to *H. erectus* and *H. habilis* (Curnoe 1991); and to the Dmanisi group. A cladistic analysis is undertaken but the cranium has too few measurement data to be included in a morphometric analysis. Although the cranium has

been repaired with one mis-alignment this does not impact on the character states used in the cladistic analysis.

3.6.2 Results

In the following analyses, I include Olduvai Hominid 9 (OH9) so that Clarke's (1994) hypothesis, that SK 847 is virtually identical to KNM-ER 3733 and that these are females of the species in which OH 9 is a male, may be tested.

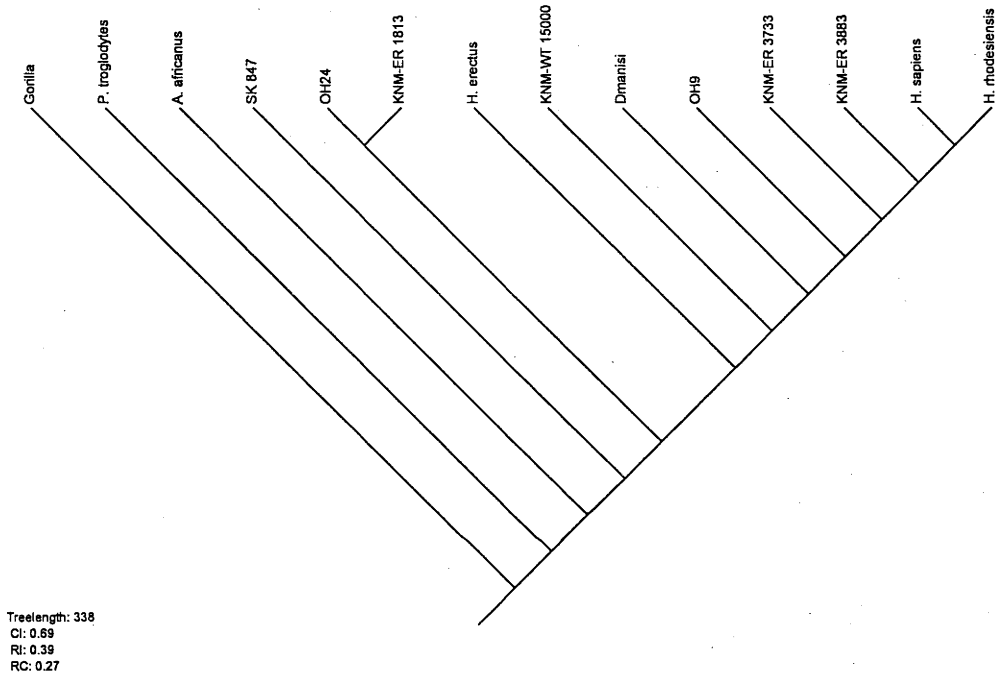


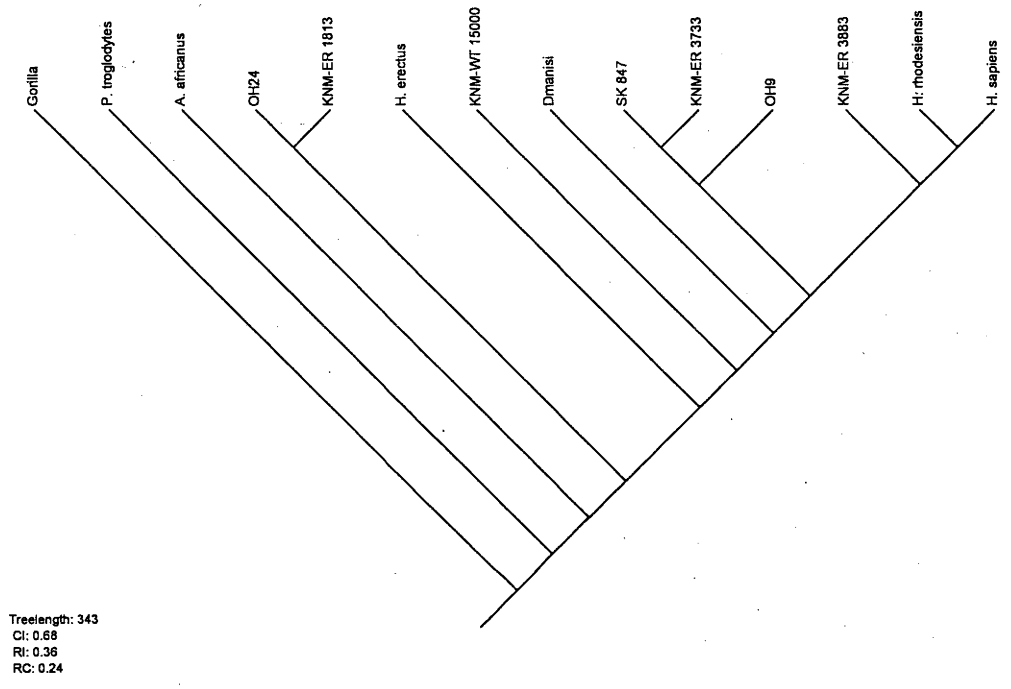
Figure 3-11 SK 847: shortest tree

In the shortest tree, SK 847 branches at the base of *Homo*, and OH 9 branches after Dmanisi. The tree is one step longer if KNM-ER 3733 and KNM-ER 3883 form a clade (not shown).

Analyses are now undertaken to test the two hypotheses for SK 847.

a) That SK 847 is phylogenetically related to KNM-ER 3733 (Clarke 1994) in a species in which OH 9 is the male. In this case there are three shortest trees (L = 343) (Figure 3.12).

These trees are 5 steps longer than the shortest tree (L = 338) and are therefore unlikely to represent the most parsimonious solution for SK 847. I also tested the possibility that SK 847 is phylogenetically related to KNM-ER 3733 but not necessarily OH 9. The shortest tree in this case is L = 340 (Figure 3.13), 2 steps longer than the shortest tree (L = 338); the T-PTP for {SK 847, KNM-ER 3733} is p = 0.26.



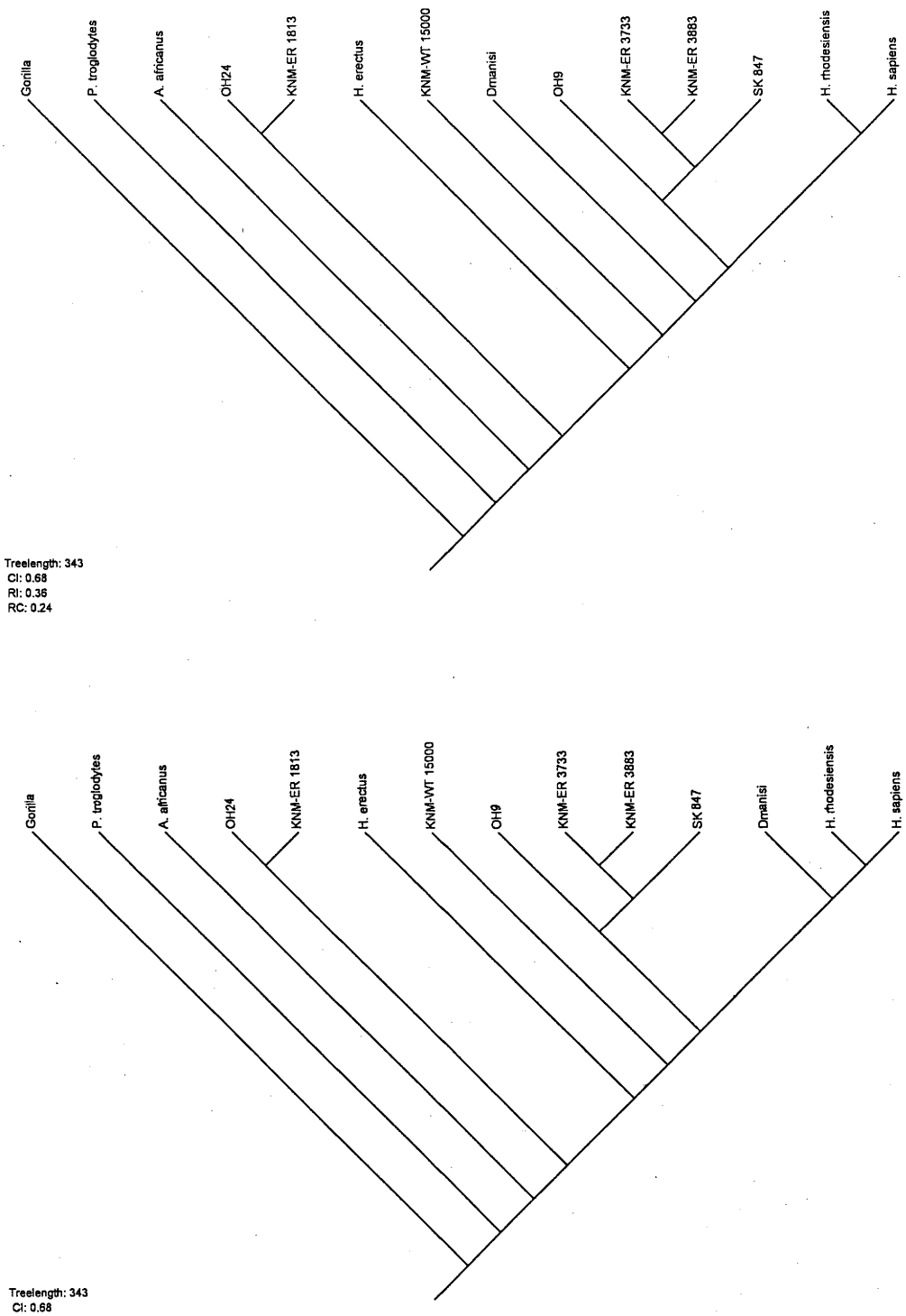


Figure 3-12 SK 847, KNM-ER 3733, KNM-ER 3883, OH9.

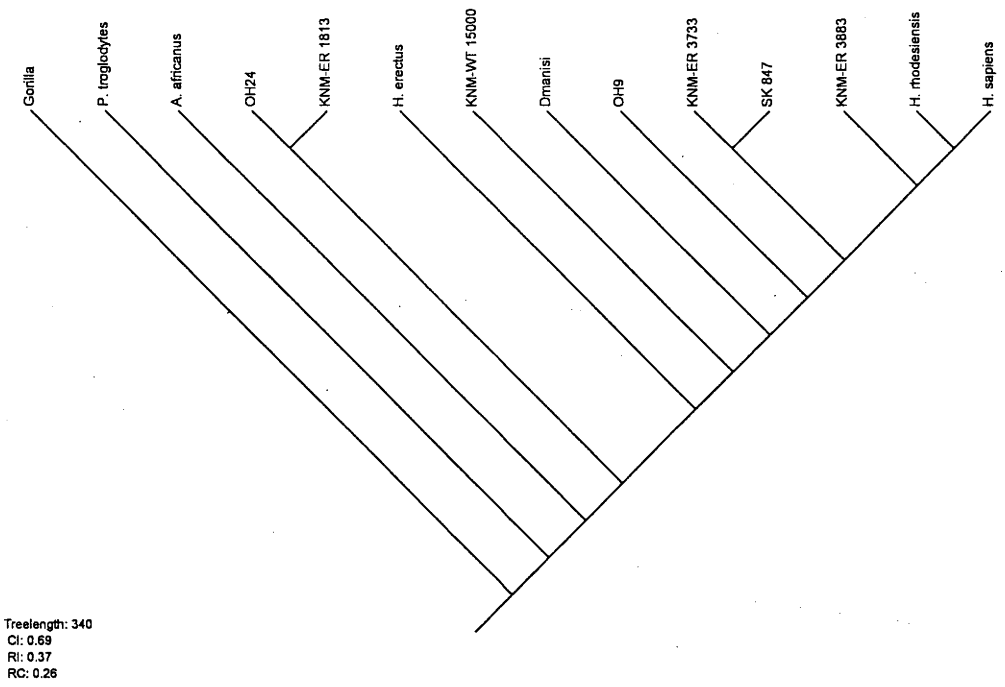


Figure 3-13 SK 847 and KNM-ER 3733

b) That SK 847 is a common ancestor to *H. erectus* and *H. habilis* (Curnoe, 1991) or *H. erectus* (Robinson, 1961). In the former case there is one tree of length 342 which is 4 steps longer than the shortest (L = 338) (Figure 3.14). In the latter case, the tree length is 340 (Figure 3.15).

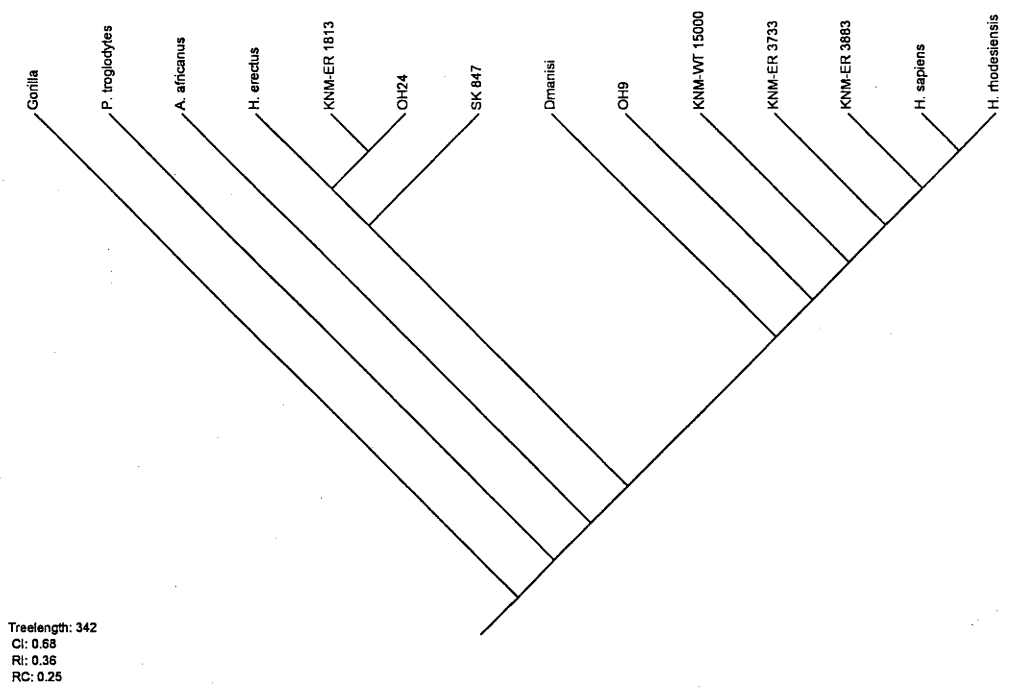


Figure 3-14 SK 847, *H. erectus*, OH 24 and KNM-ER 1813

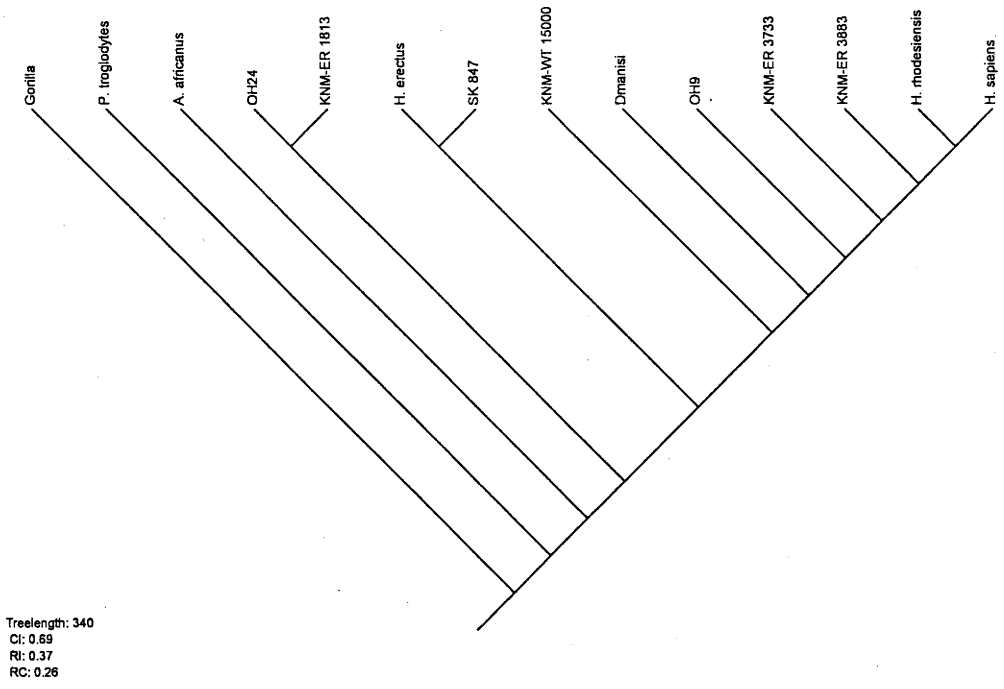


Figure 3-15 SK 847 and *H. erectus*

The T-PTP for the {SK 847, *H. erectus*, OH 24, KNM-ER 1813} clade is p = 0.18; the null hypothesis that they would come together only by chance is not rejected. It appears unlikely that SK 847 shared an immediate common ancestor with *H. erectus*, OH 24 and KNM-ER 1813; nor is it likely that it shared an immediate common ancestor with *H. erectus* (Figure 3.15).

c) that SK 847 and Dmanisi share a common ancestor. In this case there is one tree of L = 342:

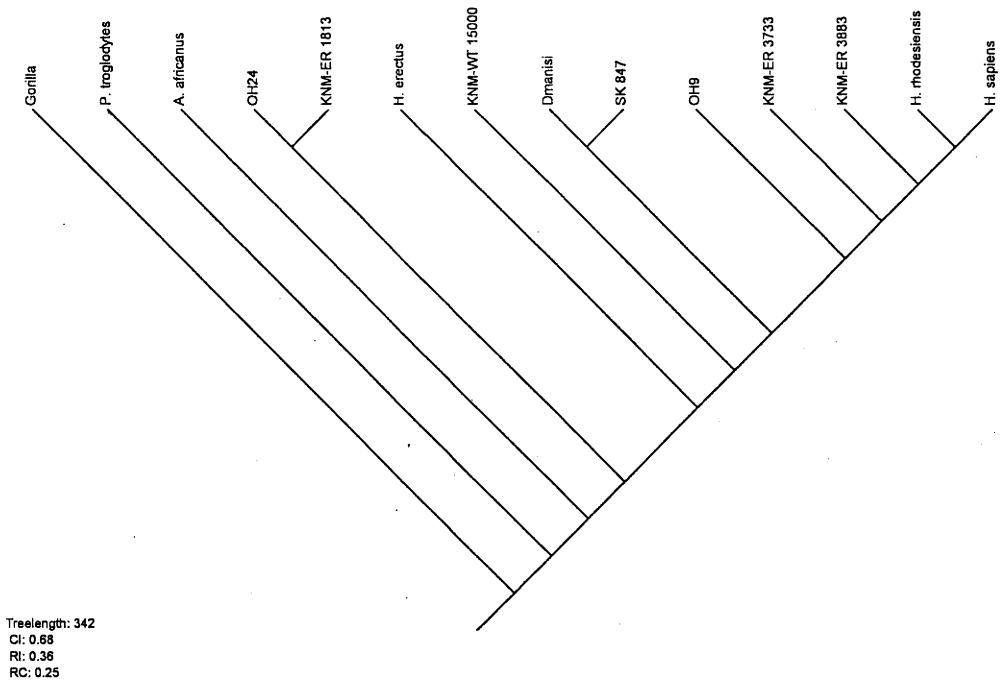


Figure 3-16 SK 847 and Dmanisi

T-PTP {SK 847, Dmanisi} is p = 0.71; the null hypothesis that this branch would form by chance is not rejected.

d) that SK 847 and *A. africanus* form a clade. In this case there is one tree, L= 342; this is 4 steps longer than the shortest (L = 338) (Figure 3.17). The T-PTP is p = 0.74; again, the null hypothesis is not rejected.

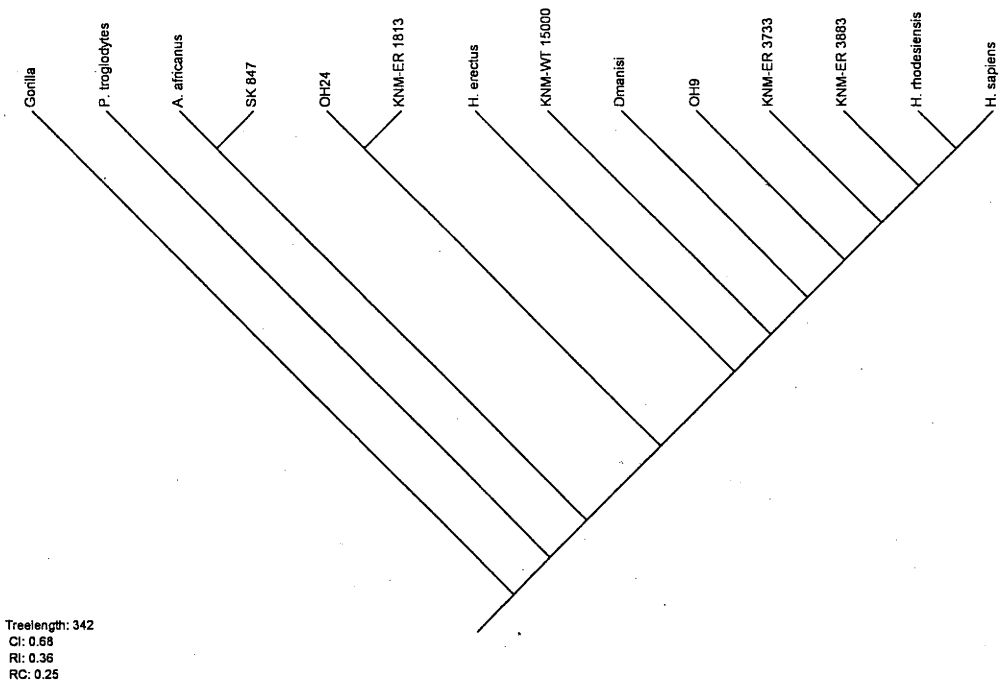


Figure 3-17 SK 847 and *A. africanus*

In summary, then, the trees that test for {SK 847, KNM-ER 3733}; {SK 847, Dmanisi}; {SK 847, *A. africanus*}; and for SK 847 as common ancestor to *H. habilis* and *H. erectus* show that none of these hypotheses seem likely, on the available evidence, to explain the phylogenetic relationships of SK 847; it is most likely that SK 847 is a separate lineage. It has the following possible derived characters: the height of articular eminence is higher relative to posterior wall of glenoid fossa (in basal view); anterior-posterior concavity of the mandibular fossa is round (parallel with *H. sapiens*, *H. rhodesiensis*); and the *jugum alveolare* forms a narrow ridge.

3.7 Olduvai Hominid 9 (OH 9)

3.7.1 Background and Observations

Olduvai Hominin 9 (OH 9) is from Upper Bed II at Olduvai and dated to 1.5-1.4 Mya (Schwartz and Tattersall, 2002), contemporaneous with KNM-WT 15000 and a little younger than KNM-ER 3883. Leakey (1961) interpreted it as evidence for a

'Pithecanthropine stage' of human evolution; and Heberer (1963) conditionally attributed it to *H. leakeyi*.

Stringer (1984) observed that OH 9 lacks a number of *H. erectus* apomorphies, although Rightmire (1990:153-163) suggested that it is most reasonably compared to the larger Indonesian hominins (Sangiran 17, 2, 12, Sambungmacan and several Ngandong crania) and concluded that OH 9 should be considered *H. erectus* (op. cit. 18).

Groves (1989:279) also assigned OH 9 to *H. erectus* as the only non-Asian representative of this taxon.

In summary then, there are three hypotheses or suggestions for the phylogenetic position of OH 9: it is *H. erectus* (Groves 1989; Rightmire 1990); it is probably not *H. erectus* (no alternative attribution was proposed) (Stringer 1984); it is a separate species (Heberer 1963; Kretzoi 1984).

Observations

The observations were made on a cast from the National Museum of Kenya and a photo of the basicranium of the original skull supplied by Professor Colin Groves.

The cranium has a massive appearance, primarily resulting from the large, flaring and projecting supraorbital torus which forms a shelf-like appearance, although it is interrupted in the medial zone.

In lateral view, the cranium, as far as can be interpreted from the partial reconstruction on the parietal and occipital, is rounded from the posterior of the supraorbital sulcus to the nuchal region, where it becomes convex. In posterior view the cranium is relatively low and long, widest at the mastoid region. The temporal lines, posttoral sulcus, and lateral flaring of the supraorbitals are the most notable features in coronal view.

There is a marked depression at glabella. The superior surfaces of the orbit margins flow smoothly onto the frontal squama. The temporal lines are prominent and sweep around from the anterior frontal region to the mastoid crest. There is a deep postorbital constriction. There is no metopic keeling; bregma is missing, so whether there was a bregmatic eminence is not known.

There is an angular tuber in the asterionic region, separated by a groove from, and following, the alignment of the lateral edge of the temporal line. The external occipital crest is comprised of two parallel crests separated by a depression. Although broken, it would appear that the mastoid process was very large.

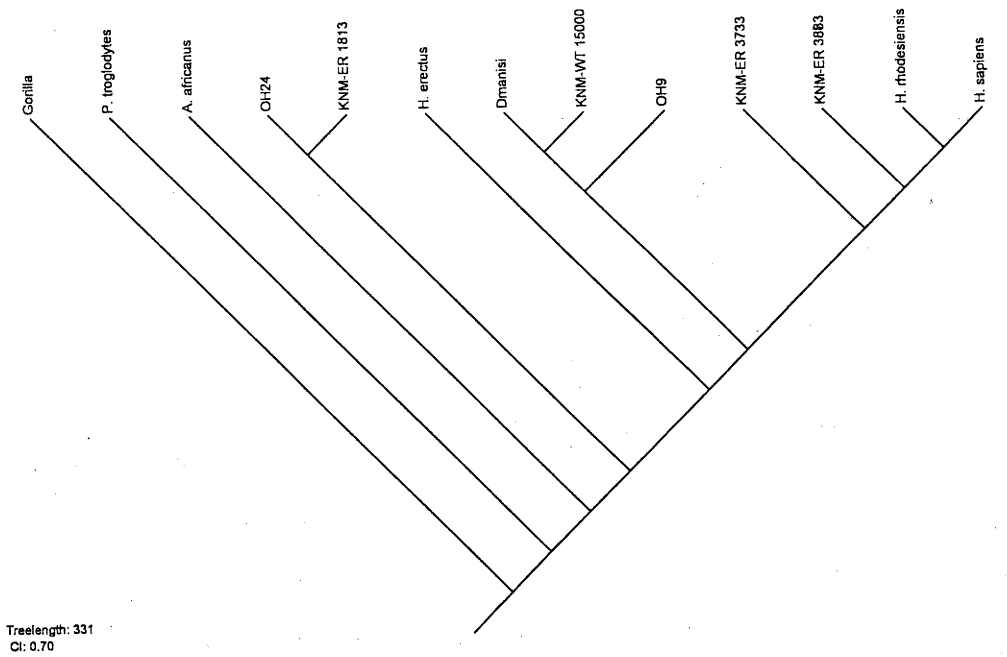
An inferior-temporal *planum* precedes the mandibular fossa. There is a well-projecting vaginal crest with a styloid foramen behind. The entoglenoid formation is prominent, pointed on the right hand side and more rounded on the left; they are separated from the sphenoid edge by a groove. The anterior wall of the mandibular fossa is almost vertical and at the same level as the crest of the articular eminence. There is no postglenoid process and the tympanic makes up the mandibular fossa wall. The mandibular fossa itself is wide. The base of the mandibular fossa follows a sigmoid line, winding around the entoglenoid formation, similar to Daka, KNM-ER 3733, and KNM-ER 3883. There is a deep, U-shaped digastric fossa and a large juxtamastoid eminence.

The morphometric analysis is based upon measurements from the cast, crosschecked with published measurement data. The cladistic and morphometric analyses are designed to test the hypotheses for this fossil (above, and Chapter 2).

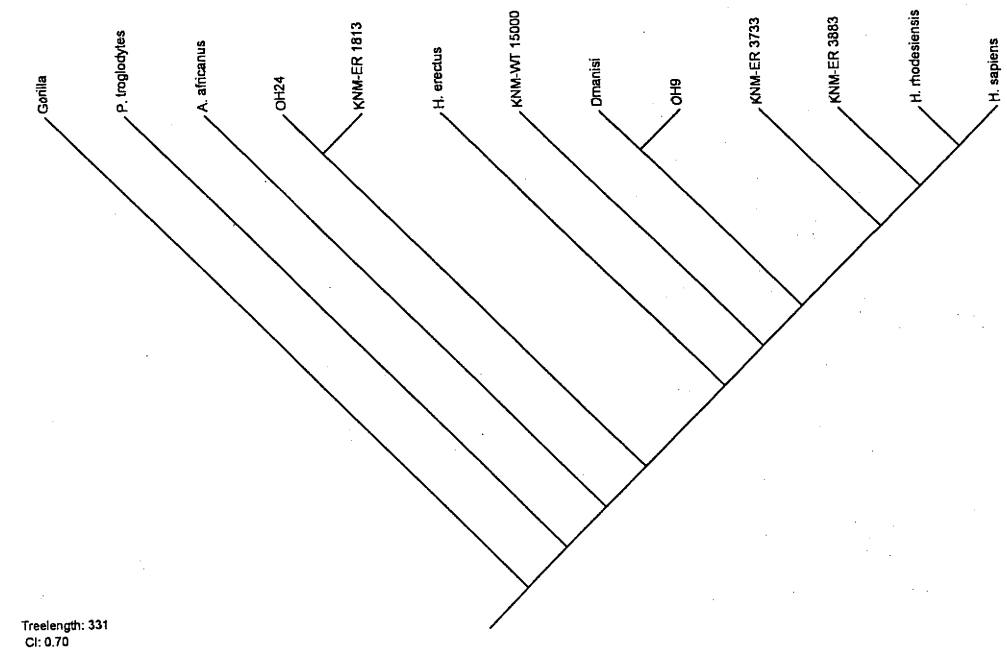
3.7.2 Results

Cladistic analyses

There are three shortest trees for OH 9:



Treelength: 331
CI: 0.70
RI: 0.39
RC: 0.27



Treelength: 331
CI: 0.70
RI: 0.39
RC: 0.27

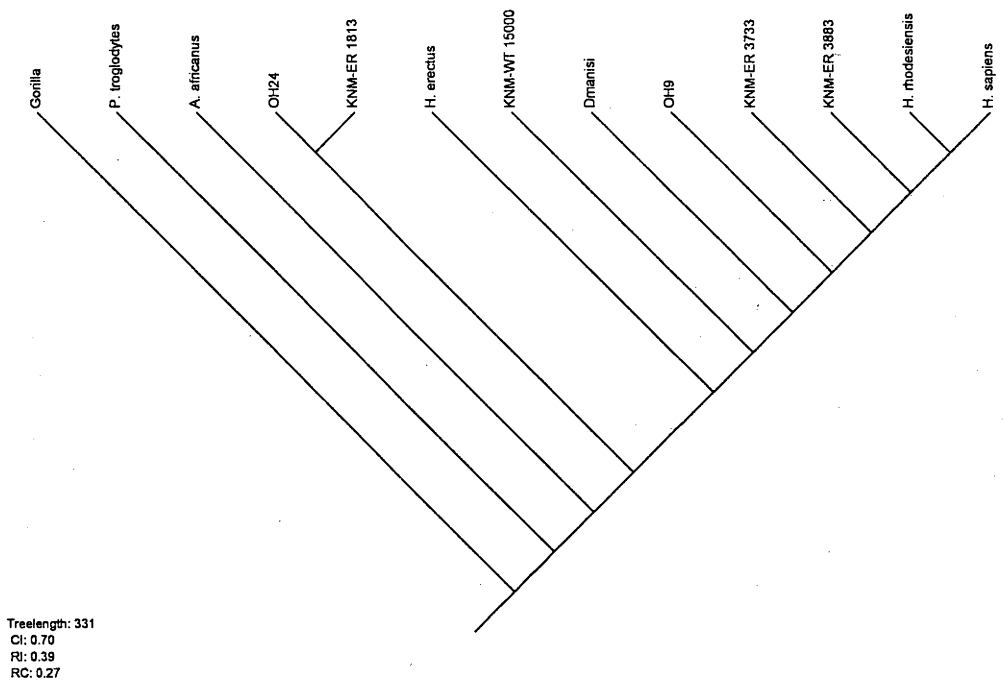


Figure 3-18 OH 9: shortest trees

In one of these OH 9 is sister taxon to {Dmanisi, KNM-WT 15000}, but the T-PTP for KNM-WT 15000 and Dmanisi is p = 0.33, so this part of the clade, at least, is likely to come together by chance alone, suggesting the branch represents an unsupported phylogeny.

In another OH 9 forms a clade with Dmanisi alone. The T-PTP for the clade {OH 9, Dmanisi} is, in this case, p = 0.58; the null hypothesis that these OTUs would come together by chance is not rejected. Again this branch is likely to represent an unsupported phylogeny.

The third possible phylogeny for OH 9 is that it branches after Dmanisi, and is sister to KNM-ER 3733, KNM-ER 3883, *H. rhodesiensis* and *H. sapiens*. The T-PTP for this group is p = 0.03; this grouping did not come together by chance. OH 9 has the following possible derived character states:

Table 5. OH 9 shared derived and unique characters.

Character	State	Derived characters	Notes
8	0	0 = a>b, b<c and a < c	Where 'a' is central, 'b' is middle and 'c' is lateral
23	0	No external occipital protrusion	Parallel with OH 24
32	1	Continuity of the supramastoid crest with the inferior temporal line	Parallel with *H. rhodesiensis*, KNM-ER 3733
34	1	Strong mastoid crest	Parallel with *H. rhodesiensis*
35	1	Continuity between mastoid crest and superior temporal line	
39	1	Presence of suprameatum spine	
43	0	The tympanal makes up most of the wall of mandibular fossa	Parallel with Dmanisi, SK 847
44	1	Mastoid projects below base	KNM-ER 3883, *H. sapiens* , *H. rhodesiensis*
46	1	Space between the tympanal and anterior of mastoid process forms a 'split'	Parallel with KNM-ER 3883
53	1	Groove between entoglenoid formation and tympanic plate	Parallel with *H. rhodesiensis*
54	2	Anterior wall of mandibular fossa almost vertical	Parallel with *H. sapiens*
63	0	Very prominent entoglenoid formation	Parallel with *H. rhodesiensis*

The hypothesis that OH 9 is *H. erectus* is now tested in MacClade. There are two trees of length L = 335, 4 steps longer than the shortest (L = 331). The difference between the trees is the location of the manoeuvred clade comprising OH 9 and *H. erectus*. The T-PTP for OH 9 and *H. erectus* is p = 0.85; again, the null hypothesis is not refuted. This, then, is unlikely to be the most parsimonious phylogeny for OH 9.

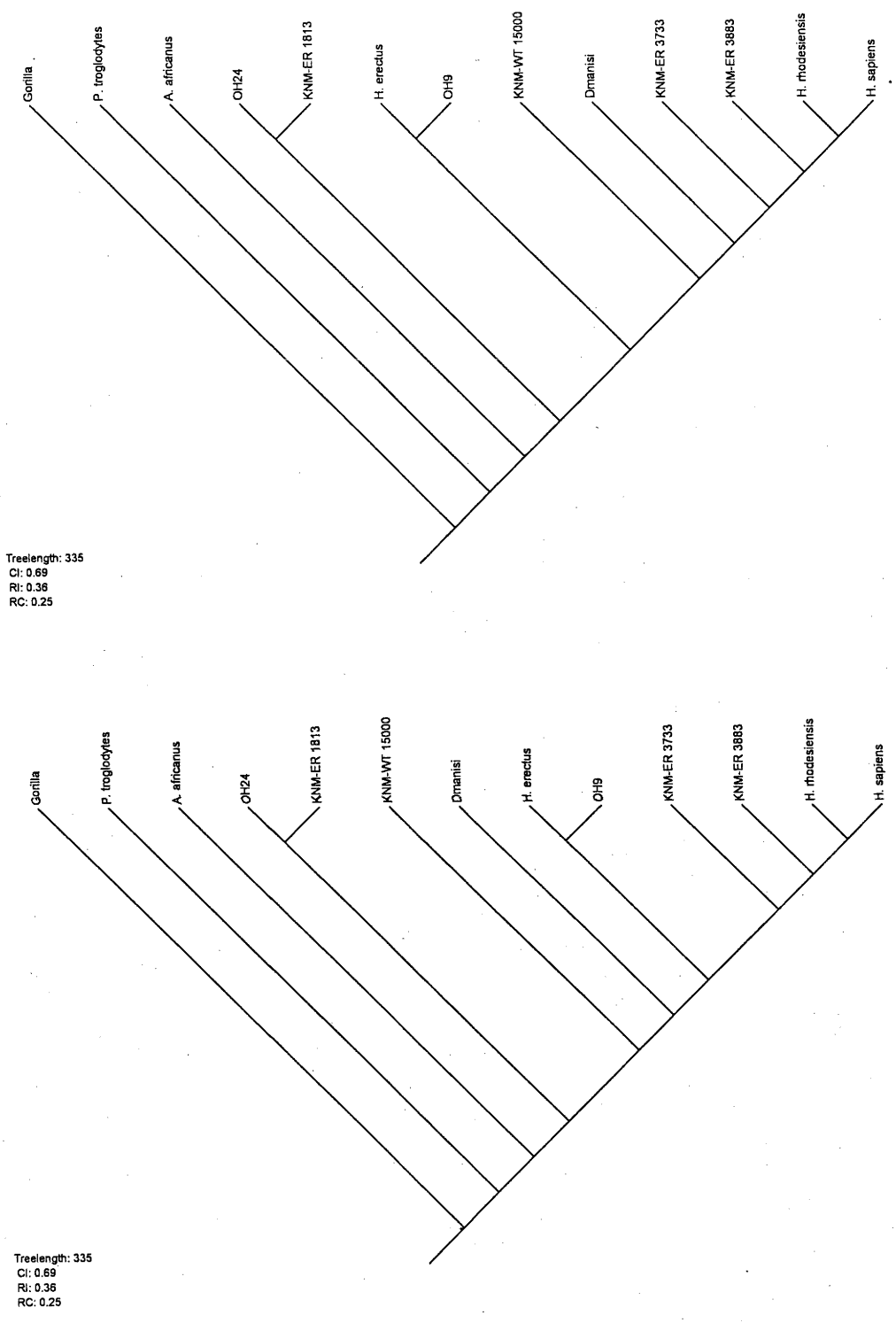


Figure 3-19 OH 9 and *H. erectus*

Nor is it likely that KNM-ER 3733 or KNM-ER 3883 would form a clade with OH 9 (Figures 3.20, 3.21). The tree length for a tree in which OH 9 and KNM-ER 3733 are constrained is L = 334 and the T-PTP for the clade is p = 0.36.

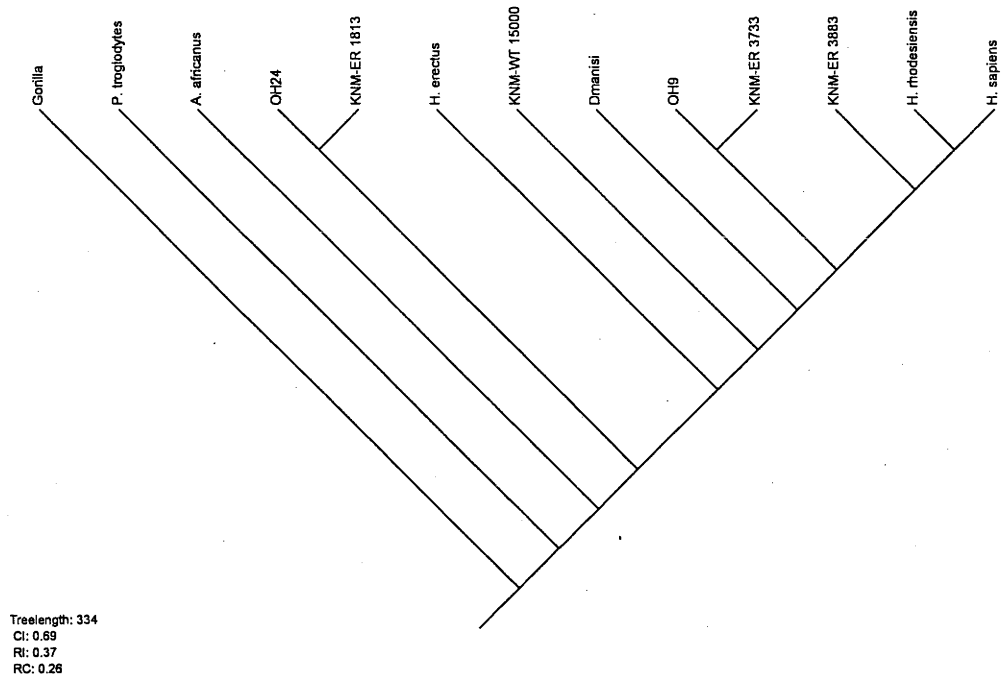


Figure 3-20 OH 9 and KNM-ER 3733

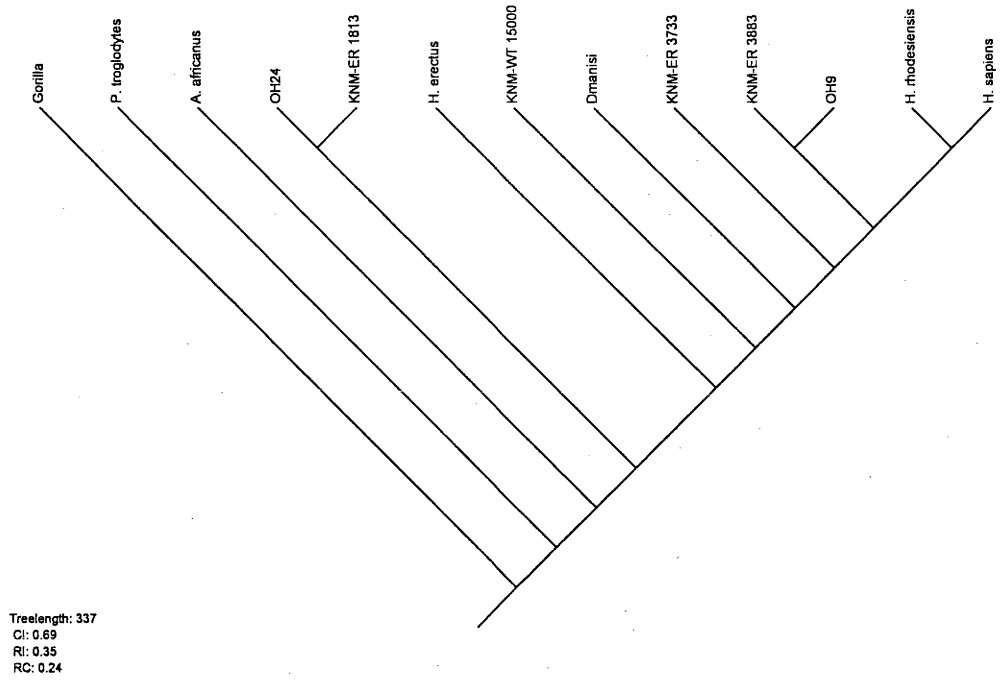
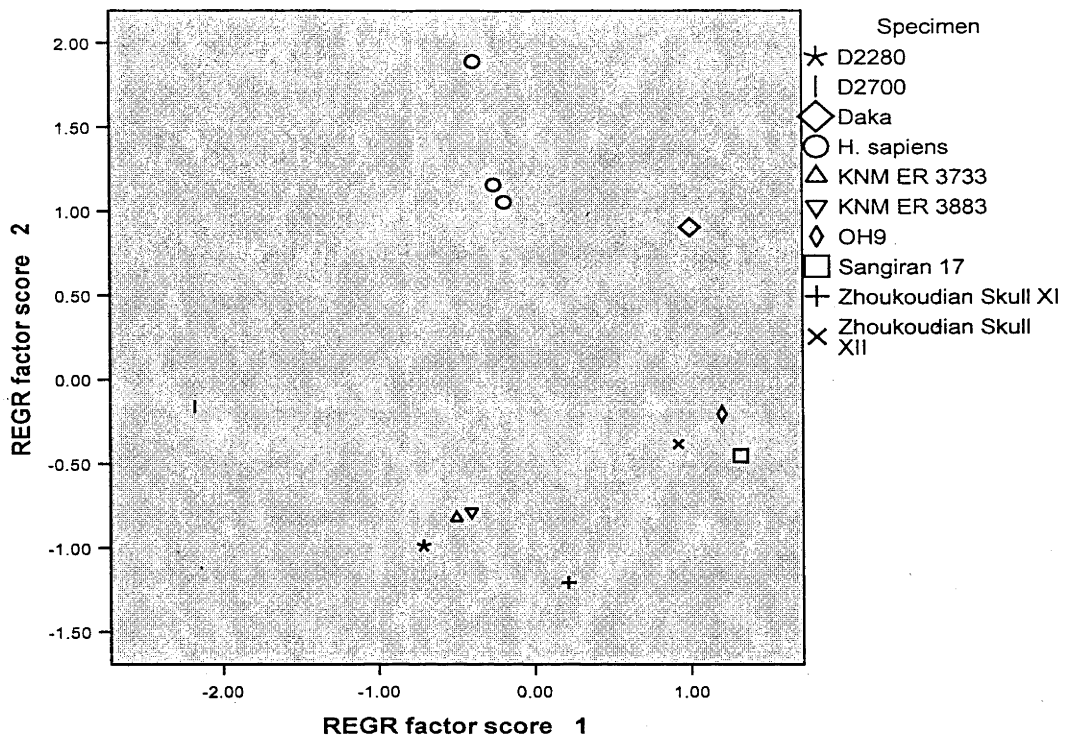


Figure 3-21 OH 9 and KNM-ER 3883

Morphometric Analysis 3. OH 9.

As OH 9 forms a clade with Dmanisi in one of the cladistic analyses, representatives of this taxon are included in the following morphometric analysis, along with *H. erectus* (Sangiran 17, *H. pekinensis* (Zhoukoudian XII, XI) and two of the Turkana crania: KNM-ER 3733 and KNM-ER 3883.



Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.216	60.226	60.226	4.216	60.226	60.226
2	1.652	23.594	83.819	1.652	23.594	83.819
3	.503	7.193	91.012	.503	7.193	91.012
4	.306	4.378	95.390			
5	.229	3.268	98.658			
6	.069	.985	99.642			
7	.025	.358	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logGOL	.913	-.226	-.130
logXCB	.755	-.490	.218
logMIN_FRONTAL_ BREADTH	.890	.305	-.171
logAUB	.633	-.670	.219
logSTB	.330	.824	.406
logFRC	.891	.256	.194
logna_br_arc	.847	.270	-.399

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

Figure 3-22 PCA Analysis 3: OH 9

Function 1 represents 60.22% of the variance and, with unequally loaded variables, this Function represents both size and shape. OH 9, Zhoukoudian XII and Sangiran 17 cluster on Function 1 and Function 2. They are similar in their biauricular:bistephanic breadth relationship and their cranial length:bistephanic breadth ratio. The group is separate from KNM-ER 3733 and KNM-ER 3883 and D2280 on Function 1; these are smaller, and have relatively narrower biauricular breadths than OH 9, Zhoukoudian XII and Sangiran 17. OH 9, although separate from D2700 on Function 1 as it is markedly larger, is similar in its bistephanic:biauricular breadth relationship.

There appears to be a conflict between the results of the cladistic analyses in that the most parsimonious solution for OH 9 in the cladistic analysis is that it is a separate taxon, but in the morphometric analysis it clusters with *H. pekinensis* and Sangiran 17 (*H. erectus*). The conflict between the results of the cladistic and metric analyses will be further discussed in Chapter 4.

3.8 KNM-OL 45500

3.8.1 Background and Observations

KNM-OL 45500 is a partial cranium found at Olorgesaillie, Kenya, comprising 11 pieces; 9 are vault fragments recovered from sieving of material 1-20m down-slope of the calvaria. KNM-OL 45500 is dated to 970,000- 900,000 (Potts et al. 2004). It is the first hominin from a site long known for dense accumulations of lithic artefacts and mammalian bones. The cranium is a very small adult or subadult that exhibits smaller frontal breadth, supraorbital torus thickness and breadth and temporal bone size than any early or middle Pleistocene adult cranium (op. cit.). It is contemporaneous with Buia and perhaps OH 12, and a little older than Daka and Ceprano (below). Based on comparative cranial morphology in Dmanisi, its estimated cranial capacity is less than 800cc. Potts et al. (op cit.) cited characters that, in their view, are like some of those in *H. erectus*, such as midline keeling of the frontal bone, shelf-like morphology of the post-toral sulcus, lack of torsion in the orbital torus, and a short temporal squama with flat superior border, but they acknowledged that its morphology would extend the known range for *H. erectus*. They

also noted that it has a double-arched supraorbital torus such as is found in Daka, Ceprano and KNM-ER 3733, and viewed it as more similar to some mid-Pleistocene hominins than *H. erectus*.

As it is a comparatively recent find, there has been little further discussion about this fossil.

Observations

It appears to have been affected by weathering; the bones are very smooth and free of muscular or other markings. It is tiny and preserves only a small proportion of the cranium, comprising part of the frontal from the coronal suture to the nasofrontal suture, although even this is fragmentary: the frontal is broken and partly missing from anterior to bregma, extending into the left side of the squama. Parts of the left temporal, basicranium, mandibular fossa, tympanic and sphenoid are preserved.

The supraorbital torus is thickest medially (10.7mm) and very thin laterally (5.1mm). It flows smoothly into the orbits, forming an 'umbrella-like' appearance over the orbits. The posttoral sulcus is continuous across glabella; the frontal rises very steeply from this. Temporal lines are visible for only 12mm. The intraorbital region is wide and bulges in a smooth left-right curve, and forms a continuous plane with glabella. In superior view the orbital arches form a smooth convex curve; it is very similar to Dmanisi D3444 and D2282 in this respect.

The mastoid projects below the base of the cranium. It has two parallel crests from its tip to the suprameatal crest, separated by a slight sulcus. The remains of the digastric fossa indicate that it is U-shaped. The tympanic appears to have been joined to the mastoid.

The glenoid fossa is short, with the posterior wall comprising the tympanic plate. There is no indication of a postglenoid process. The articular tubercle forms a very curved arc (side to side); the entoglenoid and tuburculum zygomaticum are in the same plane.

The cranial wall extends outward above the zygomatic root.

Internally there is a strong sharp fine ridge that is 10mm high that extends from behind the centre of the nasal bones and proceeds along the frontal for 45mm. The cranial thickness on the frontal is 5.5mm (behind mid-torus on right hand side); 7.5mm on temporal behind the lateral edge of the torus, but only 4.6 on the opposite side of the cranium; and 6.1mm at the centre of the most posterior point of the broken frontal.

In summary, cranium is tiny but appears robust, especially in the glabella region. It has an unusual crest and sulcus feature on the mastoid process.

KNM-OL 45500 is here compared to the standard OTUs in MacClade. The fossil has too few data to be compared in a morphometric analysis.

3.8.2 Results

The shortest tree (L = 323) is formed when KNM-OL 45500 and *H. sapiens* form a clade.

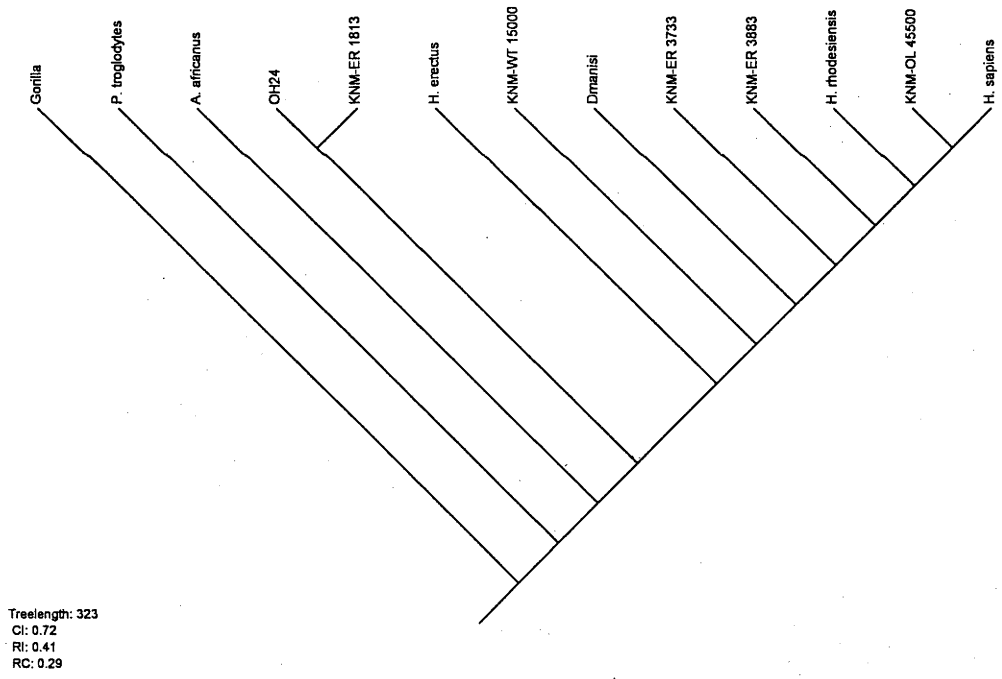


Figure 3-23 KNM-OL 45500: shortest tree.

Although the T-PTP for KNM-OL 45500 and *H. sapiens* is p = 0.03, they share only one possible synapomorphy: the size of the articular eminence is shorter than the opposite side

of the mandibular fossa (parallel with KNM-WT 15000). It seems unlikely that KNM-OL 45500 and *H. sapiens* share an immediate common ancestor. I therefore test the phylogenetic position of KNM-OL 45500 in MacClade. The next shortest tree (L = 325) is formed when KNM-OL 45500 and KNM-ER 3733 form a clade, the T-PTP for which is p = 0.04.

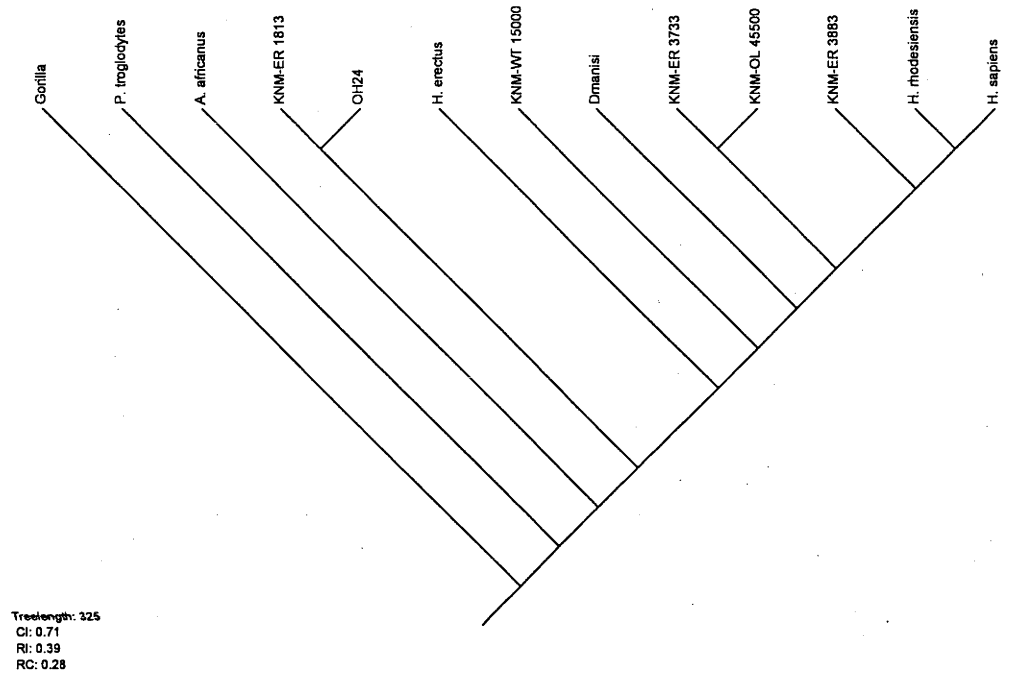


Figure 3-24 KNM-OL 45500: shortest tree omitting *H. sapiens*

The clade {KNM-OL 45500, KNM-ER 3733} shares four possible synapomorphies:

Table 6. KNM-OL 45500 and KNM-ER 3733 possible synapomorphies.

Character	State	Synapomorphy	Notes
3	1	Depression at glabella	Parallel with KNM-ER 3883, KNM-ER 1813, *H. sapiens*
34	1	Strong mastoid crest	Parallel with parallel with *H. rhodesiensis*
59	2	A sigmoid shape of posterior edge of the tuberculum articular in *norma basilaris*	Parallel with KNM-ER 3883, *H. sapiens*

64	1	Entoglenoid is marginally extended posteriorly	Parallel with KNM-ER 3883

As KNM-ER 3733 and KNM-ER 3883 are often referred to *H. ergaster*, I again examine this hypothesis in the light of the results for KNM-OL 45500 and KNM-ER 3733 by testing a clade comprising KNM-OL 45500, KNM-ER 3733, and KNM-ER 3883:

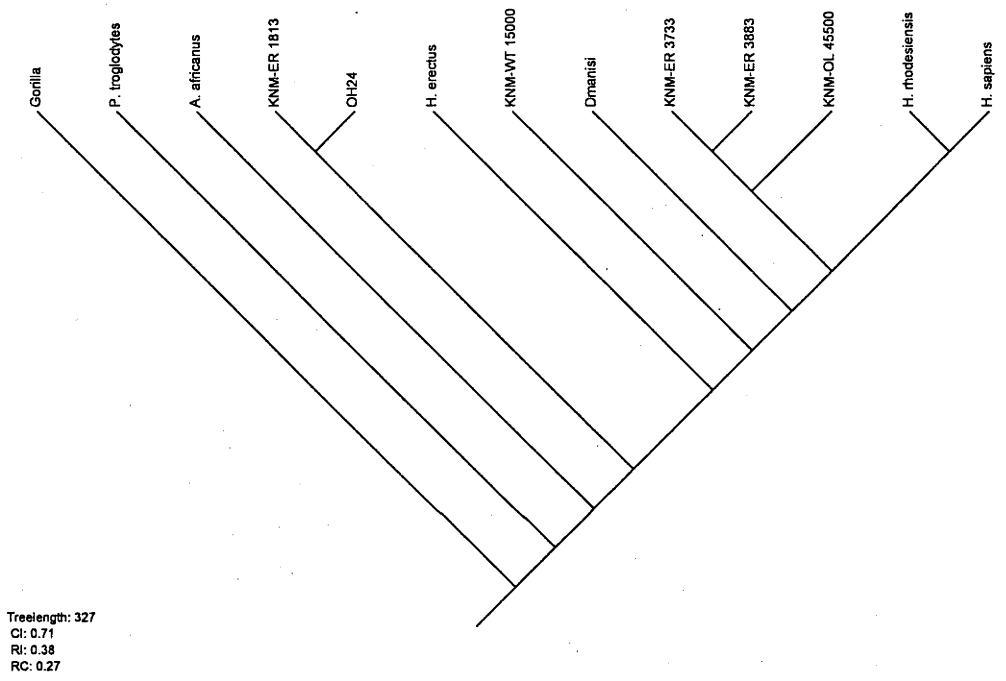


Figure 3-25 KNM-OL 45500, KNM-ER 3733 and KNM-ER 3883

This tree length is 327 steps, 2 steps longer than the most parsimonious tree (omitting *H. sapiens*; L = 325) and the T-PTP for the clade is p = 0.31; the null hypothesis that the clade would come together by chance is not rejected. That is, it seems unlikely that KNM-ER 3883 shared a unique common ancestor with {KNM-ER 3733, KNM-OL 45500}.

All other configurations for KNM-OL 45500 yield longer trees: if it is manoeuvred to form a clade with:

- *H. erectus* or {OH 24, KNM- ER 1813}: the tree length is 329, 4 steps longer than the shortest (L=325);
- Dmanisi or KNM-WT 15000: the tree length is 327, 2 steps longer than the shortest.

The most parsimonious solution for KNM-OL 45500, then, is that it is a sister taxon to KNM-ER 3733.

3.9 Ceprano, Daka and Bodo

3.9.1 Background and Observations.

The calvaria found near Ceprano, Italy, is estimated to be > 700,000 and probably slightly over 800,000 years old[6] (Ascenzi et al. 1996) and is therefore roughly contemporary with Daka (below) from Ethiopia, and Gran Dolina (below) from Atapuerca, Spain. Bodo, also from Ethiopia, is somewhat younger, ~640,000 – 550,000 years old.

3.9.2 Ceprano

Ascenzi et al. (op. cit.) attributed Ceprano to *H. erectus*, particularly to late *H. erectus*, in which they include the Middle Pleistocene fossils Arago, Petralona, and contemporaries which they acknowledged are attributed by some to *H. heidelbergensis*. Clarke (2000) noted that the orbits on Ceprano are unnaturally elongated mesiodistally and that there was asymmetry of the calvaria due to errors of reconstruction, rather than to congenital deformation and post-mortem deformation as Ascenzi et al (1996:416) had supposed. With the support of Ascenzi and colleagues, Clarke undertook a reconstruction during 1997 which resulted in a revision of the reported metric values of the calvaria. One outcome from the reconstruction is a reduced, but as yet unmeasured, cranial capacity, suggested to be similar to OH 9 and within the *H. erectus* range. Greatest cranial width is now noted to be across the supramastoid region (as opposed to the temporal squama per Ascenzi et al.; p. 419) and the parietal profile slopes medially (Clarke, 2000). The attribution by Ascenzi et al. (1996) nevertheless remained unchallenged.

Using a neighbour joining and unweighted pair method, Manzi et al. (2001) found that Ceprano grouped with the later specimens from Africa: Kabwe, Saldhana and Bodo. The only other sample known from Europe from this period is from Gran Dolina (Spain),

including the ATD6-69 juvenile which is the type specimen of *H. antecessor* (Burmudez de Castro et al., 1999); though noting that none of this material is directly comparable to Ceprano, Manzi et al. (2001) predicted that affinities will emerge to show that this cranium would represent the adult form of *H. antecessor*.

Mallegni et al. (2003) undertook a cladistic analysis using 30 characters in which a strict-consensus tree placed the Ceprano cranium with the Daka cranium as an 85% supported monophyletic group that is itself monophyletic with a group comprising Arago, Petralona, Kabwe, Saldhana and Bodo. They named Ceprano *H. cepranensis sp. nov.* (op. cit 154-159) and hypothesised that it is representative of an African population that migrated about 1.0 Mya and that did not contribute to the human population of Europe as the typical characters of European *H. heidelbergensis* are not present.

When the calvaria was subjected to morphological comparisons made possible by computer tomography (CT), Bruner and Manzi (2005) corroborated earlier hypotheses that it shares a number of plesiomorphies with early *Homo* taxa and some derived features suggesting a phylogenetic relationship with *H. heidelbergensis* but they concluded that a proper taxonomic interpretation remains puzzling (op. cit. 643-656).

Observations

Ceprano lacks the base, face, and various parts of the skull; the supraorbitals are intact but bone at bregma is missing, so measurements and observations about this part of the cranium cannot be made with any certainty and are not used in this analysis. As well, no observations can be made in the asterionic region as it is composed of tiny fragments and it is difficult to discern features accurately. There is some plastic deformation causing asymmetry in the skull that is most noticeable in frontal and occipital view. The calvaria is of massive appearance; the bone thickness is 100mm at the top of the parietal and 150mm in the temporal region. The supraorbitals also contribute to the massive appearance; they are very thick medially and narrow centrally and laterally.

[6] See addendum at the end of this Chapter

In frontal view the calvaria is relatively high, the parietals curve gently. On the more complete left side of the calvaria, the cranial wall angles sharply at the temporal line and is almost straight-sided until the temporal squama is reached, at which point it slopes inwards. There is a 9mm x 13mm rounded tubercle on the frontal 40mm above right supraorbital.

In lateral profile, the frontal rises steeply from just posterior to the supraorbitals, and the calvaria is relatively high and short with a prominent occipital torus and sharply angulated nuchal region. There is little post-orbital constriction.

Although the supraorbitals appear flat in frontal view, they are curved superiorly-inferiorly in lateral profile. There is a slight depression within these at each extremity, and there is a depression at glabella. There is no real sulcus, the supraorbital margin flows into the frontal after a very slight convex curve in the region above the orbits; the metopic keel commences at glabella. The lower border of the supraorbital torus forms an angle with the orbital roof.

The greatest width of the cranium is difficult to gauge as there is some deformation of the skull and some missing fragments. At best, the measurements are estimates and the greatest width may be high on the temporals (~156mm) or at the supramastoid crest (~160mm). It is probably misleading to simply state that the widest part of the cranium is at the supramastoids, as it these that contribute to the measurement. Rather, it is more important to note the widest part of the cranium appears to be at mid-parietal; the temporal bones converge inferiorly to a small extent; the small postorbital constriction; and the relatively expanded form of the cranium compared to earlier hominins.

The temporal lines (l.h.s.) are raised and continue to form a marked raised area on the occipital region of the cranium. In occipital view, the occipital torus is above the superior nuchal line and extends for the width of the cranium; a slight sulcus lies above, but does not extend laterally as far as the torus. There are two equally proportioned bilateral longitudinal depressions within the torus. Below the torus the nuchal surface commences with a very sharp undercut to the cranium; it is concave at first, then swells and retreats inferiorly. Inion is difficult to identify as there is a 'free flowing' or 'island' piece of bone

in the immediate vicinity and the location of inion depends on whether it is placed correctly in the otherwise open space. There is a tubercle where the supramastoid crest stops at the squamosal suture. The mastoid process is large and projects inwardly below the base. The anterior part of the tympanic joins the anterior part of the mastoid process.

The mandibular fossa is very shallow and relatively short; there does not appear to be a postglenoid process; the tympanic makes up the wall of the fossa. On the left there is a styloid pit incised as a groove into the low, flat vaginal process. The articular tubercle slopes gently into the mandibular fossa after a sharp angulation with the pre-glenoid plane. The entoglenoid forms a sharp high point. The digastric fossa is deep, U-shaped and long.

3.9.3 Daka

The Daka cranium, BOU-VP-2/66, (Ethiopia), was found *in situ* in sediments with a basal $^{40}Ar/^{39}Ar$ age of 1.042 ± 0.009 Myr; the sediments are reverse polarity and their minimum age is therefore estimated to be ~.8 Myr (Asfaw et al. 2002). The calvaria is well preserved although it has some distortion.

Asfaw et al. (op. cit.) found that Daka shares many derived characters with *Homo erectus*, based on an analysis of 22 characters they asserted to be widely used in cladistic analyses of *Homo erectus* and close relatives (op. cit. 318). To perform this analysis, they included Daka in a polymorphic deme with OH 9 and Buia, so the analysis did not test the phylogenetic relationships for Daka as such. Although the authors concluded that the cladistic method failed to support a division of *Homo erectus* into African and Asian clades and that the Daka calvaria is consistent with the hypothesis of a widespread polymorphic and polytypic species existing 1 million years ago, the analyses show Kabwe (*H. rhodesiensis*) and Dali as sister taxa, from which it could be hypothesised that they share a unique common ancestor; the same situation occurs for KNM-WT 15000 and the Trinil/Sangiran deme, Daka/Buia/OH 9 and Ngandong, and KNM-ER 1813 and KNM-ER 1470 (refer their Figure 2). Each of these clades is on a separate branch. Further, Trinil/Sangiran is widely separated from *H. pekinensis* and one could hypothesise that they did not share a unique common ancestor. In other words, there are several hypotheses arising from Asfaw et al.'s (op cit) analysis of these hominins.

Observations

In frontal profile, the calvaria is somewhat steep sided with the parietals forming a low peak superiorly. In lateral profile, the frontal slopes moderately steeply from glabella to mid-frontal, after which the slope moderates. The occipital is smooth and rounded but with a bun-like formation above the nuchal region. In coronal profile the calvaria is almost straight-sided in the parietal region with a low, flat slope to sagittal suture; the greatest breadth is low on the skull.

The supraorbitals are arched and thick, superiorly/inferiorly flat, with maximum thickness at the midline of each. There is a marked depression at glabella. The supraorbital sulcus is pronounced above the orbital region but interrupted in the medial zone, above glabella.

The frontal rises relatively steeply posterior to glabella. The temporal lines are pronounced and extend to the lambdoid suture; there is a tubercle at frontotemporale on both sides of the calvaria.

The interorbital region is relatively wide above the frontonasal suture and has a deep superior-inferior sulcus which gives a 'double-arched' appearance to the supraorbital torus.

A small amount of bone (9.7mm x 12.0mm) is missing at bregma. Nevertheless, judging from the lack of swelling adjacent this region, it seems unlikely that a bregmatic eminence was present. There is some frontal and parietal bossing, but no keeling posterior to bregma.

There is no angular tuber on the left hand side and only a slight swelling on the right hand side in this region. There is no occipital torus, rather, the superior nuchal line projects somewhat sharply above a convex nuchal region; I could not discern an inferior nuchal line. There is a depression at each lateral extremity of the nuchal line, where the nuchal line splits somewhat below, and medial to, asterion. At the lateral extremity of the nuchal line is a foramen (5mm x 4mm); below and anterior to this are two parallel superior-inferior grooves adjacent and posterior to what remains of the eroded mastoid process.

There is no occipital sulcus. Below inion is a triangular region from which a low, rounded external occipital crest extends to the foramen magnum. The foramen magnum is oval shaped. There is little evidence of a supramastoid crest and no supramastoid sulcus.

The mandibular fossa is deep, with a groove between the entoglenoid and tympanic plate. The base of the mandibular fossa follows a sigmoid line, winding around the entoglenoid formation, similar to OH 9. The postglenoid process is relatively small on the left side and of medium size on the right side. The styloid pit is surrounded by thick bone, 1.7mm wide, which extends laterally and melds with the vaginal process. The vaginal process peaks just sagitally from the styloid foramen. The tympanic, where present, is thick.

Bone thickness at coronal suture anterior to the temporal line is 7.6mm.

3.9.4 Bodo

Bodo (Bodo d'Ar, Ethiopia) is younger than those examined thus far. Rightmire (1996) reports an estimated age for the remains to be 600 Kya. In their original announcement of the cranium, Conroy et al. (1976) refrained from making a taxonomic determination. Later, Kalb et al. (1982) assigned Bodo to *H. sapiens rhodesiensis,* including it in a taxon with Kabwe, whose age is unknown (see Chapter 4; Kabwe discussion). Groves (1989) also attributed Bodo to such a taxon, as did Adefris (1992) in his dissertation on Bodo, although he preferred the term 'archaic *Homo sapiens'*.

The specimen consists of an almost complete face and partial neurocranium, including most of the frontal bone, basicranium, nasal bones and the left zygomatic except for the temporal process and parts of the maxilla. Although it is younger than other fossils in this study, it is included here as it has been conditionally compared to *H. erectus s.s.* by Stringer (1984) based upon its robusticity, in terms of keeling, thickness and dimensions for facial breadth and the degree of prognathism, but only if its more *H. sapiens* characters (large cranial capacity, relatively high vault, and supraorbital torus morphology) are considered to be of less phylogenetic importance than the *H. erectus* characters (op. cit. 140-141).

Rightmire (1996) undertook a detailed description and comparative analysis of the Bodo cranium, concluding that it seems most reasonable to group Bodo with Kabwe and similar specimens from the Middle Pleistocene sites in Africa and Europe.

That is, the general consensus appears to be that Bodo is a more derived form of the Early Pleistocene fossils. This is tested in the following analyses in which Bodo is compared to Kabwe and earlier hominins.

Observations

In frontal view, the cranium appears massively built. The interorbital region is very wide, the tori are flaring and wide superiorly with a flat anterior surface; the arches are fused at glabella. The facial region is relatively complete on the right/left side. The maxilla is inflated and puffy, with a flaring (incomplete) zygomatic, and this contributes to the massive appearance of the skull. There is a slight depression at glabella. Each temporal band is 11mm wide, consisting of parallel, slightly raised lines, flanked internally by a depression with a central raised area.

In lateral view the frontal rises obliquely from a posttoral plane posterior from the orbits, and immediately from glabella, where the posttoral plane is interrupted. The frontal forms a low, elongated rise that peaks posteriorly on the vault, to descend gradually into a relatively smooth occipital region, or what remains of it.

What remains of the basicranium is comprised of many tiny pieces of bone; the mandibular fossa region presents as a most unusual, simple, dish-like, featureless depression comprised of one fragment. While this seems unusual, I assume that the reconstruction is accurate.

Cranial thickness is 13mm just lateral to bregma, 12.5 in the right parietal region, and 9.1 at the posterior region of the available cranium; other cranial thicknesses vary between 9.8 mm and 9.5mm. Posterior to the bregmatic eminence the cranium is relatively flat in the sagittal region for a short distance whereupon sagittal keeling recommences. The cranium is also relatively flat as it slopes from the sagittal plane to the temporal region. There is a marked postorbital constriction.

The *facies anterior* has an inflated appearance but there is a flat region below the medial orbital regions, below which is a depressed canine fossa. The superior margin of the orbits is linear. The nasal bones are laterally convex. There is a short, broad nasal aperture with sharp margins; a nasal spine is present.

The naso-alveolar clivus is flat anteriorly and laterally, and the skull is very prognathic. Although the anterior pillars are not marked, there is a longitudinal swelling adjacent the aperture.

The palate is massive in appearance, anteriorly rounded, and slopes gently posteriorly from the incisor area, whereas the sides of the palate slope vertically.

3.9.5 Results.

1. Cladistic analysis

The shortest tree that includes Daka, Ceprano and Bodo is L = 369, and it forms when Bodo, Daka, and Ceprano form a clade.

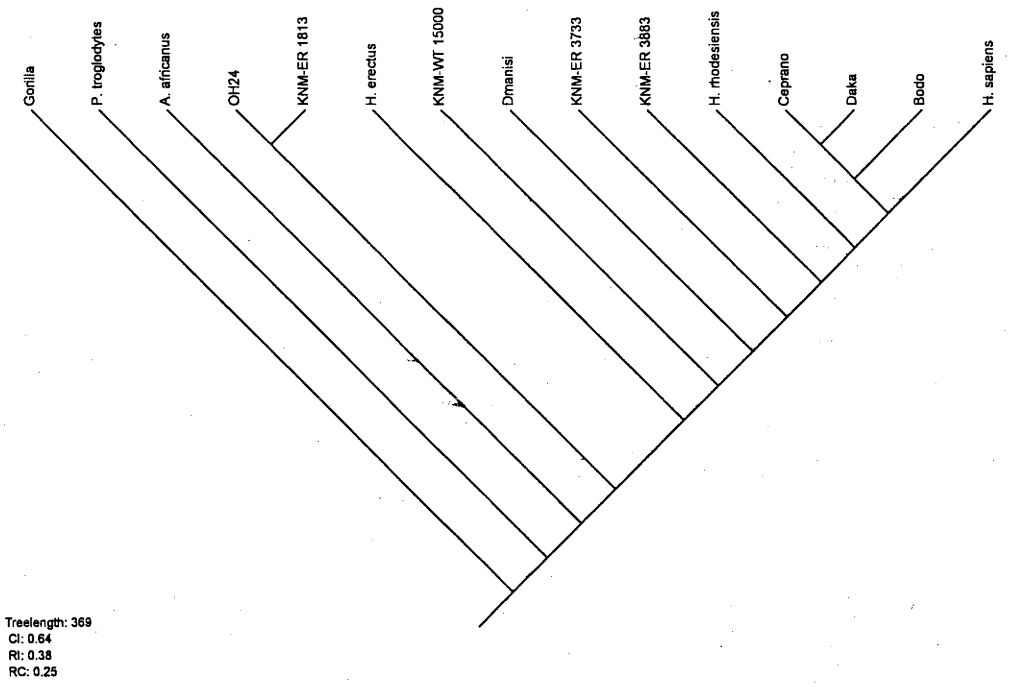


Figure 3-26 Ceprano, Daka, Bodo: shortest tree

The T-PTP for the clade is p = 0.04; it is unlikely that this clade would form by chance alone. Daka, Ceprano, and Bodo share the following five possible synapomorphies:

Table 7. Daka, Ceprano, and Bodo possible synapomorphies

Character	State	Synapomorphy	Notes
4	1	The frontal edge is linear in *norma verticalis*	parallel with Dmanisi, *H. sapiens*
6	1	The supraorbital torus is interrupted in the medial zone, forming two 'mono-tori'	parallel with KNM-ER 1813
46	0	Posterior part of tympanic join the anterior part of the mastoid process	Parallel with Dmanisi, *H. sapiens*
60	1	Angulation between the pre-glenoid planum and the posterior slope of the articular tuberculum	Parallel with *H. rhodesiensis*, OH 24, *H. sapiens*
77	1	The supraorbital margin is thick, rounded and not demarcated from the roof of the orbit	Parallel with *H. erectus, H. rhodesiensis*

The T-PTP for {Daka, Ceprano} is p = 0.04; and they share five possible synapomorphies:

Table 8. Daka and Ceprano possible synapomorphies.

Character	State	Synapomorphy	Notes
4	1	Frontal edge is linear in *norma verticalis*	Parallel with Dmanisi
6	1	There are two 'mono-tori'	In common with Bodo; parallel with *H. habilis*
20	1	Presence of angular tuberosity	
46	0	Posterior part of tympanic joins anterior of mastoid process	Parallel with Dmanisi
63	0	very prominent entoglenoid formation	Parallel with *H. rhodesiensis*

In summary, the most parsimonious solution for Daka, Ceprano and Bodo is that they form a supported clade which is more derived than most of the other OTUs in the study. Other hypotheses that have been presented for Bodo, Ceprano and Daka have been proposed and these are now tested.

Testing other hypotheses for Bodo

Kalb et al. (1982) assigned Bodo to *H. sapiens rhodesiensis*; Groves (1989) also in effect attributed Bodo to this taxon, as did Adefris (1992) in his dissertation on this fossil (although he preferred the term 'archaic *Homo sapiens*'); while Stringer (1984) conditionally compared Bodo to *H. erectus s.s*, although he recognized the possible phylogenetic significance of some *H. sapiens* features of this cranium. The difference between the trees is the position of the clade on the tree.

1. Bodo and *H. rhodesiensis*: There are two shortest trees of length 378 found when Bodo and *H. rhodesiensis* are manoeuvred to from a clade. This is 9 steps longer than the shortest tree (L = 369), and the T-PTP is p = 0.90. It is likely that these OTUs would form a clade by chance alone.

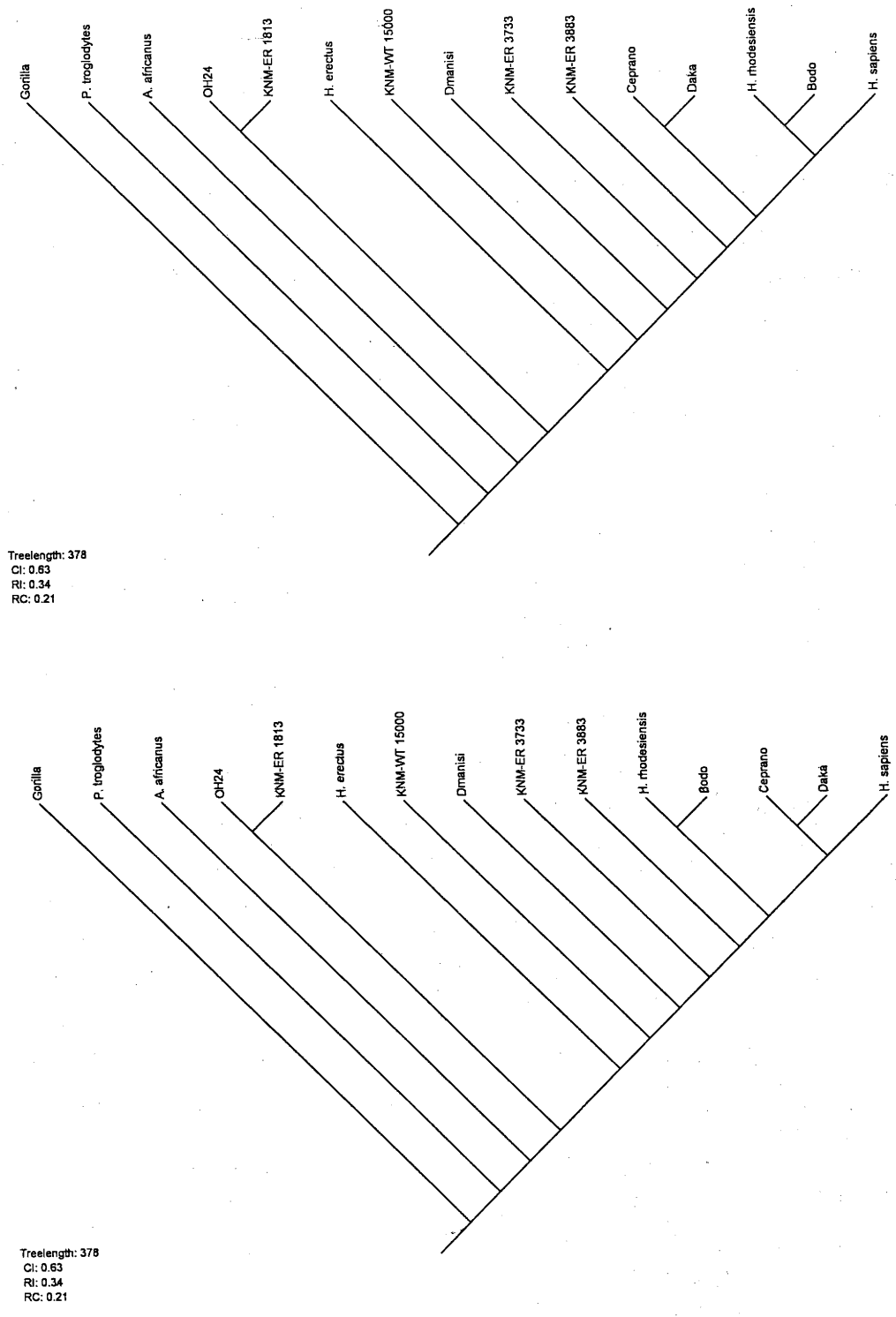


Figure 3-27 Bodo and *H. rhodesiensis*

2. Bodo and *H. erectus*

The shortest tree in which Bodo and *H. erectus* are manoeuvred to form a clade is L = 373, 4 steps longer than the shortest tree (L = 369) for Bodo. The T-PTP = 0.18. This is, therefore, an unlikely solution for Bodo.

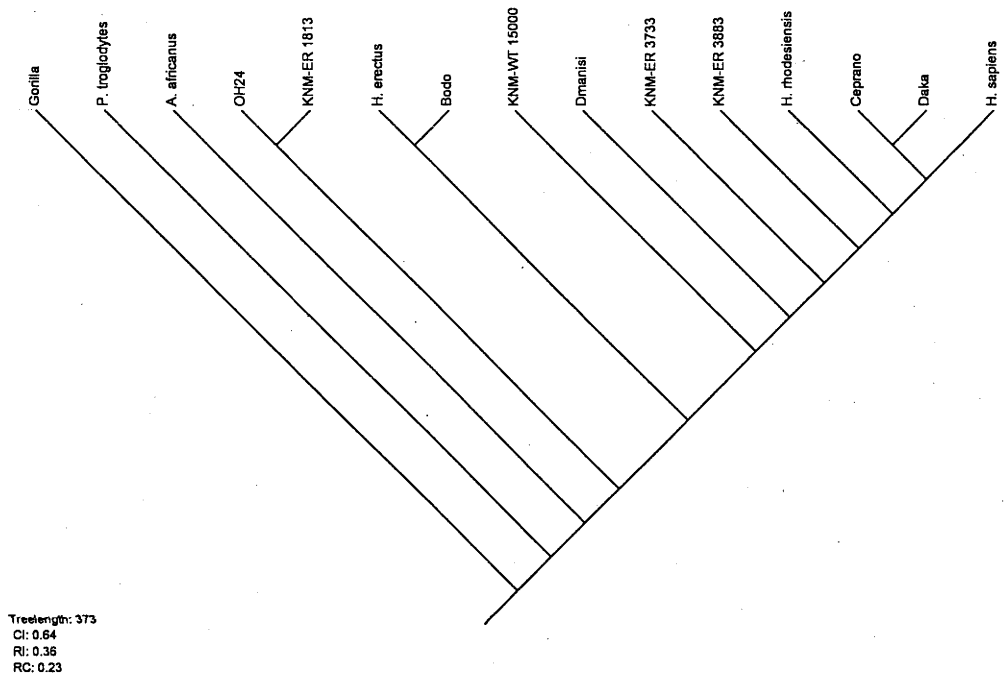


Figure 3-28 Bodo and *H. erectus*

Testing other hypotheses for Daka

Daka and *H. erectus.*

Asfaw et al. (2002) proposed that Daka is *H. erectus*. When this hypothesis is tested in the present study by manoeuvring Daka to form a clade with *H. erectus* the shortest tree length is 373; this is 4 steps longer than the most parsimonious tree (L = 369), and the T-PTP is p = 0.27; the null hypothesis that Daka and *H. erectus* would form a clade by chance is not rejected.

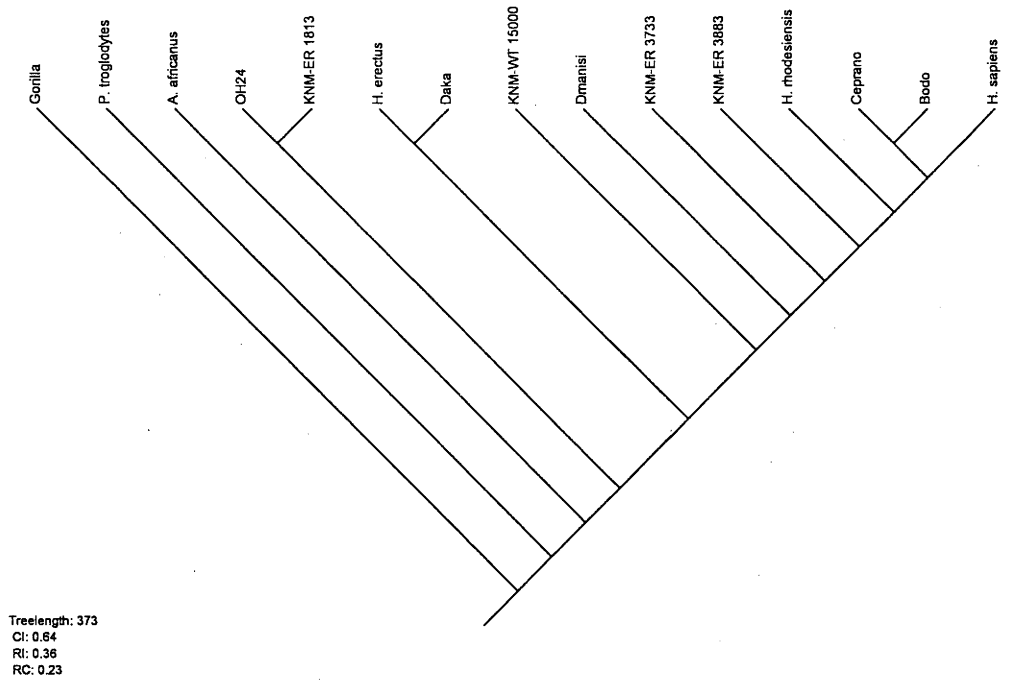
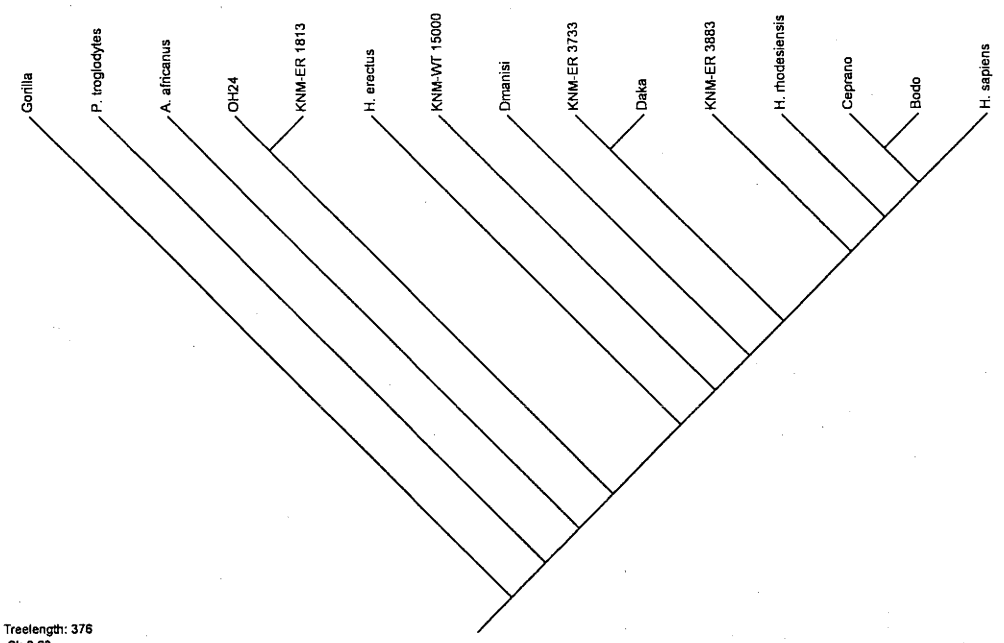
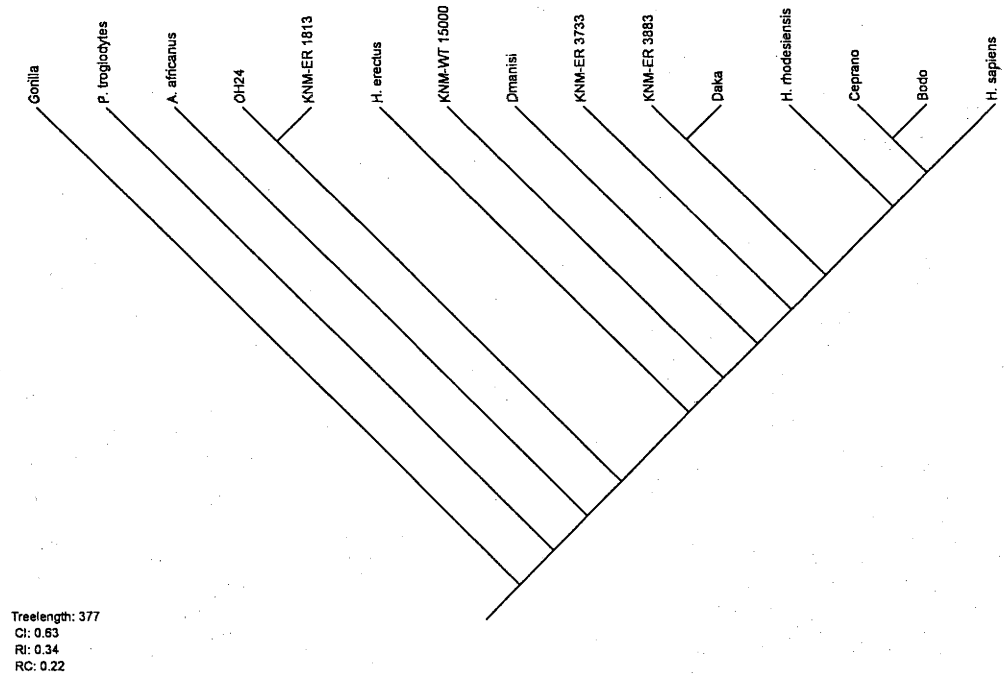


Figure 3-29 Daka and *H. erectus*

Daka and *H. ergaster*

Although it has not been hypothesised that Daka and *H. ergaster* share a common ancestor, I nevertheless explore this possibility as Asfaw et al. (2002) posit a chronological and anatomical morphocline for KNM-ER 3733/KNM-ER 3883 to OH9, to Daka/Buia, sampling a single evolving species. If this is the case, then it could be surmised that Daka would share a unique common ancestor with KNM-ER 3733 and KNM-ER 3883. I test this in MacClade by testing clades {Daka, KNM-ER 3733} and {Daka, KNM-ER 3883} taking into account that in my earlier analyses these OTUs do not form a clade.


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
H. erectus
KNM-WT 15000
Dmanisi
KNM-ER 3733
Daka
KNM-ER 3883
H. rhodesiensis
Ceprano
Bodo
H. sapiens
Treelength: 376
CI: 0.63
RI: 0.35
RC: 0.22


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
H. erectus
KNM-WT 15000
Dmanisi
KNM-ER 3733
KNM-ER 3883
Daka
H. rhodesiensis
Ceprano
Bodo
H. sapiens
Treelength: 377
CI: 0.63
RI: 0.34
RC: 0.22

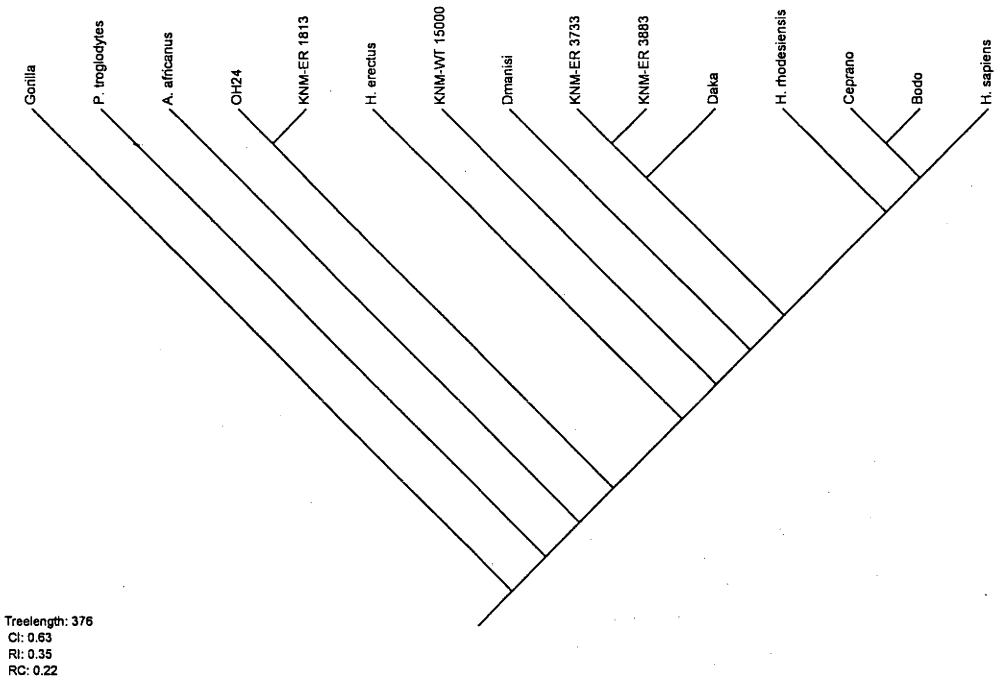


Figure 3-30 Daka and KNM-ER 3733, KNM-ER 3883

When Daka is manoeuvred to form a clade with KNM-ER 3733 the tree length (L = 376) is 7 steps longer than the shortest tree that includes Daka, Ceprano and Bodo (L = 369) and 8 steps longer (L = 377) for a clade {Daka, KNM-ER 3883}. It is most unlikely that there is a close phylogenetic relationship between Daka and any of these OTUs.

A test clade (Daka, KNM-ER 3733, KNM-ER 3883} yielded a tree length of 376, again, 7 steps longer than the most parsimonious.

Testing other hypotheses for Ceprano:

Ascenzi et al. (1996) attributed Ceprano to *H. erectus*, although they were referring, in fact, to the Middle Pleistocene hominins such as Arago and Petralona. I nevertheless tested for a possible phylogenetic relationship between Ceprano and *H. erectus s. s.*, followed by a test for Ceprano and *H. rhodesiensis*. The shortest tree that includes the clade {Ceprano, *H. erectus*} is 377 steps (Figure 3.31). This is 8 steps longer than the shortest tree (L = 369) and is an unsupported phylogeny.

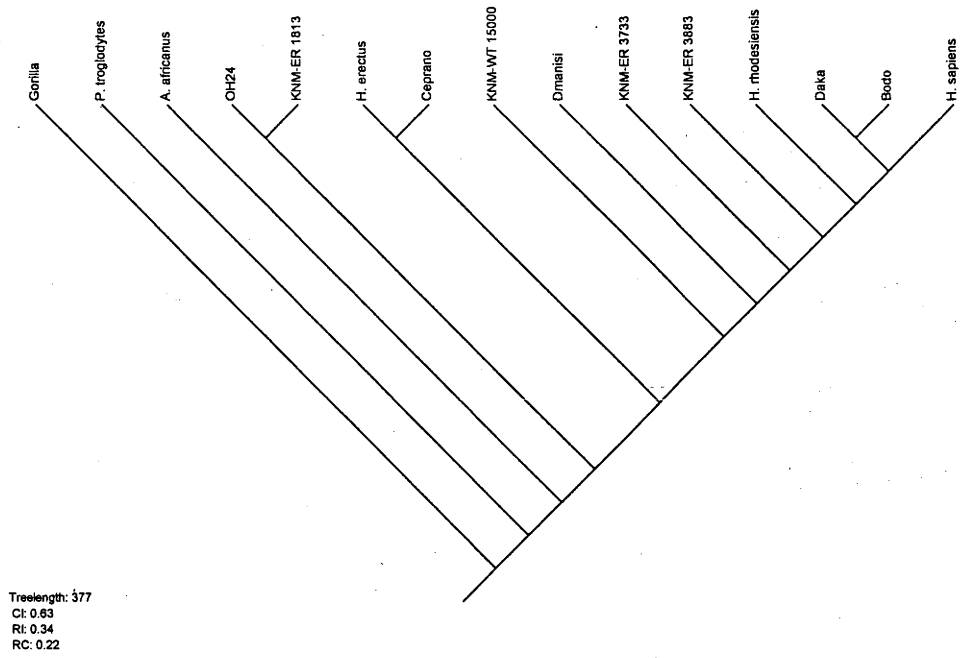


Figure 3-31 Ceprano and *H. erectus*

The shortest tree for a constrained clade comprising Ceprano and *H. rhodesiensis* is also L = 377, 8 steps longer than the shortest tree for Ceprano.

Figure 3-32 Ceprano and *H. rhodesiensis*

Finally if a clade comprising KNM-ER 3733 and KNM-ER 3883 is incorporated into the shortest tree for Daka/Ceprano/Bodo the tree is 2 steps longer (L = 371) than the shortest (L = 369): the T-PTP for {KNM-ER 3733, KNM-ER 3883} is p = 0.34.

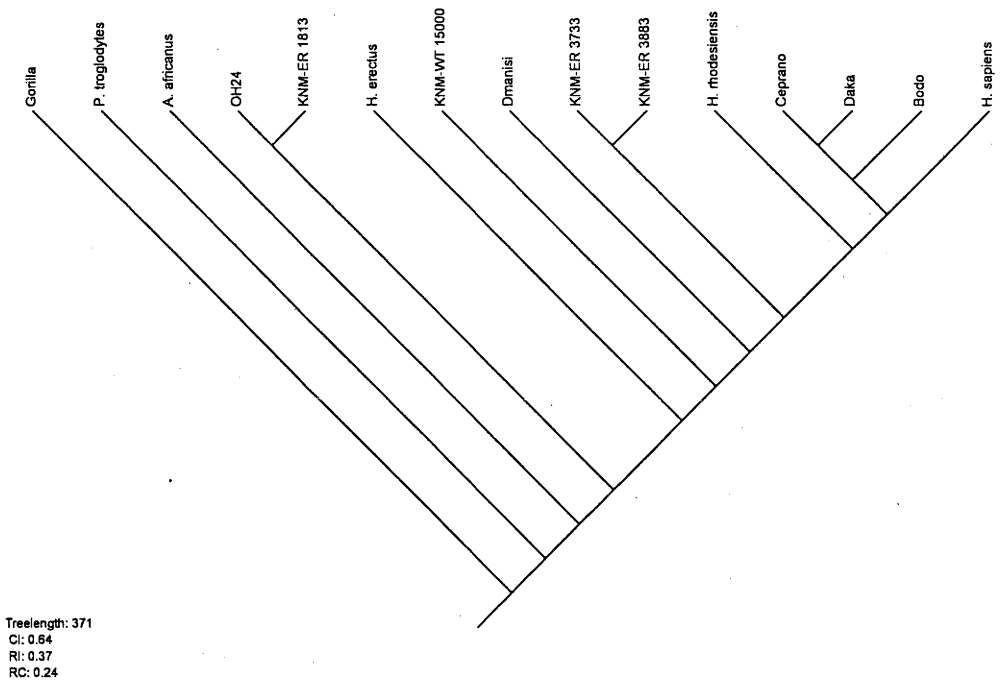
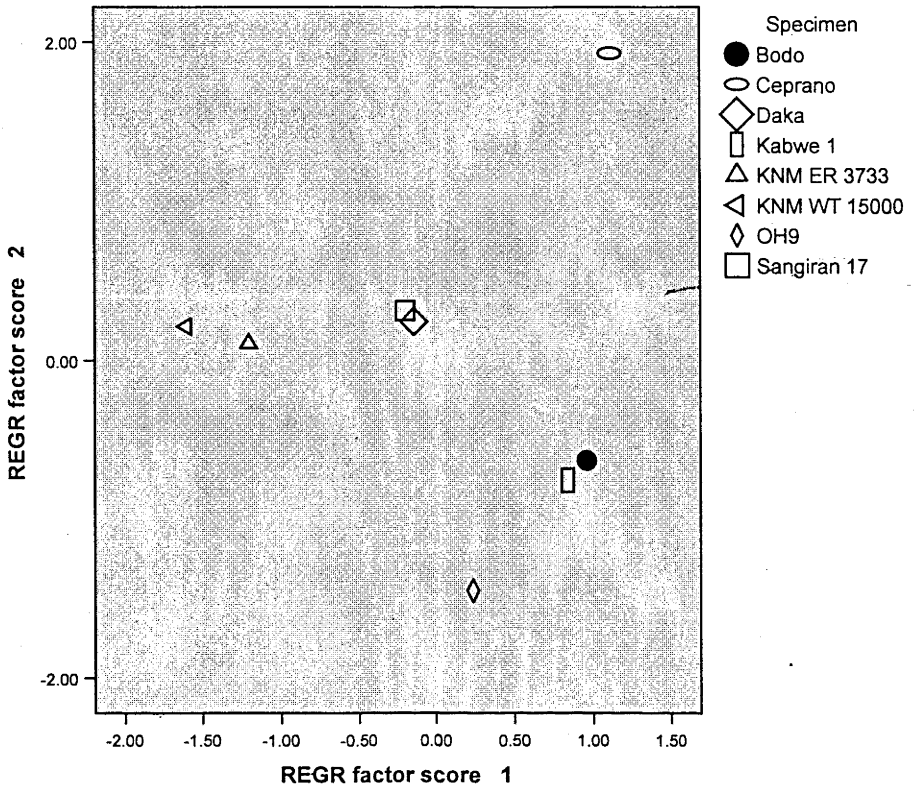


Figure 3-33 Test for a clade KNM-ER 3733/KNM-ER 3883

The most parsimonious solution for Daka, Ceprano and Bodo, then, is that they form a separate clade; tests for any of these forming a sister taxon to *H. erectus* indicate that a hypothesis that any of these crania are *H. erectus* is unlikely.

Morphometric analyses for Bodo, Daka and Ceprano.



Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.311	86.227	86.227	4.311	86.227	86.227
2	.380	7.591	93.818	.380	7.591	93.818
3	.239	4.770	98.588	.239	4.770	98.588
4	.047	.937	99.525			
5	.024	.475	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logTor_central	.913	.038	.400
logMax_supra_br	.926	-.363	-.016
logUpper_facial_br	.947	-.161	-.248
logMIN_FRONTAL_ BREADTH	.982	.047	-.002
logXCB	.872	.467	-.130

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

Figure 3-34 PCA Analysis 4: Daka, Bodo and Ceprano

Most of the variance is on Function 1 and, as these components are more or less equally loaded, they probably represent differences in cranial size. Bodo and Ceprano are similar in overall size and both are similar to Kabwe in this respect. Bodo and Ceprano are separate, however, on Function 2 which accounts for 7.5% of the variance; Ceprano has a relatively wide supraorbital breadth, and, to a lesser extent, broader upper facial region, than Bodo. In fact, Bodo clusters with Kabwe; they are similar in their supraorbital breadth: cranial width relationship.

Ceprano, Bodo and Daka are well separated on Function 2 in this analysis. Ceprano is somewhat larger than Daka, and has a relatively wide vault in relation to its supraorbital breadth than Daka. Daka and Sangiran 17, however, are tightly clustered on both Functions, similar in size and shape.

KNM-ER 3733 and KNM-WT 15000 cluster on Function 2; they are similar in their cranial breadth:supraorbital breadth relationship.

3.10 Gran Dolina (ATD 6-15 + 6-69).

3.10.1 Background and Observations

Human fossils recovered from the excavation TD6 level at Gran Dolina in the Sierra de Atapuerca in Spain comprise neurocranial, mandibular, facial and dental material and many postcranial bones (Bermudez de Castro, 1999) representing six individuals (Bermudez de Castro, 1997), dated to between 780 – 857 Kya by Falguèrès (1999). The

remains were attributed to a new species, *H. antecessor*, based upon a unique combination of cranial, mandibular, dental and postcranial traits, all of which Burmudez de Castro et al. (1999) viewed as different from *Homo erectus* and *Homo ergaster*. Although the holotype is the mandibular fragment ATD6-5, it is the partial face of a juvenile, ATD6-69, that has been taken more widely to define the species. The name of the new species, *H. antecessor*, was chosen to reflect that the authors considered it to be the common ancestor of *Homo neanderthalensis* and modern humans. A revision of the dates for the nearby Sima de los Huesos (HS) fossils, purportedly descendants of Gran Dolina, to an earlier time frame of 400-500 Kya (Bischoff et al., 2003) impelled Burmudez de Castro et al. (2003) to review their hypothesis regarding phylogenetic position of Gran Dolina. They compared the dental sample from Gran Dolina (eight permanent and two deciduous from six individuals) and the SH sample of 467 permanent and eight deciduous teeth (op. cit.). They observed clear morphological differences between the two, within the relatively short time frame. This marked difference, in their opinion, suggests that the Gran Dolina and SH sample belong to different populations, and perhaps to distinct palaeospecies. I was unable to study the SH fossils, nor the more recently announced Sima del Elephante partial mandible (Bermúdez de Castro et al., 2009)

Observations

ATD6-69 comprises the cranial remains of an adolescent or child; the third molar is present but has not erupted. The primary remains consist of a partial vault and separate right maxilla, but there are fragments from other individuals. The latter were examined and photographed but are not used in the analysis as the material does not possess the relevant characters.

The maxilla.

The lower orbital border is lined by rounded swollen bone; the infraorbital immediately below this slopes inwardly; within this region is a very prominent thumb-shaped depression (~15mm x 12mm), which gives the infraorbital region a 'pinched in' effect. Between the canine fossa are two lines of raised bone, extending from the *alveolare* region to lower nasal aperture; there is also a marked ridge above the left canine.

The lateral and lower orbit margins are sharp; there is a slight depression before the orbital slopes inwardly. The right lateral orbital border slopes steeply anteriorly to form what remains of the outer orbital border. The zygomatic faces laterally from the zygomaxillary suture. The malar notch forms an arch flanked by an inferiorly extending tubercle at the zygomatic/maxilla suture.

The nasal aperture ranges from a sharp to a rounded edge at various points; the *margo limitans* forms a sill above a flat naso-alveolar clivus. The tip of the nasal spine projects beyond the naso-alveolar clivus and is very marked.

The palate is somewhat squared off in front with divergent alveolar processes; the form of the arcade is similar to *H. sapiens*. There is an unusual small oval-shaped bone (tooth?) encased in the posterior part of the third molar within the crypt, and extending posteriorly from it. The molar seems to be wrapped around it.

Frontal (ATD6-15)

The calvaria is very small and incomplete. In frontal view the vault is low and rounded; much of the supraorbital region is missing but enough remains to indicate that there is no supraorbital torus. There is a supraorbital sill that comprises a slightly rising surface with a minor longitudinal depression before flowing onto the frontal squama. It would appear that postorbital constriction is not marked. The temporal lines are distinct but not salient. There is no keeling or bossing; there are no depressions.

The paucity of the vault remains means that there are few cranial characters available for the cladistic analysis, and not enough to perform metric analyses.

3.10.2 Results

The shortest tree shows Gran Dolina forming a clade with *H. sapiens*.

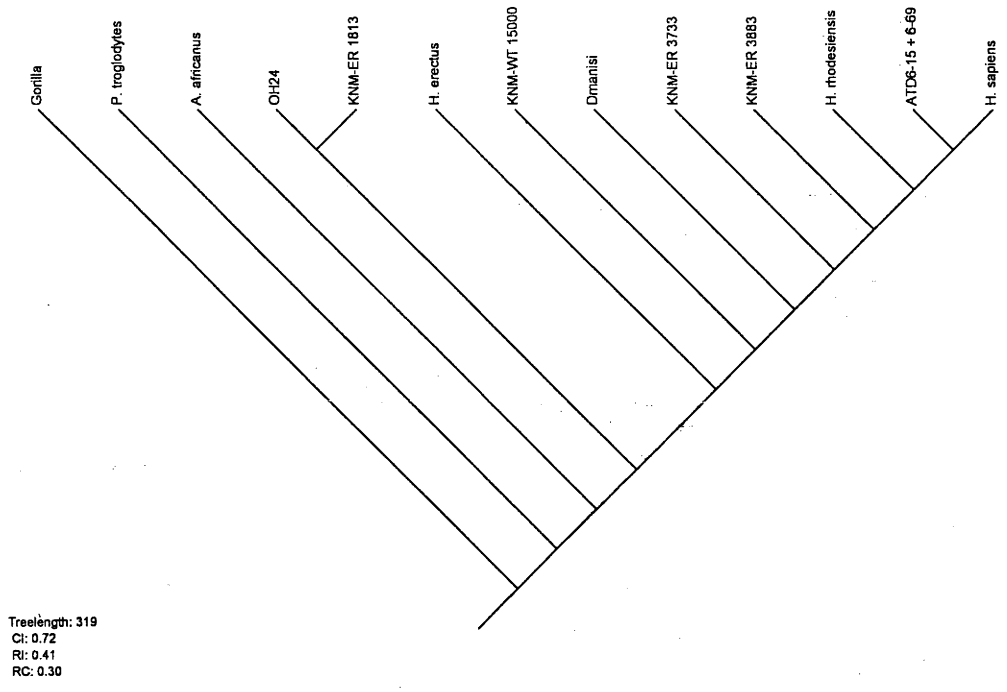
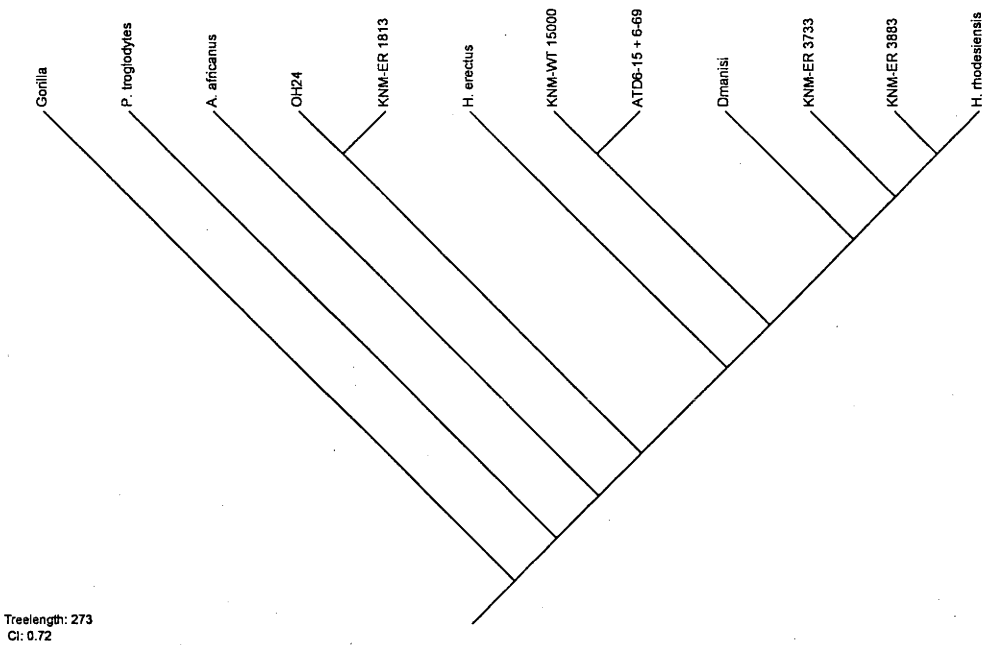
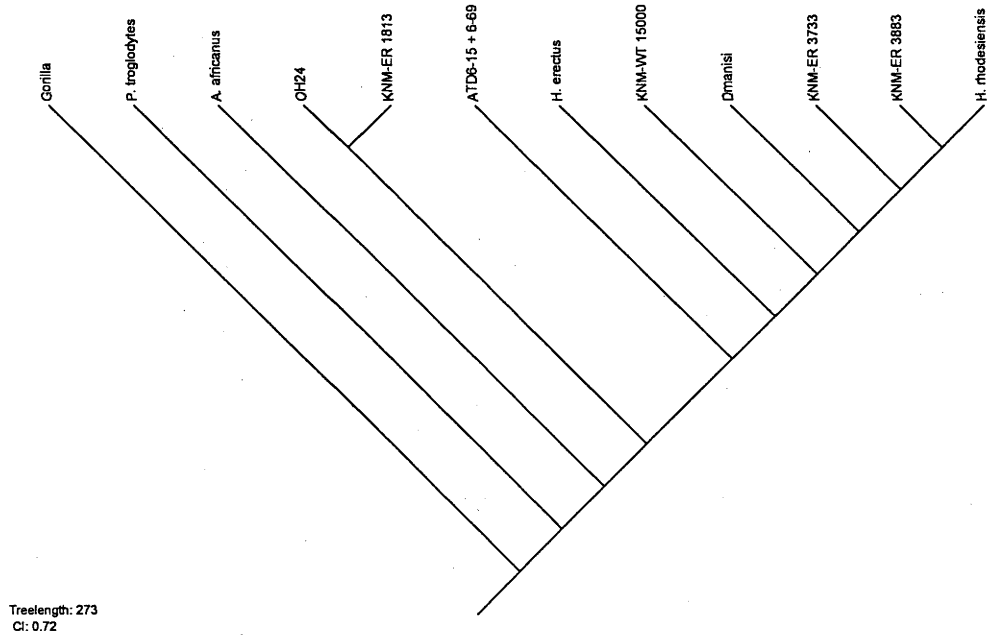


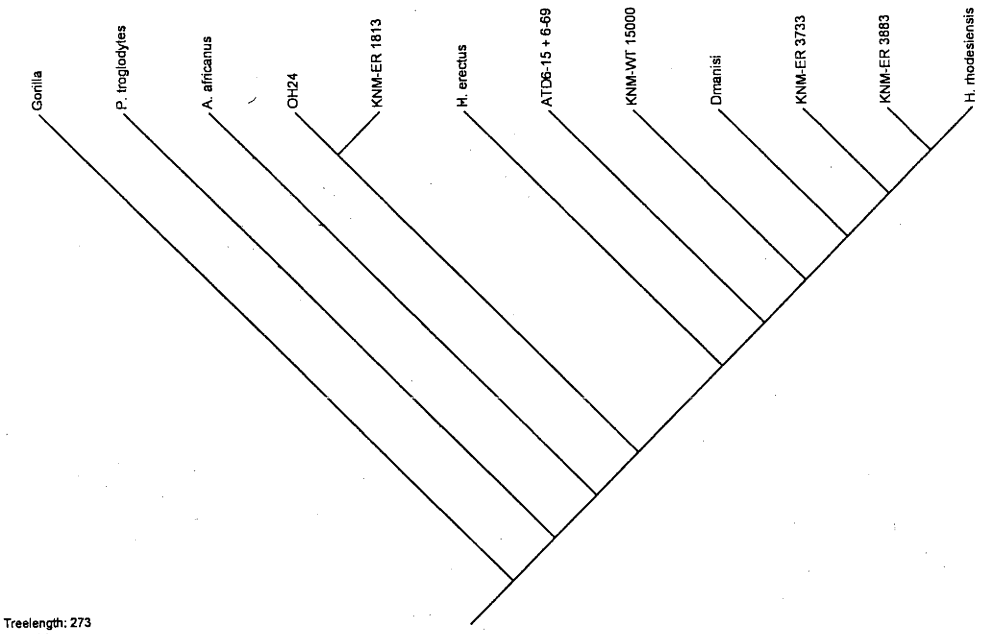
Figure 3-35 Gran Dolina: shortest tree

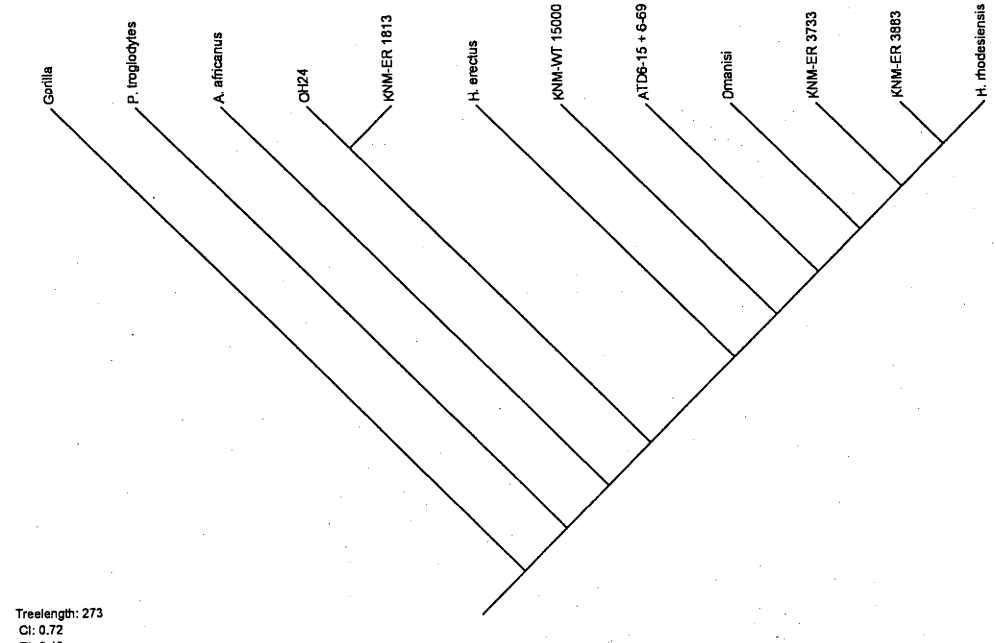
The T-PTP for the clade Gran Dolina/*H. sapiens* clade is p = 0.01 and they share two possible synapomorphies: the malar notch forms an arch, rather than being curved, an arc, or absent (*H. sapiens* is polymorphic for this state); and neither has a supraorbital torus. On the other hand, Gran Dolina is a juvenile and unlikely to represent the adult form. In particular, it is probable that the form of the supraorbitals is undeveloped and that is what partly produces the clade.

For exploratory purposes, then, *H. sapiens* is omitted from the tree. The result is 5 shortest trees; in these Gran Dolina either forms a separate taxon branching from various parts of the tree, or forms a clade with KNM-WT 15000 or *H. erectus*.


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
H. erectus
KNM-WT 15000
ATD6-15 + 6-69
Dmanisi
KNM-ER 3733
KNM-ER 3883
H. rhodesiensis
Treelength: 273
CI: 0.72
RI: 0.40
RC: 0.29


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
ATD6-15 + 6-69
H. erectus
KNM-WT 15000
Dmanisi
KNM-ER 3733
KNM-ER 3883
H. rhodesiensis
Treelength: 273
CI: 0.72
RI: 0.40
RC: 0.29


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
H. erectus
ATD6-15 + 6-69
KNM-WT 15000
Dmanisi
KNM-ER 3733
KNM-ER 3883
H. rhodesiensis
Treelength: 273
CI: 0.72
RI: 0.40
RC: 0.29


Gorilla
P. troglodytes
A. africanus
OH24
KNM-ER 1813
H. erectus
KNM-WT 15000
ATD6-15 + 6-69
Dmanisi
KNM-ER 3733
KNM-ER 3883
H. rhodesiensis
Treelength: 273
CI: 0.72
RI: 0.40
RC: 0.29

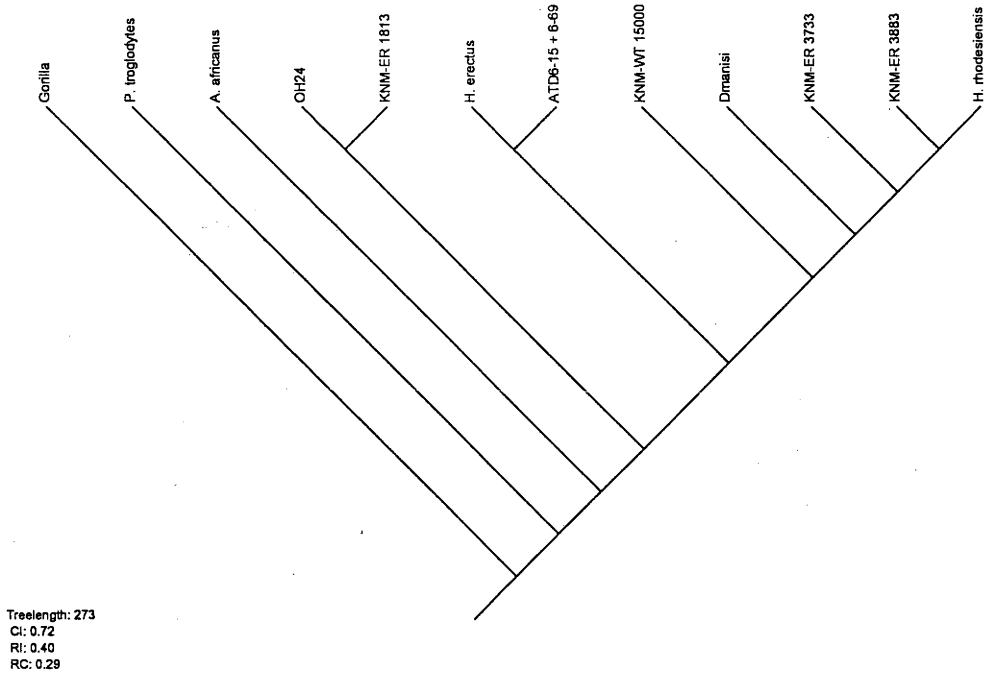


Figure 3-36 Gran Dolina: shortest trees (omitting *H. sapiens*)

The T-PTP for {Gran Dolina, KNM-WT 15000} is p = 0.30 and the T-PTP for {Gran Dolina, *H. erectus*} is p = 0.46; the null hypothesis that Gran Dolina would form a clade with either of these by chance is not rejected.

Burmudez de Castro et al. (2003) included Ceprano in their proposed Gran Dolina population. Trees in which Gran Dolina and Ceprano are constrained, however, yield a tree length of 336 (Figure 3.37; below) and a T-PTP p = 0.81, while the two shortest trees with Ceprano and Gran Dolina included are L = 330 (Figure 3.38; below).

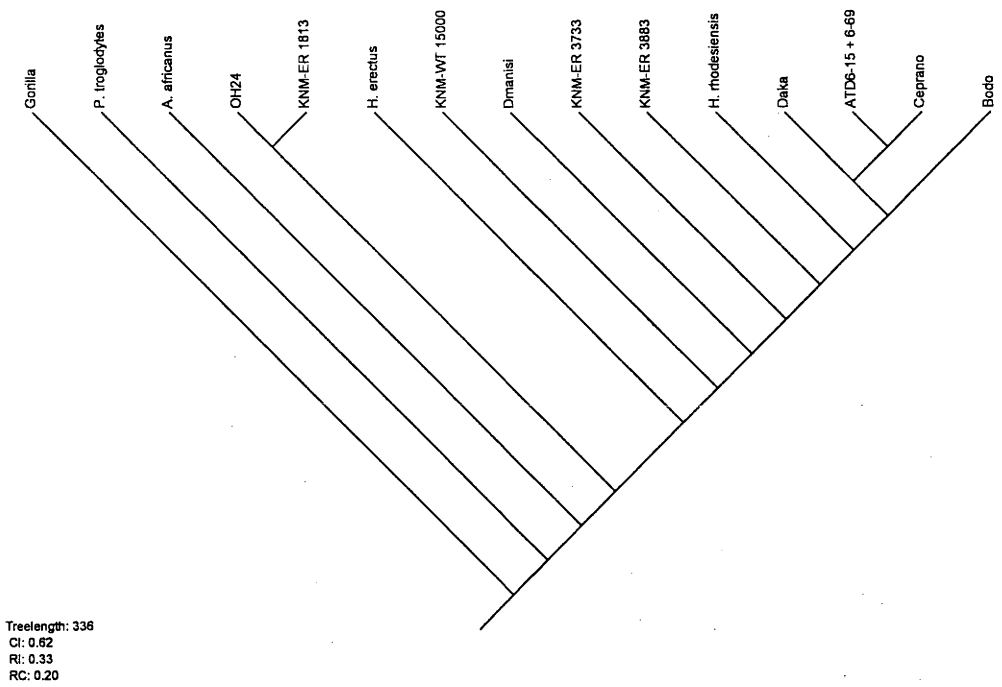


Figure 3-37 Gran Dolina with Bodo, Daka and Ceprano included

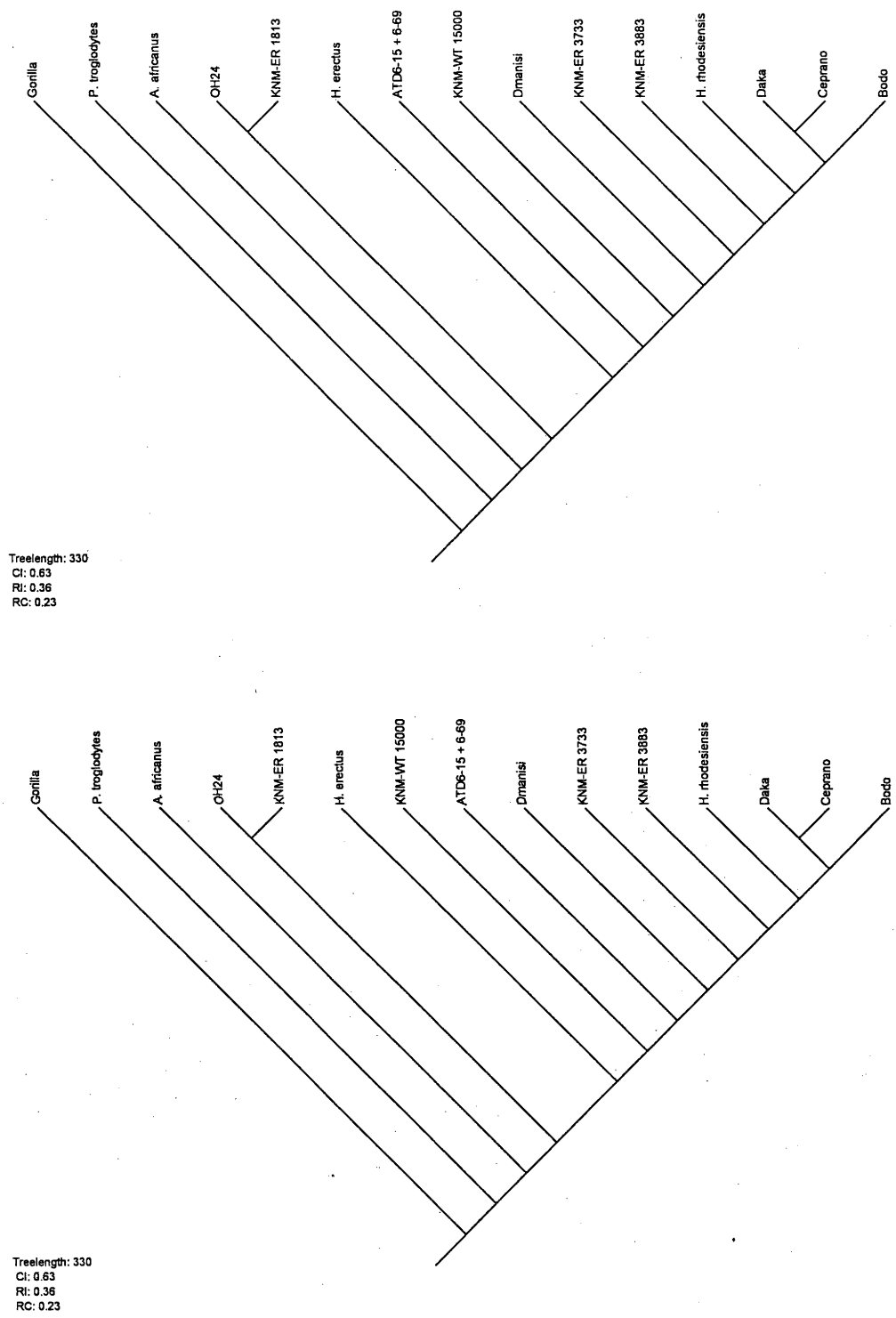


Figure 3-38 Shortest trees Gran Dolina and Ceprano.

The possible phylogenetic positions of Gran Dolina, then, are that it branches before *H. erectus*, after *H. erectus* and before KNM-WT 15000; and after KNM-WT 15000 and before Dmanisi. It has the following possible derived characters:

Table 9. Gran Dolina possible derived characters:

Character	State	Derived character	Notes
68	1	the *margo limitans* forms a sill	Parallel with KNM-ER 1813, *H. sapiens*, *H. rhodesiensis*
71	1	there is no *sulcus infraorbitalis*	Parallel with *H. sapiens*, *H. rhodesiensis*
72	4	zygomaticoalveolar crest forms an arch	*H. sapiens* polymorphic
75	1	orifice of incisive canal is immediately posterior to incisors	Parallel with KNM-WT 15000, KNM-ER 3733, KNM-ER 3883
85	0	No supraorbital torus	Parallel with *H. sapiens*

3.11 Kabwe

3.11.1 Background and Observations

Kabwe 1 was found during mining operations in the basal wall of a steeply sloping cleft emanated from a cave within a small hillock at Broken Hill, Zimbabwe (then Rhodesia). It has not been dated, and, as it seems to have rolled down the cleft at an unknown time, and was annually inundated by a high water table (Hrdlicka 1928) which compromises attempts to date it using ESR, and the hillock no longer exists, having been completely mined, it has not been possible to reliably estimate Kabwe's age.

Kabwe is a relatively large cranium, with an ECV of 1285cc (Holloway, 2000). In lateral profile, the cranium is relatively long, with a gently rising frontal. There is slight occipital 'bun' present. The superior border of the temporal is relatively high in relation to vault height and is rounded. There is no real supratoral sulcus, but the supraorbitals appear massive and protrude. In frontal view, the supraorbitals appear/are flattened towards glabella, and are of similar form to Daka and Ceprano in this respect. In occipital view, the vault is relatively high and rounded, with almost parallel walls. There is a slight

depression on the parietals which gives the impression of a raised area on the midline, reminiscent of Daka. In superior view, postorbital constriction is reduced, and temporal lines are marked, continuing to asterion. Overall, the cranium appears massive.

3.11.2 Results

Kabwe was included in all cladistic analyses and two metric analyses. In the metric analyses (Figures 3.9; 3.10), it is separated from all other specimens on Function 1; it has a broad vault in relation to its post-orbital constriction (Figure 3.9; Analysis 2a) and in relation to vault height and length (Figure 3.10; Analysis 2b). It is similar to KNM-WT 15000 in its vault breadth: frontal arc relationship on Function 2, although it is a much larger skull (Figure 3.9); and similar to KNM-ER 3733 and KNM-ER 3883 in its vault height; length relationship, although, again, it is a much larger skull than these (Figure 3.10).

In the cladistic analyses it branches closest to *H. sapiens*, but when Ceprano, Daka, Bodo and Gran Dolina are introduced into the analyses, it branches before these OTUs. Although it has been referred to the same taxon as Bodo, *H. heidelbergensis*, the test tree for this clade is 9 steps longer (Figure 3.27) than the shortest when the two are constrained to form a clade. In the preferred phylogeny (Figure 3.50), Kabwe branches before Gran Dolina, Daka, Ceprano and Bodo.

Kabwe has the following possibly autapomorphic characters:

Character	State	Autapomorphic characters	Notes
5	1	glabella is neither depressed or protruding	Parallel with *A. africanus*
10	2	Strong metopic keeling	Parallel with KNM-ER 3733, Daka
11	0	Metopic keeling has parallel edges	
19	1	Parietal bosses	Parallel with Daka, Dmanisi
28	0	High temporal squama in relation to vault	Parallel with KNM-ER 3883, *H.*

			sapiens
41	2	Backwardly sloping orientation of main axis of tympanal in *norma lateralis*	Parallel with *H. floresiensis* Dmanisi
129	3	Nasospinale lies behind rhinion	

It would appear, then, that Kabwe shares no immediate ancestors with any other OTU in the analyses and may represent a separate lineage to those in the analyses; its separation from other skulls in the metric analysis would support this conclusion. Its phylogenetic attribution will be explored in Chapters 4 and 5.

3.12 Homo floresiensis

3.12.1 Background and Observations

The following discussion in part incorporate the results of publications prepared during the course of this study (Argue et al., 2006; Argue et al, 2009). *H. floresiensis* comprises a number of individuals[7] dated to between 13.4-10.2 Kya and about 100 Kya (Roberts et al., 2009) excavated from Liang Bua cave on the island of Flores, Indonesia.

The referral of the Liang Bua hominins to a new species is based upon a unique mosaic of primitive and derived features compared to any other hominin. The announcement precipitated widespread interest, and attention quickly focused upon its possible affinities. LB1, a partial skeleton, is a small-bodied hominin with an endocranial volume of 380–410 cm^3, a stature of one metre, and an approximate geological age of 18,000 years. The describers (Brown et al., 2004) originally proposed that *H. floresiensis* was the end product of a long period of isolation of *H. erectus* or early *Homo* on a small island, a process known as insular dwarfism. More recently, Morwood, Brown, and colleagues (2005) reviewed this assessment in light of new material from the site and concluded that *H. floresiensis* is not likely to be descended from *H. erectus*, with the genealogy of the species remaining uncertain.

In 2006, Colin Groves, Denise Donlon, Richard Wright and I published a paper in which we presented morphometric and morphological analyses of the LB1 cranium

[7] Actual number yet to be calculated; M. Morwood, pers. comm..

and postcranial remains (Argue et al. 2006). We concluded that that this skeleton is unlikely to be a microcephalic *H. sapiens,* as had sometimes been maintained (Henneberg and Thorne 2004; Jacob et al. 2006), the only similarity it shows to this morphology being a small endocranial volume; nor does LB1 approximate pygmy or 'pygmoid' morphologies. On the contrary, it shows many characters found in early *Homo*. Our analyses also showed that LB1 probably did not evolve from *H. erectus* as originally proposed (Brown et al. 2004); it differs in cranial shape, degree of prognathism, and limb proportions (the latter inferred from the condidion in *H. ergaster*). The cranial morphology of LB1 is different from all archaic *Homo* specimens in this study, although there are indications that it may be most similar to *H. ergaster* KNM-ER 3733. Postcranially, it exhibits primitive limb proportions most similar to the fossils attributed to *A. garhi*; it has a long radius relative to its femur, assuming the estimated length for the radius is correct. LB1 is short in stature; it has a small cranial capacity but the brain nevertheless is suggested to be neurologically complex. This combination of cranial and postcranial traits is unique, and we supported the attribution by Brown and colleagues (2004) of LB1 to a new species: *H. floresiensis*. We also suggested a number of possible hypotheses for the evolution of *H. floresiensis,* concluding that it most likely represents a previously unknown early hominin likely evolved in Africa and diffused to Southeast Asia before the disappearance of *A. garhi* (or an unknown, similarly-proportioned species) in Africa. We presented three possible scenarios for *H. floresiensis*:

1. The morphology of *H. floresiensis* may have evolved from a founder population of archaic *Homo* that possessed, or developed, a more advanced endocranial anatomy in relation to its postcranial characteristics, either on Flores or in some intermediate region, if Falk et al.'s (2005) assessment of its cranial potential proves correct.

2. *H. floresiensis* represents a previously unknown early hominin that shares cranial similarities with KNM-ER 3733 and limb proportions with *A. garhi*. In this case, it likely evolved in Africa and diffused to Southeast Asia before the disappearance of *A. garhi* (or an unknown, similarly-proportioned species) in Africa.

3. *H. floresiensis* represents a previously unknown hominin that was in the process of evolving from *Australopithecus* to *Homo* when it diffused from Africa. In this case, diffusion would have occurred before the appearance of the fully derived *Homo* morphology, that is, prior to about 2 Mya.

Each of these possible explanations implies a relatively early diffusion from Africa.
Using Principle Components Analysis and Euclidean distance, Gordon et al. (2008) demonstrated that LB1 appears most similar to non-Asian early hominin specimens D2700 (from Dmanisi, Republic of Georgia) and KNM-ER 3733 (from Koobi Fora, Kenya). Recognising that these results might be affected by scaling relationships, they scaled the variables for modern human crania to the size of the LB1 cranium; LB1 remained significantly different from the (non-pathological) modern human cranial shape. That is, regardless of the potential confounding issue of scaling, Gordon et al. (op. cit.) concluded that LB1 is significantly different in cranial shape to modern humans. This provided corroborative support for their conclusions that LB1 is similar to early hominins: Dmanisi 2700, KNM-ER 3733 and *H. habilis*.

Analysis of individual bones of LB1 has provided further insights about this skeleton. Larson et al. (2007) examined LB1's clavicle (LB1/5) and humerus (LB1/50), and LB6's scapula (LB6/4). They showed that this complex is similar to the 1.5 million year old *H. ergaster* fossil skeleton (KNM-WT 15000) and, like this individual, *H. floresiensis* did not have the same shoulder geometry and rotational ability as modern humans; they hypothesised that *H. floresiensis* retained a functional complex that characterised *H. ergaster*. The wrist bones of *H. floresiensis* also appear to be primitive. Tocheri et al. (2007) described three complete carpal bones from the left wrist of LB1. None show modern human features; instead the bones show a pattern found in all African apes as well as fossil hominins 'that preserve the comparable wrist morphology and date before 1.7 Mya.' (op. cit. 1743).

The brain of LB1 also has some primitive characteristics. Falk et al. (2005) studied a virtual endocast of the brain of LB1 using morphometric, allometric and shape data, and concluded that the endocast of LB1 resembles that of *H. erectus* (their sample was Zhoukoudian III, X, XI, XII, and Trinil 2). LB1 does, however, have derived frontal and temporal lobes and a

lunate sulcus in a derived position; brain characteristics that are consistent with higher cognitive abilities (op. cit.). They propose that the shape features of LB1 are consistent with its assignment to another species (*H. floresiensis*) (Falk et al. 2007) and that *H. erectus* and *H. floresiensis* shared a common ancestor that was an unknown small-bodied and small-brained hominin (Falk et al. 2005).

Henneberg and Thorne (2004) had previously proposed a very different hypothesis. They compared skull measurements of LB1 with those of a 2,000-year-old microcephalic skull from Crete described by Poulianos (1975), concluding that both skulls are characterised by very small braincases but their faces are within 3 standard deviations of the normal human range. They cited small braincases and normal-sized faces as characteristics of secondary microcephaly, and therefore suggested that LB1 is a microcephalic modern human. Jacob et al. (2006) and Martin et al. (2006) concurred that this is the most likely explanation for *H. floresiensis*.

Richards (2006) suggested that it appears biologically reasonable that the craniofacial skeleton of *H. floresiensis* could have derived from a *H. sapiens* template. The presumed 'primitive' features of the postcranium, he proposed, are consistent with a stature reduction resulting from a growth hormone deficiency caused by modification of the GH-IGF-I axis, although he was unable to find a match for the size or shape modification. Hershkovitz et al. (2007) compared the skeletal remains of *H. floresiensis* and a large cohort of patients with Laron Syndrome, an autosomal recessive condition that is expressed in consanguineous families (op. cit.) that causes short stature, underdeveloped musculature, hip dysplasia, shallow orbits, small hands and feet, and other symptoms. Hershkovitz et al. (op. cit.) compared the characteristics of the skeleton from Liang Bua with the symptoms of Laron syndrome and proposed the Flores sample may represent a local, highly inbred *H. sapiens* population in which a mutation occurred in one of the gene loci, causing this syndrome. A claim that *H. floresiensis* was part of a long-term population that suffered from cretinism has also been proposed (Obendorf et al. 2008).

Lyras et al. (2008) revived the hypothesis that *H. floresiensis* represents a morphological response to the Island Rule (see Brown et al. 2004; Morwood et al. 2005; Argue et al. 2006). The Island Rule refers to a biological phenomenon whereby large mammals on

islands decrease in size and, conversely, some small mammals increase in size, over a long period of evolution acting on a small gene pool in relative isolation, particularly in an island environment. Argue et al. (2006) refuted this argument for *H. floresiensis*. Lyras et al. (2008) re-asserted it based upon their geometric morphometric analysis of the LB1 skull with skulls of *H. sapiens*, Sangiran 17 (*H. erectus*), KNM-ER 1813 (*H. habilis*) and Sts 5 (*A. africanus*) and concluded that it was not possible to separate *H. floresiensis* from *H. erectus*. Their analysis (op cit.; Figure 2), in fact, shows that *H. floresiensis* and *H. habilis* are similar on PC1, and *H. floresiensis, H. erectus* and *A. africanus* are similar on PC2. Their Euclidean distances analysis, based on these PCs, show *H. floresiensis* and Sangiran 17 (*H. erectus*) clustering (op cit. Figure 4).

Observations

The skeletal remains of *H. floresiensis* were found during an archaeological excavation of Liang Bua cave, on the island of Flores, Indonesia, and announced in 2004 (Brown et al. 2004). *H. floresiensis* comprises an incomplete, partially articulated adult skeleton, Liang Bua 1 (LB1) bracketed by luminescence ages of 34 ± 4 ka and 14 ± 2 ka (Morwood et al. 2004), and more than 30 bones including another mandible, an ulna, femur, fibula, scapula, various phalanges, radii, pelvic fragments and several bones of one or more children[8]; these date from at least 18,000 ya to 95 ± 13 kyr (Morwood et al. 2004).

LB1 represents a person of 1m height (Brown et al 2004) who had an endocranial volume of 417cc (Falk et al. 2005). In lateral view, the LB1 cranium rises relatively steeply from a narrow postorbital plane. There is post-depositional[9] damage at bregma, which might contribute to the relatively flat appearance of the apex of the skull. The lower facial region is prognathic; and there is no chin formation.

In frontal view, the cranium is low, forming a peak superiorly; there is some metopic keeling. The external nasal and right supraorbital regions were damaged during excavation, nevertheless it is clear that the supraorbitals framed the orbits, rather than forming a shelf-like structure. The orbits are rounded and appear relatively large in

[8] List supplied to me by M. Morwood

[9] Some of the bregmatic bone was found in an unassociated position in the stratum (M. Morwood pers. com. 7/12/06)

relation to the face; the superior fissure is round and large. The internal orbital[10] and nasal regions retain fine detail. The malar region extends in a fan like, deep depression inferiorly and laterally from the larger of the infraorbital foramina (reminiscent of the Gran Dolina juvenile); the zygomatic bones flare but are relatively gracile and turn sharply; in lateral view they have an unusual raised tubercle on the superior posterior margin. The malar pillars are prominent.

In occipital view, the cranium is a globular shape, widest at the mastoids. There is a mound extending laterally 3cm and 3.5cm in each direction laterally from the junction of the nuchal lines that comprises the occipital torus. There is a marked, large depression which extends from the obelionic region and, inferiorly, across lambda for some distance; this depressed area is approximately 22mm x 11mm and is somewhat unusual in its size and location if it is considered to be an obelionic depression.

The nuchal surface comprises two large mounded areas each side of the external occipital crest; there is some damage in this region, but there is a small pit either side of the external occipital crest near the foramen magnum. Evidence for occipital condyles comprises a low, thin, sharp, raised bony extrusion that extends from just right of basion to about halfway along the left side of the foramen magnum. It originates as an overhang on the foramen, but as it extends around the foramen it becomes separated from it by a slight groove. A depression is also present along the left lateral edge of the bony extrusion. On the opposite side of the foramen, apart from a small protuberance, the bone is flush with the opening of the foramen. Although this cranium has been damaged since it was excavated (Morwood and Van Oosterzee, 2007), there is no evidence of damage in this region: the bone retains the same mottled appearance as the rest of the basicranium and the area around the foramen magnum, both on the outer and inner edges, retains fine structural detail that appears intact. This form of LB1 condyles is similar to those of modern human neonates, but before I diagnose this as a paedomorphic trait for LB1 further comparative research is necessary.

The mandibular fossa forms a large arc anteriorly and a straight line between tuberculum zygomaticum and the entoglenoid process, rather like a 'D' shape. The mandibular fossa,

[10] Including cribra on the upper surface

undertemporal planum, and zygomatic in this region of the cranial base is very similar to KNM-ER 1813. The auditory meatus is round, unlike either *H. sapiens* or *H. erectus*.

LB1 has a fissure-like feature that extends along the midsection of the tympanal in basal view. This feature also appears to occur on D2700 (Dmanisi group), KNM-WT 15000 and Zhoukoudian Skull III (Weidenreich 1943:54) to varying degrees. These are all subadults. Tobias (1991a) describes it also for *Zinjanthropus boisei* (Olduvai Hominid 5), suggesting that it results from a poor or incomplete fusion between the two moieties of the tympanic bone, and for Olduvai Hominid 24 (Tobias 1991b). The two parts of the tympanic bone meet and fuse after birth (Wilson 2007). The distribution of the trait might, again, suggest a paedomorphic condition for LB1.

The mastoid process has two superior/inferior orientated ridges or crests in lateral view, separated by a sulcus. The more posterior crest originates just anterior to the base of the mastoid and the more anterior crest commences about halfway along the anterior edge of the process. The posterior crest joins a narrow horizontal crest that extends across the top of the mastoid process.

The palate has a strong median palatine ridge that has a very narrow median suture. The palantine ridge is flanked by marked elongated parallel depressions, adjacent which are sharp high elongated ridges, each with a rounded pit adjacent the 3rd molar. The general appearance is of a 'ridges and furrow' pattern on the palate.

3.12.2 Results

1. **Cladistic analysis.**

There are 7 shortest trees (L = 338), all of which show *H. floresiensis* at the base of the *Homo* clade, but 6 contain the clade {Dmanisi, KNM-WT 15000}. This clade has a T-PTP of p = 0.33: the null hypothesis that these would come together by chance is not refuted (this is also discussed above where Dmanisi and KNM-WT 15000 are examined). The remaining tree, then, represents the most parsimonious solution for *H. floresiensis*:

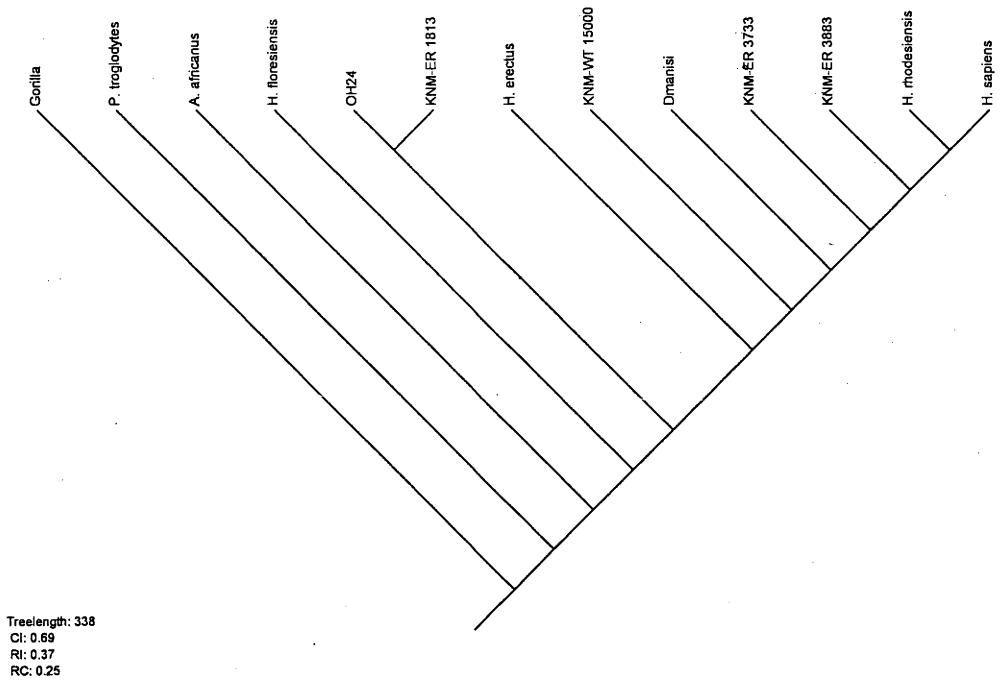


Figure 3-39 *H. floresiensis*: most parsimonious of the 7 shortest trees.

H. floresiensis is at the base of the genus *Homo*. It has the following possible autapomorphic characters in this analysis:

Table 10: *H. floresiensis* cranial characters.

Character	State	Characters	Notes
6	1	There are two distinct tori	Parallel with KNM-ER 1813
10	1	Weak metopic keeling	Parallel with *H. erectus*
21	0	Nuchal plane convex posteriorly in *norma lateralis*	
24	2	Strong degree of relief of tuberculum linearum	
25	1	No depression above where nuchal lines meet	Parallel with KNM-ER 3733
32	1	there is continuity of the supramastoid crest with the inferior temporal line	Parallel with KNM-ER 1813, *A. africanus*
34	1	Strong mastoid crest	Parallel with KNM-ER 3733, *H. rhodesiensis*
41	1	Main axis of tympanic in *norma lateralis* is vertical	Parallel with Dmanisi, *H. rhodesiensis*
42	0	Thin tympanic in *norma lateralis*	
53	1	Groove between entoglenoid and tympanic plate	Parallel with *H. rhodesiensis*
64	1	Lateral extension of entoglenoid slightly extended backward	Parallel with KNM-ER 3733. KNM-ER 3883
65		No postglenoid process	Parallel with KNM-WT 15000
70	3	Jugum alveolar forms a broad and prominent ridge	Parallel with Dmanisi
72	2	they have curved malar notches (as opposed to no malar notch, very curved or arched notches)	
74	1	Palate surface has low irregular crests/fine longitudinal ridges	
75	4	Orifice of incisive canal is parallel with 2nd premolar	

H. floresiensis has been referred to *H. sapiens* by several authors (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Richards, 2006; Hershkovitz et al., 2007;

Obendorf et al. 2008). When *H. floresiensis* and *H. sapiens* are manoeuvred to form a clade, the tree length is L = 345, 7 steps longer than the shortest tree (L = 338):

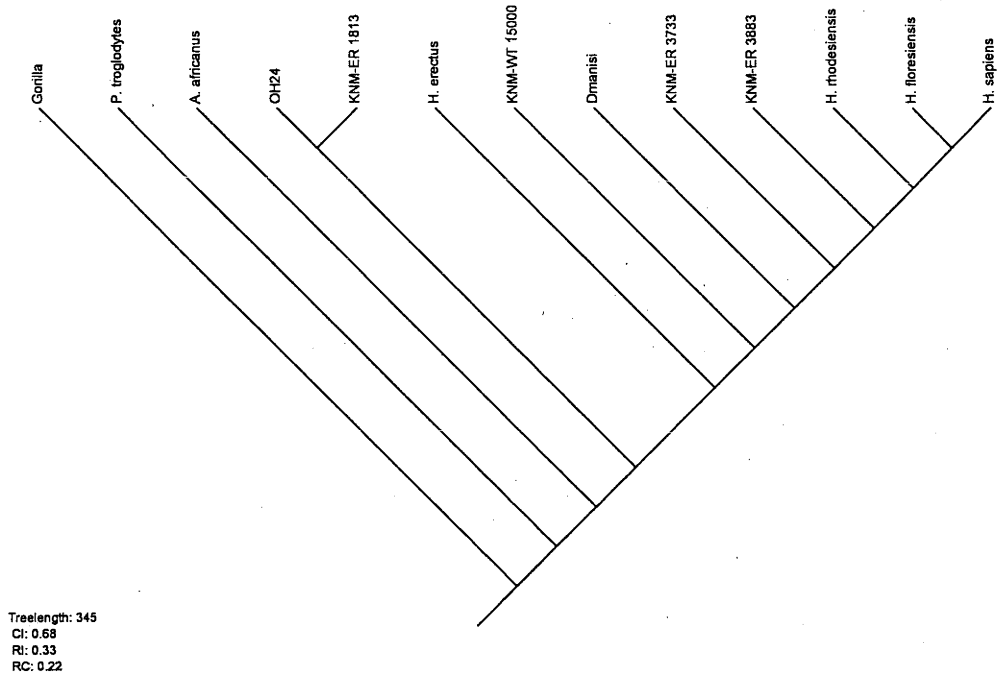


Figure 3-40 *H. floresiensis* and *H. sapiens*

The T-PTP for {*H. floresiensis*, *H. sapiens*} is p = 0.77; the null hypothesis that these would form a clade by chance is supported. Further, the hypothesis that LB1 is a modern human with pathology (microcephaly) was tested in our earlier paper (Argue at al., 2006) and rejected.

Brown et al. (2004) suggested that *H. floresiensis* may have been derived from *H. erectus* although this was later rescinded in the light of further information. Lyras et al. (2008) revived the hypothesis (see above, this section).

To test this hypothesis, *H. floresiensis* is manoeuvred to form a clade with *H. erectus*:

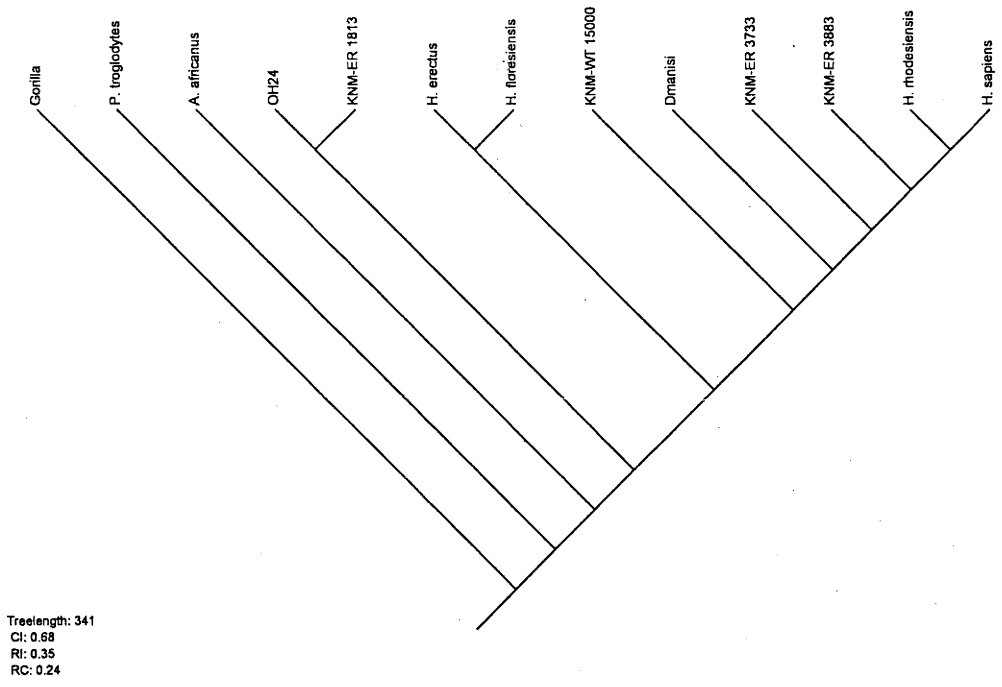


Figure 3-41 *H. floresiensis* and *H. erectus*

This tree length is 342, 4 steps longer than the most parsimonious. The T-PTP for {*H. erectus, H. floresiensis*} is p = 0.53; the null hypothesis that *H. floresiensis* and *H. erectus* would form a clade by chance is not rejected.

I also explore the possibility that *H. floresiensis* could share a common ancestor with *A. africanus*, given that it has been compared to *Australopithecus* by Jungers et al. (2009), although they did not hypothesise that it is on the same branch as *H. floresiensis*; it nevertheless seems worth testing. Possible phylogenetic relationships with *H. habilis* and the Dmanisi group are also investigated.

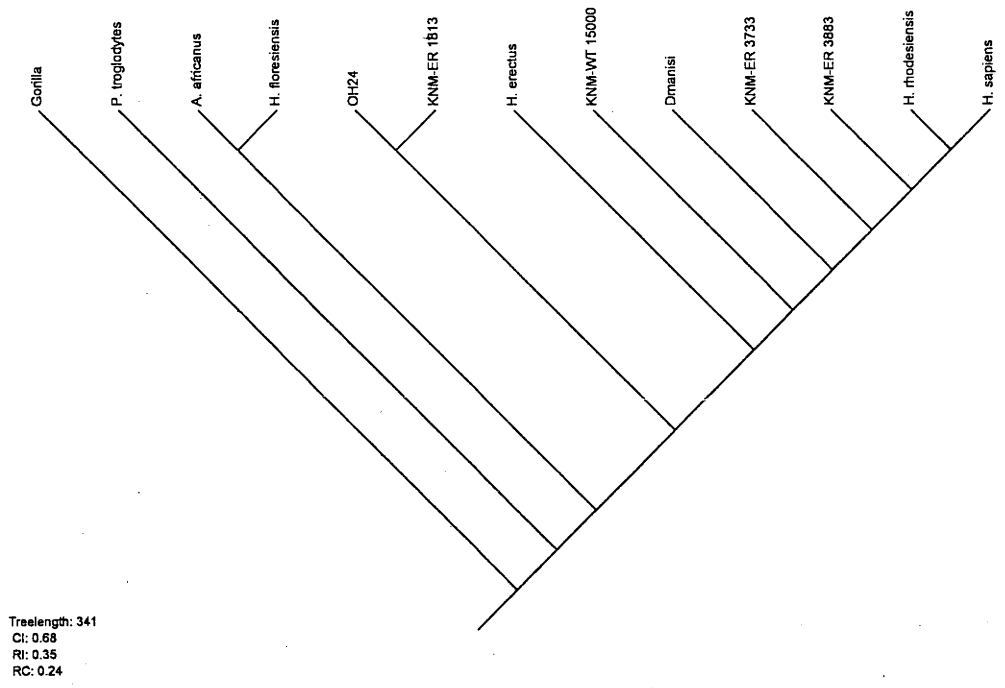


Figure 3-42 *H. floresiensis* and *A. africanus*

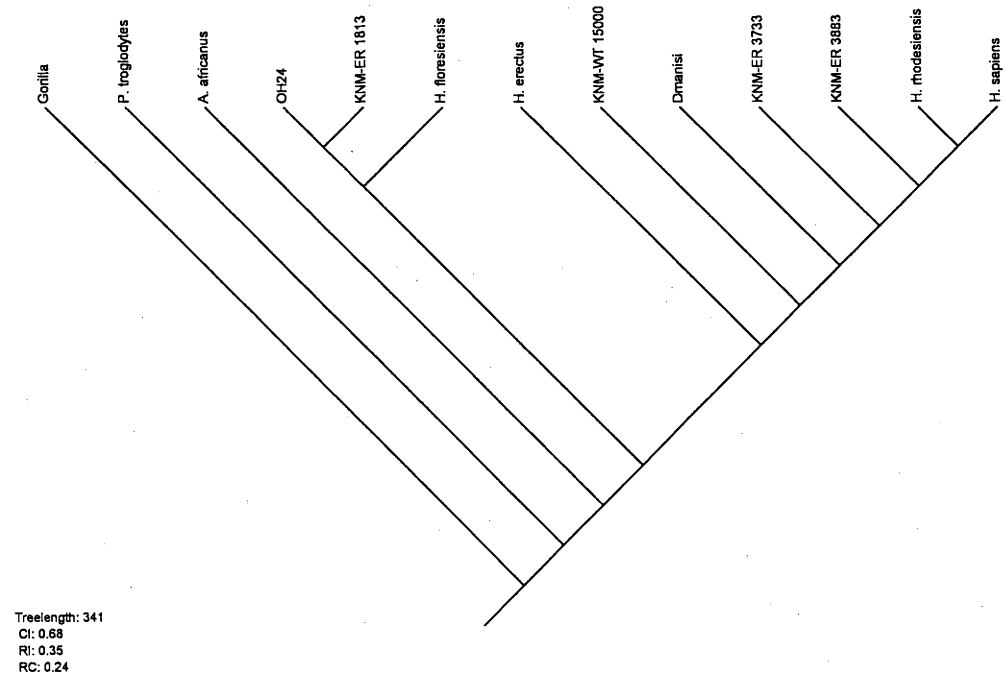


Figure 3-43 *H. floresiensis* and *H. habilis*

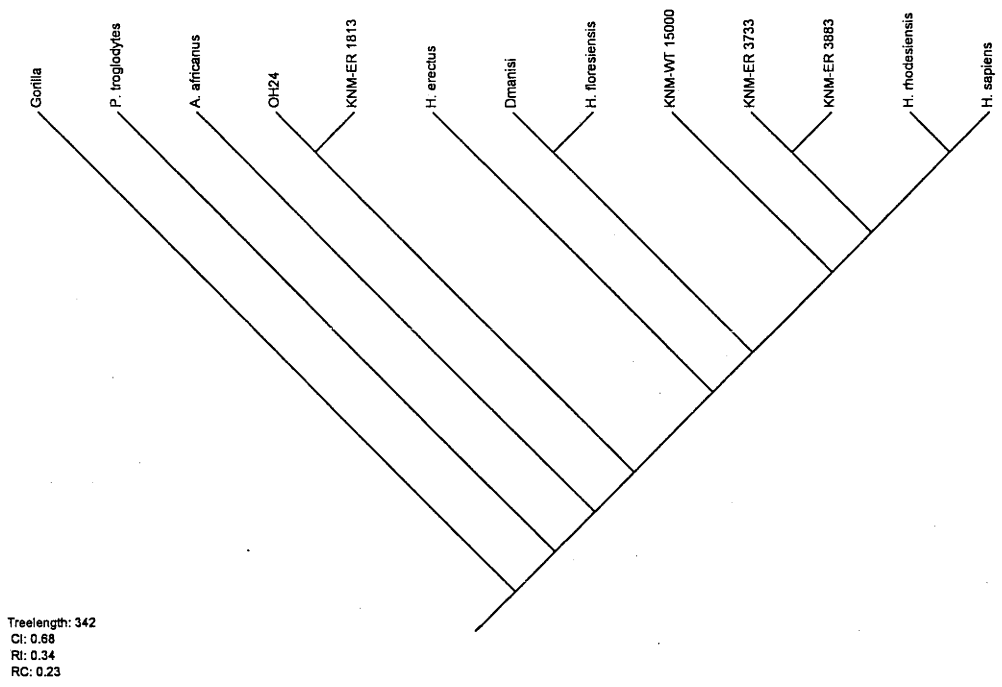


Figure 3-44 *H. floresiensis* and Dmanisi

When *H. floresiensis* is manoeuvred to form a clade {*H. floresiensis*, *A. africanus*} or {*H. floresiensis*, *H. habilis*} each tree is 5 steps longer than the most parsimonious, and the shortest tree with a manoeuvred clade {*H. floresiensis*, Dmanisi} is 4 steps longer than the shortest tree for *H. floresiensis*.

Morphometric Analysis 5. *H. floresiensis*.

The results of four morphometric analyses are presented in our published paper (Argue et al. 2006). These showed clearly that LB1 clusters with early hominins, and well separated from modern humans including microcephalics and pygmoid forms, and that it is likely to represent a distinct species, *H. floresiensis*. This is now examined further.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	6.517	72.406	72.406	6.517	72.406	72.406
2	1.780	19.783	92.189	1.780	19.783	92.189
3	.411	4.571	96.760	.411	4.571	96.760
4	.162	1.804	98.563			
5	.067	.741	99.305			
6	.040	.446	99.751			
7	.015	.171	99.921			
8	.007	.079	100.000			
9	3.1E-006	3.43E-005	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logGOL	.978	.043	.033
logXCB	.805	-.314	.486
logBBH	.792	-.588	-.118
logBPL	.580	.783	-.121
logAUB	.785	.515	.269
logFRC	.952	-.204	-.135
logna_br_arc	.925	-.320	-.187
Min_frontal_breadth	.982	-.120	-.087
Upper_facial_br	.779	.546	-.109

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

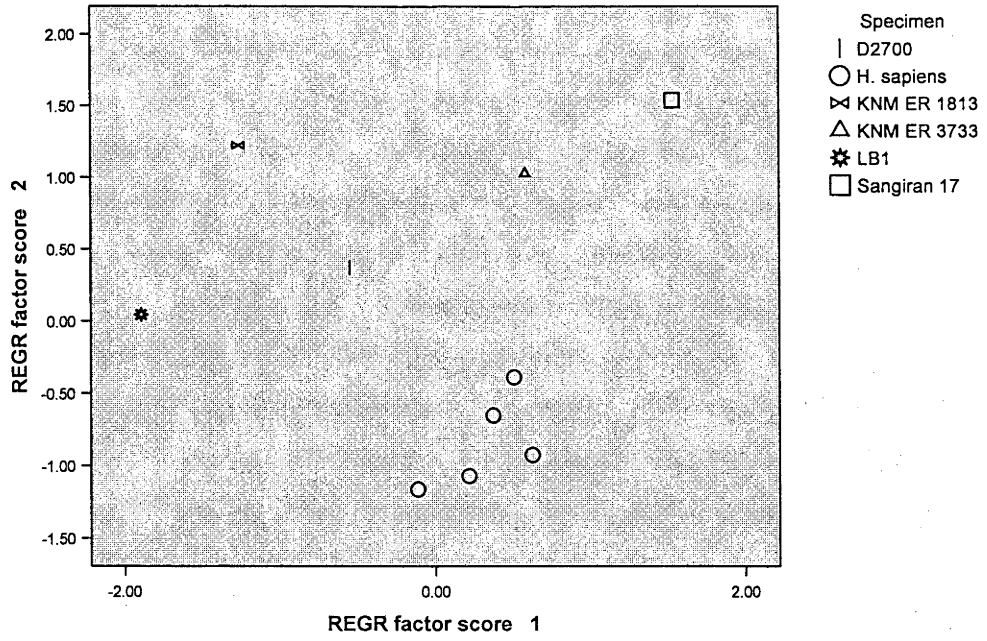


Figure 3-45 PCA Analysis: *H. floresiensis*

LB1 is separate from all other crania in the analysis. This might relate partially to its small size (Function 1) but on Function 2 (19.7% of the variance) it differs from all but D2700 in its basion prosthion length (BPL) in relation to basion bregma height (BBH). That is, it is relatively more prognathic than modern humans but less so than the earlier hominins, except perhaps, Dmanisi D2700. LB1 differs from KNM-ER 3733 in size and shape: the latter is more prognathic and has a relatively lower vault than LB1.

H. floresiensis is well separated from *H. sapiens*; it has a relatively wider biauricular breadth in relation to its prognathism, that is, *H. sapiens* has reduced prognathism and narrower biauricular breadth compared to *H. floresiensis*.

LB1 is also well separated from Sangiran 17 (*H. erectus*), partly resulting from size differences, but also because LB1 has a relatively lower cranium than Sangiran 17, and is less prognathic.

3.13 KNM-ER 42700

3.13.1 Background

In August 2007[11] the discovery of two new cranial fossils from the Koobi Fora Formation was reported (Spoor et al. 2007). One of these is a small, well preserved calvaria (KNM-ER 42700) of a young adult or subadult dated to between 1.53 and 1.61 Myr. Spoor et al. (op cit.) assigned the calvaria to *H. erectus*, in which they include KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, OH 9, Dmanisi D2280 and D2700, Sangiran 17, Ngandong 1, 6, 7, 11, 2, Ngawi, Sambungmacan 3, and Zhoukoudian III, XI, XII, based upon the presence of features such as frontal and parietal keeling, the medio-laterally narrow temporomandibular joint, the distinct coronal and sagittal orientation of the tympanic and petrous bones, respectively, and a posterior midsagittal profile with a low occipital upper scale and opisthocranium positioned close to lambda. Its endocranial capacity is 691 cm^3, the smallest known calvaria to be attributed to *H. erectus*, and is closer in overall size to *H. habilis* (op. cit.); that is, Spoor et al. found that *H. erectus* and *H. habilis* overlapped in cranial size, and they hypothesised that there was a large degree of sexual dimorphism in *H. erectus* (as inferred by the authors in their sample selection, above).

[11] I have not studied this cranium as it was published well after the completion of my fieldwork program.

Baab (2008), noting that the inclusion of KNM-ER 42700 in *H. erectus* significantly expands the range of variation in this species, and that Spoor et al. (2007) attributed the absence of certain features diagnostic of *H. erectus* to the presence of allometric scaling in early *Homo*, has undertaken a series of analyses to test these findings. Firstly she performed a multivariate regression of all shape variables to predict the shape of a hypothetical specimen of *H. erectus* the same size as KNM-ER 42700. She found that KNM-ER 42700 falls outside the 95% prediction for *H. erectus* cranial shape predictions, and that the result is due to the greater expansion of the posterior vault, and a steeper, wider frontal; and the skull is wider across the temporals and has thinner supraorbitals (op. cit.). Baab (op. cit.) concluded that it is preferable to assign KNM-ER 42700 to *Homo sp.* in order to emphasise its uniqueness. Of further interest is that one of Baab's analyses, using a wider range of variables than that used by Spoor et al. (2007), shows KNM-ER 42700 close to the c. 100,000 year old early modern human, Skhul 5 on both Functions, although Baab did not discuss this outcome from the analysis.

3.13.2 Results

Morphometric Analysis 6. KNM-ER 42700

I took relevant measurements from Spoor et al. (2007) and entered them into a morphometric analysis. The first analysis compares KNM-ER 42700 to *H. erectus* (although not with all of the specimens that Spoor et al. inferentially included in *H. erectus*); the second includes *H. habilis* (KNM-ER 1813) as Spoor et al. (op cit.) have said that the calvaria overlaps in size with this species but is distinct from it.

Total Variance Explained

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.229	64.573	64.573	3.229	64.573	64.573
2	1.153	23.056	87.630	1.153	23.056	87.630
3	.394	7.884	95.514	.394	7.884	95.514
4	.146	2.924	98.438			
5	.078	1.562	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix[a]

	Component		
	1	2	3
logGOL	.946	-.109	-.144
logXCB	.861	.009	.494
logBBH	.290	.944	.066
logMIN_FRONTAL_ BREADTH	.891	.224	-.354
logAUB	.845	-.448	.008

Extraction Method: Principal Component Analysis.

a. 3 components extracted.

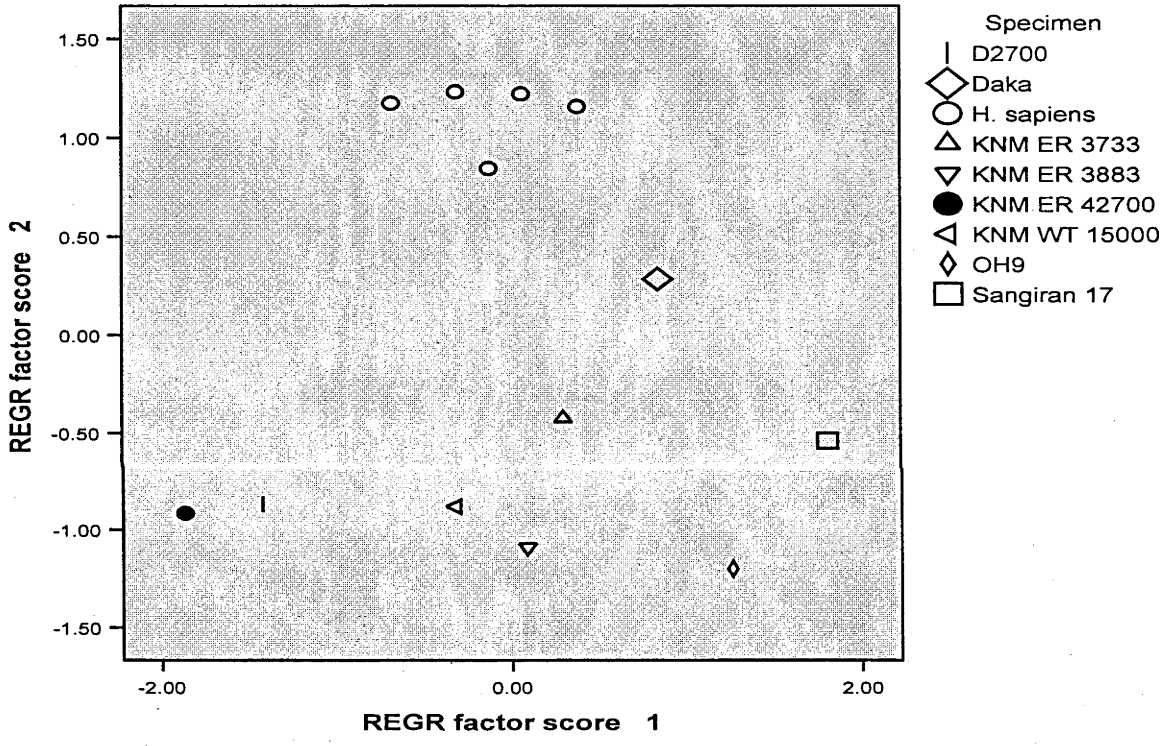


Figure 3-46 PCA Analysis: KNM-ER 42700

Factor 1 accounts for 64% of the variance but is unevenly weighted (e.g. BBH = .290, GOL = .946) and therefore reflects some degree of cranial shape difference. KNM-ER 42700 is relatively close to the sub-adult Dmanisi cranium D2700. It is separate from the other Turkana crania and Sangiran 17, having a relatively low cranium in relation to its cranial length. Function 2 (23% of the variance) shows that the calvaria is relatively broad on the biauricular plane with a low cranium. In this it is similar to KNM-WT 15000, KNM-ER 3883 and D2700, but differs somewhat from KNM-ER 3733 and Sangiran 17.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.731	74.618	74.618	3.731	74.618	74.618
2	.842	16.845	91.464	.842	16.845	91.464
3	.260	5.200	96.663	.260	5.200	96.663
4	.115	2.295	98.958			
5	.052	1.042	100.000			

Extraction Method: Principal Component Analysis.

Component Matrix(a)

	Component		
	1	2	3
logGOL	.956	-.175	.084
logXCB	.893	.050	-.447
logBBH	.673	.716	.097
logMIN_FRONTAL_BREADTH	.957	.078	.191
logAUB	.807	-.539	.088

Extraction Method: Principal Component Analysis.
a 3 components extracted.

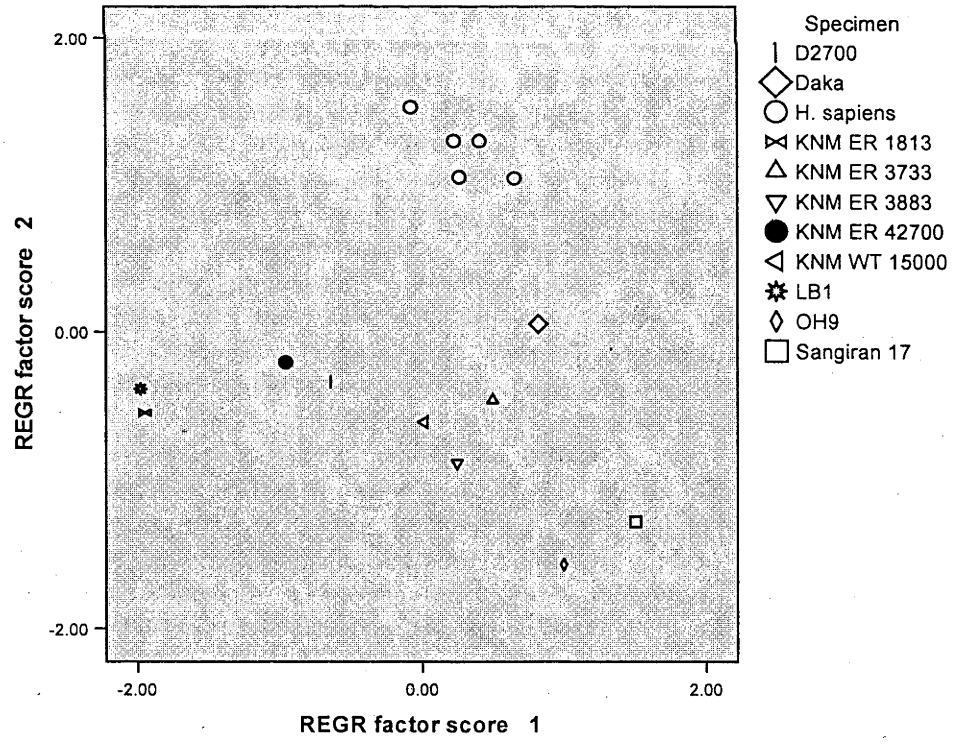


Figure 3-47 PCA Analysis: KNM-ER 42700 and *H. habilis*

In Figure 3.47 KNM-ER 42700 is close to D2700 on both Functions; they are similar in the relationship between cranial height, minimum frontal breadth and lower cranial (biauricular) width, and cranial length.

KNM-ER 42700 is separate from *H. erectus/H. ergaster* crania on Function 1 (74.6% of the variance). The variables on this Function are unevenly weighted (e.g. GOL = .965; BBH = .673) and some information about shape differences is present. KNM-ER 42700 has a shorter cranium in relation to vault height compared to KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, Daka, Sangiran 17 and OH 9.

KNM-ER 1813 and *H. floresiensis* cluster. They are similar to KNM-ER 42700 on Function 2, with a comparable height:biauricular breadth and height:length relationship.

KNM-ER 42700 is closest to D2700 in both size and shape in these analyses. Spoor et al. (2007) also note the overall similarity between KNM-ER 42700 and D2700, and that KNM-ER 42700 is slightly smaller.

3.14 SYNTHESIS

I now synthesise the results of the cladistic analyses to present the most parsimonious trees for the early Pleistocene hominins.

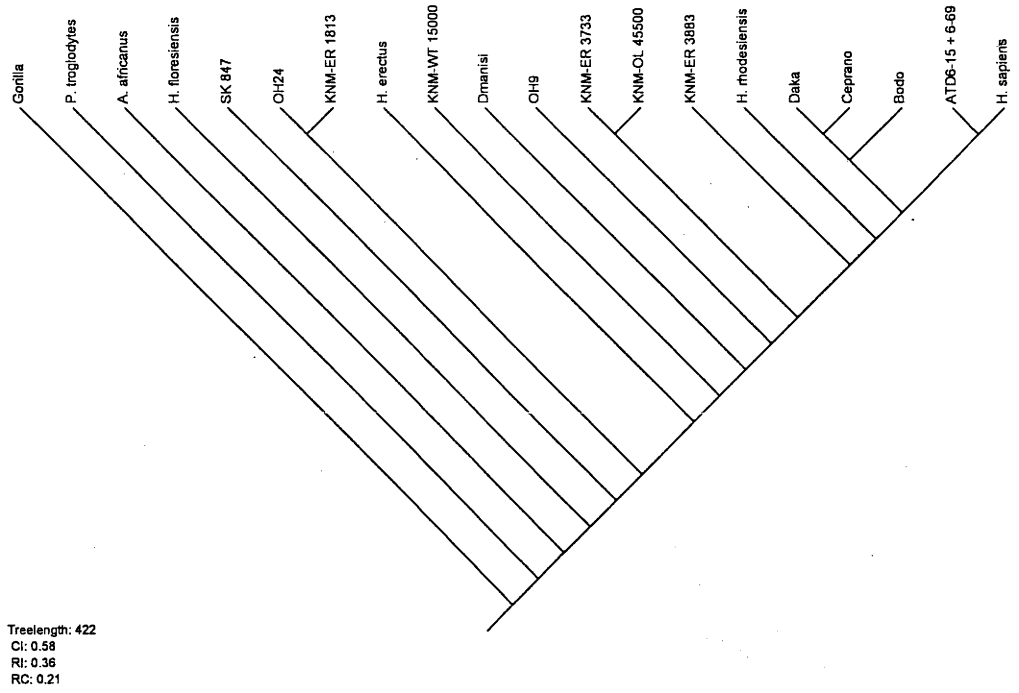


Figure 3-48 Synthesis: shortest tree

The shortest tree shows Gran Dolina sharing a common ancestor with *H. sapiens*. The improbability of this relationship is discussed above; I therefore present the next shortest trees:

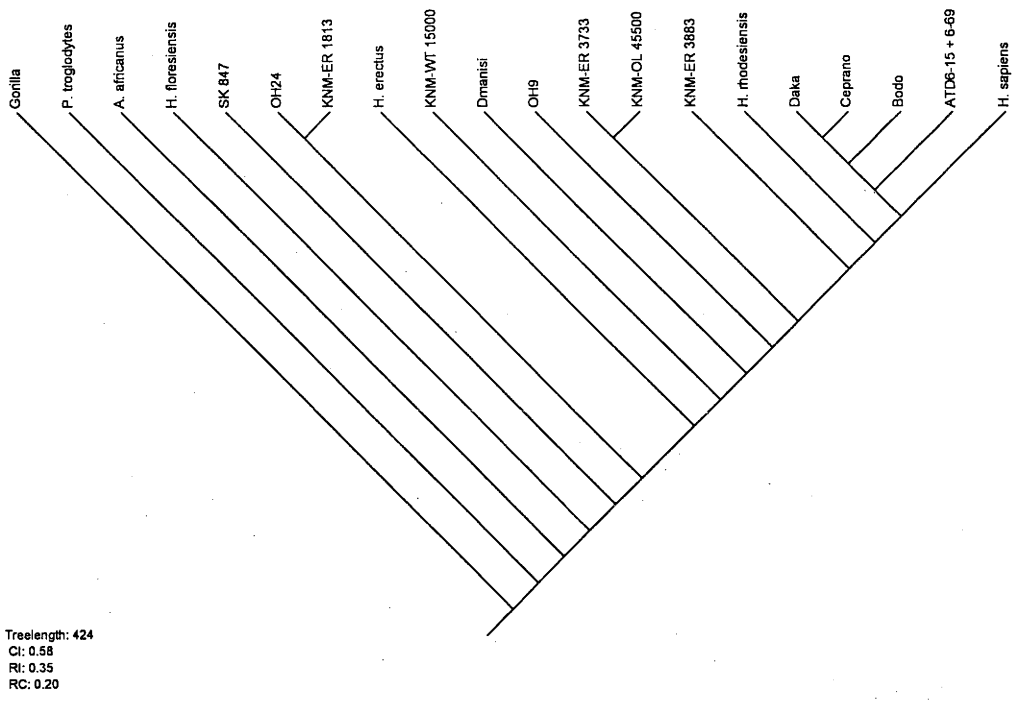


Figure 3-49 Synthesis. Shortest trees: Tree A (above)

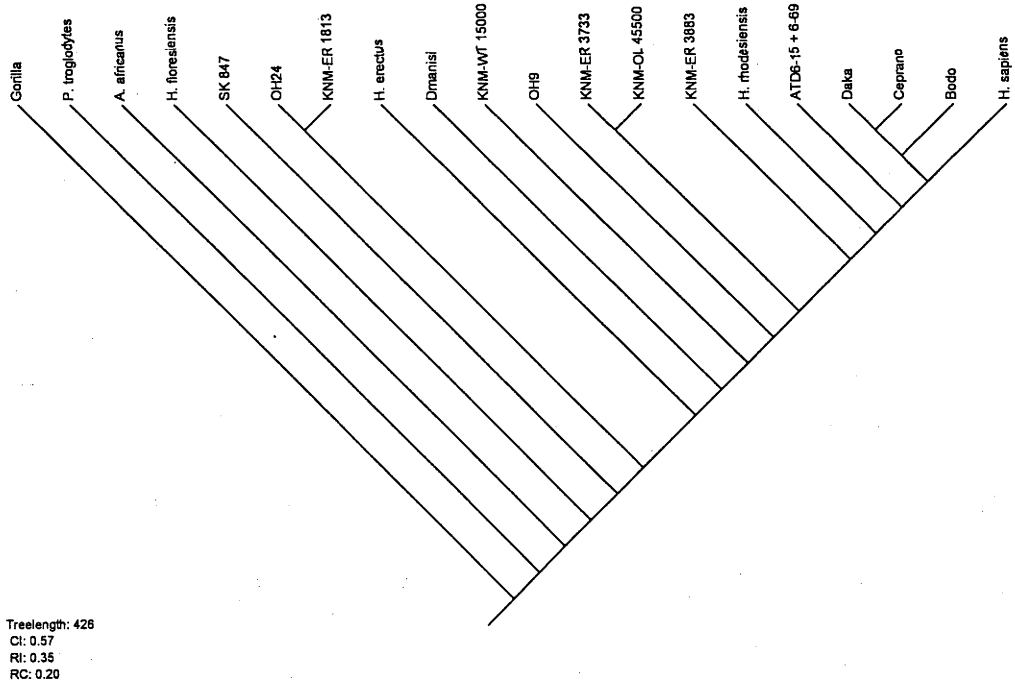


Figure 3-50 Synthesis. Shortest trees. Tree B.

The difference between the trees is the position of Gran Dolina; it is on a branch with Daka, Ceprano and Bodo in the first tree; and it forms a separate lineage in the second tree. The T-PTP for Gran Dolina, Daka, Ceprano and Bodo is p = 0 .41. It is likely that Gran Dolina would form a clade with these OTUs only by chance. The second of the trees (Tree B), therefore, is my preferred phylogeny.

B. MANDIBULAR ANALYSES

Nine Early Pleistocene hominin mandibles from the region and period under consideration are available for cladistic analysis. These are KNM-ER 992, KNM-WT 15000, the Dmanisi mandibles (D211, D2600, D2735), and the Tighenif mandibles (1, 2 and 3). Two mandibles of *H. floresiensis* (LB1 1/2, LB1 6/1) are included to further elucidate the affinities of this species. Sangiran 9 (*Pithecanthropus* C), two *H. pekinensis* mandibles (P696, P695) and two *H. sapiens* mandibles are included for comparative purposes. Refer Table 1, Cranial and mandibular specimens, Chapter 2.

Background and Observations

3.14.1 Dmanisi mandibles

In late 1991 a well preserved human mandible, D211, was excavated from the site of Dmanisi, Georgia, (Gabunia, 1995) from levels now dated to 1.76 to 1.77 Mya (van Arsdale 2006:32). This mandible is the earliest evidence for *Homo* outside Africa. It comprises a thick corpus with a damaged base and rami but the dentition is intact; it is distinctive in the marked distal reduction in tooth area and size, small teeth, its small but robust corpus, narrow alveolar arcade and anteriorly placed origin of the ramus (Gabunia and Vekua 1995). Gabunia and Vekua (op. cit.) concluded that it is early *Homo* based upon its overall size, robustness, dental proportions and symphysis and that it is most similar to what they call African *H. erectus* (KNM-ER 730, KNM-ER 992, KNM-WT 15000, OH 22). They also noted that, to a lesser extent, it has similarities to what they call Asian *H. erectus* (Zhoukoudian G1-6), and to the Tighenif, Mauer, Arago and Sangiran specimens (op cit p. 510).

Bräuer and Schultz (1996) compared the Dmanisi mandible to the those of 11 *H. habilis*, 10 early (1.8-0.9 Mya) specimens referred to *H. erectus* and *H. ergaster* (from Swartkrans, 'East Rudolf' (= East Turkana) and Olduvai) and 15 later (0.9 – 0.25 Mya) remains referred to *H. erectus* from Africa and China (Zhoukoudian, Lantian 1, Sangiran 6 and 1b, BK 67, OH23, OH22 and Tighenif 1, 2, 3). They concluded that, as the Dmanisi mandible possesses a combination of derived characters as well as affinities to the later erectines, it represents a 'progressive' (op. cit. 487) form of *H. erectus* or even archaic *H. sapiens* (now generally referred to *H. heidelbergensis*).

Perceiving a contradiction between the ancient age and derived morphology of the mandible, Rosas et al. (1998) compared the Dmanisi mandible with a large range of Australopithecines and *Homo* (*H. habilis*, *H. rudolfensis*, and *H. ergaster*). They also noted that the mandible has a unique combination of traits; the architecture of the mandible being primitive while the distally decreasing molar series seems to be derived. The structure of the mandible is close to that of *H. ergaster* or *H. habilis* and it is especially similar to KNM-WT 15000. The immaturity of KNM-WT 15000, they suggested, does not affect these features as they develop early in the postnatal growth period. Rosas et al. (op cit.) observed similarities between Dmanisi and the larger mandibles from Java and dissimilarities between D211 and the more gracile Sangiran 1 and 22. They suggested that the similarities are primitive characters and therefore proposed that there was a very early differentiation of the Asian branch of *Homo*; they classify D211 as *Homo sp. indet. (aff. ergaster)*.

In 2000, a second more complete and robust adult mandible, D2600, was excavated at the Dmanisi site (Gabounia et al., 2002). This mandible is much larger than D211 and Gabounia et al. (op. cit.) raised the possibility of the co-existence of two groups or two hominin species in this region. They listed a number of characters in which the new mandible differs from D211, including: a long and high corpus, a long post-symphysis extension, an inferior transverse torus and weak superior transverse torus, and large canines. They concluded, however, that these differences relate to sexual dimorphism within a single species which they name *H. georgicus, sp. nov* (op. cit. 244), although co-

author Abesolom Vekua is later represented in Rightmire (2006: 130) as placing only D2600 in this species.

A cranium, D2700[12], and an associated mandible, D2735, were discovered in 2002 in the same horizon as the previous hominin crania and mandibles (Vekua et al., 2002); that is, the material is contemporaneous. As the maxillary M^3s are only partially erupted, Vekua et al. (op. cit.) identified the individual as a young person whose age lies between those of KNM-WT 15000 and D2282. The mandible resembles D211 in dimensions; and in size and appearance it is very similar to KNM-WT 15000, and Vekua et al. (op. cit.) assigned all specimens to *H. erectus* (= *H. ergaster*), suggesting that they are likely to be the ones most similar to a presumed *H. habilis* stem and that the ancestors of the Dmanisi population dispersed from Africa before the emergence of the *H. erectus* grade.

The sediments containing the hominins at Dmanisi were deposited and sealed by groundwater calcretes in less than 10,000 years (Lordkipanidze et al. 2006). All fossils were found in lateral and stratigraphic proximity. They, and associated faunal bones, exhibit little evidence of erosion and some faunal bones are articulated; there is no evidence for geological transport or post burial damage (op. cit.). That is, they were buried rapidly after death, within a short interval and with minimum transport.

The considerable difference in size between D2600 and the other Dmanisi mandibles has generated investigation into whether D2600 may be accommodated within the same species as the other Dmanisi mandibles and crania. Gabunia et al. (2002) (above) attributed the differences to sexual dimorphism within *H. georgicus*. Vekua et al. (2002) argued for a single population at Dmanisi assigned to *H. erectus* (= *H. ergaster*) and suggested that the group is also closely related to *H. habilis* (*senso stricto*) as known from Olduvai Gorge in Tanzania, Koobi Fora in Kenya and possibly Hadar in Ethiopia (op. cit.) (although see above for Vekua's more recent view). Skinner et al. (2006) assessed size and shape differences in the Dmanisi mandibles and found that the variation is significantly greater than that of modern humans and any extant ape species and that they are more dimorphic in size compared to other fossil *Homo* species. They concluded that

[12] The third to be discovered, see above Chapter 2.

expectations of sexual dimorphism in the genus *Homo* need be re-examined to account for the marked size and shape differences between D2600 and D211; that is, they were suggesting that sexual dimorphism in early hominins, as represented by the Dmanisi mandibles, might be larger than previously understood. Van Arsdale (2006), in his doctoral study of all Dmanisi mandibles, also proposed that the variation observed within the Dmanisi population results from a greater degree of sexual dimorphism than is evident in modern humans and chimpanzees, and that this may be of significance for the interpretation of early *Homo* (op. cit. 202).

Rightmire et al. (2006) have undertaken a full comparative study of the Dmanisi crania and mandibles. While noting the similarity of the Dmanisi skulls to *H. habilis* in some respects, they viewed the population as a single paleodeme best classified as *Homo erectus*, in particular, as a subspecies of *H. erectus* that is close to the stem from which *H. erectus* evolved.

In 2006, a fifth cranium (D3444) with associated mandible (D3900) was excavated from the same stratum as the other crania and mandibles (Lordkipanidze et al., 2005). The dentition of the maxilla and most of the mandible had been lost before death and sockets resorbed (except for the canine) (op. cit. 718; Lordkipanidze et al., 2006). Lordkipanidze et al. (op. cit.) referred all specimens to a single Dmanisi paleodeme, with the possible exception of D2600, following Rightmire (2006); the group is close to the stem for *H. erectus*, the later *H. erectus* being more derived. D3900 was not included in this study as its morphology is compromised as a consequence of the remodelling process; it has been reduced in size, the symphysis is altered and the wall of the body is eroded (Lordkipanidze et al. 2006).

3.14.2 KNM-ER 992

This adult mandible is dated to 1.55 – 1.49 Mya (Feibel et al., 1989) and is thus contemporaneous with KNM-ER 3883, KNM-WT 15000, OH9 and, possibly, SK 847 if the latter is at the younger limit of its possible range of 1.8 – 1.5 Mya.

Groves and Mazák (1975) made the specimen the type of a new species, *H. ergaster*. The attribution is based mainly upon a comparative study of the dentition of Plio-Pleistocene hominins using statistical parameters (op. cit. 110). The hypodigm includes a number of mandibular and maxillary fragments and dentitions as well as a parietal fragment (KNM-ER 734) and perhaps the skull KNM-ER 1805 (op. cit. 120), to which Groves (1989:272) later added the cranium KNM-ER 1813.

Wood (1992) at first rejected KNM-ER 992 as belonging to a separate species; his view was that KNM-ER 992 resembles *H. erectus*, although is not conspecific with it; but later he recognized *H. ergaster* (Wood et al., 2000).

3.14.3 Tighenif (formerly Ternifine)

Three mandibles were excavated from a sand extraction site near Palikao, Algeria (Arambourg, 1955a; 1956). Geraads et al. (1986) placed the Ternifine deposits, in which the mandibles were found, in a normal period, either the Brunhes epoch (from 780,000 y.a.) or the Jaramillo event (1.0 – 1.1 Mya) based upon geometric polarity.

Arambourg (1954) provisionally named the Tighenif fossils *Atlanthropus mauritanicus* but he did not list characters purporting to differentiate the new species, and in addition the name was used conditionally; either circumstance would be sufficient to render the name unavailable under Article 13 of the International Code of Zoological Nomenclature (Clarke 1994:190). He concluded that the three mandibles are very closely related to Pithecanthropus (*H. erectus*) and Sinanthropus (*H. erectus* or *H. pekinensis*), that the robust and massive character is reminiscent of *Telanthropus* (now regarded as early *Homo* (Grine et al. 1996)) but that they tend towards a more progressive state.

3.14.4 H. floresiensis

There are two *H. floresiensis* mandibles. LB1/2 is part of the LB1 skeleton that is bracketed by luminescence ages of 34 ± 4 Kya and 14 ± 2 Kya (Morwood et al. 2004). The mandible is complete but I observed that it is narrower than the bi-mandibular fossa breadth and no longer fits the cranium. There are three vertical repaired breaks to the inferior border of the mandible: one originates at the (missing) right P_4; one from between

the left P_1 and P_2; and one from below the left M_2. This damage does not, however, affect the identification of the mandibular characters used in this analysis.

The lower dental arcade is relatively short, wide, and broadly curved at front. The symphyseal region has no mental protuberance or keeling and retreats. There is a marginal torus. In lateral view the ramus is relatively wide with marked muscle scarring that is particularly notable towards the base of the ramus (origin of masseter muscle) but there is no anterior notch or any marked swelling. The coronoid process is higher than the mandibular condyle; the sigmoid notch is a 'U' shape, but lowest towards coronoid process. The mental foramina are anterior to P_3. There is a relatively wide sulcus extramolaris and the lateral prominence is under M_2. Internally the post-incisal plane is somewhat inclined and there is a bulbous mylohyloid ridge; there are superior and inferior transverse tori.

LB6/2 is incomplete; the mandibular condyle on the left hand side is broken, and most of the ramus on the right hand side is missing. This mandible has also sustained post-excavation damage, such that the shape of the mandible is now parabolic, bearing no resemblance to its original shape. Repaired vertical breaks are visible: one on the right hand side originating between the premolars; and three on the left hand side: originating between M_1 and M_2, between P_1 and P_2, and between the canine and I_2.

LB6/2 differs from LB1/2 in two characters, although not all states for LB6/2 are known: the post-incisive plane appears to be more vertical; and the single digastric fossa is shallow, whereas on LB1/2 there are two shallow fossae separated by a tubercle.

The attributions of the other mandibles in the following analysis are as described above (Analysis A) for the crania with which they either belong or are associated.

3.15 Mandibular Analyses Results

Nine equally parsimonious trees[13] are found using PAUP*; these are summarised in the Majority Rule consensus tree.

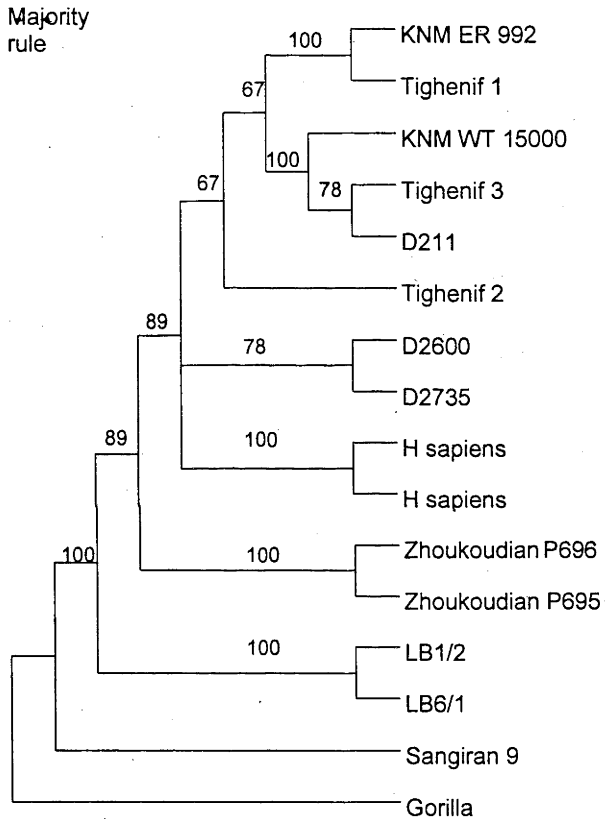
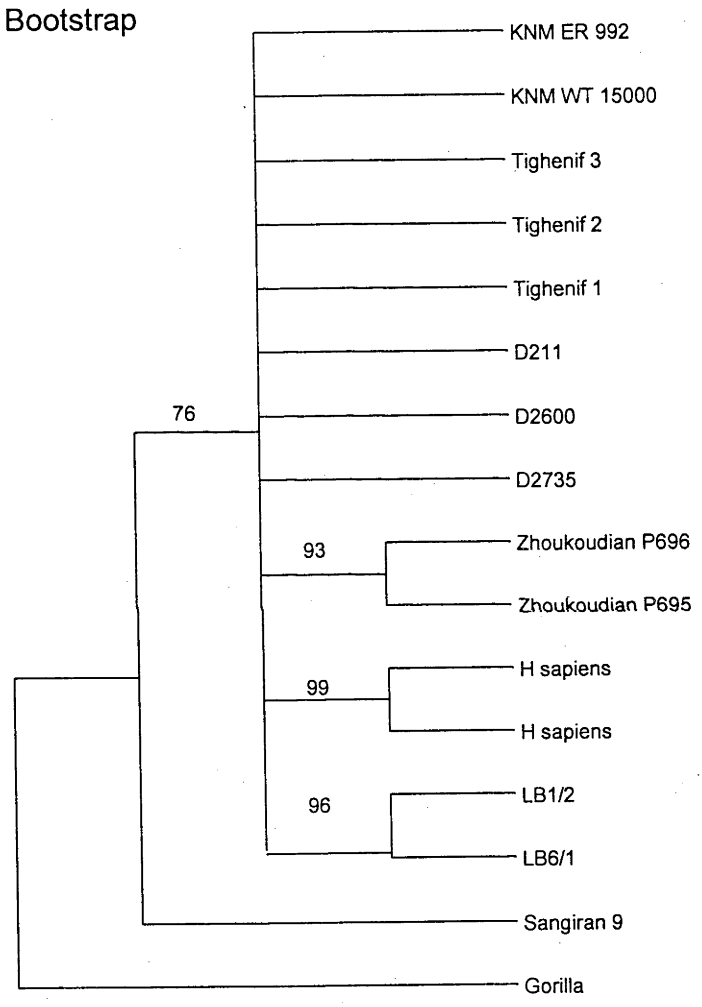


Figure 3-51 Mandibular cladistic analyses: Majority Rule (above); Bootstrap (below)

[13] Length = 77; CI = 0 60; HI = 0.39; RI = 0.65; RC = 0.40.


Bootstrap
KNM ER 992
KNM WT 15000
Tighenif 3
Tighenif 2
Tighenif 1
D211
76
D2600
D2735
93
Zhoukoudian P696
Zhoukoudian P695
H sapiens
99
H sapiens
LB1/2
96
LB6/1
Sangiran 9
Gorilla

KNM ER 992 and Tighenif 1 form a clade in all most parsimonious trees. This clade is within a branch comprising all Tighenif mandibles, KNM-WT 15000 and D211. The clade {KNM- ER 992, Tighenif 1} has a T-TPT of value p = 0.01.

This clade is sister to a clade comprising (KNM-WT 15000, {Tighenif 3, D211}) which also occurs in all of the most parsimonious trees with a T-PTP value of p = 0.01; that is, the null hypothesis that these came together by chance may be rejected although the clade has no Bootstrap support. The clade {Tighenif 3, D211} within this branch, however, has a T-PTP value of p = 0.17. The null hypothesis that these two mandibles came together by chance is *not* rejected and it is probable that this is not the most parsimonious explanation for D211. This will be explored below.

The largest of the three Dmanisi mandibles, D2600, and the sub-adult D2735, form a separate clade to those above in 78% of the most parsimonious trees. {D2600, D2735} has a T-PTP value of p = 0.01 although they share no synapomorphies.

The *H. floresiensis* mandibles form a clade in all the most parsimonious trees. The clade is separate from all other clades, has a Bootstrap value of 96% and shares the following possible synapomorphies:

- Sigmoid notch deepest towards condyle (Character 26; state 3)
- Marked muscle scarring on ramus
- Mylohyloid ridge bulbous superiorly/inferiorly (parallel with KNM-ER 992) (Character 29; State 2)
- Lateral prominence under M^2 (*H. pekinensis* polymorphic) (Character 31; State 2)
- Origin of *sulcus extramolaris* is at central posterior edge of alveolus at M^3 (parallel with KNM-WT 15000, D211) (Character 33; State 2)
- Double mental foramina (parallel with KNM-WT 15000, D211) (Character 34; State 2)

The *H. pekinensis* mandibles[14] also form a separate clade in all the most parsimonious trees. The Bootstrap support is 93% and they share the following synapomorphies:

- Mental foramina are under M^1 (Character 6, State 1)
- Gonial region flares outwards (Character 13, State 2)
- Coronoid process is higher than the mandibular condyle (Character 17, State 2)
- From below, the symphyseal region is uniformly thick front to back (Character 22, State 2)
- Sigmoid notch is deepest centrally (parallel with Tighenif 1) (Character 26, State 2)

And the following possible derived states:

- There is no protuberance in the symphyseal region and it retreats (parallel with LB sample) (Character 3, State 3)
- There is no symphyseal keel (parallel with Sangiran 9, LB sample) (Character 4, State 2).

H. sapiens forms a separate clade in all most parsimonious trees with a Bootstrap support of 99%.

I also used T-PTP tests for the larger clades to assess the phylogenetic support for the tree. The clade (KNM-ER 992, Tighenif 1, KNM-WT 15000, Tighenif 3, D211, Tighenif 2, D2600, D2736, *H. sapiens*) has a T-PTP value of $p = 0.01$; the clade comprising this group and *H. pekinensis* has a T-PTP value of $p = 0.02$; the clade comprising this and *H. floresiensis* has a T-PTP value of $p = 0.03$. That is, these successively larger clades are unlikely to have been generated by randomness in the data; the phylogeny is supported.

To test the various hypotheses proposed for the OTUs the Majority Rule consensus tree is transferred into MacClade. There is shortest tree of length 80 steps:

[14] I initially included Zhoukoudian crania in the cranial analyses but incurred an irretrievable data error. The Zhoukoudian crania are highly apomorphic but retain basic features of *H. erectus*.

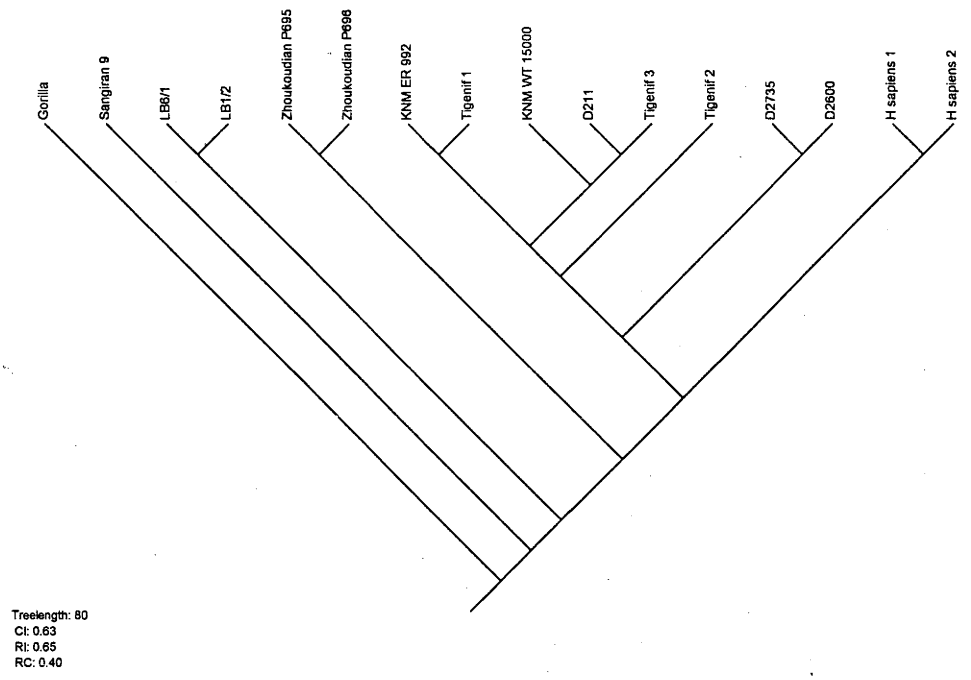


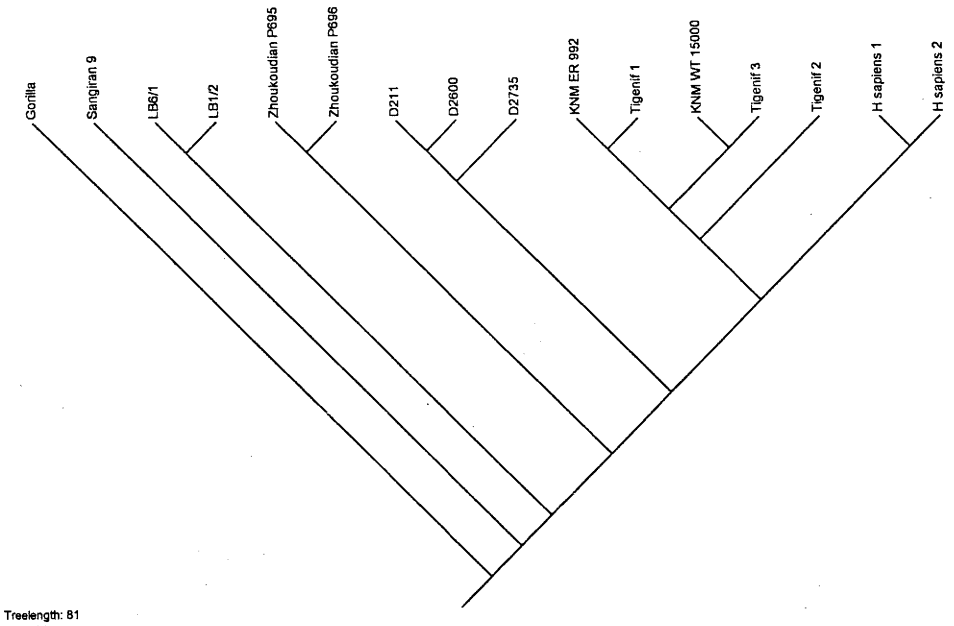
Figure 3-52 PAUP Mandibular Consensus tree transposed to MacClade

Hypothesis tests

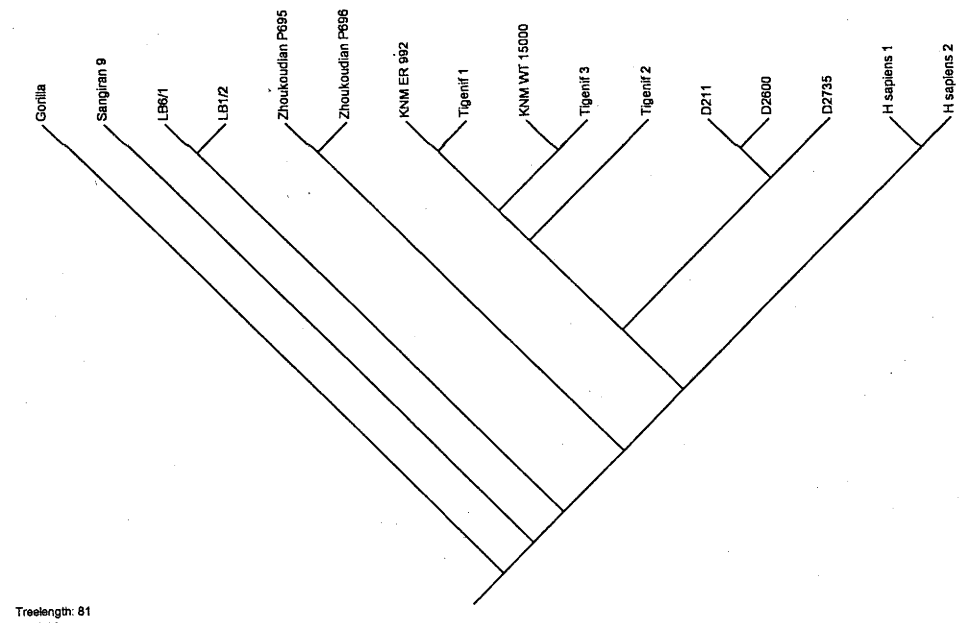
1. Dmanisi

1.1 Test for homogeneity

Gabunia et al. (2002), Vekua et al. (2002), Skinner et al. (2006), Van Arsdale (2006), Rightmire et al. (2006) and Lordkipanidze et al. (2006) attribute the Dmanisi mandibles to a single paleodeme, although they differ somewhat in attribution of affinities of the Dmanisi fossil remains. The T-PTP for D211 and Tighenif 3, a clade in the Majority Rule consensus tree, shows that it is likely they came together by chance (T-PTP p = 0 .17; see above), suggesting that D211 is not a sister taxon to Tighenif 3. I therefore manoeuvred D211 to from a clade with the other Dmanisi mandibles to test for their homogeneity. In this case, there are 3 trees one step longer than the shortest:



Treelength: 81
CI: 0.62
RI: 0.64
RC: 0.39



Treelength: 81
CI: 0.62
RI: 0.64
RC: 0.39

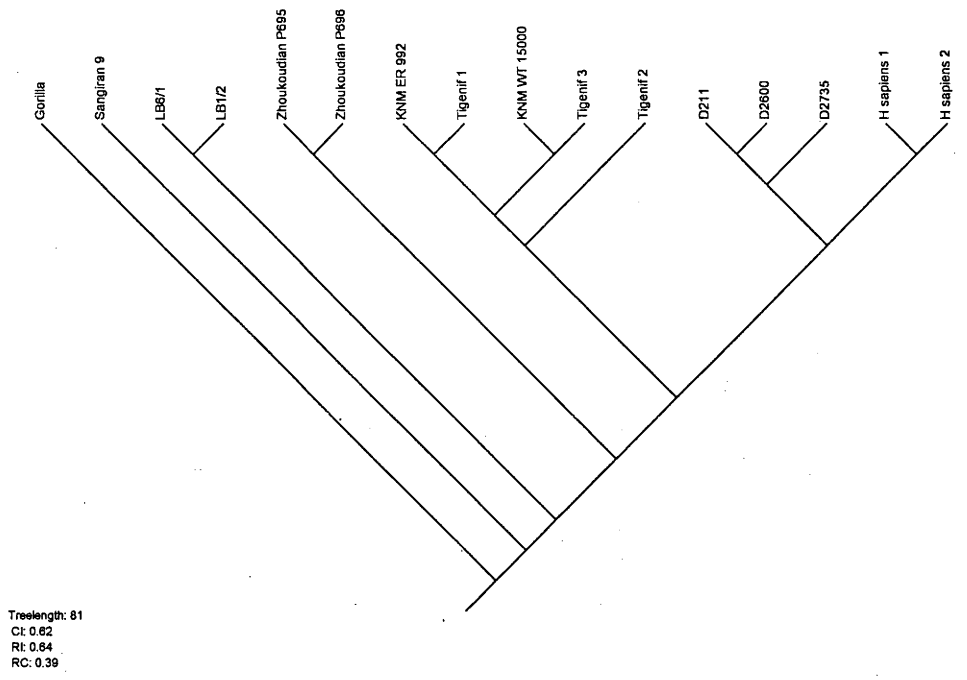


Figure 3-53 Three trees with Dmanisi constrained

The differences between the trees are the relative positions of the Dmanisi clade, and the position of Tighenif 2.

The T-PTP for {D2600, D2735, D211} is p = 0.065. Although this is not a strong result, it is better than {D211, Tighenif 3}. The three Dmanisi mandibles share two synapomorphies: the digastric fossa is shallow (parallel with LB6/1; *H. sapiens* polymorphic); and the symphyseal region is uniformly thick inferiorly (parallel with *H. pekinensis*).

On one of the shortest trees, the Dmanisi clade is on the branch containing KNM-ER 992, KNM-WT 15000, and the Tighenif mandibles. The T-PTP for this branch is p = 0 .01; the null hypothesis that the group would form by chance alone is rejected.

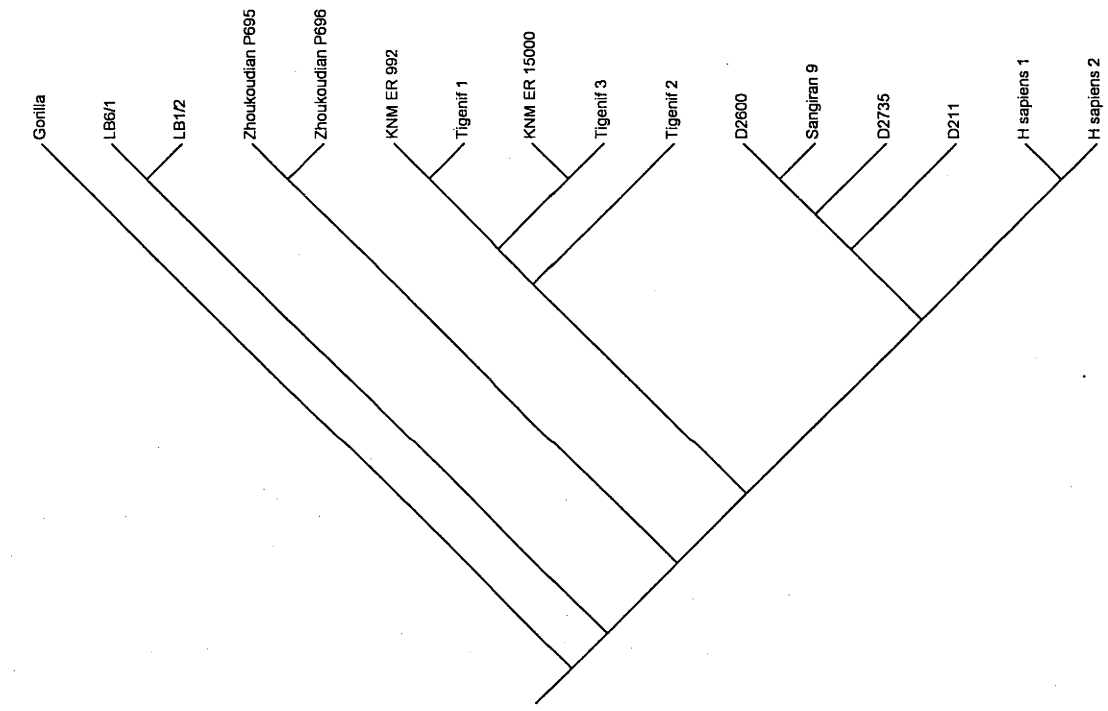
There are, then, three possibilities for the phylogenetic position of the Dmanisi clade on the tree:

- Sister to {KNM-ER 992, KNM-WT 15000, Tighenif 1, 2, and 3}

- A separate clade that branches after the KNM-ER 992 branch
- A separate clade that branches before the KNM-ER 992 branch

1.2 Dmanisi and H. erectus

The Dmanisi group has been compared to *H. erectus* (Gabunia and Vekua, 1995). This hypothesis is tested by constraining the three Dmanisi mandibles to form a clade with Sangiran 9.



Treelength: 85
CI: 0.59
RI: 0.60
RC: 0.35

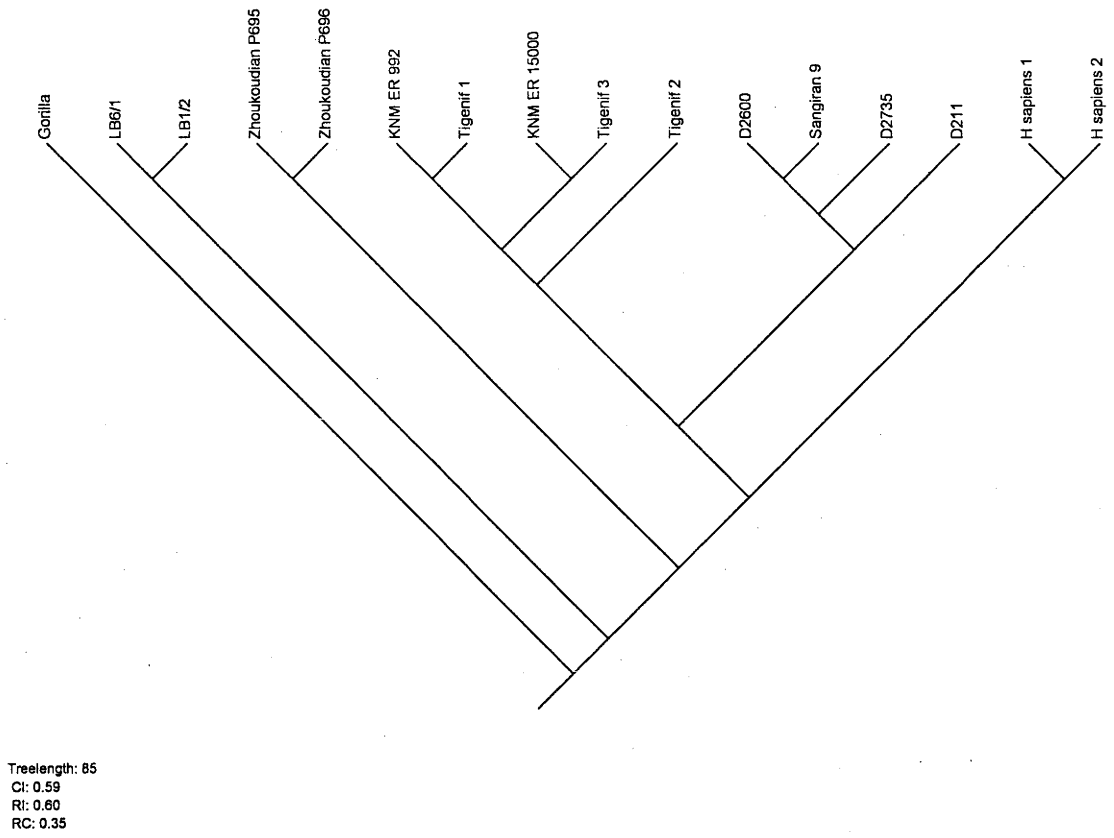


Figure 3-54 *H. erectus* and the Dmanisi group

There are two trees of equal length, 85 steps; the difference between them is the position of the subject clade on the tree. The trees are three steps longer than the shortest trees (L = 81; in which the Dmanisi mandibles are constrained). The T-PTP for the Dmanisi mandibles and Sangiran 9 is p = 0.14; the clade is not supported.

Although a phylogenetic relationship has not been presented for Dmanisi and *H. pekinensis*, Gabunia et al. (1995) noted some similarities of D211 and *H. pekinensis* mandibles. I therefore explore for any possible phylogenetic relationship for these OTUs. There is one tree that is L = 82, one step longer than the shortest tree (L = 81):

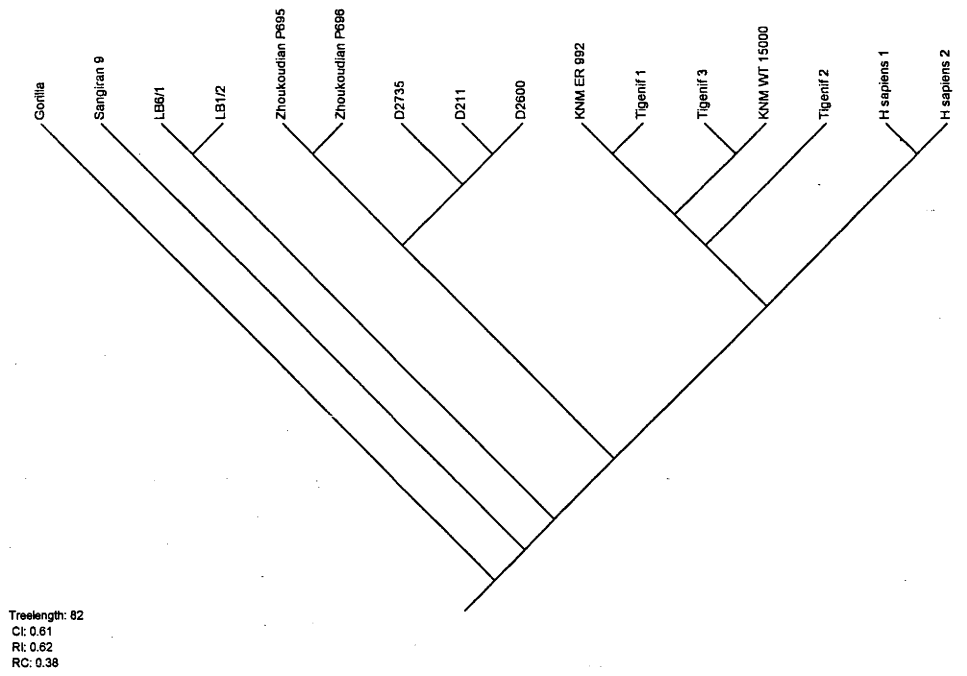


Figure 3-55 Dmanisi and *H. pekinensis*

The subject clade however, has a T-PTP p = 0.19 and the null hypothesis, that the clade would come together by chance, is not rejected.

In summary, then, although there is a marked size difference between the Dmanisi mandibles, the most parsimonious phylogeny is that they form a clade. In subsequent analyses, then, they will be constrained to form an OTU.

2. KNM-WT 15000, KNM-ER 992, and the Tighenif mandibles

As discussed above, D211 is most likely to form a sister OTU with the other Dmanisi mandibles rather than with Tighenif 3. With D211 manoeuvred to form a clade with the other Dmanisi mandibles, the branch now comprises KNM-ER 992, KNM-WT 15000, Tighenif 1, 2, and 3. This has a T-PTP value of p = 0.01 and the clade shares four possible synapomorphies:

- the mandibular corpus is of uniform height;
- the gonial region has no flaring (condition for Dmanisi is not known);
- the symphyseal region in basal view is thickest at the midline

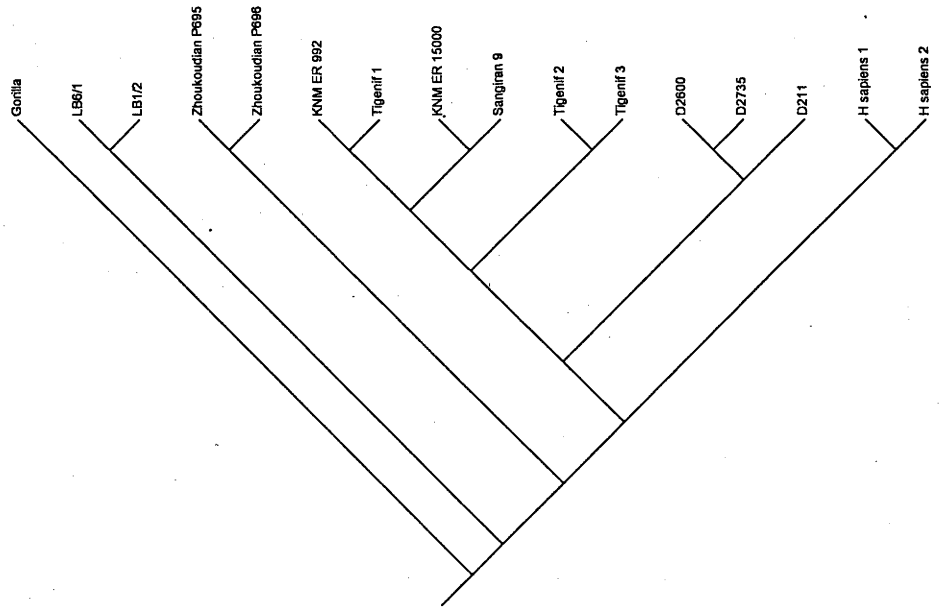
- the submandibular fossa is wide (the condition for Dmanisi, Zhoukoudian P695 and Sangiran 9 is not known; parallel with Zhoukoudian P696).

Further, as discussed above, one of the three possible solutions for the Dmanisi mandibles is that they are sister to this clade. In this case, the branch shares 4 possible synapomorphies:

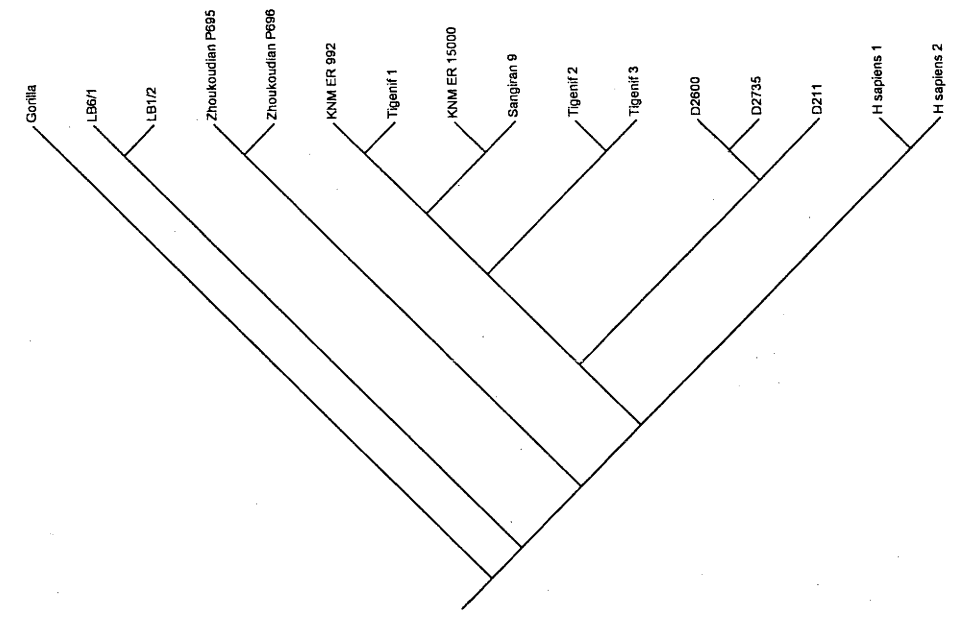
- the lower dental arcade is tightly curved (parallel with Sangiran 9; *H. pekinensis* polymorphic);
- there is no mental protuberance and the symphysis retreats
- they have symphyseal keels (condition for KNM-ER 992 unknown; parallel with *H. sapiens*; the keel on KNM-WT 15000 is short and low).
- no subalveolar depression (parallel with *H. floresiensis*, *H. pekinensis*)

2.1 KNM-WT 15000 and *H. erectus*

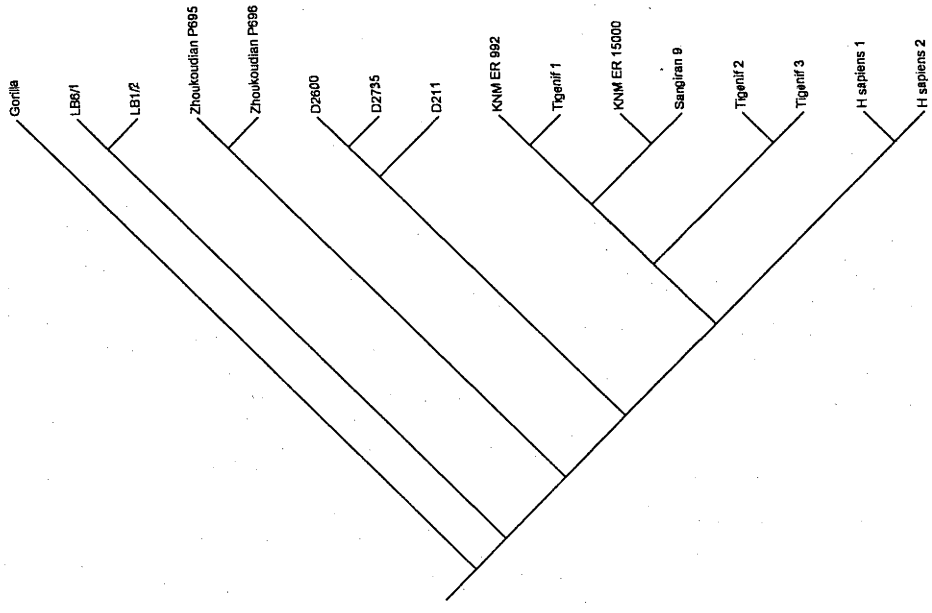
KNM-WT 15000 is attributed to *H. erectus* by Walker and Leakey (1993) and Rightmire (1990). This is now tested by constraining KNM-WT 15000 with Sangiran 9 to form a clade. In this case, there are three shortest trees of length 86 steps:



Treelength: 86
CI: 0.58
RI: 0.58
RC: 0.34



Treelength: 86
CI: 0.58
RI: 0.58
RC: 0.34



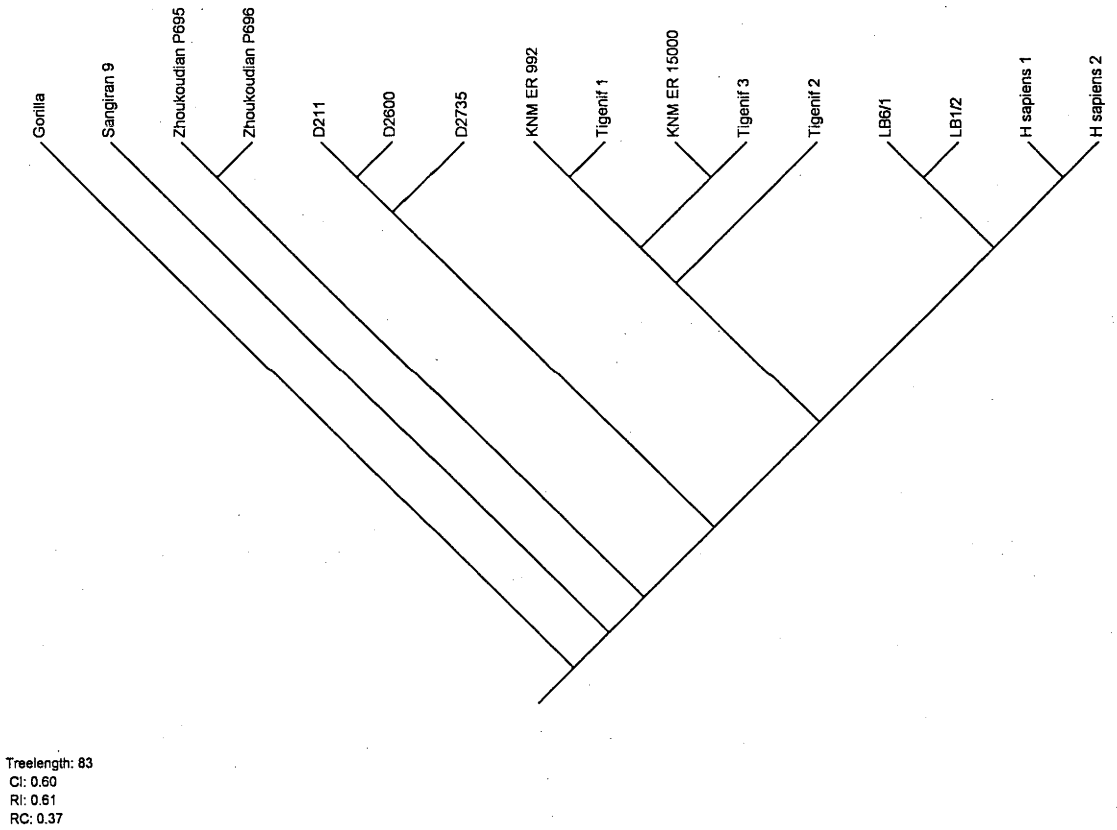
Treelength: 86
CI: 0.58
RI: 0.58
RC: 0.34

Figure 3-56 KNM-WT 15000 and *H. erectus*

The trees are 5 steps longer (L = 86) than the most parsimonious trees (L = 81); this is considerably longer than the shortest tree. The T-PTP for {KNM-WT 15000, Sangiran 9} is p = 0 .92 and they share no synapomorphies; the phylogeny is not supported.

3. *H. floresiensis* and *H. sapiens*

H. floresiensis has been attributed to *H. sapiens* by Henneberg and Thorne (2004); Jacob et al. (2006); Martin et al. (2006); Richards (2006); Hershkovitz et al. (2007); and Obendorf et al. (2008). This hypothesis is tested below:



Treelength: 83
CI: 0.60
RI: 0.61
RC: 0.37

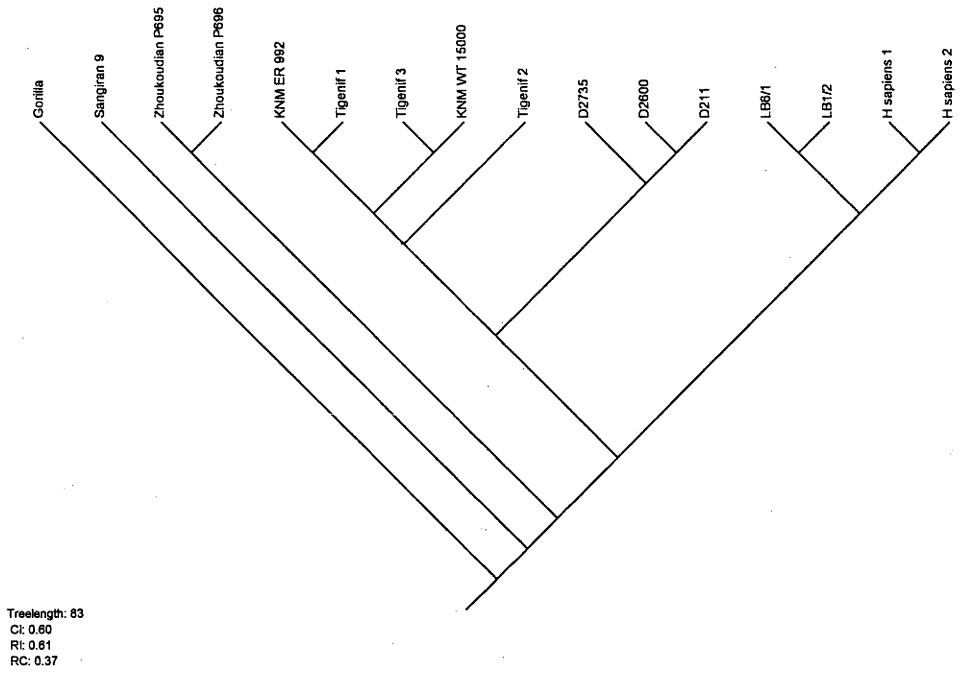
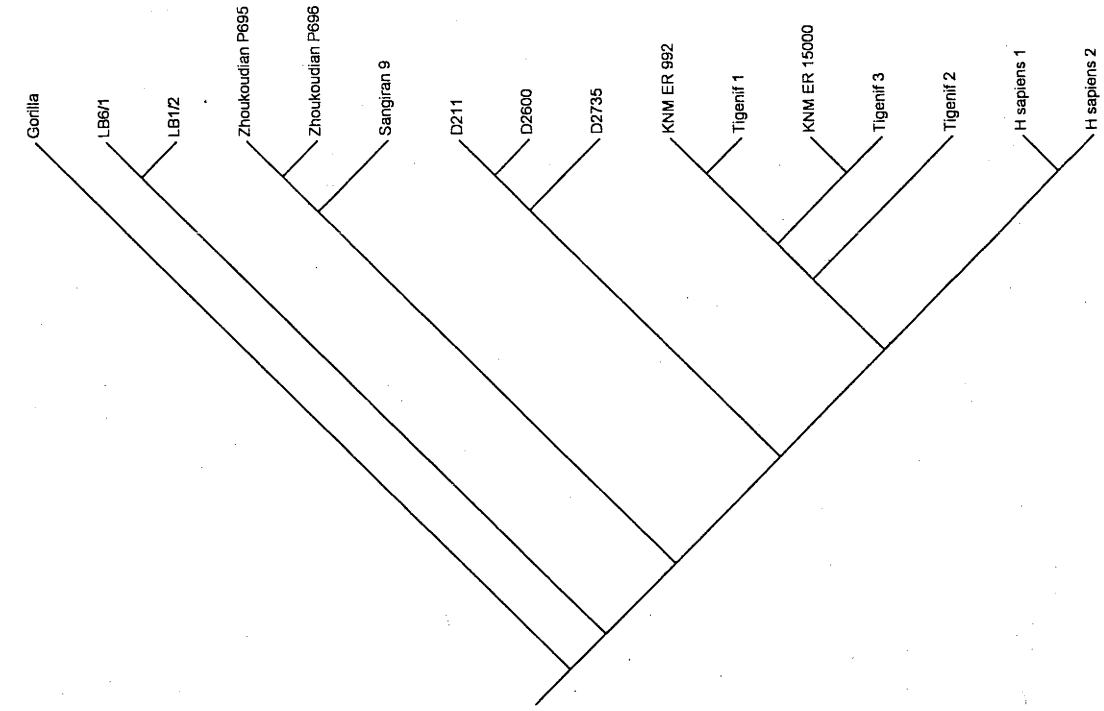


Figure 3-57 *H. floresiensis* and *H. sapiens*

The shortest trees with *H. floresiensis* (LB6/1, LB1/2) constrained to form a clade with *H. sapiens* are 2 steps longer (L = 83) than the shortest tree L = 81). The difference between the trees is the relative position of the Dmanisi group. The T-PTP for {*H. floresiensis*, *H. sapiens*}, however, is p = 0.15; the null hypothesis that *H. floresiensis* and *H. sapiens* would form a clade by chance alone is not rejected. The clade {(LB6/1, LB1/2), *H. sapiens*} shares two possible synapomorphies: the lower dental arcade is tightly curved at front; submandibular fossa is narrow, although the state for LB6/1 unknown.

4. *H. erectus* and *H. pekinensis*



Treelength: 84
CI: 0.60
RI: 0.60
RC: 0.36

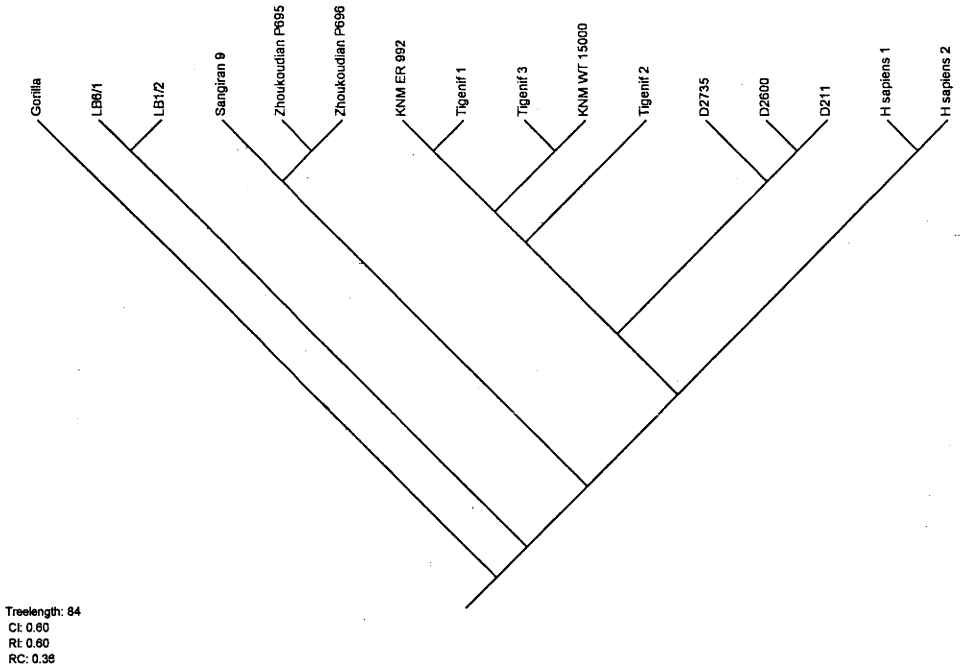


Figure 3-58 *H. erectus* and *H. pekinensis*

The shortest trees when Sangiran 9 is manipulated to form a clade with *H. pekinensis* is L = 84, 3 steps longer than the shortest tree (L = 81). Again, the difference between the trees is the position of the Dmanisi branch. The T-PTP for {Zhoukoudian P695, Zhoukoudian P696, Sangiran 9} is p = 0.43; the clade is not unlikely to form by chance alone.

In summary, the most parsimonious phylogeny for the mandibles is a tree, or trees, comprising the following clades or lineages:

- Dmanisi: D211, D2600, D2735;
- KNM-ER 992, KNM-WT 15000, Tighenif 1, Tighenif 2, Tighenif 3, with or without the Dmanisi mandibles;
- *H. floresiensis*: LB6/1, LB1/2;
- Zhoukoudian P696, 695;
- Sangiran 9;
- *H. sapiens.*

The most parsimonious trees are, therefore:

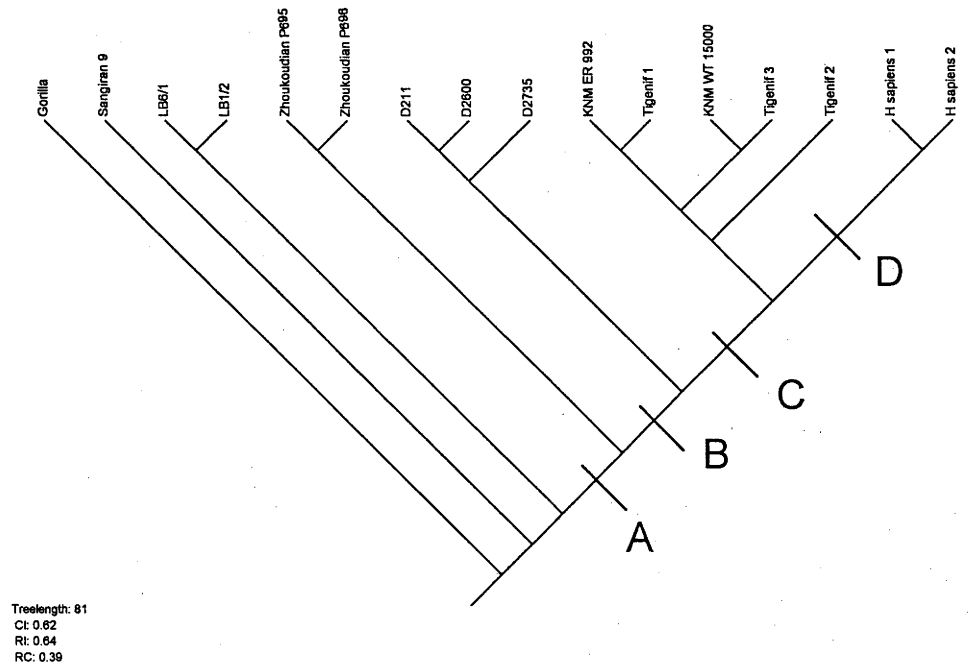


Figure 3-59 Mandibles: Most parsimonious solutions
(Nodes indicated 3rd tree)

In view of the most parsimonious solution for the crania (above Figure 3.50), in which *H. georgicus* branches before *H. ergaster*, the preferred tree for the mandibles is the last of the three trees in Figure 5.39, but also see discussion in Chapter 4.

Table 10a: Mandibular character changes at nodes

Node	Character	Change at node	Synapomorphies for the node	Notes
A	1 3 10 28 29	1→2 3→2 2→1 2→1 2→1	Lower arcade short/wide Symphyseal vertical No anterior notch No muscle scarring on ramus Narrow mylohyoid ridge	Parallel with (pw) D2600 D2600 = 3 Pw KNM-ER 992
B	4 26	2→1 2→1	Symphyseal keel Sygmoid deepest centrally	
C	8 22	1→3 2→3	Mandib. corpus uniform ht Symphys. thickest midline	
D	2 3 5 13 20 22 35 36	2→1 2→1 2→1 4→1 2→1 3→1 2→1 2→1	Lower arcade broad-curved Chin Subalveolar depression Gonial flares out Post-incis. plane vertical Symph. thickest at molars No ant. marginal tubercles	

The implications of these phylogenies and those for the cranial analyses will be discussed in the next Chapter; nodal changes are discussed in Chapter 5.

Addendum: Too late to be included in this chapter, a paper has been published suggesting that Ceprano dates to the Middle Pleistocene, rather than the terminal Early Pleistocene (Muttoni et al., 2009).

4 DISCUSSION

Identifying relationships between taxonomic units is of critical concern to the study of *Homo*. Cranial and mandibular cladistic and metric analyses were undertaken so that predictions could be made about the phylogenetic relationships between OTUs. Possible clades identified in the cladistic analyses were tested using the T-PTP test, which tests the support for clades, or sister taxa, shown in the cladogram (Faith and Cranston, 1991; Faith, 1991; also see Chapter 2). The initial analyses tested the homogeneity of the known or hypothesised species: *H. erectus*, *H. ergaster*, and *H. georgicus*. In cases where any generally accepted members of any of these species could not be securely attributed to their proposed species, they were retained as separate OTUs so that their affinities could be further tested.

This chapter begins with a discussion of the OTUs and follows with a discussion about individual phylogenetic attributions. Chapter 5 will present a framework for the evolution of *Homo* during the early Pleistocene based upon the outcomes of this discussion.

4.1 KNM-ER 1813 and OH 24

Two *H. habilis* skulls are included in this analysis: KNM-ER 1813 and OH 24. *H. habilis* is known from Olduvai, Tanzania; Koobi Fora, Kenya; Hadar, Ethiopia; and Uraha, Malawi. It is best known from 1.9-1.8 Mya at Koobi Fora and Olduvai, East Africa (Feibel et al., 1989; Feibel et al., 2009). In this analysis OH 24 and KNM-ER 1813 formed sister taxa in all most parsimonious trees and share three possible synapomorphies: no preglenoid plane precedes the glenoid cavity (parallel with KNM-ER 3733, KNM-ER 3883; KNM-WT 15000); the *facies anterior* and alveolar process form a flat surface (parallel with *A. africanus*); and a sharp high line divides the floor of the orbit from the facial part of the malar (parallel with Dmanisi). *H. habilis* branches after SK 847 (Chapter 3; Figure 3.50; Tree B); it does not share a common ancestor with any OTU in the analysis.

4.2 Turkana crania and mandibles

The Turkana crania KNM-WT 15000, KNM-ER 3733 and KNM-ER 3883 are usually referred to *H. ergaster* (e.g. Wood, 1991), but are also referred to *H. erectus* (e.g.

Rightmire 1990). Their phylogenetic relationships are explored to determine whether they might be attributable to either of these or another, unnamed, species. To resolve this, the following process is followed.

1. Establish if KNM-ER 3733, KNM-ER 3883, KNM-WT 15000 are distinct or not from *H. erectus*.
2. If they are distinct from *H. erectus*, establish whether or not they comprise a single homogeneous group. In this case, the analysis must show the three as sister taxa in a clade, and they should cluster in the metric analyses.
3. Establish whether or not they represent *H. ergaster*. This cannot be done directly from cranial comparisons, as the hypodigm for *H ergaster* is the mandible KNM-ER 992. Of the three crania generally attributed to *H. ergaster*, only KNM-WT 15000 has an associated mandible, so it is this that needs to be compared to KNM-ER 992 in the first instance. This will test the attribution of one of the specimens in question, KNM-WT 15000, to that species. The same process will also test the hypothesis that KNM-ER 992 could share a common ancestor with *H. erectus*, as Sangiran 9 is included in the mandibular analyses.
4. Should it be determined that KNM-WT 15000 represents *H. ergaster*, test whether KNM-ER 3733 and KNM-ER 3883, usually attributed to *H. ergaster*, do indeed belong in that species.

The process outlined above is now followed.

1. Are KNM-ER 3733, KNM-ER 3883 or KNM-WT 15000 distinct or not from *H. erectus*?

The three Turkana crania are separate in the PAUP* Consensus tree (Figure 3.1; Chapter 3): they do not form a clade. In the four equally parsimonious trees, KNM-ER 3733 forms a sister taxon to the Sangiran group and KNM-ER 3883 is sister to this group.

This result was tested in MacClade by placing the Turkana crania on a branch with *H. erectus*. In this case, the tree length is 6 steps longer than the most parsimonious tree, and the T-PTP is $p = 0.35$. It seems unlikely, then, that the Turkana group shared a unique common ancestor with *H. erectus*. Further, when each of the Turkana crania was

individually constrained to form a clade with *H. erectus* the tree lengths were greater than the shortest tree and the T-PTP results would also suggest that none of the Turkana crania are *H. erectus*.

The Turkana and Sangiran crania share only one possible synapomorphy in the analysis: the posterior slope of the articular tuberculum is continuous with the pre-glenoid planum (although *H. erectus* is polymorphic for this state). KNM-ER 3733 and *H. erectus* also share only one possible synapomorphic state: they have metopic keeling (parallel with Dmanisi and *H. rhodesiensis*), while KNM-ER 3883 and *H. erectus* share no synapomorphic states in this analysis. Although KNM-WT 15000 and *H. erectus* share three possible synapomorphies (the superior surface of the orbital margin forms a horizontal posttoral plane from which the frontal rises, as opposed to the frontal flowing smoothly into the frontal squama or there is a posttoral sulcus; weak temporal bands, parallel with *H. habilis*, *H. sapiens*, *A. africanus*; and the temporal squama is triangular); there is no T-PTP support for the clade, as discussed above.

Rightmire (1990), in his morphological comparison of KNM-ER 3733 and KNM-ER 3883 with the *H. erectus* type specimen from Trinil and the *H. erectus* fossils from Sangiran, observed that the African and Asian crania are broadly similar, sharing characters such as thick supraorbital tori, low frontal profiles, maximum breadth at supramastoid crests, strongly developed supramastoid crests, a wide occipital bone, a developed juxtamastoid eminence, a narrow glenoid cavity and a thick tympanic plate. Although he noted some differences between them he was uncertain as to what emphasis should be placed on these, and suggested that such variation could be expected over such a wide geographical range (op. cit. 96). All these characteristics, however, occur in other species, e.g. thick supraorbital tori are found in Ceprano, Daka, Kabwe, Bodo; a low frontal profile is found on Kabwe and *H. habilis*; maximum breadth at the supramastoid crests characterises all crania until, arguably, Ceprano, or later hominins, appear; strong juxtamastoid eminences are found on SK 847, and *H. habilis*, *H. rhodesiensis*, and *H. sapiens* are polymorphic for this state. While I do not know how Rightmire defined 'thick tympanic plate', I defined this as >2mm at the outer anterior edge of the tympanic, based upon Zeitoun's (2000) work.

That is, although KNM-ER 3733 and KNM-ER 3883 might be similar to *H. erectus* in these characters, the characters do not serve to differentiate a group consisting of *H. erectus* and the Turkana crania from other OTU.

Two morphometric analyses (Chapter 3; Figures 3.9; 3.10) were designed to focus on the Turkana crania. In one analysis, the three Turkana crania cluster and they are separate from Sangiran 17 on both axes; they are relatively smaller but have relatively higher vaults and narrower supraorbital widths than *H. erectus* (as represented by Sangiran 17). In the other morphometric analysis, KNM-ER 3733 and KNM-ER 3883 form a cluster with Zhoukoudian Skull XI and Dmanisi D2280 (Sangiran 17 is not represented for want of comparative data). KNM-ER 3733 and KNM-ER 3883 are similar to the *H. pekinensis* crania in their cranial width:frontal arc relationship. This distinguishes them from *H. sapiens*, *H. rhodesiensis*, KNM-WT 15000, the subadult D2600 and *H. floresiensis*.

Four other metric analyses include two or more of the Turkana crania. In Figure 3.22 (Chapter 3) KNM-ER 3733 and KNM-ER 3883 cluster and they are well separate from Sangiran 17; in Figure 3.34 the three Turkana crania cluster; and in Figure 3.46 and 3.47 (in which the same variables are used, but Figure 3.47 incorporates more crania) the three Turkana crania form a group that is separate from Sangiran 17, although KNM-ER 3733 is similar to Sangiran 17 in its vault height: biauricular breadth relationship. In summary, the Turkana crania are separate from Sangiran 17 in these analyses.

The hypothesis that the Turkana group are *H. erectus* can be further tested cladistically by analysing the mandibles. There is one mandible available for the Turkana group, KNM-WT 15000; and there is one available for *H. erectus*: Sangiran 9. By constraining KNM-WT 15000 and Sangiran 9 to form a clade, the shortest tree is 5 steps longer than the (T-PTP supported) shortest tree, in which KNM-WT 15000 is on a branch with KNM-ER 992 and the Tighenif mandibles, and the T-PTP for {KNM-WT 15000, *H. erectus*} is $p = 0.92$; it is likely that such a clade would form by chance alone. The results of the mandibular analyses support those of the cranial cladistic analyses: KNM-ER 992, the Turkana mandible, cannot be attributed to *H. erectus*.

The cranial and mandibular cladistic analyses undertaken in this study have shown that the Turkana crania and *H. erectus* share very few potential synapomorphies, and the trees in which the Turkana crania and *H. erectus* are constrained to form a clade are significantly longer than the shortest tree. Further, the T-PTP tests show that there is no evidence that a clade comprising the Turkana and Sangiran fossils would come together any way but by chance. That is, the Turkana group and *H. erectus* are unlikely to have shared an immediate common ancestor; there is no evidence that the Turkana group is closely related to *H. erectus*.

2. Do KNM-ER 3733, KNM-ER 3883, KNM-WT 15000 all belong to *H. ergaster*?

As KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 are distinct from *H. erectus*, the hypothesis that they are *H. ergaster* is now tested; firstly by comparing the hypodigm for *H. ergaster*, the KNM-ER 992 mandible, with its contemporary KNM-WT 15000, the only mandible available for the Turkana group.

a) Comparison of KNM-ER 992 and KNM-WT 15000 mandibles

The mandibular analysis Majority Rule consensus tree (Chapter 3; Fig. 3.51) shows KNM-ER 992 and KNM-WT 15000 are in the same clade in all most parsimonious trees. This branch comprises the clade {KNM-ER 992, Tighenif 1; KNM-WT 15000, Tighenif 3, D211; Tighenif 2}, with a sister clade comprising the Dmanisi mandibles, D2375 and D2600.

Within the branch, KNM-ER 992 forms a well supported clade with Tighenif 1, while KNM-WT 15000 forms a clade with Tighenif 3 and Dmanisi D211. Tighenif 2 is sister taxon to these two clades. Tighenif 3 and D211, however, are likely to have come together by chance (refer Chapter 3). When D211 is excluded the branch shares four possible synapomorphies: the mandibular corpus is of uniform height; the gonial region has no flaring (condition for Dmanisi is not known); the symphyseal region in basal view is thickest at the midline; the submandibular fossa is wide (although the condition for Dmanisi, Zhoukoudian P695 and Sangiran 9 is not known; parallel with Zhoukoudian P696).

Although it is possible that KNM-ER 992 and Tighenif 1 share an immediate common ancestor, and KNM-WT 15000 and Tighenif 2 share an immediate common ancestor, while Tighenif 3 branched off earlier than these four (implying evolutionary changes through time for the Tighenif group), it is far more likely that these are all from the one closely related group that shares an immediate common ancestor. The Tighenif mandibles are the same age (either from the Brunhes Normal Chron (800,000 Kya); or from the Jaramillo Normal Subchron (1.0-1.1 Mya), see Geraads et al. 1986), and from a localised area (a hillock 20km east of Mascara, Algeria; op. cit.). It is difficult, then, to argue that they represent evolutionary change through time; they most likely sample the same biological population and that the 'spread' of the Tighenif mandibles through the branch represents intra-species variation. The branch (without D211) has a T-PTP of $p = 0.02$ and was therefore not likely to be generated by randomness in the data. I propose that all OTUs on the branch shared a common ancestor. As the type specimen for *H. ergaster* is on this branch and Tighenif mandibles are interspersed within the branch, I further propose that all members of the branch are *H. ergaster*. That is, KNM-WT 15000 is *H. ergaster*.

b) Are KNM-ER 3733, KNM-ER 3883, KNM-WT 15000 sister taxa?

The mandibular analysis strongly suggests that KNM-WT 15000 and *H. ergaster* shared an immediate common ancestor. To test whether KNM-ER 3733 and KNM-ER 3883 shared a common ancestor with *H. ergaster*, these crania are now compared to the cranium of KNM-WT 15000, and to each other.

Morphometric results

There are four morphometric analyses that include the three Turkana crania. In the first analysis (Chapter 3, Figure 3.9), designed to include all three crania, KNM-ER 3733 and KNM-ER 3883 cluster but KNM-WT 15000 is separate from them; KNM-WT 15000 has a relatively rounder and more tightly curved occiput compared to the others. Nevertheless they form a group in several other analyses (Figures 3.22, 3.34, 3.47). Further, KNM-WT 15000 and KNM-ER 3733 cluster in Analysis 4 (Figure 3.34) - they are similar in cranial breadth:supraorbital breadth relationship although KNM-WT 15000 is slightly smaller than KNM-ER 3733 and has a relatively lower vault in relation to cranial length. In

summary, then, the three crania generally cluster but there are several differences between KNM-WT 15000 and KNM-ER 3733.

Cladistic analysis results

The three Turkana crania are separate in the most parsimonious (equally shortest) trees (Chapter 3; Figure 3.3). When KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000 are constrained to form a clade, the tree is 3 steps longer than the most parsimonious tree and the T-PTP is p = 0.25, suggesting that they would only come together by chance. The cladistic analyses, then, do not support the hypothesis that KNM-ER 3733, KNM-ER 3883 and KNM-WT 15000 share an immediate common ancestor.

KNM-ER 3733 and KNM-ER 3883.

KNM-ER 3733 and KNM-ER 3883 do not form a clade in the shortest trees. When they are tested as sister taxa the tree is three steps longer than the most parsimonious tree and the T-PTP is p = 0.19. It is not unlikely then, that they could only form a clade by chance although they do share 8 possible synapomorphies (see Chapter 3).

I also tested for the clade {KNM-ER 3733, KNM-ER 3883} when other OTUs were being separately examined. When the KNM-ER 3733 and KNM-ER 3883 were thus constrained in the SK 847 analysis (Figure 3.12), the tree was one step longer than the most parsimonious; for the KNM-OL 45500 phylogeny it was 2 steps longer when KNM-ER 3883 is added to the KNM-OL 45500/KNM-ER 3733 clade (Figure 3.25); and it is also 2 steps longer (Figure 3.33) than the most parsimonious tree for Ceprano, Daka and Bodo. As the T-PTP for {KNM-ER 3733, KNM-ER 3883} is >.05 and tree lengths increase by either two or three steps if the two are placed in a clade in a range of cladistic analyses, it is difficult to argue that KNM-ER 3733 and KNM-ER 3883 shared a unique common ancestor.

Further, KNM-ER 3733 and KNM-ER 3883 differ in the following characters:

KNM-ER 3733	**KNM-ER 3883**
Metopic swelling	No metopic swelling
Supraorbitals of even thickness	Supraorbitals thickest centrally
Frontal rises after posttoral sulcus	Frontal rises immediately post-glabella
Naso-frontal suture takes a 'V' course	Naso-frontal suture takes a horizontal course
Bone thickness adjacent nasal aperture 0.97mm (taken 1cm in from nasal edge and 33mm below nasion).	Bone thickness adjacent nasal aperture 0.39mm (taken 1cm in from nasal edge and 33mm below nasion) although I am not certain that this bone fragment is, in fact, correctly placed on the cranium).
Precoronal depression	No precoronal depression
Prominent temporal lines	Temporal lines less marked
Low temporal squama	High temporal squama
Tympanic projects forward inferiorly	Tympanic projects back inferiorly
No digastric fossa	U-shaped digastric fossa
No juxtamastoid eminence	Juxtamastoid eminence
External occipital crest from superior nuchal line to rim of foramen magnum	External occipital crest only from inferior nuchal line to rim of foramen magnum
Strong tuberculum linearum	Moderate tuberculum linearum
Strong supramastoid and mastoid crests	Weak supramastoid and mastoid crests
Narrow supramastoid sulcus	Wide supramastoid sulcus
Supramastoid and mastoid crests divergent anteriorly	supramastoid and mastoid crests parallel

That KNM-ER 3733 and KNM-ER 3883 are not *H. ergaster* has been advocated by Groves (1989), Zeitoun (2000), and Schwartz and Tattersall (2002:136-138; 143-145). Holloway et al. (2004:129) show that the KNM-ER 3883 endocast differs from KNM-ER 3733 in size and shape - particularly in its relative flatness of the frontal lobe, while noting their general similarity. Groves (1989) placed KNM-ER 3733 and KNM-ER 3883 in *Homo sp. (unnamed)* as they share derived traits of *H. ergaster* (arched or ridged nasals, broad upper face, endinion lower than ectinion; op. cit. 271), as well as sharing derived traits with *H. erectus* and *H. sapiens* (mastoid process more than 12mm long, occipital scale shorter than the nuchal scale and others; op. cit. 276).

Zeitoun (2000) separated the two crania into different species based upon the outcome of a cladistic analysis of *Homo* using 468 cranial characters; KNM-ER 3733 is made the type of *H. kenyaensis nov. sp.* and KNM-ER 3883 is of *H. okotensis nov. sp.* (op. cit. 148). To ascertain if they could represent different species or lineages I undertook two further tests. By constraining KNM-ER 3733 and KNM-WT 15000, the tree was 3 steps longer and there was no T-PTP support. Secondly I compared KNM-ER 3883 and KNM-WT 15000. This comparison is particularly important as KNM-ER 3883 and KNM-WT 15000 are contemporaneous. When they were constrained in the cladistic analysis, the tree was 5 steps longer. Moreover, they differ in 20 characters that relate primarily to the basicranium; and also to the frontal and temporal regions. Although KNM-WT 15000 is sub-adult, only one character difference, the presence of a tympanic trough in KNM-WT 15000, could be attributed to developmental age differences. There is then, no evidence that KNM-WT 15000 and KNM-ER 3883 belong together.

4.3 Homo ergaster

The mandibular cladistic analyses, in which the type specimen for *H. ergaster*, KNM-ER 992, was included, produced a supported phylogeny that included a branch ({KNM-ER 992, Tighenif 1}{KNM-WT 15000, Tighenif 3}, Tighenif 2). I concluded (as above), then, that these specimens shared an immediate common ancestor.

This group may be characterised by the following possible synapomorphies:

- the mandibular corpus is of uniform height;
- the gonial region has no flare, suggesting a weakly developed masseter;
- the symphyseal region in basal view is thickest at the midline (parallel with *H. erectus*)
- the submandibular fossa is wide (parallel with Zhoukoudian P696)
- tympanic trough (parallel with OH 24, *H. floresiensis*; Dmanisi polymorphic)

To further assess the proposed phylogenetic relationship between the Tighenif mandibles, KNM-ER 992, and KNM-WT 15000 I examined them for morphological differences in the characters available for most of them: the position of the mental foramina varies; there are differences in the form of the posterior marginal tubercles and relative rugosity of the

gonial region; and they are variable for the origin of the *sulcus extramolaris* and form of *torus lateralis superior*. Tighenif 1 has a narrow *sulcus extramolaris* compared to the others; the lateral prominence is greatest below M_3 in Tighenif 1 but below M_1 in the others; and the mylohyloid ridge is narrow on Tighenif 1 and 3 and wide KNM-ER 992. The distinct diversity in size would suggest sexual dimorphism in the species.

The remains from Tighenif include a right parietal bone (Arambourg 1955). In view of the hypothesised phylogenetic relationship between Tighenif and KNM-WT 15000 it would seem useful to compare this parietal with the parietal of KNM-WT 15000, specifically its left parietal which is the more intact (Walker and Leakey, 1993). The sutures of the Tighenif parietal are not closed, indicating that the bone is from a relatively young individual (Arambourg, 1955); KNM-WT 15000 is a sub-adult. Both[15] parietals are relatively square in shape, convex anteriorly/posteriorly and superiorly/inferiorly; in each the convexity changes to a steeper slope just below the temporal line; the frontal borders are straight, while the sagittal and occipital borders are irregular; the surfaces on the squamous sutures of both have many ridges and grooves, with fine striations running diagonally back for up to about 20mm (parietal striae?). There are differences between the parietals: the Tighenif parietal is thinner than KNM-WT 15000 at bregma and near the sphenoid angle, and thicker at asterion.

There are differences in the reported cranial capacities. The cranial capacity for KNM-WT 15000 is 909cc (Walker and Leakey, 1993; p 347) and for Tighenif it is 1300cc (Kochetkova, 1968). The Tighenif cranial capacity seems to be a rather large estimate for a pre- *H. sapiens* juvenile hominin and, in fact, lies within the range of *H. sapiens* adult cranial capacities (1166-1659cc, Holloway 1981a:156; 1156-1775cc, Falk 1987:20). The estimated breadth for the Tighenif endocranium is 137mm (Kochetkova 1968) which is within the range for modern human adult crania, greater than that for *H. erectus* crania (Trinil, 125mm; Sangiran 2, 120mm; Sangiran 4, 125mm; Sangiran 10, 117mm; Sangiran 12, 130mm; Sangiran 17, 129mm) (Holloway 1981b:518), and closer to adult Neanderthals Spy 1 (144mm) and Spy II (136mm) (Holloway 1981c:391). The estimated endocranial height is 103mm. This is considerably shorter than *H. sapiens* (eg 110-

[15] Ternifine parietal: pers. obs; Arambourg, 1955. KNM-WT 15000; Leakey and Walker, 1993.

156mm, Bruner et al., 2003), *H. erectus* (117-130mm, Holloway 1981b:518), and Spy 1 and Spy 2 (116mm; 113mm respectively; Holloway 1981c:391). That is, the estimated cranial capacity of the sub-adult Tighenif is similar to adult *H. sapiens*, although the parietal itself is considerably shorter, and a different shape. The estimate for its endocranial width is within the range of modern human adults but its endocranial height is extremely low. It appears to me that there is some error in either the estimated height or width (or both) of the endocranium, and that this may have resulted in an overestimate of the cranial capacity. From this point of view, conclusions cannot be drawn from comparisons of the cranial capacities of KNM-WT 15000 and Tighenif. In summary, then, there are similarities and differences between the Tighenif and KNM-WT 15000 parietals; and no further conclusions may be drawn.

In summary, there is cladistic and morphological support for KNM-ER 992, KNM-WT 15000, Tighenif 1, Tighenif 2 and Tighenif 3 being con-specific. The name that has priority is *H. ergaster* (Groves and Mazak, 1975); this is the available name for this con-specific group.

4.4 Dmanisi crania and mandibles

There are two key issues for the Dmanisi hominins. The first is whether the striking differences between D2600 and the other mandibles signify that two species were present at this site; the second is the taxonomic affinity of the hominin material. The latter issue is dependant upon the resolution of the former; this is now addressed.

The tight chronological period and constrained depositional stratigraphy strongly suggest the Dmanisi assemblage samples a single population, but the differences between the mandible D2600 and the other Dmanisi mandibles has generated debate as to whether it may be accommodated within the Dmanisi paleodeme (Gabounia et al., 2002; Rightmire et al., 2006). Further, there is some uncertainty about the provenance of D2600 (van Arsdale 2006), and at the time of its discovery some debate occurred as to whether it came from the earlier (basal) layer A1, in which case it would be the only hominin to come from this layer. It was discovered during a post-field season soil sampling program and, at the time, was identified as coming from stratigraphic layer 5, now denoted Layer A2 (op. cit. 45), based upon field notes that provided its stratigraphic co-ordinates. Van Arsdale

suggested that, as well as the evidence from the field notes, there is other material (unpublished) associated with D2600, and it is likely D2600 is after all from stratigraphic level A2, and therefore contemporaneous with the other Dmanisi crania and mandibles.

Skinner et al. (2006) and Martinón-Torres et al. (2008) hypothesised that D2600 represents a separate paleodeme, and Rightmire et al. (2006) concluded from their comparative analyses of the skulls that, while it is appropriate to group the skulls, D2600 may not be from the same population, although, if it is included, since it is the type of *H. georgicus*, the nomen *H. erectus georgicus* is applicable given that, in their view, Dmanisi is a subspecies of *H. erectus*. Skinner et al. (2006) used four linear size measurements to compare the Dmanisi mandibles to three *Gorilla* subspecies, five *Pan* subspecies, *H. sapiens*, *Australopithecus*, *Paranthropus*, *H. habilis* and *H. erectus* (in which they included Sangiran, *H. pekinensis*, OH 23, OH 51, SK 15, KNM-ER 992, and the Tighenif mandibles) to test the probability that size and shape differences between the largest (D2600) and the smallest (D211) mandibles are not significantly greater than those found in comparative taxa. They proposed two hypotheses:

a) that the degree of sexual dimorphism in the Dmanisi sample exceeds expectation for a species of *Homo*, and

b) that two species of *Homo* are sampled. The latter hypothesis would be more likely if D2600 came from an earlier stratigraphic level (op. cit.). Van Arsdale (2006), however, as discussed above, provided fairly conclusive stratigraphic information to show that D2600 is from level A2 (although his assertion that it is associated with other Dmanisi material in this level is not substantiated).

Van Arsdale (2006) also found that the variation within the mandibles is greater than expected for a comparative sample of humans or chimpanzees (but not of gorillas), and hypothesised that sexual dimorphism in early *Homo* is greater than previously recognised. Martinón-Torres et al. (2008), however, separated D2600 from the rest of the Dmanisi sample on the basis that it alone of the Dmanisi mandibles shares the primitive $M_2 < M_3$ pattern with *Australopithecus*, *Paranthropus* and early *Homo*, and that there are differences in dental dimensions and root morphology (e.g. bifurcated P_3s); and supported the hypothesis that two distinct paleodemes are represented at Dmanisi, although they also found that the other Dmanisi dentition displays conservative morphology that overlaps

with *Australopithecus* and *H. habilis*, which somewhat weakens their argument that D2600 is more primitive than the other Dmanisi mandibles.

In this study D2600 and the sub-adult D2735 form a clade in 78% of the most parsimonious trees (Chapter 3; Figure 3.51), with a T-PTP value of p = 0.01 and therefore is unlikely to have formed by chance alone. That is, the mandible that led Martinón-Torres et al. (2008) to hypothesise that two taxa are represented, and Skinner et al. (2006) to consider this as a possibility, and Rightmire et al. (2006) to express some reservation about its inclusion in the deme, seems highly likely to have shared an immediate common ancestor with the subadult mandible D2735. Further, when the other Dmanisi mandible D211 was constrained with D2600 and D2735 the 3 equally parsimonious trees were only one step longer than the shortest and the T-PTP for the three Dmanisi mandibles was p = 0.065. The clade also shares two possible synapomorphies: the digastric fossa is shallow (parallel with LB6/1; *H. sapiens* polymorphic); and the symphyseal region is uniformly thick inferiorly (parallel with *H. pekinensis*).

The Dmanisi crania also formed a separate clade, with 68% Bootstrap value, in all most parsimonious trees in the PAUP* cranial analysis (Chapter 3; Figure 3.1); and they share 14 possible synapomorphies

- zygomaticoalveolar crest forms an arch
- sharp high line divides the floor of the orbit from the facial portion of the malar
- shallow digastric fossa
- frontal edge in norma verticalis is linear (parallel with *H. sapiens*, KNM-ER 1813)
- supraorbital form is a>b, b<c and a>c (where 'a' is central, 'b' is middle and 'c' is lateral; parallel with *A. africanus*)
- bregmatic eminence (*H. erectus* polymorphic)
- vertical axis of main axis of tympanic (parallel with *H. rhodesiensis*)
- strong occipital torus (parallel with *H. erectus*)
- main axis of tympanal in norma lateralis is vertical (parallel with *H. sapiens*)
- postglenoid process is strongly involved in the wall of the mandibular fossa (parallel with *A. africanus*)
- posterior part of tympanal joins anterior part of mastoid process (D2282 n/a)

- the *jugum alveolar* forms a broad and prominent ridge (D2280 n/a)
- glasserian fissure

I hypothesised, then, that the Dmanisi crania and mandibles formed a single taxonomic unit, and treated them as such in the analyses, leaving discussion of their attribution and possible phylogenetic relationships until all analyses had been completed. The available nomen for the assemblage is *H. georgicus* Gabunia et al., 2002).

Nevertheless, I tested the hypotheses that Dmanisi is *H. erectus* (Gabunia and Vekua, (1995; Bräuer and Schultz, 1996; Rightmire et al., 2006) and that it is *Homo ex. gr. ergaster* (Gabounia et al., 2000).

The PAUP* cranial cladistic analyses show no phylogenetic relationship between Dmanisi and *H. erectus* (Figure 3.1). When the Dmanisi mandibles and the *H. erectus* mandible Sangiran 9 were constrained to form a clade the two shortest trees (Figure 3.54) are 4 steps longer than the most parsimonious (Figure 3.52) and have no T-PTP support. The hypothesis that the Dmanisi mandibles have a phylogenetic relationship with *H. erectus* is, then, highly unlikely.

When the three Dmanisi mandibles are constrained (Figure 3.53), however, they form a sister clade to KNM-ER 992, KNM-WT 15000 and the Tighenif mandibles on one of the 3 equally parsimonious trees. This branch has a T-PTP p = 0.01 and shares 3 possible synapomorphies:

- the lower dental arcade is tightly curved (parallel with Sangiran 9; *H. pekinensis* polymorphic);
- they have symphyseal keels (condition for KNM-ER 992 unknown; parallel with *H. sapiens*; the keel on KNM-WT 15000 is short and low).
- no subalveolar depression (parallel with *H. floresiensis*, *H. pekinensis*).

On the other two equally parsimonious trees, they branch either before or after *H. ergaster*.

It is possible to suggest from the mandibular analyses that *H. georgicus* and *H. ergaster* share a common ancestor, but in the cranial analyses, *H. ergaster* and *H. georgicus* are on separate lineages (in all cranial analyses). Further, the T-PTP for the Dmanisi crania and the *H. ergaster* cranium KNM-WT 15000 is p = 0.66, suggesting that this clade would come together by chance alone.

That there are close similarities between the mandibles of the two species is clear: they share a number of synapomorphic states, notably an incipient symphyseal keel – the earliest *Homo* in which this occurs. KNM-WT 15000 and *H. georgicus* also share some postcranial traits, some of which are shared with *H. sapiens*: they have modern postcranial proportions (Ruff and Walker, 1993; Lordkipanidze et al., 2007); the Dmanisi adult right scapula (D4166) shows a glenoid orientation relative to the spine, and a breadth-to-width ratio of the spine, similar to KNM-WT 15000 (at the lower end of modern human variation), and humeral torsion is virtually absent in *H. georgicus* and KNM-WT 15000 (as well as *H. floresiensis* and some Australopithecines). The Dmanisi clavicles (D4161, D4162), however, are more similar to modern humans than to KNM-WT 15000.

Nevertheless, the cranial, mandibular and postcranial evidence for a phylogenetic relationship between *H. georgicus* and *H. ergaster* is equivocal, and I cannot show that it is not due to chance alone.

If *H. georgicus* and *H. ergaster* do not share a unique common ancestor, there are two remaining possibilities for the phylogenetic position of *H. georgicus.* The mandibular analysis does not rule out the alternatives that it branched after or before *H. ergaster* (as represented by KNM-WT 15000), while the preferred phylogenetic tree for the crania (Figure 3.50) shows *H. georgicus* branching before *H. ergaster* (KNM-WT 15000).

The *H. georgicus* hypodigm includes adolescents (D2700/D2735, D2282), a prime adult (D2280), and an aged adult (D2600); that is, it provides a relatively good range of comparable morphology within the species. Gabounia et al. (2002) describe the species as highly sexually dimorphic comprising a gracile group, D211, D220, D2282, D2700 and D2735, and a more robust group represented by D2600. As noted above, the variation among the mandibles is outside the previously known range for *Homo* (Skinner, 2006;

Martinón-Torres et al., 2008) yet they are clearly a member of this genus. I conclude that sexual dimorphism in at least some of the Early Pleistocene hominins is greater than generally acknowledged to date.

4.5 SK 847

SK 847, from the site of Swartkrans, South Africa, is dated to between 1.63 Mya and 2.1 Mya, roughly contemporaneous with *H. habilis*, *H. georgicus*, and KNM-ER 3733, and KNM-ER 992, although the upper limit would make it older than these OTUs.

There are six hypotheses for SK 847: that it is *H. erectus* (Robinson (1961), *H. habilis* (Clarke and Clark Howell, 1972), *Homo incertae sedis* (Clarke et al., 1970; Groves and Mazák, 1975), *H. africanus* (Olson, 1978), or nearly identical to KNM-ER 3733 (Clarke, 1994), while Curnoe (1999) proposed that it shared a common ancestor with *H. habilis* and *H. ergaster*.

SK 847 forms a separate lineage on the shortest tree (Figure 3.11). It branches off early in the genus *Homo*: before *H. habilis* and after *H. floresiensis* (Figures 3.11, 3.50). Nevertheless I tested the competing hypotheses for SK 847. The tree is 2 steps longer under the hypothesis that SK 847 is related to *H. erectus* (Robinson, 1961) (Figure 3.15), 4 steps longer when it is sister to a clade combining *H. erectus* and *H. habilis* (Curnoe 1999) (Figure 3.14); 4 steps longer when SK 847 and *A. africanus* are constrained (Olson 1978) (Figure 3.17); 5 steps longer when SK 847 was constrained with KNM-ER 3733 and OH 9 (Clarke, 1994) (Figure 3.12); and 2 steps longer when constrained with only KNM-ER 3733 (Figure 3.13). There was no T-PTP support for these clades. As well, there was no support for SK 847 and *H. georgicus* sharing a common ancestor (Figure 3.16).

The most parsimonious solution for SK 847 is that it forms a separate *Homo* lineage. It has three possible uniquely derived characters: there is no variation in the superior-inferior thickness of the supraorbitals; the *jugum alveolare* forms a narrow ridge (as opposed to there being no *jugum alveolare*, or the *jugum* forming a broad and prominent ridge); and the posterior part of the tympanic joins the anterior part of the mastoid (parallel with Dmanisi). I, therefore, follow Groves and Mazák (1975) and Clarke et al. (1970) who attribute SK 847 to *Homo incertae sedis*.

Of interest, SK 847 shares some characters with *H. sapiens* that other fossil specimens in this study do not: the malar notch forms an arch with a sharp angular and downward projecting tubercle anterior to the malar-zygomatic suture; the zygomatic forms a straight line after turning sharply, without any flaring, from the maxilla (assuming the reconstruction is correct); the nasal bones are wider towards nasiospinale and are raised to form a central superior/inferior ridgeline; and the orbit forms a square shape with a sharp lateral edge and a slightly rounded inferior lip. At this stage, these must be considered as parallelisms, but it would be worth exploring the implications in a future study.

4.6 KNM-ER 42700

KNM-ER 42700 is a small well-preserved calvaria from the Turkana Basin dated to between 1.53 and 1.61 Mya, referred to *H. erectus* (Spoor et al., 2007). It is more or less contemporaneous with OH 9 and KNM-WT 15000, and a little younger than SK 847 and *H. georgicus*.

In the metric analyses it clusters with the sub-adult Dmanisi cranium, D2700 (no other Dmanisi crania could be included in the analyses whilst retaining a reasonable number of variables). Both PC axes reflect shape differences and similarities; KNM-ER 42700 and D2700 are similarly broad on the biauricular plane in relation to their vault height, but have relatively high vaults in relation to cranial length (Chapter 3; Figure 3.46), similar to KNM-ER 1813 and LB1; and postorbital constriction (in relation to vault height) is not as marked as occurs on KNM-ER 1813 and LB1, but is more pronounced than for the Turkana crania, OH 9, and Sangiran 17 (Chapter 3; Figure 3.47).

KNM-ER 42700 and D2700 are sub-adults (Spoor et al 2007; Rightmire et al., 2006): the sphenoccipital synchronosis on KNM-ER 42700 is two-thirds fused (Spoor et al., 2007) and on D2700 it is unfused and the M^3s on D2700 are only just erupting (Rightmire et al., 2006).

To further explore for similarities and differences between KNM-ER 42700 and D2700, I compiled the following table from the morphological descriptions by Spoor et al. (2007) (KNM-ER 42700) and Rightmire et al. (2006:124-128) (D2700).

Table 11. KNM-ER 42700 and D2700

KNM-ER 42700	D2700
ECV 691cc	ECV 600cc
Uniformly thin supraorbitals	Supraorbitals thicker centrally
Shallow supratoral sulcus	?
Flattened supraglabella region	Flattened supraglabella region
Projecting glabella	Projecting glabella
Frontal keel	Trace of frontal keel
Sagittal keel	Sagittal keel
No occipital torus	No occipital torus
Ovoid calvaria in lateral view	Ovoid calvaria in lateral view
Upper part of occipital scale vertical	Upper part of occipital scale vertical
Sloping frontal	Sloping frontal
Flattened parietal	Flattened parietal
Moderately angled occipital	Moderately angled occipital
Greatest breadth at supramastoids	Greatest breadth at supramastoids (Vekua et al. 2002; Figure 2E)
Temporal squama low and gently convex	Temporal squama low with a straight superior border (Vekua et al., 2002:88)
Well developed postglenoid process	Marked postglenoid process
Tympanic has faint petrous crest	Thin petrous crest
Short slender mastoid process	Mastoids eroded
Thin cranial vault	?
Mediolaterally narrow mandibular fossa	?

From published images of KNM-ER 42700 and D2700, the frontal profile of KNM-ER 42700 appears less rounded than D2700, and it has a flattened temporal region, whereas D2700 appears more rounded here (refer Spoor et al., 2007; Figure 1a; Vekua et al., 2002 Fig 2A); the lateral profiles are very similar but the frontal of KNM-ER 42700 might rise a little more steeply than on D2700 (refer Spoor et al., 2007; Figure 1b; Rightmire et al., Figure 3); in superior profile they appear to be almost identical (Spoor et al., 2007, Figure 1a; Rightmire et al., 2006, Figure 3) with almost matching frontal forms (Spoor et al., 2008, Figure 3b, 3c). It is not possible to compare the occipital profiles as the published images for this aspect of the cranium are taken from different angles (refer Spoor et al., 2008, Figure 1c; cf Vekua et al., 2002, Figure 2E), although it is clear they are both widest at the supramastoids.

They have many other characters in common: their lateral and superior profiles are almost identical; they have a flattened supraglabella region; project at glabella; a trace of a frontal keel; a sagittal keel; no occipital torus; the upper part of their occipital scales are vertical; greatest breadth is at the supramastoids; inion and opisthion do not coincide; the parietals are flattened; they have moderately angled occipitals; marked postglenoid processes; and thin petrous crests. They differ, however: KNM-ER 42700 (ECV 691cc) is a relatively larger cranium than D2700 (ECV 600cc); KNM-ER 42700 has uniformly thin supraorbitals while D2700 supraorbitals are thicker centrally; there appear to be differences in the frontal profile in lateral view, although from bregma the lateral profiles are very similar; the superior borders of the temporal squama differ; and KNM-ER 42700 has an incipient angular torus while D2700 has none.

The number of similarities between them would suggest that further study is warranted when the Dmanisi and KNM-ER 42700 crania are made available.

Spoor et al. (2007) attribute KNM-ER 42700 to *H. erectus* based upon a comparison with *H. erectus s. l.* that includes KNM-ER 3733, KNM-ER 3883, OH9, D2280 and D2700, Sangiran and Ngandong skulls, Ngawi, Sambumacan, 3 *H. pekinensis* skulls, and KNM-WT 15000. That is, their *H. erectus* sample includes all the skulls that others have ever attributed to other species, and may mask important variation in the Early Pleistocene record, and obscure any sexual dimorphism at this time. My preferred procedure in phylogenetic analyses is to compare fossil material to the type specimen or the particular species *senso stricto*; my metric analysis included Sangiran 17, which is unequivocally referred to *H. erectus*. KNM-ER 42700 is well separated from Sangiran 17 in both analyses – they differ not only in size, but in their cranial length-vault height relationship, and biauricular breadth-vault height relationships. Overall, the cranial shape differences are too great to argue for a close phylogenetic relationship between KNM-ER 42700 and *H. erectus s. s.*.

In the absence of a cladistic analysis that could shed more light on KNM-ER 42700, I would concur with Baab (2008) in assigning KNM-ER 42700 simply to *Homo sp.*. The degree of phenetic similarity to Dmanisi D2700 is interesting, and deserves further evaluation based upon observations on the original material.

4.7 Olduvai Hominid 9

Olduvai Hominin 9 (OH 9) is from Upper Bed II dated to 1.5-1.4 Mya (Schwartz and Tattersall, 2002), hence is contemporaneous with KNM-WT 15000 and a little younger than KNM-ER 3883.

The three hypotheses for the phylogenetic position of OH 9 are: that it is *H. erectus* (Groves 1989; Rightmire 1990); that it is **not** *H. erectus* (Stringer 1984); that it is a separate species (Heberer 1963; Kretzoi 1984).

In the three shortest trees (Figure 3.18) OH 9 is either sister taxon to Dmanisi, or is sister taxon to a clade comprising Dmanisi and *H. ergaster,* or forms a separate lineage. T-PTP tests for the latter trees suggest that an OH 9/Dmanisi clade and an OH 9/Dmanisi/KNM-WT 15000 (*H. ergaster*) clade would come together only by chance.

In no tree did OH 9 and *H. erectus* form a clade. When they were constrained, the two trees thus formed were 4 steps longer than the shortest and, again, the T-PTP result indicated that this clade would come together only by chance.

Nor are clades comprising OH 9 and KNM-ER 3733, or OH 9 and KNM-ER 3883 likely: when OH 9 was constrained with KNM-ER 3733, the tree was 3 steps longer than the shortest and the T-PTP was $p = 0.36$, and when it was constrained with KNM-ER 3883 the tree length was 2 steps longer, and the T-PTP = 0.70.

OH 9 has 9 possibly derived characters shared with a range of *Homo* (Chapter 3; Table 2) and three characters that may be uniquely derived: the form of the supraorbital torus, continuity between the mastoid crest and superior temporal line, and the presence of a suprameatal spine.

The morphometric analysis (Figure 3.22) does not appear to support the most parsimonious solution in the cladistic analyses for OH 9 (Figure 3.18; third tree): in the metric analysis OH 9 clusters with Sangiran 17 and one of the *H. pekinensis* skulls

(Zhoukoudian XII). They are similar in their biauricular:biasterionic breadth relationship and their cranial length:bistephanic breadth ratio, and differ from other crania in the analysis, including Zhoukoudian Skull XI. The analysis included a relatively wide range of data: cranial length, breadth, minimum frontal breadth, biauricular breadth, bistephanic breadth, and frontal arc and chord. There are, then, strong similarities in the cranial shape of OH 9, *H. erectus*, and *H. pekinensis*; the cladistic analysis, however, shows that OH 9 is unlikely to be phylogenetically related to *H. erectus*. In the cladistic analysis 89 characters are used from the frontal, parietal, occipital, temporal and basal regions of the cranium; the morphometric analyses use far less data, and, while they show cranial shape similarities and differences, they are not designed to identify sister taxa. From this point of view, while I note the phenetic similarity between OH 9, *H. erectus* and *H. pekinensis*, they can not be shown to be phylogenetically related based on the cladistic analysis. OH 9, I propose, represents a separate lineage. Should the lineage comprise a species, the available name is *H. louisleakeyi*, proposed by Kretzoi (1984) (Groves, 1999).

4.8 KNM-OL 45500

Although KNM-OL 45500 is a small calvaria (<800cc; Potts et al., 2004) Potts et al. (op. cit.) conclude that it is an adult or near adult: its bony superstructures are developed, its post-toral sulcus is as developed relative to the rest of the frontal bone as in adult *H. erectus,* and its interorbital region is wide, prominent and convex (op cit.0. It is dated to 970-900 Kya (op cit.), younger than SK 847, KNM-ER 3733, KNM-ER 3883, or KNM-WT 15000, and contemporaneous with OH 12 and Buia, and somewhat older than Daka and Ceprano. Potts et al. (op. cit.) noted some similarities to Daka and Ceprano. There are relatively few cladistic data for KNM-OL 45500, and too few metric to enable a Principal Components analysis to be performed.

Although KNM-OL 45500 and *H. sapiens* formed a clade in the shortest tree in the cladistic analysis (Figure 3.23), they share only one possible synapomorphy (the size of the articular eminence is shorter than the opposite side of the mandibular fossa, parallel with KNM-WT 15000). The next shortest tree, only one step longer, presents a clade comprising KNM-OL 45500 and KNM-ER 3733 (to the exclusion of KNM-ER 3883) (Figure 3.24), the T-PTP for which is $p = 0.04$; they share four possible synapomorphies:

depression at glabella, a strong mastoid crest, the posterior edge of the *tuberculum articulare* is a sigmoid shape, and the entoglenoid is extended posteriorly. KNM-OL 45500 is unlikely to form a clade with *H. habilis*, *H. georgicus*, or *H. ergaster* (results listed in Chapter 3). The most parsimonious hypothesis, then, is that KNM-OL 45500 and KNM-ER 3733 shared an immediate common ancestor although there is a considerable difference in age between them, and a paucity of cladistic data for KNM-OL 45500. If KNM-ER 3733 is found to be a species, and KNM-OL 45500 belongs with it, the available nomen is *H. kenyaensis* Zeitoun, 2000.

The ECV of KNM-OL 45500 is <800cc based upon comparisons with the cranial capacity of Dmanisi D2282 and D2280, whose frontal tori, vault and temporal bone sizes match those of KNM-OL 45500 (Potts et al., 2004). The ECV of KNM-ER 3733 is 848cc (Holloway 2000). In view of the sexual dimorphism apparent in *H. georgicus*, and assuming the ECV for KNM-OL 45500 is a reasonable estimate, the difference in the sizes might represent a sexually dimorphic lineage and we could suppose that a degree of sexual dimorphism is retained in *Homo* until this period, i.e. until 970-900 Kya, at least.

4.9 Kabwe

The affinities of the Kabwe skull have been based to some extent upon the supposedly associated postcranial material and its dating has been reliant upon the supposed association of faunal remains. It is appropriate, then, to provide the background to the circumstances of the find.

In 1921 a miner at the Broken Hill lead and zinc mine in (then) Northern Rhodesia, Southern Africa, carefully extracted an isolated cranium from the basal wall of a deep, steeply descending cleft emanating from a cave or cleft within a hill (Hrdlicka, 1930; see Appendix 6 for a site diagram). Recognising the unusual morphology of the cranium, the miner presented it to the mine manager, who took it to the British Museum (Natural History) five months later. Only a brief note of the event was recorded in the mine records at the time (Hrdlicka 1930:105). Smith Woodward (1921) provided the first scientific report, followed by Pycraft (1928), Hrdlicka (1930) and, later, others (discussed below).

In 1925 Hrdlicka (op. cit.) visited the mine in order to discover as much about the discovery as possible. He interviewed five persons involved in the discovery. Mr Zwigelaar, the miner who extracted the skull, reported that there were no other bones close to or near the skull. The next day the miners had unsuccessfully looked for the lower jaw and later in the day found a human leg bone at an undisclosed depth below the cranium. Mr Barron, the mining captain at the time, entered the event into the mines records two or three days after the event, mentioning bat bones surrounding it, and a lion's skull, but not the leg bone (op. cit. 106). In a letter he wrote to a Mr Moffatt in December 1921, Mr Barron wrote that the skull, and a number of other fossilised bones that Dr Wallace (doctor at the Broken Hill mine) considered of great interest, were packed in a box to be taken to the British Museum (Natural history (BMNH) (op. cit. 107). That is, there is no intimation that the bones were associated with the skull (op. cit.).

Loose bones had been collected and stored in offices and tool huts of the mine during the course of mining. Their provenance within the cave is unknown. Some were enclosed in mineral matrix, others were unencrusted and covered in earth and dust; all were more or less mineralised. Amongst these were a large portion of a distal end of a humerus (found in the tool house) and a piece of parietal (found in the hut). As there was not any evidence that any of these bones came from anywhere near the skull, Hrdlicka (op. cit.) believed that they probably came from other parts of the cave. Further, Hrdlicka dug the mine tailings and from this numerous bones and teeth were added to the collection; he reported that a large number of animal bones were found in the cave, and this is also indicated by Clark et al. (1947; Fig 2), where bones are indicated throughout the cave, both in the horizontal floor area and in the descending shaft.

There are, as well, long bones (a left and a right femur, left tibia, and humerus), a second (much smaller) maxillary fragment, two innominates, a sacrum, and an immature parietal from the Broken Hill mining works. Two human fragments and mammalian teeth and a selection of the animal bones were deposited in the British Museum (Natural History) by Hrdlicka, who intended that they be kept with the skull and other specimens collected from the mine previously. Keeping all the bones in what might have appeared as a single site collection from Broken Hill may have perpetrated the misunderstandings that developed about the association of the skull with a range of human and animal bones, as

well as the stone artefacts. There is, in fact, no evidence for any bones associated with the Kabwe skull. This is important, as referrals of Kabwe to a separate and relatively derived species have been to a certain extent based on the assumed association of (modern) postcranial bones with the skull (eg Smith-Woodward, 1921; Pycraft, 1928). This assumption is still apparent. Yokley and Churchill (2006) assumed that the Broken Hill humerus belongs with the skull; they undertook a range of analyses to test the taxonomic utility of humeri as discriminator of archaic and modern humans, and concluded that, while Neanderthal humeri appear distinct from other groups, the Kabwe humerus does not; and they concluded that a modern/archaic dichotomy, as previously reported for proximal ulnar morphology, is not supported in respect of human distal humeri. These conclusions are based on the assumption that the humerus stored with the Kabwe skull is associated with it, whereas it could have come from any part of the Broken Hill mine, including the modern human skeletal material from the cave floor in the Broken Hill knoll.

In view of Hrdlicka's (1928) conclusion that no other bones were found with or near Kabwe, and that those bones assumed to be associated with the skull were from the tailings and cave, and, being of some interest, were at various times packed up and sent to the British Museum, Clark et al. (1947) tested the lead and zinc content of the skull and postcranial bones. Only lead was being smelted at the Broken Hill mine in 1921 when the skull was found and the discarded material thus comprised zinc impregnated material. Clark et al. (op cit.) therefore resolved to test the possibility of association of the post cranial material. Microsamples of all bones and the artefacts from the Broken Hill mine held at the BMNH were assayed for their lead and zinc content. The results were:

- the skull is **high in zinc** (my emphasis) and the matrix inside the skull contains no lead;
- the maxilla is **low in zinc** and high in lead;
- one left femur and the left tibia are **low in both lead and zinc**
- the sacrum, the 2 innominates, humerus, right femur and the immature parietal are high in lead and very **low in zinc**, (op. cit. 10).
- the animal bones are high in lead although where matrix is identified it is higher in zinc.

Clark et al. (op. cit.) proposed an association of the maxilla with the left femur, the sacrum, and the male innominate as they have similar proportions of lead and zinc. Despite the difference between these and the lead/zinc ratios of the skull and tibia, they concluded that together they form one contemporary group, in defiance of the fact that the skull is the only bone to be high in zinc, while all the others are either high in lead or contain equal proportions of lead and zinc. In other words, I would conclude that there is no support for the skull to have been associated with any of the postcranial material based on its mineral content. The postcranial material from Kabwe should not be used to assess the phylogenetic position of the cranium.

The deeply inclined cleft (Appendix 6) from which Kabwe had been extracted was inundated with water each wet season, forming a well. Seasonal soaking of the Kabwe skull means that it cannot be reliably be dated by Electron Spin Resonance, and, as the site no longer exists, dating methods such as potassium-argon cannot be applied. We therefore do not know the date for Kabwe.

The results of the metric and cladistic analyses in this study suggest that Kabwe represents a separate lineage to others in the study. Of particular importance, it cannot be argued from the cladistic results that Kabwe is phylogenetically related to Bodo, despite both of them being often placed in *H. heidelbergensis*. If Kabwe is indeed on a separate lineage within *Homo*, then the available name is *H. rhodesiensis* (Smith-Woodward, 1921). It is characterised by a glabella region that is neither depressed nor protruding; strong metopic keeling that has parallel edges; parietal bosses; high temporal squama in relation to vault; posteriorly sloping orientation of main axis of tympanal in *norma lateralis*; and nasospinale lies behind rhinion. It is probably more closely related to Daka, Ceprano, and Bodo, branching before these, than to the OTUs that branch earlier in the tree (Chapter 3; Figure 3.50). It has a large ECV of 1185 (Holloway, 2000).

4.10 Daka, Ceprano, Bodo, Buia

Ceprano, Daka and Bodo have variously been attributed to *H. erectus*, or *H. heidelbergensis* (*H. rhodesiensis*) or have been thought phylogenetically related to each other in some way.

The large, robust, cranial morphology of Bodo (0.64 ± 0.04 – 0.55 ± 0.03 Mya; Conroy et al., 2000) has resulted in inconclusive discussions about its attribution. When first describing it, Conroy et al. (1978) refrained from a taxonomic determination, but observed similarities to *H. erectus* and to the more derived Broken Hill skull (Kabwe or *H. rhodesiensis*); they stressed the potential for Bodo to document a *H. erectus/H. sapiens* transition. Stringer (1984) placed the skull in *H. erectus* but he qualified this significantly by observing Bodo's more derived *H. sapiens* features, such as a large cranial capacity, relatively high vault, and more derived supraorbital torus morphology. Adefris (1992) also recognised Bodo's more derived characters and placed Bodo in the (taxonomically unsatisfactory) group 'archaic *Homo sapiens*'[16]. Rightmire (1995) noted Bodo's *H. erectus* characteristics, but pointed out that some characters appear in 'archaic' *H. sapiens*, such as expansion of the parietal walls relative to bi-temporal breadth, high squamosal suture, and parietal bossing.

The Ceprano calvaria (Italy; > 700 Kya and probably slightly over 800 Kya; Ascenzi et al., 1996) is roughly contemporaneous with Daka and Gran Dolina, and somewhat older than Bodo. Ascenzi et al. (op. cit.) attributed Ceprano to *H. erectus* although differences from *H. erectus s. s.* were noted, e.g. a larger cranial capacity (1185cc compared to not more than 1000 for Javan *H. erectus*; Rightmire, 1990), no sagittal keel or parasagittal depression on frontal squama, and a lessened post orbital constriction (Ascenzi et al., 1997). Mallegni et al. (2003), however, proposed a new species for Ceprano, *H. cepranensis*, based upon their assessment that it possesses a unique suite of characters, identified from a cladistic analysis in which Ceprano is sister taxon to Daka, and this clade is monophyletic with a group comprising Arago, Petralona, Kabwe, Saldhana and Bodo. The only other species known from Europe at this time is that represented by the juvenile attributed to *H. antecessor*, Gran Dolina (ATD6-69; Spain; Bermúdez de Castro et al., 1997). Although no comparable parts of this specimen and of Ceprano are represented, Manzi et al. (op. cit.) predicted that affinities will emerge with Ceprano,

[16] This term was used for a relatively short period to set Middle Pleistocene non-*H. erectus* hominins apart and to emphasize their closer phylogenetic relationships with *H. sapiens* within a theoretical framework for human evolution that included an ancestor-descendant relationship of *H. erectus* to *H. sapiens*.

suggesting that this cranium would describe the adult form of *H. antecessor*. I examine this proposal below (Gran Dolina section).

Daka (Ethiopia), dated to 1.042 ± 0.009 Mya (Asfaw et al., 2002), was attributed to *H. erectus* when announced by the describers who proposed a single evolving species, *H. erectus,* that includes KNM-ER 3733/KNM-ER 3883, OH 9, Daka, Buia, and Bodo. The only challenge to this hypothesis, as discussed above, is Mallegni et al.'s (2003) view that Daka is monophyletic with Ceprano.

Because Daka, Ceprano and Bodo are proposed to have been phylogenetically related (op. cit.), or, alternatively, may represent *H. erectus* (Asfaw et al., 2002), I tested for a phylogenetic relationship between them and for a relationship between them and *H. erectus*; and for a relationship between them and Kabwe (*H. rhodesiensis* in these analyses).

The results show that Daka and Ceprano form a clade, to which Bodo is sister taxon. This clade is on a separate branch from *H. rhodesiensis* (Chapter 3; Fig 3.26). The T-PTP for a Ceprano/Daka clade is p = 0.04, and they share five possible synapomorphies: frontal edge is linear in *norma verticalis* (parallel with Dmanisi, *H. sapiens*), there are two 'mono-tori'(parallel with KNM-ER 1813), presence of angular tuber, posterior part of tympanic joins anterior of mastoid process, and a very prominent entoglenoid formation. The T-PTP for the Daka/Ceprano/Bodo clade is again p = 0.04, suggesting that it is unlikely that the OTUs came together by chance alone. The clade shares the possible synapomorphies: the frontal edge is linear in *norma verticalis*; the supraorbital torus is interrupted in the medial zone, forming two 'mono-tori'; the posterior of tympanic joins the anterior part of the mastoid process; there is an angulation between the pre-glenoid planum and the posterior slope of the articular tuberculum; and the supraorbital margin is thick, rounded and not demarcated from the roof of the orbit.

I could here hypothesise that Daka and Ceprano shared an immediate common ancestor, and Bodo shared a common ancestor with Daka and Ceprano, and that they do not share a common ancestor with *H. rhodesiensis* or *H. erectus*, or any other OTU in the analyses, but before doing so, I will examine the results of tests for other hypotheses for each OTU.

4.11 Daka

When Daka and *H. erectus s. s.* were constrained, the tree was 4 steps longer than the most parsimonious, and there was no T-PTP support (p = 0.27). That is, it would be difficult to argue that Daka shared a unique common ancestor with *H. erectus.* Asfaw et al. (op. cit.), however, also include KNM-ER 3733 and KNM-ER 3883 in their definition of *H. erectus.* I therefore tested for a phylogenetic relationship between Daka and these OTUs, to assess whether they might share a common ancestor which would be a requirement to satisfy Asfaw et al.'s (op. cit.) morphocline hypothesis for *H. erectus*. I initially constrained Daka with these OTUs in a separate analyses (as KNM-ER 3733 and KNM-ER 3883 did not form sister taxa in my Turkana analyses, above). In each case, the trees were considerably longer than the shortest tree for Daka (7 and 8 steps respectively; Figure 3.30). When Daka was constrained with both KNM-ER 3733 and KNM-ER 3883 (to test Asfaw et al., 2002 using their hypothesis regarding the relationship between KNM-ER 3733 and KNM-ER 3883) the tree was 7 steps longer than the most parsimonious (Figure 3.30). That is, there is no phylogenetic relationship between Daka and KNM-ER 3733 or KNM-ER 3883, other than belonging in the genus *Homo*.

4.12 Ceprano

I tested Ceprano and *H. erectus s.s.*, and Ceprano and *H. rhodesiensis*. When Ceprano and *H. erectus* were constrained, the tree length was 8 steps longer than the shortest tree for Ceprano (Figure 2.31); and when Ceprano and *H. rhodesiensis* were constrained, the tree was also 8 steps longer (Figure 3.32). It is unlikely, then, that Ceprano shared an immediate common ancestor with *H. erectus s.s.* or *H. rhodesiensis.*

4.13 Bodo

When Bodo was constrained with *H. erectus* (Figure 3.28) the tree was 4 steps longer than the shortest for Bodo; and the Bodo/*H. erectus* clade had a T-PTP of p = 0.18. When Bodo was constrained with *H. rhodesiensis* the tree was 9 steps longer (Figure 3.27). That is, neither the hypothesis is supported in these cladistic analyses.

The most parsimonious solution for Ceprano, Daka and Bodo is that they form a clade. Mallegni et al. (2003) had a comparable result from their analyses and named the Ceprano

OTU *H. cepranensis*. While I here propose that Daka shares a common ancestor with Ceprano, it differs from Ceprano in that, while it has the same parallel-sided cranial walls that angle steeply from the temporal lines, the cranium does not contract inferiorly and the widest part of the cranium is low. Put another way, Ceprano appears to be the earliest of the early hominin crania to have a somewhat expanded upper braincase, while Daka retains the more primitive condition with the greatest width low on the cranium. Daka does, however, express some characters associated with an expanded braincase: reduced post-orbital constriction, a rounded occipital, relatively high contour of the temporal squama and some parietal bossing (after Rightmire 1995:32). That is, Daka is more derived than earlier taxa and *H. rhodesiensis* but is not as derived as *H. cepranensis*.

Bodo, somewhat younger than Daka and Ceprano, shares a common ancestor with them. It does not form a clade with *H. erectus*, *H. ergaster*, KNM-ER 3733, KNM-ER 3883, Dmanisi or *H. rhodesiensis*.

None of the crania, however, cluster in the morphometric analyses. Rather, Bodo and Kabwe (*H. rhodesiensis*) cluster; and Daka and Sangiran 17 cluster. Each cluster is similar in its vault width:maximum supraorbital breadth relationships, and Daka/Sangiran 17 showing most extreme supraorbital breadths. Ceprano is well separate from these clusters; it has a relatively wide vault and a narrower supraorbital width. That is, despite their relatively close phylogenetic relationships, Daka, Ceprano and Bodo show fairly broad differences in some cranial shape attributes, indicating a relatively large degree of variation within this group.

4.14 Buia

The Buia cranium from Eritrea (Abbate et al., 1998) has not been fully described and is hence unavailable for study (Lorenzo Rook, pers. comm. 2004). It is estimated to date from 992 Kya (Albianelli et al., 2004) and is thus close to Daka (1.042 ± .009 Mya; Asfaw et al., 2002) in geological age. The remains comprise a cranium and a large part of the facial skeleton and the base (Macchiarelli et al., 2004); and a left symphysis, that shows that Buia is a male (Bondioli et al., 2006). Preliminary descriptions (Abbate et al., 1998; Macchiarelli et al., 2004) indicate that the braincase is very long (204mm) compared to its width (130mm), and is relatively high (Abbate et al., 1998).

Buia and Daka share many similarities. While the Buia cranium is longer than Daka (180mm; Asfaw et al., 2002), both have an ECV of 995 cc (Daka, op. cit.; Buia, Macchiarelli, 2004). In lateral view the frontal profiles are rounded and rise relatively steeply from the supraorbital sulcus; the occipital profiles are rounded with an incipient bun. In frontal profile, both crania are widest inferiorly and have relatively straight-sided parietal walls but Buia's lateral walls converge inferiorly reminiscent of Ceprano. Both Buia and Daka have reduced post-orbital constriction. The only section of the supraorbital available for Buia, the right lateral half, closely matches the form of the same region on Daka. There are, then, a number of phenetic similarities between these almost contemporaneous *Homo*, that lived 600 kms apart in the Danakil Depression, making it difficult to argue that they are from separate populations. A more detailed comparative analysis may show otherwise, of course, when Buia is available for study.

Buia and Ceprano also share a number of similarities: the parietals converge slightly inferiorly (Buia: Macchiarelli, 2004; Ceprano, pers. obs.); they have a small depression on the same area laterally on the front of the supraorbitals (Ceprano, pers. obs.; Buia, Macchiarelli et al., 2004, Fig 1); on both the frontals rise steeply; supraorbitals are interrupted at glabella (Buia: Macchiarelli, op. cit.); they have reduced post-orbital constriction; mastoid processes are short and broad; there are only modest external occipital protrusions, and slight angular tori. Ceprano has a slightly greater ECV, of 1185cc (72cc larger than Buia and Daka). They differ, however, in that the temporal lines on Buia disappear early on the parietals, whereas Ceprano's temporal lines continue to asterion; Buia does not have an occipital torus (Macchiarelli, 2004), whereas Ceprano does; glabella is in a forward position on Buia (op. cit.), while this area is depressed on Ceprano; and Buia has an occipital 'bun' (Fig 2b, Abbate et al., 1998), which is absent on Ceprano.

I propose that Daka shared a common ancestor with Ceprano but is not as derived, and they shared a common ancestor with Bodo, a chronologically younger specimen that nevertheless appears less derived despite its cranial expansion. Daka and Buia, which are fairly contemporaneous, and Ceprano and Buia, share many phenetic similarities, but tests

for any phylogenetic relationships between Buia and these OTUs must await a full description of Buia.

4.15 Gran Dolina (ATD 6-15 + 6-69)

Gran Dolina comprises six individuals (Bermudez de Castro, 1997), dated to 780 – 857 Kya by Falguèrès (1999); this study includes ATD6-69 (partial face) and the frontal (ATD6-15) from the same individual. The remains were attributed to a new species, *H. antecessor* (Bermúdez de Castro et al., 1999). In 2008 Bermúdez de Castro et al. (2008) revised their assessment of Gran Dolina, in light of evidence from a new mandibular specimen – a young adult – ATD6-113. In their view the latter is almost identical to an earlier mandible, ATD6-5 (same location of the lateral prominence, position of mylohyoid line in relation to the alveolar margin, relief of the pterygoid fossa, position of the plane of the postmolar trigone, relief of the masseteric fossa, depth of the posterior subalveolar fossa, and spatial relationship between M_3 and the ascending ramus (op. cit.)). ATD6-113 has a derived morphology compared to *H. habilis*, *H. rudolfensis,* Dmanisi mandibles, *H. ergaster*, and most of the Sangiran mandibles (*H. erectus*) (op. cit.). That is, in their view Gran Dolina represents a different lineage from African and Asian species. Bermúdez de Castro et al. (2008) also noted that ATD6-113 does not have the apomorphic features of European Pleistocene hominins (op. cit.). (ATD6-113 was published very recently and is not included in the analyses).

Although Gran Dolina (ATD6-5) formed a clade with *H. sapiens* in the shortest tree, I consider that this most likely resulted from its juvenile characters, particularly the lack of a supraorbital torus. I therefore omitted *H. sapiens* from the Gran Dolina cladistic analyses.

The subsequent analyses yielded no single most parsimonious solution for Gran Dolina (Figure 3.36); there are five shortest trees in which it is either on separate lineages at different places on the tree, or forms a clade with KNM-WT 15000 (*H. ergaster*) or *H. erectus*. There is, however, no T-PTP support for a close phylogenetic relationship between Gran Dolina and the latter OTUs. I tested for a relationship between Ceprano and Gran Dolina (tentatively suggested by Manzi et al. (2001) as a possible alternative to

Ceprano representing a new species), by constraining them to form a clade, but the tree length was longer by six steps and the T-PTP for the clade was p = 0.81. This, then, does not support a proposal that there might be a close phylogenetic relationship between Gran Dolina and Ceprano, although the different personal ages must be borne in mind. When the preferred phylogeny for all taxa is resolved (Chapter 3; Figure 3.50) Gran Dolina is on a separate lineage that branches after *H. rhodesiensis* and before the Daka/Ceprano/Bodo clade. While it is difficult to know how much weight to give to this phylogenetic position given that Gran Dolina is a juvenile, and is relatively unstable on the tree, it appears to be more derived than *H. habilis*, *H. georgicus*, *H. erectus*, KNM-ER 3733, KNM-ER 3883 and *H. rhodesiensis*. Its phylogenetic position could be further refined should Middle Pleistocene *H. neanderthalensis* be included in analyses; and when adult crania from the Gran Dolina site are discovered and described.

4.16 Olduvai Hominid 12

The OH 12 calvaria is too fragmentary to be included in the metric or cladistic analyses. It was found on the surface of Bed III, Olduvai Gorge, but a gritty matrix adhering to the fragments suggested that the material originated in Lower Bed IV (M. Leakey, 1971:230). It appears, then, to be contemporaneous with *H ergaster* (Tighenif population, at least) and the KNM-ER 3733/KNM-OL 45500 lineage.

Overall, Antón (2004) found that the greatest facial similarities of OH 12 are with KNM-ER 3733 in the supraorbital torus, glabella region, interorbital breadth, and occipital torus. I therefore looked into whether OH 12 shared other similarities with KNM-ER 3733 (Table 12; columns 1, 2) and found that there are also similarities in the mastoids and naso-alveolar clivus. There are, however, many cranial differences: in nuchal line form; position of temporal lines; form of auditory meatus; route of lambdoid suture; and presence/absence of suprameatal crests and postglenoid processes – which might weigh against any suggestion of overall similarity.

Table 12: characters available for OH 12 compared to KNM-ER 3733, KNM-OL 45500, and OH 9. N/a = character not available; ? = character not discernable.

OH 12. Antón (2004); Schwartz and Tattersall (2002).	KNM-ER 3733; after Antón (2004), Schwartz and Tattersall (2002).	KNM-OL 45500. pers. obs.	OH 9. pers. obs.; Schwartz and Tattersall (2002).	Notes
Continuous torus	Yes	Yes	No – separated at glabella	
Continuous and wide supratoral sulcus	Yes	Yes	Yes	different from KNM-ER 3883 and D2280
Broad interorbital	Yes	Yes	Yes	Similar KNM-ER 3883
(likely)Non-projecting glabella	Yes	Likely	Indented	
Convex lateral malar region	N/a	N/A	N/a	
Flat infraorbital plate	N/a	N/A	N/a	
Swelling at bregma	N/a	No	N/a	
Occipital torus	Yes	N/a		
Sharply angled medial superior orbital	No	No	No	KNM-ER 3733; KNM-OL 45500 rounded
Extremely thick bone	?	Yes	Yes	
Nasoalveolar clivus long and anteriorly sloping	Yes	N/a	N/A	
Steeply, inwardly sloping nuchal plane	Yes	N/a	Yes	
Thin, bow-shaped superior nuchal line	No	N/a	Yes	KNM-ER 3733 keel-like ridges
Shallow, scallop shaped depressions	Yes	N/a	Yes	

either side of occipital protuberance				
Skull would have been broadest across mastoids	yes	N/a	Yes	
Temporal line low on side of skull	No	No	No	3733 well above squamosal suture; OL 45500 high on skull (Potts et al., 2004; Fig 1A)
Lambdoid suture rose steeply from asterion; probably arced smoothly across lambda	No	N/a	?	KNM-ER 3733 apex at lambda
Mastoid process thickened externally, downward pointing, not projecting or long a/p	Yes	?	?	
Large auditory meatus	No	?	Yes[17]	
Postglenoid plate probably	No	N/a	Yes	
No suprameatal crest	No	?	No	KNM-ER 3733; OH 9 have crests

As Antón (2004) found similarities between OH 12 and KNM-ER 3733, and KNM-ER 3733 and KNM-OL 45500 formed a supported clade in my cladistic analyses, it also seems useful to compare KNM-OL 45500, KNM-ER 3733, and OH 12 (Table 12) for those characters available in all. Of the synapomorphies for the latter group (depression at glabella; strong mastoid crest; sigmoid shape of posterior edge of the tuberculum articular in *norma basilaris*; and entoglenoid is marginally extended posteriorly), only the mastoid

[17] I superimposed a cast of OH 12d (Antón, 2004) over a cast of OH 9; it is clear the OH 9 auditory meatus has a larger diameter.

and glabella are available for OH 12. OH 12 has a mastoid crest, but information about a depression (or not) is not available.

While it can be seen that the three crania have similar supraorbital and supratoral forms, non-projecting glabella, and broad interorbital regions (Table 12), and that KNM-ER 3733 and KNM-OL 45500 differ from OH 12 in the available orbital characters, there are very few other comparative cranial characters available for all three. No conclusions, then, can be made about any possible phylogenetic relationships between them at this stage.

As OH 9 is also from Olduvai Gorge, although dated to 1.4 – 1.5 Mya and therefore considerably older than OH 12, I investigated whether OH 12 has the derived character states of OH 9 (Table 12a).

Table 12a. OH 9 derived characters compared to OH 12.

Derived character states of OH 9	Present on OH 12?
0 = a>b, b<c and a < c	n/a
No external occipital protrusion	n/a
Continuity of the supramastoid crest with the inferior temporal line	n/a
Strong mastoid crest	Yes
Continuity between mastoid crest and superior temporal line	n/a
Presence of suprameatum spine	n/a
The tympanal makes up most of the wall of mandibular fossa	n/a
Mastoid projects below base	n/a
Space between the tympanal and anterior of mastoid process forms a 'split'	Yes
Groove between entoglenoid formation and tympanic plate	n/a
Anterior wall of mandibular fossa almost vertical	n/a
Very prominent entoglenoid formation	n/a

It can be seen that only two of the derived characters for OH 9 are available for OH 12, and that they share these characters: a space between the tympanal and anterior of mastoid process forms a 'split'; and strong mastoid crest. The supraorbital for OH 12 is moderately tall (superiorly/inferiorly) which differs from the very tall supraorbital torus on OH 9 but

they have comparable posttoral planes. OH 12 and OH 9 are similar in other respects (Table 12): a broad interorbital; extremely thick cranial bone; steeply, inwardly sloping nuchal plane; thin, bow-shaped superior nuchal line; shallow, scallop shape depressions either side of occipital protuberance; skull broadest across mastoids; large auditory meatus; and (probably for OH 12) a postglenoid process. They differ in ECVs, superior orbital borders, and position of the temporal lines. As OH 12 and OH 9 share two possible synapomorphies, and many other similarities, it is just possible that they are phylogenetically related.

4.17 Homo floresiensis

The hominin bones from Liang Bua cave on the island of Flores in Indonesia (Brown et al., 2004) are in stratigraphic levels dated to between 13.4-10.2 Kya and about 100 Kya (Roberts et al., 2009); that is, they represent a population that existed for a period of approximately 86,000 – 90,000 years. A critically important component of the assemblage is a partially articulated skeleton, Liang Bua 1 (LB1), found at 6 m depth and bracketed by calibrated radiocarbon ages of between 19.0 Kya and 17.1 Kya (op. cit.).

The species is characterised by small endocranial volume (417cc; Falk et al., 2005) and short stature (106 cm; Brown et al., 2004) similar to *Australopithecus afarensis*; and robust limb bones similar to the australopithecines. Unlike *Australopithecus afarensis*, however, *H. floresiensis* shows more derived states such as reduced prognathism and facial height, along with smaller postcanine teeth. Indices of cranial shape, including for example maximum cranial breadth at the supramastoid region and a broad vault relative to height, reflect those for *H. erectus* (Brown et al., 2004).

That an apparently primitive hominin survived until relatively recent times appears to violate two paradigms of human evolution. The first stipulates that the specimens from Dmanisi (~1.77 Mya; Rightmire et al., 2006), who had modern body proportions (Lordkipanidze et al., 2007), were the earliest member of our genus to emerge from Africa. The existence of *H. floresiensis* in South East Asia could indicate that a more primitive hominin emerged from Africa (Morwood et al., 2005; Argue et al., 2006). The second major paradigm, that *H. sapiens* was the sole remaining species of *Homo* since the

demise of *H. erectus* in Asia and *H. neanderthalensis* in Europe around 30,000 years ago, is also contradicted by *H. floresiensis*. That a hominin lineage is hypothesized to have emerged in the Early Pleistocene and continued living, to the best of our knowledge, until the terminal Pleistocene, that is, 1.3 - 1.8 million years after its hypothesised first appearance, and well after the arrival of *H. sapiens* in the region, is an extraordinary concept in palaeoanthropology.

These discoveries generated a robust body of papers, setting the stage for opposing views. Alternative interpretations include the possibility that the Liang Bua fossils represent a new hominin species, *H. floresiensis* (Brown et al., 2004; Morwood et al., 2004, 2005; Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007; Baab et al., 2009) or that the holotype specimen, LB1, was a modern human, possibly afflicted with a pathological condition (Henneberg and Thorne, 2004; Jacob et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al., 2008). These conflicting hypotheses are based on comparative analyses of the morphology of the bones with both archaic and modern *Homo*, generally using statistical methods to compare the Liang Bua bones with other hominins.

I tested the hypotheses that *H. floresiensis* is an archaic species of *Homo*, and that it is *H. sapiens*. The cladistic analyses found seven trees of equal length for *H. floresiensis,* but six of these included an unsupported clade (Dmanisi/KNM-WT 15000). In all trees, including the most parsimonious (Chapter 3; Figure 3.39) *H. floresiensis* is at the base of the genus *Homo*.

The mandibular cladistic analysis also shows *H. floresiensis* towards the base of the *Homo* clade. The two *H. floresiensis* mandibles form a clade with 96% bootstrap support; they are on a separate lineage to any other OTUs in the analysis and share a number of synapomorphies (the sigmoid notch deepest towards condyle; marked muscle scarring on the ramus; the mylohyloid ridge is bulbous superiorly/inferiorly (parallel with KNM-ER 992); lateral prominence is under M^2 (*H. pekinensis* polymorphic); the origin of the *sulcus extramolaris* is at central posterior edge of alveolus at M^3 (parallel with KNM-WT 15000, D211); and double mental foramina (parallel with KNM-WT 15000, D211)).

The two other hypotheses for *H. floresiensis* are that it is *H. sapiens*, and that it is derived from *H. erectus*. Those who oppose *H. floresiensis* as a new species propose that it is either a dwarfed *H. sapiens* or is a modern human with pathology; and typically focus only on the one specimen, LB1 (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al. 2008). As pygmoid or pathological modern humans would not be outside the normal range of modern *H. sapiens*, I do not include these in the comparative sample. My cladistic analyses show no support for *H. floresiensis* and *H. sapiens* sharing a unique common ancestor. Specifically, tree lengths are considerably longer when such a clade is interjected, and the T-PTP test does not support *H. floresiensis* and *H. sapiens* as sister taxa or sister OTUs. Just as importantly, *H. floresiensis* has several characters that are, to my knowledge, never observed in *H. sapiens*. It has internal mandibular buttressing comprising a sub-alveolar plane with inferior and superior transverse tori (Brown et al., 2004; DA pers. obs.) with no external mandibular buttressing. *H. sapiens'* mandibular buttressing is on the external symphysis only, never internally, and takes the form of a chin which has a distinctive inverse "T" formed by a raised central keel that flows into a distended inferior margin (Schwartz and Tattersall, 2000), and all *H. sapiens* have this (op. cit.) regardless of any degree of projection or retrenchment of the chin. *Homo floresiensis* also has marked, sharp ridges and relatively deep longitudinal furrows in the palate; strongly developed nasal pillars; supraorbital and occipital tori; the cranium is widest at biauricular region, while the cranium of *H. sapiens* is widest at the parietals; and relatively long arms in relation to legs, outside the range of modern humans (Brown et al., 2004; Argue et al., 2006). As my cladistic analysis shows, *H. floresiensis* and *H. sapiens* are unlikely to be sister taxa, and *H. floresiensis* has characters that are not found on *H. sapiens*. On this basis, I strongly reject the hypothesis that *H. floresiensis* is *H. sapiens*, either with or without pathology.

That *H. floresiensis* is the end product of a long period of isolation of *H. erectus* was the original hypothesis for *H. floresiensis* (Brown et al., 2004) but it was later modified in the light of further information (Morwood et al., 2005). The evidence of a new humerus and ulna, along with the previously described femur, tibia and pelvis, enabled Morwood et al. (op. cit.) to estimate limb and body proportions for LB1. The humerus and ulna are long relative to femur length, with an estimated the humerofemoral index (humerus length x 100)/femur length) of 85.4 (equal to *A. afarensis* AL288-1) (op. cit.). Although the

postcrania of *H. erectus* are poorly known, body proportions for *H. erectus* probably approximate means for adult modern humans for most limb shaft proportions (Ruff and Walker, 1993; Haeusler and McHenry, 2004). Furthermore, limb bones are robust relative to length and differ from predictions for *H. sapiens* of similar body size. Specifically, femur robusticity falls in the range of *Pan paniscus* with humerus robusticity midway between *Pan paniscus* and *H. sapiens* (Morwood et al., 2005). Based on these observations, Morwood et al. (op. cit.) concluded that *H. floresiensis* is not an allometrically scaled *H. erectus*.

Nevertheless Lyras et al. (2008) argue for island dwarfing of *H. erectus*. The Island Rule stipulates that insular dwarfism of large mammals may occur when a founder population reaches an island and becomes reproductively separated. In the case of *H. floresiensis*, the assumed founder population is *H. erectus*, the only known early hominin candidate in South East Asia. The stature for *H. erectus* is generally assumed to be similar to *H. sapiens*, based upon the almost complete sub-adult skeleton of a related species, *H. ergaster*, from Koobi Fora, Africa, KNM-WT 15000, whose height is estimated to be ~1.60m (Ruff and Walker, 1993) although stature estimates from other postcranial remains attributed to *H. ergaster* are between 157cm and 171cm (females) and 180cm - 181cm (males) (McHenry, 1991). *H. erectus* cranial capacity is between 813 cc and 1059 cc (Sangiran crania; Holloway, 1981). That is, estimated stature and cranial capacity of *H. erectus* are far greater than for *H. floresiensis*.

To invoke the Island Rule to explain the morphology of *H. floresiensis* necessitates an ancestor-descendant phylogenetic relationship between *H. erectus* and *H. floresiensis*. This relationship cannot be supported based solely on Lyras et al.'s (2008) geometric morphometric comparisons of the LB1 skull with skulls of *H. sapiens*, Sangiran 17 (*H. erectus*), KNM-ER 1813 (*H. habilis*), and Sts 5 (*A. africanus*): their analysis, in fact, shows that *H. floresiensis* and *H. erectus* are *separated* on Principal Component Axis I (PCI), while *H. habilis* appears to be most similar to *H. floresiensis* on this axis (Lyras et al., 2008 Figure 3; cf. Baab and McNulty, 2009). On PCII three hominins appear to cluster, namely *H. floresiensis*, *A. africanus* and *H. erectus* (Lyras et al., 2008 Figure 3). The Principal Components Analysis fails to support the conclusion for exceptional phenotypic similarities between *H. floresiensis* and *H. erectus*, although a weighted pair-

group cluster analysis based on Euclidean distances does group *H. floresiensis* with Sangiran 17.

Beyond Lyras et al.'s hypothesis and empirical results, the status of the "Island Rule" remains poorly established (Lawlor, 1982; Meiri et al., 2008). Meiri et al. (op. cit.) found no evidence for a general rule: while there appear to be some clade-specific patterns in island rodents, carnivores, and lagomorphs, they found few significant factors affecting insular size. Insularity does not result in simple patterns of size change, and there is enormous variation in size evolution, rather than a general rule for morphological change in island environments. Island area, island isolation, species trophic level, and carnivore numbers do not appear to affect body size (op. cit.). Other studies show that there are contradictory explanations for size reduction or increase in mammals on islands (see Dayan and Simberloff, 1998; Sondaar, 1977; Heaney, 1978; Melton, 1982; Libois et al., 1993; Wassersug et al., 1979). Consequently, the causes and effects of the 'rule' on mammals are far from resolved. Nevertheless, as the hypothesis that *H. floresiensis* as a dwarfed form of *H. erectus* remains viable, the idea that *H. floresiensis* and *H. erectus* are sister taxa should be evaluated.

For this hypothesis to be sustained in the cladistic analysis, *H. floresiensis* and *H. erectus* would be expected to form sister OTUs with T-PTP support. In other words, the analyses must demonstrate that they share a common ancestor. The results of the cladistic analyses, however, show the shortest tree with a constrained *H. floresiensis/H. erectus* clade is 4 steps longer than the most parsimonious and the T-PTP is $p = 0.53$ – the clade is likely to form by chance alone. It is unlikely that *H. floresiensis* and *H. erectus* shared a common ancestor and I would argue against any close phylogenetic relationship between these species and cannot support the *H. erectus* island dwarfing hypothesis.

I examined other possible phylogenetic relationships for *H. floresiensis*. Despite some morphological similarities with *Australopithecus*, *H. floresiensis* does not share an immediate common ancestor with either *Australopithecus africanus* or *Australopithecus afarensis*. The trees in which *H. floresiensis* was manoeuvred to form a clade with each of these are also considerably longer than the most parsimonious and, again, lack T-PTP support. Finally, I tested for possible phylogenetic relationships of *H. floresiensis* with *H.*

habilis and the hominins from Dmanisi, but again, the relevant trees were longer than the most parsimonious trees, and unsupported.

Cranial shape changes may be correlated with size and these compounding effects of allometry might have affected the outcome of this cladistic analysis, especially as the LB1 cranium is so small compared to most of the other hominids. A problem with dealing with allometry in analyses such as this is that we do not know *a priori* which characters might be influenced by size. Gilbert and Rossie (2007) have recently presented a method by which control for body size can be managed in cladistic analyses without loss of phylogenetic information, performing Pearson correlation analyses of all isometrically size-adjusted shape characters against geometric mean of all cranial measurements. Those characters that were found to be allometrically influenced were then subjected to a coding procedure aimed at offsetting the effects of allometry. Gordon et al. (2008) also recognised that metric analyses might be affected by scaling relationships for crania as small as LB1, and they scaled variables from modern humans to the size of LB1 to test this possibility. They found that the LB1 cranial shape is even more distinct from modern human cranial shape when scaling is taken into account, concluding that LB1 cannot lie within the range of shape of nonpathological modern humans. Gilbert and Rossie (2007) used metric-based cladistic characters, and Gordon et al. (2008) use statistical methods when testing for scaling relationships. I, on the other hand, use qualitative characters such as presence or absence of a trait, or the form of a trait. Just how scaling can be dealt with when morphological, rather than morphometrical, characters are used, is unclear, but as scaling relationships did not affect the outcome of Gordon et al.'s (op. cit.) analyses for LB1 I suggest that my analyses are unlikely to be affected by scaling issues.

The morphometric analysis of *H. floresiensis* shows that it differs metrically from other species in the analysis. Compared to *H. habilis*, *H. floresiensis* is less prognathic (basion-prosthion length) in relation to its cranial height. It differs from KNM-ER 3733 and Sangiran 17, which are larger and have a greater degree of prognathism; and from *H. sapiens* which have greater vault height and reduced prognathism. Although LB1 is overall a smaller cranium than Dmanisi D2700, the two are similar in their degree of prognathism in relation to vault height, but there is no support for a phylogenetic relationship between them in the cladistic analyses.

I hypothesise that *H. floresiensis* is a late surviving species of *Homo* relatively little changed from an ancestral form that separated either in the Late Pliocene or in Early Pleistocene. This crucial conclusion has major implications for our understanding of the evolution of our genus. More specifically, these results strongly imply that:

- A very early member of the *Homo* lineage diffused from Africa to Indonesia; this species was more primitive than our current paradigm - that *H. georgicus* was the first species to emerge from Africa - proposes. I cannot say when diffusion occurred, but, assuming it was before the evolution of *H. habilis*[18] this may have been as early as 1.9 Mya (Feibel et al., 1989; Feibel et al., 2009)
- This very early member of the *Homo* lineage survived on Flores until between 13.4-10.2 Kya at the very least (Roberts et al., 2009). We do not know when it arrived in South East Asia, only that its earliest appearance at Liang Bua could be as late as ~ 100 Kya (Roberts et al., 2009). Nevertheless, it is clear that an early species of *Homo* existed at the same time as *H. sapiens* in the same region (although evidence from the Liang Bua excavations suggest that on Flores *H. sapiens* appeared after *H. floresiensis*). We had thought that *H. sapiens* was the sole remaining member of our genus since the demise of *H. neanderthalensis* in Europe and *H. erectus* in Asia, at around 30,000 years ago.
- The hypothesis that *H. floresiensis* is a very early hominin from the late Pliocene or Early Pleistocene would predict a greater range of hominin variation during the Early Pleistocene than hitherto has been conceptualized by hypotheses of human evolution. *H. floresiensis* has an extremely small stature (106 cm; Brown et al., 2004) similar to the "Lucy" specimen of *A. afarensis* (105 cm; McHenry, 1992) and a little shorter than *A. africanus* (estimated 110-134 cm; McHenry, 1991) and a small cranial capacity estimated at 417 cc (Falk et al., 2005, 2009) which is within the *A. afarensis* range of 343 cc (AL 333-45; Falk, 1987) to 500 cc (AL 444-2; Johanson and Edgar, 1996). The cranial capacity and stature of *H. floresiensis* fall outside the known ranges for *Homo*, taking the size of *H. habilis*, the earliest species of *Homo*, as a "Rubicon", or immutable lower limit, for the stature and cranial capacity (600 cc; Leakey et al., 1964; although the ECV for KNM-ER 1813 is

[18] And assuming non coexistence between *H. floresiensis* and *H. habilis*.

505cc, Holloway et al., 2004) for our genus. *H. floresiensis* has, however, been placed in *Homo* (Brown et al., 2004) and my analyses strongly support its placement within this genus. To place a hominin with a cranial capacity of 417cc in *Homo* might be considered a very challenging proposal, but Falk et al. (2005; 2009) have shown that the brain had an expanded prefrontal cortex and temporal lobes relative to fossil hominins and the capacity for higher cognitive processes.

In summary, there is no evidence of a close phylogenetic relationship of *H. floresiensis* to *H. sapiens*, and I reject the idea that the Liang Bua remains represent a pathological modern human. I am also unable to link *H. floresiensis* phylogenetically to *H. erectus*, rejecting the hypothesis *H. floresiensis* resulted from insular dwarfing of the latter. My results support *H. floresiensis* as a new species (Brown et al., 2004; Morwood et al., 2005) and favor the hypothesis that it descended from an early species of *Homo* (Falk et al., 2005; Argue et al., 2006; Larson et al., 2007; Tocheri et al., 2007). *H. floresiensis* challenges several paradigms in human evolution and may cause us to revise our hypotheses for the evolution of our genus.

4.18 Phylogeny of the Early Pleistocene hominins

I synthesised the outcomes of the cranial cladistic analyses discussed in this chapter. The shortest tree (Figure 3.48) was not the most parsimonious, as it included the unsupported Gran Dolina/*H. sapiens* clade (see above; Gran Dolina discussion). Of the two shortest trees that did not contain a Gran Dolina/*H. sapiens* clade, one has an unsupported clade comprising Gran Dolina, Daka, Ceprano and Bodo Figure 3.49; Tree A); it is Gran Dolina's inclusion in the clade that is not supported. The preferred phylogeny, then, is:

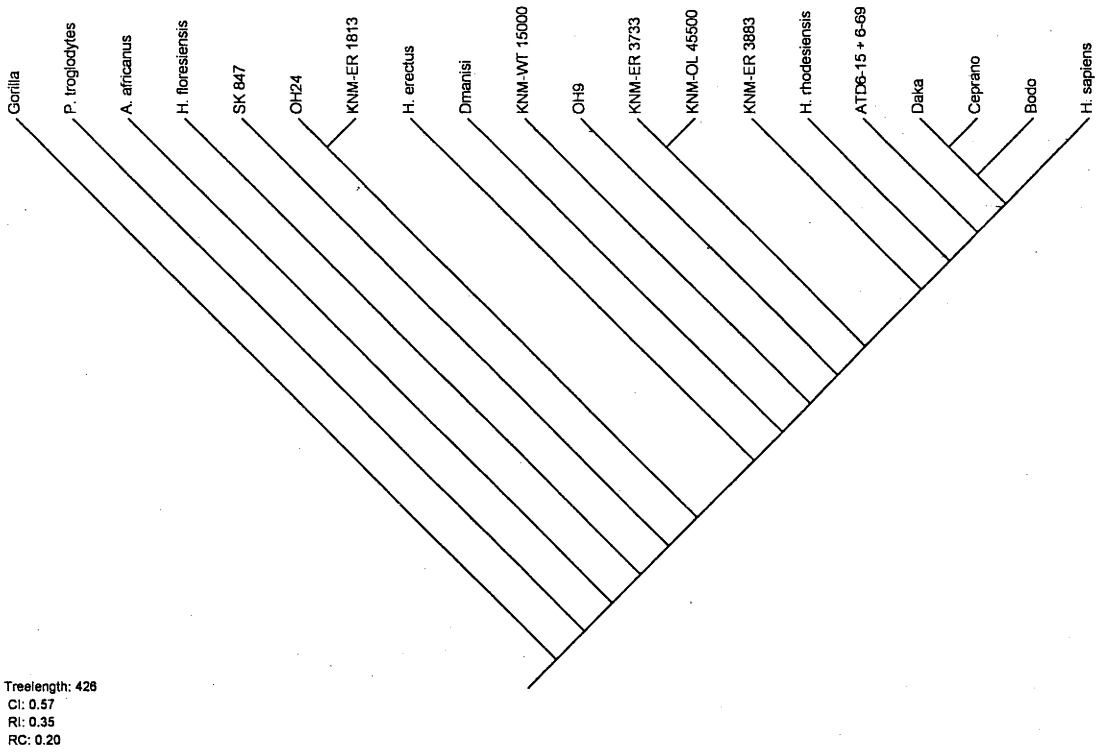


Figure 4-1 Most parsimonious phylogeny

Gran Dolina is very unstable on the tree: the tree is only 1-2 steps longer when it is moved to any other part of the tree. I anticipate that it may be difficult to assess its phylogenetic position.

Below is a schematic diagram representing human evolutionary relationships in the Early Pleistocene.

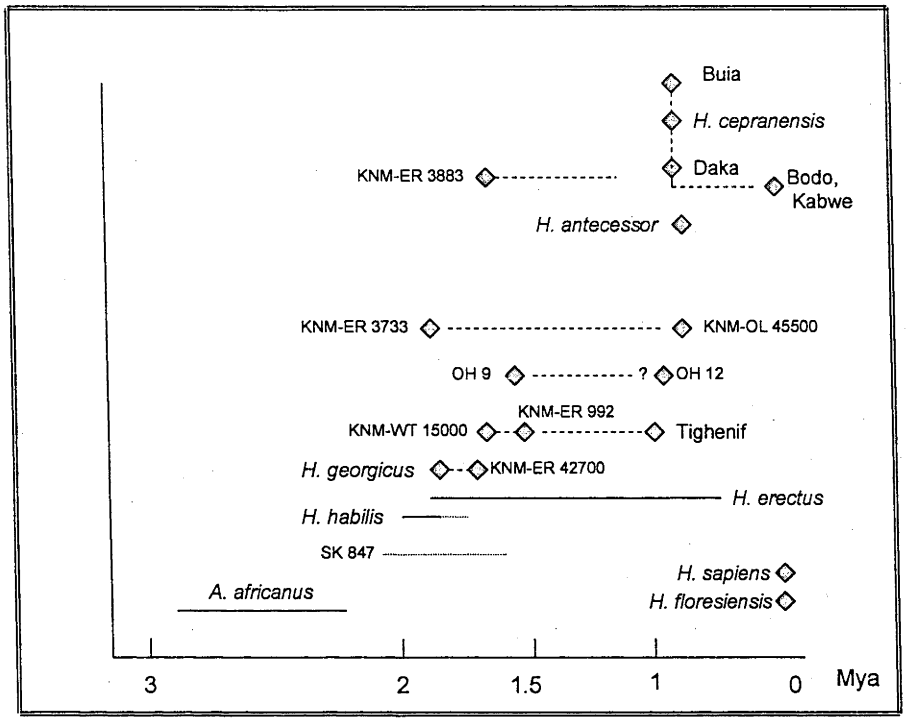


Figure 4-2 Schematic diagram of human evolutionary relationships in the Early Pleistocene.(Dotted line: possible time period; dashed line: possible phylogenetic relationships; filled line: known time period).

The schematic diagram illustrates the species, lineages and possible relationships for *Homo* in the Early Pleistocene identified in from the analyses. Whether the lineages represent species, and the implications for human evolution from the synthesis of the cranial analyses together with the results of the mandibular analyses, will be presented in the next Chapter.

5 HUMAN EVOLUTION IN THE EARLY PLEISTOCENE

Phylogenetic hypotheses must be grounded in some theoretical concept of units of diversity, among which the patterns of phylogenetic relationships are sought (Kimbel and Rak, 1993); it is the goal of taxonomy to establish biologically significant patterns – species and lineage patterns – as the fundamental units for reconstructing evolutionary relationships. Darwin (Darwin and Wallace, 1858) hypothesised that nature is comprised of morphological diversity that results from descent with modification in response to a struggle for existence. Wallace (Darwin and Wallace, 1858) articulated speciation as occurring as descent with modification forming either a straight line of descent, or a forked or many branched line; and he used the concepts now applied in taxonomic assessments and classifications – analogies, affinities and parallelisms, and he recognised the difficulties that must be faced in identifying these.

As units of evolutionary change, species are the fundamental level of biological organisation for phylogenetic reconstruction. Delineation of species is thus of crucial concern to understanding human evolution but the concept of species – what a species really is – has not been resolved and a number of concepts have been suggested. These may be divided into theoretical concepts (what a species is) and operational concepts (how a species may be recognised) (Groves 2001). The most influential and dominant of the theoretical concepts (op cit.) is the Biological Species Concept (BSC) (Mayr 1942; 1963). While Darwin's[19] theory envisaged species as arising out of a gradual accumulation of phenotypic change resulting from natural selection that produces a *continuum* of morphological variation, Dobzhansky (1937) observed that there are indeed discrete entities that have been called species, and that this implies discontinuity rather than continuity. Dobzhansky (op cit.) and Mayr (1942) viewed species as reproductively isolated groups that would otherwise show a smooth adaptive continuum of phenotypic diversity, i.e. the BSC was imposed upon Darwin's theory of evolution so that observed discontinuity could be explained (Eldredge, 1993). In the BSC species are defined by having biological gaps between them that resulted from reproductive isolating

[19] Alfred Wallace's theory of evolution appears to have only recently attracted widespread appreciation.

mechanisms, whether pre-mating (failure to come together because of ecological separation, ethological incompatibility, mechanical barriers to fertilisation), or post-mating (failure of hybridisation; hybrid inviability; hybrid sterility) (Groves, 2001).

The BSC is applicable to extant species and could be extended in time only through inference (Rose and Bown, 1993). Simpson (1961), therefore, proposed the Evolutionary Species concept (ESC), defining an evolutionary species as a lineage of an ancestor-descendant sequence of populations evolving separately from others. He divided lineages into successive species; classification of these should be based on morphological variation consistent with that in biological species (Rose and Bown, 1993). It is essentially a variation of the BSC that includes a time dimension (Groves, 2001).

Other theoretical concepts of species include the Ecological Species Concept (ESC) (Van Valen, 1976) and the Recognition Species Concept (RSC) (Paterson, 1986). The ESC proposes that species are populations that occupy distinct ecological niches. This is difficult to apply to extant species, let alone extinct species, and in effect does not really define a species, but may provide insight to an element – the ecological niche - under which speciation might occur in, for example, Darwin's and Wallace's theory of evolution. Further, it may not be known if species in distinct ecological niches would interbreed if they came into contact (Groves, 2001). Under the RSC, however, reproductive isolation is a by-product of the divergence of two populations, and a species is thus the most inclusive population of biparental organisms that share a common fertilisation system. This appears to be very similar to the BSC, rather like a mirror image of it, under which species do not interbreed with each other (Groves, 2001).

None of these species concepts is applicable to the fossil record; they emphasise processes thought to produce the results of evolution, rather than the results of evolution (Cracraft, 1983). Evolution produces taxonomic entities, defined in terms of their evolutionary differentiation from other such forms, and these entities, in Cracraft's image of it, should be called species. By emphasising differentiated taxonomic units (species) comparison between diverse groups become possible, even when the processes that produced them may differ even if they are known at all (op cit.). Cracraft (1989) found that controversy had arisen over the species concepts because many evolutionary biologists and

systematists had found the BSC untenable in theory and unworkable in practice, and he argued for abandoning the BSC and its variants in favour of a Phylogenetic Species Concept (PSC), an operational species concept, in which a species is considered an irreducible cluster of organisms, diagnostically distinct from other such clusters, and with which there is a parental pattern of ancestry and descent (1983; 1989). That is, the speciation process produces differentiated taxa – populations of interbreeding organisms having one or more novelties distinguishing this new unit from all other similar units. Species, thus, are equivalent to evolutionary taxa. The PSC emphasises character variation for individuating taxa and it is testable: assigning a differentiated population to a species rank under PSC will always be dependant on the data available and the rigour of the interpretation (op cit.). It has been criticised, however, on the grounds that it cannot deal with gradually evolving sequences of species (Rose and Bown 1993), and, as with other species concepts, it does not provide an infallible method of attributing individual organisms to species (Kimbel and Rak, 1993).

Nevertheless, the PSC can be usefully applied to the question of species in the fossil record as, while we cannot perceive whole species in that the fossil record is incomplete, we can infer their existence by proper use of characters (op cit.). The PSC is reflected in most of the basic premises, and the implementation, of cladistic analyses, which uses character state variation to identify phylogenetic relationships between taxonomic units. Species must be diagnosable entities, identified by the features by which the species may be infallibly recognised (Groves, 2001). Diagnostic characters are signs of reproductive cohesion that enable the grouping of organisms by virtue of uniquely shared ancestry and descent (Kimbel and Rak, 1993).

The question is, then, are the lineages identified in this study likely to represent species? Do any lineages possess a unique combination of characters not found in other taxa (Kimbel and Rak, 1993) that may be declared diagnosable for that group (Groves, 2001).

Character analysis shows that the basal branching pattern comprises a number of species – *H. floresiensis, H. erectus*, *H. georgicus*, *H. ergaster*, and *H. habilis*, and a lineage represented by SK 847. As will be argued, the later part of the tree shows a degree of

homoplasy that suggests that the identified lineages reflect a polymorphic population for much of the African population; and two species, *H ergaster* and *H. cepranensis*.

5.1 H. floresiensis

H. floresiensis is characterised by a short stature (106cm; Brown et al., 2004), small endocranial volume (417cc; Falk et al., 2005), short legs in relation to arms (Brown et al., 2004), and archaic wrist (Tocheri et al., 2007), shoulder (Larson et al., 2007, 2009), and lower limb morphology (Jungers et al., 2009). The tori arch over the orbits; there is weak metopic keeling, a convex nuchal plane in *norma lateralis,* a strong degree of relief of the tuberculum linearum, no depression above the confluence of the nuchal lines, continuity of the supramastoid crest with the inferior temporal line, strong mastoid crest, a vertical main axis of tympanic in *norma lateralis;* there is a groove between entoglenoid and tympanic plate; the lateral extension of entoglenoid slightly extended backward; there are broad and prominent jugum alveolare, curved malar notches, low irregular crests/fine longitudinal ridges on palate surface, orifice of incisive canal parallel with 2nd premolar, and absence of a postglenoid process.

My results supported the species *H. floresiensis*, as originally proposed by Brown et al. (2004; Morwood et al., 2005). I concluded (Chapter 4) that *H. floresiensis* is a late surviving lineage of *Homo* that evolved in the Early Pleistocene or late Pliocene; there is no evidence of a close phylogenetic relationship to *H. sapiens*, and I reject the idea that the Liang Bua remains represent a pathological modern human. I am also unable to link *H. floresiensis* phylogenetically to *H. erectus*, and cannot support the hypothesis that it resulted from insular dwarfing of *H. erectus*.

The results strongly imply that a very early member of the *Homo* lineage diffused from Africa to South East Asia. We had thought that more derived hominins, with an expanded braincase and modern body proportions, were the first to emerge from Africa. Until the Dmanisi hominins were discovered, this paradigm was based upon the appearance of *H. erectus* in Asia, at 1 Mya (Watanabe and Kadar, 1985; Pope, 1988) or 1.8 Mya (Swisher et al., 1984); the discovery of the Dmanisi hominins shifted the paradigm somewhat, in showing us that hominins with smaller ECVs had diffused from Africa, and that this had

occurred earlier (i.e. at 1.77 Mya) than previously thought (this under the assumption that *H. erectus* in SE Asia appeared 1 Mya). We cannot say when diffusion of *H. floresiensis* occurred, but, assuming it was before the evolution of SK 847 and *H. habilis* as suggested by the cladistic analyses, this may have been as early as, or earlier than, 2.1 Mya (if the earliest possible date for SK 847 is 2.1 Mya; Curnoe et al., 2001).

H. floresiensis shows that a much more archaic species of *Homo* had emerged from Africa than we had previously understood. We do not know when *H. floresiensis* left Africa, or when it arrived in South East Asia, only that its earliest appearance at Liang Bua could be as late as ~ 100 Kya (Roberts et al., 2009).

The hypothesis that *H. floresiensis* is a very early hominin, relatively little changed from the late Pliocene or Early Pleistocene would predict a greater range of variation in *Homo* during the Early Pleistocene than hitherto has been conceptualized by hypotheses of human evolution. The cranial capacity and stature of *H. floresiensis* fall outside the known ranges for *Homo*; but Falk et al. (2005; 2009) have shown that the brain had an expanded prefrontal cortex and temporal lobes relative to fossil hominins, and the capacity for higher cognitive processes.

This taxon survived on Flores until between 13.4-10.2 Kya at the very least (Roberts et al., 2009). *H. sapiens* were in nearby Australia, New Guinea, and SE Asia by 40,000 years ago (Mulvaney and Kamminga, 1999). That is to say that, although there is no evidence for any overlap between *H. floresiensis* and *H. sapiens* on Flores in the Liang Bua excavations, there is no doubt that *H. sapiens* shared its world with another species of *Homo*. This challenges yet another paradigm in human evolution: we had thought that we, *H. sapiens*, had been the sole remaining species of *Homo* since the demise of *H. neanderthalensis* and *H. erectus* in Asia.

5.2 H. habilis

Although I did not set out to study *H. habilis*, I included two crania referred to this species in the analyses retrospectively when similarities between *H. floresiensis* and *H. habilis* were observed. I concluded from the analyses that OH 24 and KNM-ER 1813 form a clade, with the following diagnostic characters:

- the *facies anterior* and alveolar process forms a flat surface
- there is no *jugum alveolare*
- presence of *tuberculum linearum*

There is little doubt that this clade corresponds to the species *Homo habilis*.

H. habilis is towards the basal region of the tree. I further tested this by assessing if there is any consistency of characters between *H. habilis* and higher elements on the tree (*H. georgicus*, *H. erectus*, *H. ergaster*, OH 9, KNM-ER 3733, KNM-ER 3883, KNM-OL 45500, *H. rhodesiensis*, Gran Dolina, *H. erectus*, *H. cepranensis*), and for consistency between SK 847 and this group. There are four characters in which *H. habilis* was similar to the higher group, and two characters in which SK 847 was consistent with it. It seems, then, that the position of *H. habilis* on the tree is supported, and that it is the more likely of the two taxa to share an immediate common ancestor with the group that is higher on the tree.

SK 847

SK 847 is not closely phylogenetically related to any other hominin in the study; it is likely to represent a separate, very early lineage, but whether it is a separate species is not resolved. It has a number of characters that other OTUs do not, and, of possible significance, it has a number of *H. sapiens*-like characters (refer Chapter 4) which suggests an interesting line of inquiry worthy of further examination.

5.3 H. erectus

This study is concerned with solving the phylogenetic position of the African/European Early Pleistocene hominins. I included the Javan *H. erectus* material so that KNM-ER 3733, KNM-ER 3883, Daka, Ceprano, OH 9 and others variously referred to *H. erectus* could be tested against this species. The Sangiran/Trinil crania clustered, and tests indicated that they formed a supported group; I combined them as a polymorphic species, *H. erectus*. The potential diagnosable character set is somewhat limited by the paucity of characters for the Trinil and Sangiran 2 calottes; for Trinil, Sangiran 2, 4, and 17 it comprises:

- superior-inferior length of nuchal dominates over superior-inferior length of occipital
- weak metopic keeling that is wider and flatter posteriorly,

as well as character states relating to the supraorbital region as noted by Stringer (1984).

H. erectus is an exclusively SE Asian species that is not closely related to any other hominins in the study; in particular, it is not closely related to KNM-ER 3733, KNM-ER 3883, or KNM-WT 15000, as is often assumed (e.g. Walker, 1981; Brown et al., 1985; Rightmire 1984). There is no support for *H. floresiensis*, *H. ergaster*, or *H. georgicus* as *H. erectus*; nor is there any support for the inclusion of Daka, Ceprano, KNM-ER 42700, OH 9, OH 12, SK 847, or KNM-OL 45500 in this species. Clearly, the practice of referring new hominin fossils to *H. erectus* based simply on a linear model of human evolution cannot be sustained.

5.4 H. georgicus

The Dmanisi crania and mandibles share a number of synapomorphies; while each of these is shared by one or two other taxa, overall the separation of these crania and mandibles from other taxa led me to conclude that they represent a single species. The species is diagnosable by the combination of the following character statis; this combination does not occur in other taxa in the study:

- bregmatic eminence
- the *jugum alveolare* forms a broad and prominent ridge
- zygomaticoalveolar crest forms an arch
- sharp high line divides the floor of the orbit from the facial portion of the malar
- glasserian fissure
- shallow digastric fossa
- small ECVs.

The nomen *H. georgicus* (Gabounia et al., 2002) is available. *H. georgicus* is not phylogenetically related to *H. erectus* (as suggested by Bräuer, 1996), or *H. habilis* (suggested by Gabunia and Vekua, 1995), or *H. floresiensis*. The evidence for a

phylogenetic relationship between *H. georgicus* and *H. ergaster* is equivocal. There is some support for a *H. georgicus/H. ergaster* clade in the mandibular analysis and they share a number of synapomorphic states, including an incipient symphyseal keel – the earliest *Homo* to possess this derived state. The cranial cladistic analyses, however, show *H. georgicus* and *H ergaster* on separate lineages, and T-PTP tests would suggest that the two species might form a clade only by chance. Nevertheless *H. georgicus* and *H ergaster* possess modern body proportions (Ruff and Walker, 1993; Lordkipanidze et al., 2007) in contrast to the earlier species, *H. habilis* and *H. floresiensis*. The morphology of the *H. georgicus* postcranium became available only after the completion of my analyses; including these characters in any future cladistic analyses could help clarify any question of possible relationship between this species and *H. ergaster*.

There is a notable variation in mandibular size in *H. georgicus* that lends support to the proposal of Gabunia et al. (2002) and Van Arsdale (2006) that *H. georgicus* was a highly sexually dimorphic species. The size variation is outside the previously known range for *Homo* (Skinner, 2006; Martinón-Torres et al., 2008). Further, as *H. georgicus* had modern body proportions, and incipient chin structure, we may assume that these derived characters of *Homo* evolved prior to the reduction in sexual dimorphism.

5.5 H. ergaster

This study found that *H. ergaster* is limited to KNM-ER 992, KNM-WT 15000, Tighenif 1, Tighenif 2, Tighenif 3; it is unlikely to include KNM-ER 3733 or KNM-ER 3883 as is commonly supposed. *H. ergaster* is united by three mandibular characters: the mandibular corpus is of uniform height; there is no flaring in the gonial region; and the symphyseal region is thickest at the midline in basal view. It is unfortunate that, apart from KNM-WT 15000, crania from the African population (below) do not have associated mandibles. No other crania could be shown to form a sister taxon to KNM-WT 15000; KNM-ER 3733, KNM-ER 3883, OH 9, *H. rhodesiensis*, Gran Dolina, Bodo, Daka, or Ceprano cannot be referred to *H. ergaster*.

The degree of difference in the sizes of the Tighenif mandibles (Arambourg 1955c) suggests that there was a relatively large degree of sexual dimorphism in *H. ergaster*, as in *H. georgicus*.

We do not know if any of the members of *H. ergaster* represent the first and/or last appearances of this species, but we may propose that it lived from at least 1.56 Mya (KNM-WT 15000) to either ~1.0 Mya or 750 Kya (Tighenif population; Geraads et al., 1986). If KNM-WT 15000 is the earliest representative, however, it branched after *H. georgicus* (1.76 to 1.77 Mya) and before KNM-ER 3733 (1.78 Mya). It is possible, then, that *H ergaster* emerged close to the time of the African population (below) and *H. georgicus*, i.e. close to 1.8/1.78 Mya. It could, then, have existed for a period of 800,000 – one million years, if it emerged before KNM-ER 3733 and survived until the later possible date (700 Kya) for the Tighenif hominins, in which case it would have co-existed with at least some of the African population discussed below.

5.6 African population

Using the character tracing attribute in MacClade an examination of character changes shows that, while there is some evidence for a few pairings, such as KNM-ER 3733 and KNM-OL 45500; and Bodo, Daka, Ceprano, there is an increasing amount of homoplasy in the mainly African group comprising OH 9, KNM-ER 3733, KNM-ER 3883 KNM-OL 45500, Bodo, Daka, Ceprano. Nevertheless they are united by the following characters:

Character 32, which changes from state 1 (continuity of the supramastoid crest with the inferior temporal line) to 0 (no direct link) above the *H. habilis* level, although the state for OH 9 is equivocal. (Figure 5.1; Node A)

Character 75, which above Dmanisi changes from state 3 (orifice of incisive canal is on a plane with 1st premolar) to state 1 (orifice of incisive canal is immediately posterior to incisors), but there is a reversal at *H. rhodesiensis*. (Figure 5.1; Node B)

Above (i.e. to the right on the tree) *H. erectus* there are two character state changes:

- character 55 changes from state 1 or 2 (the entoglenoid projects to a similar or greater extent than the tuberculum zygomaticum anterior) to state 3 (entoglenoid is less projected than the tuberculum zygomaticum anterior) with some reversal; and

- character 73 changes from 2 (naso-alveolar clivus is flat) to 1 (naso-alveolar is convex), but this reverses in Bodo and *H. sapiens* (state for Daka and Ceprano not known). (Figure 5.1; Node C)

Above (i.e. to the right on the tree) *H. ergaster*, as represented by KNM-WT 15000, there are three character state changes:

- character 3 changes from state 1 (depression at glabella in *norma facialis*) from state 0 (no depression) but there is some homoplasy because this state occurs in KNM-ER 1813;
- character 44 changes from 0 (in *norma lateralis* mastoid process does not project below the base) to 1 (projects below the base); and
- character 59 changes from 0 (posterior edge of the tuberculum articular in *norma basilaris* is flat) to 2 (sigmoid shape), and occasionally 1 (arched), although *H. rhodesiensis* has reversed to 0. (Figure 5.1; Node D)

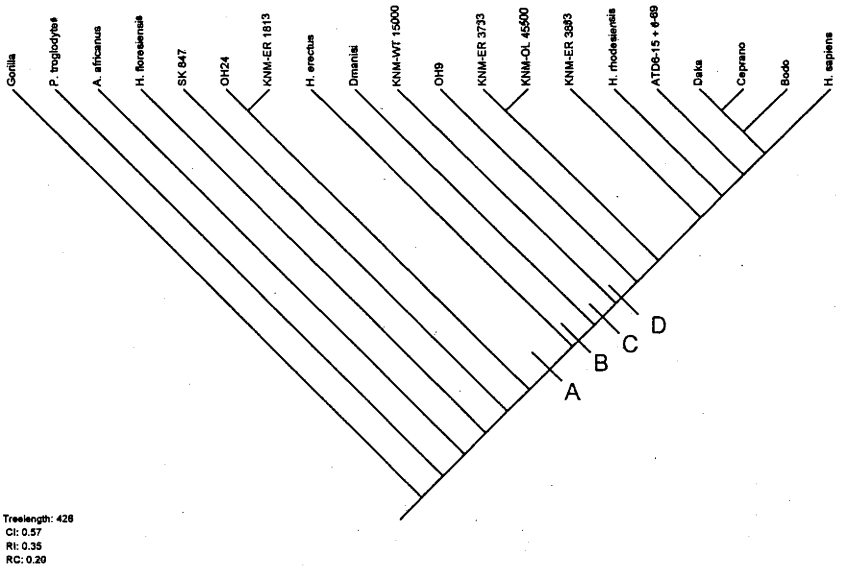


Figure 5-1 Nodes on most parsimonious phylogeny

In summary, then, none of the lineages in the African/early European clade are free from homoplasy and it most likely that there are polymorphisms in which characters sort independently. The most plausible explanation is that these penecontemporaries, KNM-ER 3733, KNM-ER 3883, OH 9, KNM-OL 45500, perhaps Kabwe, and, probably, OH 12 (in view of its similarities to OH 9) form a single polymorphic evolving African population above the split with *H ergaster* until the emergence of *H. cepranensis* (below). This group has a T-PTP of p = 0.01 and it is unlikely that they would form a clade by chance. If Kabwe is truly part of the complex, the species represented by this population would be called *H. rhodesiensis*; as this is equivocal, a safer course would be to use the next available name, *H. louisleakeyi*.

Although *H. ergaster* is based entirely on mandibular characters (above), and *H. louisleakeyi* is based upon cranial characters, the split between the two species (assuming *H. louisleakeyi* is a species) shows that the KNM-WT 15000 (*H. ergaster*) cranium does not share *H. louisleakeyi* synapomorphies.

Table 13. *H. louisleakeyi* possible synapomorphies compared to condition for KNM-WT 15000

H. louisleakeyi	**KNM-WT 15000**	***H. louisleakeyi* parallel with ?**
Depression at glabella (Character 3; state 1)	?	*H. cepranensis*, KNM-ER 1813, *H. sapiens*
Strong mastoid crest (Character 34; state 1)	Weak mastoid crest (state 0)	Ceprano
Mastoid projects below base of cranium (Character 44, state 1)	Mastoid does not project below base (state 0)	[condition for KNM-ER 3733 unknown]
Articular eminence and posterior wall of mandibular fossa similar heights (Character 49; state 1)	Articular eminence shorter posterior wall of mandibular fossa (state 0)	Dmanisi, KNM-ER 1813
Sigmoid shape to posterior edge of articular eminence in *norma basilaris* (Character 59; state 2)	Posterior edge of articular eminence in *norma basilaris* is flat (state 0)	[*H. rhodesiensis* = state 0]

Further, KNM-WT 15000 differs from all members of *H. louisleakeyi* in the following ways:

- triangular temporal squama (Character 29, State 1)
- weak juxtamastoid eminence (Character 52, State 1)
- postglenoid process does not overlap the tympanic (Character 65, State 0)
- infraorbital margin has pronounced rounding of the inferior lateral border (Character 78, State 3)
- tympanic trough (Character 81, State 1) (this might be an age-related character)
- superior-inferior length of nuchal does not dominate over superior-inferior length of occipital (Character 88, State 0)

When KNM-WT 15000 is added to the members of *H. louisleakeyi* (T-PTP p = 0.01, above) in a T-PTP test, the result is p = 0.12; it is likely *H. ergaster* and *H. louisleakeyi* would come together by chance alone.

5.7 Daka, Ceprano and Bodo

Daka, Ceprano and Bodo hold together well, although, again, there is homoplasy for each of the shared characters:

- character 6 changes from state 2 (a continuous supraorbital torus) to state 1 (two distinct tori); homoplasy with KNM-ER 1813, *H. floresiensis*
- character 46 changes from states 1 and 2 ('split' or a wide space between tympanic) to 0 (posterior part of tympanic joins anterior part of mastoid process); homoplasy with Dmanisi
- character 77 (form of the supraorbital margins) changes from state 3 to 1; homoplasy with *H. rhodesiensis* and *H. erectus*.

Each has a relatively expanded braincase, and Ceprano appears to be the earliest of the early hominin crania to have a slightly expanded upper braincase. Brain expansion in *Homo* is associated with a number of cranial characters: parietal bossing; high contour of the temporal squama; rounding of the occiput; and a relatively steeply sloping frontal

(Rightmire, 1996). *H. rhodesiensis* has the first two of these characters, and a relatively large cranium with an ECV of 1300cc (Holloway et al., 2004:120). While Ceprano and Daka differ in some aspects of cranial shape, they nevertheless represent an evolutionary shift in the overall form of the braincase. Like Kabwe, vault walls are nearly parallel in Daka, but converge slightly inferiorly in Ceprano; and postorbital constriction is reduced in both. Ceprano and Daka are more derived than *H. rhodesiensis* in that their frontals rise more steeply, and they have rounded occipitals. Ceprano also has a relatively high temporal squama but does not have parietal bossing. Daka, too, lacks some of the characters associated with cranial expansion, such as a relatively high temporal squama. Although Bodo has a relatively large cranial capacity (1250 cc; Holloway et al., 2004) it does not show some of the other characters associated with an expanded braincase such as parietal bossing, greatest width at the parietals, or reduced post-orbital constriction, although its occipital seems to be rounded and it has a relatively high temporal squama contour. That is, although Bodo, Daka, and Ceprano all show marked cranial expansion in ECVs and related characters, none show all characters (refer Chapter 4).

Daka and Ceprano seem to form a more derived clade within the African population. They share an immediate common ancestor with Bodo and I propose that Bodo, Daka, and Ceprano form a species diagnosable by the following combination of characters:

- lack of occipital torus
- posterior part of tympanic joins anterior part of mastoid process
- supraorbital margin is thick, rounded and not demarcated from roof of orbit
- sagittal keeling on first half of parietal
- angular tuberosity
- expanded braincase
- reduced post-orbital constriction
- rounded occipitals.

The prior available name for the species thus composed is *H. cepranensis* (Mallegni et al., 2003). I would also suggest that Buia is a member of the clade, and tentatively suggest it is

H. cepranensis given the similarity of its characters to Daka and Ceprano (Chapter 4), although its characters cannot yet be diagnosed satisfactorily.

The key development in the evolution of the clade exemplified by Daka, Bodo, and Ceprano is a marked expansion of the vault, and, in Ceprano and Buia, the inferior contraction in the sides of the vault. These developments appeared relatively suddenly around one million years ago, following a period of ~480,000 years (from 1.48 Mya (OH 9) to 800 Kya (Daka)) in which we know of only two hominins, OH 12 (> 1.07 Mya) and KNM-ER 42700 (970-900 Kya). This period, then, represents a significant remaining gap in our knowledge of human evolution in the Early Pleistocene.

5.8 H. antecessor

The hypodigm of *H. antecessor* at present comprises six individuals (Bermudez de Castro et al., 2008) from Gran Dolina, Spain, and is dated to 780 – 857 Kya (Falguèrès, 1999). In these analyses it was represented by the juvenile ATD6-69 + 6-15, as it had the greatest number of characters available. Its phylogenetic relationships cannot be resolved except to propose that it is probably not related to *H. ergaster* or *H. erectus.* That is, it may well represent a separate lineage but it is very unstable in the analyses, due in part to its juvenile status and in part to the small number of characters available. Nevertheless, *H. antecessor* has a relatively large cranial capacity of 1000cc (Burmudez de Castro et al., 1997), which is comparable to the more derived hominins Daka and Ceprano from the same period. It is characterised in this analysis by a sill-like form of the *margo limitans*; no *sulcus infraorbitalis*; the zygomaticoalveolar crest forms an arch; the orifice of incisive canal is immediately posterior to incisors; and no supraorbital torus, although the latter character is more likely to represent the juvenile, rather than the adult, form.

KNM-ER 3883, *H. rhodesiensis* and *H. antecessor* are closest to *H. cepranensis* and it may be supposed that *H. cepranensis* evolved from the polymorphic evolving Africa population, *H. louisleakeyi*, discussed above (KNM-ER 3733, KNM-ER 3883, OH 9, KNM-OL 45500, Kabwe), although there was no support for the closest of these, Kabwe, and *H. cepranensis* sharing an immediate common ancestor. Depending on the resolution of the phylogenetic position of *H. antecessor*, it may yet prove to present the same species as Ceprano, as indeed suggested by Manzi et al. (2001).

5.9 Kabwe

Kabwe (*H. rhodesiensis*) is characterised in this analysis by a glabella region that is neither depressed nor protrudes, strong metopic keeling that has parallel edges; parietal bosses, a high temporal squama in relation to vault; the orientation of main axis of tympanal in *norma lateralis* slopes posteriorly; and the face is tucked in under the orbits, whereby nasospinale lies behind rhinion. Although the frontal slopes only gradually, and the cranium retains a relatively long lateral profile, Kabwe has reduced postorbital constriction; no prognathism; almost parallel vault walls; a braincase that is comparatively high, with somewhat flattened parietals. Whether it represents a species, or is part of the polymorphic, evolving African population (*H. louisleakeyi*), is not determinable using the character diagnostic process, as there is only one fossil available (Kabwe), and I leave its species status as an open question. Based upon its position in the preferred phylogeny (Chapter 3; Fig 3.24), though, Kabwe is the first of the hominins to possess more derived states. It is unfortunate that we do not know its date.

5.10 Summary – human evolution in the Early Pleistocene

The following is a summary of the hypotheses presented.

Human evolution in the Early Pleistocene, then, is characterised by diffusion of a very early hominin – *H. floresiensis* - to south East Asia; and, although only known from the Late Pleistocene and the Holocene on Flores, Indonesia, *H. floresiensis* was a very early, perhaps the earliest, member of the *Homo* lineage.

Other species or lineages emerged around 1.8 Mya, or are at least evident at this time, in widely separated geographic regions: the SK 847 lineage in South Africa; *H. habilis* in East Africa; *H. georgicus* in Eurasia; and *H. erectus* in South East Asia. Of these, to the best of our knowledge, only *H. erectus* continued well into the Middle Pleistocene.

The earliest representative of the proposed species *H. louisleakeyi*, KNM-ER 3733, also appeared at this time and lived in Africa until at least 970 Kya (KNM-OL 45500), disappearing a little before the emergence of *H. cepranensis*.

H. ergaster is evident from 1.56 Mya to either 1.1 Mya or 700 Kya (depending on the date for Tighenif) and, if the former date is correct, *H ergaster* was contemporaneous with two members of the African population (*H. louisleakeyi)*, KNM-ER 3883 and KNM-ER 42700. If the latter date is correct, *H ergaster* was contemporaneous with *H. louisleakeyi*, *H. antecessor* and *H. cepranensis*.

From ~800 Kya, a new species, *H. cepranensis*, with a more expanded braincase appeared in Africa and Europe; its origin is unclear; it may have emerged from the African population represented by KNM-ER 3883 and Kabwe/*H. rhodesiensis*, although the evidence for this is weak; or, possibly, it emerged from the European species *H. antecessor*. The key period between 1.48 – 1 Mya, prior to the emergence of *H. cepranensis*, has provided very few hominin remains from which we may derive hypotheses for the notable developments evident in this species.

In summary, the earliest species to emerge in the Early Pleistocene is, in all probability, *H. floresiensis*. The other early hominins comprise a number of spatially discrete species - *H. erectus* (SE Asia), *H. georgicus* (Eurasia), *H. habilis* (East Africa); and the SK 847 lineage (South Africa). The species which should possibly be called *H. louisleakeyi* emerged with the appearance of KNM-ER 3733, 1.8 Mya. *H. ergaster* comprises KNM-ER 992, KNM-WT 15000, and the Tighenif hominins; but not KNM-ER 3733 or KNM-ER 3883, and it co-existed with at least some representatives of *H.louisleakeyi*. *H. cepranensis* appeared much later than the earlier species and lineages; it comprises Bodo, Daka, Ceprano and, most likely, Buia. The place of *H. antecessor* is unresolved, but when adult *H. antecessor* crania are discovered consideration may be given to a possible relationship of this species to *H. cepranensis*. The phylogenetic relationship of KNM-ER 42700 remains unclear.

Other questions remain: is there any phylogenetic relationship between KNM-ER 42700 and *H. georgicus*? Will a comparative analysis of *H. georgicus* and *H ergaster* that includes post-cranial characters show any phylogenetic relationship between these species? Is there any significance to the *H. sapiens*-like features in SK 847? And what happened to *H. floresiensis* between its proposed emergence in the Early Pleistocene and

its appearance on Flores just 100,000 years ago? These are intriguing questions that this study raises, and which merit future investigation.

6 CONCLUSION

Understanding the meaning of morphological variation in the Early Pleistocene has been beset by difficulties resulting from a paucity of fossil hominins - until recently - for the period 1.7 Mya – c. 700,000; the referral of new fossil discoveries, and indeed, well-known hominins, to multiple species; and a tendency for a model-dependant attribution of hominins to *H. erectus*. A number of new fossil discoveries in the last ten years, however, has substantially increased the sample for Early Pleistocene hominins, such that it was timely to review this period.

A number of hypotheses for the phylogenetic relationships of *Homo* during the Early Pleistocene have been presented. The species *H. floresiensis* evidently arose at the base of the *Homo* clade. Apart from this, several species are evident: *H. georgicus*, *H. erectus*, *H. ergaster*, *H. louisleakeyi*, and *H. cepranensis*. *H. georgicus* is a highly sexual dimorphic species comprising the fossil hominins from the site of Dmanisi in the Republic of Georgia; *H. erectus* is exclusively a SE Asia (Java) species; *H. ergaster*, also showing notably sexual dimorphism, comprises KNM-ER 992, KNM-WT 15000, and the Tighenif fossils, but not KNM-ER 3733 or KNM-ER 3883 as had been generally thought. The latter are, in fact, part of a separate polymorphic African population that comprises a number of other hominins; for which the name *H. louisleakeyi* is probably appropriate. A later species, *H. cepranensis*, comprises Ceprano, Daka, Bodo, and, perhaps, Buia; all have more expanded braincases than the earlier hominins. Unplaced, for the moment, is Kabwe. If it belongs in what is here called *H. louisleakeyi*, then the name *H. rhodesiensis* may take precedence.

The practice of placing newly discovered fossils of *Homo* into *H. erectus s. l.*, however this is construed, is unsupportable; rather, where such fossils are to be compared with *H. erectus*, the proper practice is to compare them to the type specimen, Trinil, and the other Javan fossils from Sangiran.

Some issues are not resolved, and questions remain about the phylogenetic position of *H. antecessor*; the role of SK 847 in human evolution; and the possible relationship of KNM-ER 42700 to *H. georgicus*. In particular, nothing is known about *H. floresiensis* from its

proposed emergence in the Early Pleistocene to its appearance on Flores a mere 100,000 years ago.

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APPENDICES

APPENDIX 1. Metric data

	Specimen	GOL	NOL	XCB	BBH	XFB
1	Kabwe 1	205.00	197.00	145.00	127.00	120.00
2	KNM ER 3733	182.00	177.00	136.00	113.00	107.00
3	KNM ER 3883	181.00	172.00	139.00	101.00	103.00
4	KNM WT 15000	175.00	.	133.00	101.00	101.00
5	OH9	203.00	194.00	138.00	100.00	110.00
6	Daka	180.00	172.00	140.00	120.00	110.00
7	Bodo	.	.	146.00	.	128.00
8	Ceprano	195.00	.	156.00	.	.
9	Sangiran 17	205.00	199.00	140.00	118.00	.
10	Sangiran 2	.	.	115.00	.	.
11	Sangiran 4	.	.	121.00	.	.
12	Gran Dolina	.	.	.	.	.
13	D2700	153.00	152.00	125.00	100.00	82.00
14	D2280	172.00	170.00	136.00	.	100.00
15	D2282	.	.	.	.	95.00
16	LB1	137.00	.	115.00	87.00	89.90
17	KNM ER 1813	142.00	.	98.00	90.00	.
18	KNM ER 42700	153.00	.	120.00	94.00	.
19	Tighenif 1	.	.	.	.	.
20	Tighenif 2	.	.	.	.	.
21	Tighenif 3	.	.	.	.	.
22	KNM ER 992	.	.	.	.	.
23	Zhoukoudian S...	199.00	194.00	143.00	.	110.00
24	Zhoukoudian S...	192.00	185.00	139.80	.	106.00
25	Zhoukoudian S...	195.50	192.00	141.00	.	108.00
26	H. sapiens	156.00	157.00	134.00	130.00	110.00
27	H. sapiens	176.00	175.00	126.00	130.00	106.00
28	H. sapiens	180.00	177.00	135.00	135.00	115.00
29	H. sapiens	180.00	177.00	133.00	130.00	98.00
30	H. sapiens	177.00	175.00	135.00	126.00	110.00
31		.	.	.	.	.

	Min_frontal_breadth	WCB	ZYB	BNL	BPL	ASB	AUB
1	102.00	99.00	.	107.00	115.00	.	.
2	85.00	87.00	135.00	105.00	110.00	112.90	129.00
3	82.00	100.00	.	101.50	.	114.00	125.00
4	83.00	90.00	.	.	124.00	105.00	121.00
5	96.00	.	.	107.60	.	120.00	135.00
6	94.00	.	.	95.00	.	116.00	128.00
7	107.00	104.00	.	.	.	.	.
8	106.00	.	.	.	.	.	.
9	97.00	94.00	.	115.00	127.00	.	148.00
10	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.
12	.	.	103.40	.	.	.	.
13	78.00	72.00	.	91.00	100.00	103.00	118.00
14	83.00	.	.	.	.	104.00	130.00
15	79.00	.	132.00	.	.	103.00	.
16	63.40	67.00	114.00	.	83.80	.	105.90
17	70.00	67.00	117.00	84.00	105.00	90.00	110.00
18	79.00	.	.	.	.	99.00	110.00
19	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.
23	89.00	.	.	.	.	111.00	147.00
24	84.00	.	.	105.50	.	113.00	143.00
25	91.00	.	.	.	.	115.00	151.00
26	83.00	.	117.00	85.00	90.00	95.80	113.00
27	90.00	.	128.00	93.00	94.00	107.20	113.70
28	90.00	.	132.00	97.00	93.00	.	121.50
29	90.00	.	.	96.00	103.00	.	113.60
30	85.00	.	121.00	92.00	90.00	100.00	114.60
31	.	.	.	.	.	.	.

	NPH	Upper_facial_br	STB	FMB	NLH	NLB	EKB
1	92.10	134.40	112.90	.	34.70	30.20	119.10
2	79.20	121.30	78.20	121.10	48.40	.	107.80
3	.	.	79.00	113.00	.	.	105.90
4	.	114.70	81.80	.	.	33.50	99.30
5	.	133.00	80.00	128.00	.	.	.
6	.	124.70	102.00	109.00	.	.	109.00
7	87.80	140.00	105.00	128.80	60.50	42.80	125.00
8	.	136.30	.	.	.	.	116.10
9	.	122.10	90.00	.	.	.	.
10	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.
12	.	.	.	.	.	27.50	.
13	69.00	96.00	77.00	90.00	50.00	28.00	90.00
14	.	114.00	74.00	108.00	.	.	105.00
15	.	108.00	76.00	.	.	26.00	96.00
16	.	85.60	66.10	.	.	19.50	.
17	66.00	100.00	.	.	42.00	23.00	.
18	.	96.00	.	.	.	.	.
19	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.
24	.	.	81.00	.	.	.	.
25	.	.	103.00	.	.	.	.
26	64.50	92.50	.	92.00	55.20	23.20	84.70
27	64.50	107.10	110.00	107.70	46.30	24.70	96.50
28	68.40	101.40	.	100.00	56.50	25.70	91.30
29	67.80	107.00	98.50	105.80	48.40	23.50	97.40
30	69.10	96.20	109.70	94.40	50.00	22.80	88.70
31	.	.	.	.	.	.	.

	OBH	OBB	DKB	JUB	WMH	FRC	Na_br_arc	PAC
1	40.10	44.70	30.00	132.00	58.20	120.00	138.00	110.00
2	35.00	40.00	16.80	121.90	.	95.00	115.00	86.00
3	35.00	45.40	16.90	.	.	101.00	118.00	90.00
4	43.10	37.30	.	115.00	52.00	.	.	95.00
5	.	.	.	.	.	112.00	165.00	.
6	.	36.90	30.00	.	.	130.00	141.00	95.00
7	38.40	51.30	38.20	.	46.80	105.00	125.00	.
8	.	.	.	.	.	.	.	.
9	36.90	43.00	.	.	37.90	120.60	130.00	.
10	.	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.	.
12	.	.	32.70	106.20	.	.	.	.
13	32.00	35.00	.	107.00	28.00	89.00	95.00	86.00
14	.	.	.	.	.	101.00	108.00	90.00
15	.	.	.	107.00	27.00	86.00	95.00	82.00
16	31.40	28.80	.	93.70	19.30	64.20	75.00	79.50
17	31.00	33.00	.	102.00	27.00	78.20	90.00	.
18	.	.	.	.	.	.	.	87.00
19	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.	.
23	.	.	.	.	.	115.00	129.00	106.00
24	.	.	.	.	.	106.00	122.00	86.00
25	.	.	.	.	.	113.00	124.00	91.00
26	32.60	34.60	21.10	103.00	19.30	98.00	117.00	.
27	31.20	36.80	28.50	117.00	23.50	106.00	127.00	97.30
28	36.00	35.20	24.00	109.80	21.40	114.00	135.00	102.30
29	33.50	40.00	21.70	112.70	18.20	105.00	125.00	102.80
30	31.50	34.50	20.40	102.00	21.10	106.00	125.00	105.60
31	.	.	.	.	.	.	.	.

	br_la_arc	OCC_L_O_chord	L_O_arc	L_I_chord	L_I_arc	I_O_chord
1	121.00	78.00	105.00	.	.	.
2	95.00	85.00	118.00	57.00	68.00	46.20
3	98.00	75.60	110.00	49.70	60.00	49.20
4	105.00	76.20	93.00	41.50	50.00	44.40
5	.	.	.	.	.	.
6	103.00	93.00	119.00	67.00	78.00	42.40
7	.	.	.	.	.	.
8	.	.	.	63.20	65.00	.
9	.	.	47.30	47.30	.	.
10	.	.	.	.	.	.
11	.	104.00	110.00	46.20	65.00	51.40
12	.	.	.	.	.	.
13	91.00	66.00	87.00	45.00	.	39.00
14	96.00	77.00	.	46.00	.	47.00
15	85.00	.	.	46.00	.	.
16	90.00	61.90	80.00	41.00	47.00	33.50
17	.	.	.	43.00	48.00	34.00
18	94.00	74.00	92.00	47.00	.	39.00
19	.	.	.	.	.	.
20	.	.	.	.	.	.
21	.	.	.	.	.	.
22	.	.	.	.	.	.
23	113.00	.	.	49.00	51.00	.
24	92.00	86.00	118.00	48.00	50.00	63.00
25	102.50	86.00	118.00	52.50	55.00	57.00
26	.	.	.	.	.	.
27	105.00	100.00	120.00	75.70	90.00	21.80
28	110.00	108.00	128.00	79.70	92.00	37.60
29	115.00	108.00	134.00	.	.	44.00
30	120.00	95.00	122.00	73.20	90.00	28.40
31	.	.	.	.	.	.

	I_O_arc	Tor_central	Tor_medial	Tor_lateral	Max_supra_br	Palate_length
1	.	19.70	20.10	17.90	139.00	55.00
2	46.20	8.90	11.80	7.20	117.00	37.60
3	55.00	14.30	20.30	7.60	114.00	.
4	48.00	9.00	.	13.60	114.00	46.30
5	.	17.10	20.10	15.90	133.00	.
6	42.00	18.10	17.80	12.60	123.80	37.10
7	.	16.60	19.10	11.70	137.00	62.20
8	.	21.00	19.50	9.70	130.00	.
9	.	15.90	19.20	16.00	124.40	.
10	.	.	12.30	7.20	130.00	.
11	54.00	.	.	.	.	.
12	.	.	.	.	.	.
13	.	8.00	.	6.00	.	55.00
14	.	11.00	.	9.00	.	.
15	.	.	.	.	.	54.00
16	35.00	7.40	.	9.90	84.50	52.30
17	34.00	.	.	.	.	54.20
18	.	.	.	.	.	57.00
19	.	.	.	.	.	.
20	.	.	.	.	.	.
21	.	.	.	.	.	.
22	.	.	.	.	.	.
23	.	.	.	.	.	.
24	67.00	.	.	.	.	.
25	60.00	.	.	.	.	.
26	.	.	.	.	.	48.40
27	22.00	.	.	.	.	50.90
28	39.00	.	.	.	.	47.90
29	46.00	.	.	.	.	46.30
30	30.00	.	.	.	.	49.50
31	.	.	.	.	.	.

	internal_palate_breadth	MDH	MDB	ZMB	FOL	Bicondolar_br	bigonial_br
1	40.80	24.30	15.50	.	41.60	.	.
2	32.40	.	.	.	34.50	.	.
3	.	27.50	20.60	.	30.50	.	.
4	38.10	28.40	12.00	.	32.00	115.90	95.90
5	.	.	.	.	.	.	.
6	.	.	.	.	.	.	.
7	48.10	.	.	.	.	.	.
8	.	.	.	.	.	.	.
9	.	.	16.10	.	31.30	.	.
10	.	.	.	.	.	.	.
11	.	.	14.20	.	39.70	.	.
12	63.30	.	.	.	.	.	.
13	.	.	.	97.00	32.00	.	.
14	.	.	.	.	.	.	.
15	.	.	.	99.00	.	.	.
16	.	24.40	10.70	91.90	29.60	.	.
17	38.90	.	.	.	.	.	.
18	.	.	.	.	.	.	.
19	.	.	.	.	.	.	76.00
20	.	.	.	.	.	.	.
21	.	.	.	.	.	130.00	89.00
22	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.
24	.	.	.	.	.	.	.
25	.	.	.	.	.	.	.
26	38.70	21.60	10.70	114.50	30.60	109.10	84.30
27	38.40	21.30	7.10	125.00	35.10	109.20	94.50
28	41.90	24.60	14.10	118.00	35.20	108.20	94.20
29	37.40	24.40	10.70	117.00	36.20	.	.
30	39.10	23.00	10.50	112.00	35.80	113.30	92.80
31	.	.	.	.	.	.	.

	synphysis_ht	ramus_ht	ramus_breadth	gonial_condyle_h
1	.	.	.	.
2	.	.	.	.
3	.	.	.	.
4	28.80	49.40	40.10	50.60
5	.	.	.	.
6	.	.	.	.
7	.	.	.	.
8	.	.	.	.
9	.	.	.	.
10	.	.	.	.
11	.	.	.	.
12	.	.	.	.
13	.	.	.	.
14	.	.	.	.
15	.	.	.	.
16	.	.	.	.
17	.	.	.	.
18	.	.	.	.
19	31.40	.	.	61.00
20	31.40	.	30.00	.
21	33.00	.	47.20	66.50
22	23.70	.	42.10	.
23	.	.	.	.
24	.	.	.	.
25	.	.	.	.
26	28.40	.	30.50	.
27	32.60	.	34.00	.
28	19.80	.	33.90	.
29	.	.	.	.
30	28.40	.	30.50	.
31	.	.	.	.

	symphysis_gonial_length
1	.
2	.
3	.
4	100.30
5	.
6	.
7	.
8	.
9	.
10	.
11	.
12	.
13	.
14	.
15	.
16	.
17	.
18	.
19	60.00
20	61.00
21	86.00
22	101.50
23	.
24	.
25	.
26	89.30
27	89.20
28	83.30
29	.
30	88.40
31	.

APPENDIX 2: CRANIAL CHARACTER STATES

1. continuity of post orbital sulcus
0 = absent because of continuity of frontal and supraorbital
1 = present but incomplete, interrupted in the medial zone
2 = present – complete and with a distinct edge or border

2. postorbital lateral depression (a depression on the lateral supraorbital region bounded by the temporal line)
0 = absent; 1 = present

3. depression at glabella in *norma facialis*
0 = absent; 1 = present

4. shape of frontal edge in *norma verticalis*
0 = linear; 1 = convex frontwards

5. position of glabella in *norma verticalis*
0 = glabella zone is depressed
1 = glabella is neither depressed or protruding
2 = glabella projects beyond the frontal

6. continuity of the supraorbital torus
0 = no supraorbital torus
1 = incomplete, interrupted in the medial zone – there are 2 distinct tori 'mono-orbitares'
2 = continuous torus

7. Superior surface of orbit margins
0 = flow smoothly into frontal squama
1 = horizontal posttoral plane from which squama rises posteriorly
2 = there is a sulcus between posterior aspect of elevated supraorbital rim and frontal squama

8. type of orbital arcade – supraorbitals.

Where 'a' is central, 'b' is middle and 'c' is lateral:

0 = a>b, b<c and a < c
1 = a>b, b<c and a>c
2 = a<b, b>c and a>c
3 = a>b, b>c and a>c
4 = no variation in form

The objective is to determine differences in superior-inferior height of supraorbital across the orbit. Measurements were used to determine 'a', 'b', 'c' for each specimen.

9. prominence of temporal band on the frontal.
0 = weak; 1 = very prominent
The temporal band corresponds to the insertion zone of temporal aponeurosis (tendon expanding to a sheet-like form). Weidenreich (1951) stressed that the temporal bands are prominent on Sinanthropus (*H. pekinensis*); it should be useful to compare temporal band prominence between species of *Homo*.

10. metopic keeling.
0 = absent
1 = present but weak
2 = strong

11. development of the keeling. 0 = parallel edges; 1 = wider and flatter posteriorly; 2 = absent (no keeling)

12. bregmatic eminence. 0 = absent; 1 = present

13. upper coronal reinforcement. 0 = absent; 1 = present

14. frontal bosse. 0 = absent; 1 = present

15. obelionic region.
0 = keeling present; 1 = no keeling; 2 = presence of obelionic depression

16. pre-lambdaic depression.
0 = keeling on 4th quarter; 1 = no keeling on 4th quarter; 2= present

17. presence of the temporal band after the coronal suture. 0 = absent; 1 = present

18. asterionic process. 0 = absent; 1 = present

19. parietal bosse. 0 = absent; 1 = present

20. angular tuberosity. 0 = absent; 1 = present

21. curvature of nuchal plane in *norma lateralis*. 0 = convex posteriorly; 1 = flat to lightly concave posteriorly

22. importance of the occipital torus. 0 = weak; 1 = strong 2= no occipital torus

23. extension of external occipital protrusion. 0 = absent; 1 = present

24. extension of the tuberculum linearum. 0 = absent; 1 = moderate; 2 = strong
This refers to the degree of elevation, or relief, at the junction of the superior nuchal line and occipital crest.

25. medial concavity of the occipital lip to the tuberculum linearum. Is there a depression above where nuchal lines meet? 0 = absent; 1 = depression
Is there a depression above junction of nuchal lines?

26. external occipital crest, where present
0 = absent
1 = present for whole of nuchal
2 = present above inferior nuchal line
3 = present below inferior nuchal line

27. occipitomastoid crest. 0 = absent; 1 = present.

28. height of temporal squama cf vault. 0 = up; 1 = low

29. shape of the temporal squama. 0 = polygon to round; 1 = triangular

30. strength of supramastoid crest in the region of porion. 0 = weak; 1 = strong

31. relation between the supramastoid crest and zygomatic process in lateral view.
0 = zygomatica forms an angle with supramastoid crest
1 = zygomatica is continuous with supramastoid crest

32. continuity of the supramastoid crest with the inferior temporal line.
0 = no direct link; 1 = continuity

33. tuberculum supramastoid anterius. Is there a tubercle where supramastoid crest stops at squamous suture? 0 = absent; 1 =present

34. strength of the mastoid crest. 0 = weak; 1 = strong

35. continuity between mastoid crest and superior temporal line.
0 = no direct link; 1 = continuity.

36. supramastoid sulcus, where present – does it close posteriorly or not?
0 = closed posteriorly; 1 = open posteriorly.

37. importance of supramastoid sulcus. 0 = absent; 1 = narrow; 2 = wide

38. convergence of mastoid crest and supramastoid crest. 0 = divergent anteriorly; 1 = parallel

39. suprameatum spine. 0 = absent; 1 = present

40. section of tympanic in *norma lateralis*. 0 = rounded; 1 = ellipsoid to ovoid

41. orientation of main axis of tympanic in *norma lateralis.* 0 = orientated anteriorly; 1= vertical; 2 = orientated posteriorly

42. thickness of tympanic in *norma lateralis* (anterior edge of tympanic). 0 = weak; 1 = strong (>2mm)

43. contribution of the tympanic to mandibular fossa
0 = postglenoid process is strongly involved in the wall
1 = the tympanic makes up most of the wall
2 = rudimentary or no postglenoid process

44. relative development of mastoid process in *norma lateralis*. (Is it standing out from the base or tucked in underneath? i.e. does it project below the base of the cranium? 0 = does not project below the base of the cranium; 1 = projects below base.

45. extension of the pre-glenoid planum
0 = **no** pre-glenoid planum precedes the glenoid cavity
1 = a pre-glenoid planum precedes the glenoid cavity
Is there a level surface of bone preceding the mandibular fossa from the articular eminence either for the whole, or at least half, of the width of the eminence? There are marked differences between species of *Homo* in this character.

46. space between the tympanic and anterior of mastoid process. 0 = posterior part of tympanic joins anterior part of mastoid process; 1 = 'split'; 2 = wide space

47. anteroposterior width of mandibular fossa. 0 = narrow; 1 = wide

48. deepness of glenoid fossa. 0 = very shallow; 1 = deep

49. size Height of articular eminence relative to posterior wall of glenoid fossa (basal view).
0 = slope is shorter 1= similar; 2 = higher

50. orientation of mastoid process. 0 = not orientated inwards; 1 = orientated inwards

51. deepness of digastric fossa. 1 = shallow; 2 = deep

52. (ordered) size of juxtamastoid eminence. 0 = no eminence; 1 = weak; 2 = strong

The juxtamastoid eminence is suggested to be a relatively recent acquisition (Taxman, 1963).

53. importance of deepness between entoglenoid formation and tympanic plate. (Entoglenoid is at end of glenoid fossa and on temporal bone). 0 = fused; 1 = groove; 2 = space.

54. anterior wall of glenoid fossa. 0 = the anterior wall is horizontal; 1 = oblique; 2 = almost vertical.

55. inferior projection of the entoglenoid process compared to that of the tuberculum zygomaticum anterior.

1 = entoglenoid projects to a greater extent than the tuberculum zygomaticum anterior
2 = entoglenoid is similar to tuberculum zygomaticum anterior in degree of inferior projection

3 = entoglenoid is less projected than the tuberculum zygomaticum anterior

The objective is to express the relative development of the entoglenoid formation.

56. relative position of the entoglenoid formation to the tuberculum zygomaticum anterior.
0 = the entoglenoid formation is at the same level as the tuberculum zygomaticum
1 = the entoglenoid formation is posterior to the tuberculum zygomaticum
2 = entoglenoid formation is very posterior to the tuberculum zygomaticum
In modern humans the entoglenoid spine is posterior to the transverse axis and in Australopithecines is even further recessed.

57. inferior projection of the entoglenoid process and the tuberculum zygomaticum compared to the tuberculum articulare.
0 = **very** large inferior projection relative to the tuberculum articulare
1 = large inferior projection relative to the tuberculum articulare
2 = small inferior projection relative to the tuberculum articulare

58. antero-posterior convexity of the tuberculum articular (articular eminence). 0 = the tuberculum articular is flat in *norma lateralis*; 1 = the tuberculum articular forms a large round arc; 2 = the tuberculum articular forms a small round arc

59. shape of posterior edge of the tuberculum articular in *norma basilaris*.
0 = flat; 1 = arched; 2 = sigmoid

60. continuity between the pre-glenoid planum and the posterior slope of the articular tuberclum. 0 = the two are continuous; 1 = there is an angulation between them

61. crest on lateral edge of mandibular fossa. 0 = absent; 1 = present

62. inferior projection of entoglenoid process compared to the sphenoid border/edge.
0 = the entoglenoid process projects inferiorly to a greater extent than sphenoid edge
1 = the entoglenoid process is equivalent in inferior projection to sphenoid edge
2 = the entoglenoid process is les projected than sphenoid edge
For Weidenreich (1943) the entoglenoid is not a true process but an abrupt slope entirely formed by the squamosal and a character of *H. erectus*.

63. prominence of entoglenoid formation. 0 = very prominent; 1 = not prominent

The entoglenoid process is large in the Great Apes, modest in Australopithecines and very prominent in *H. sapiens* (after Picq, 1983).

64. lateral extension of entoglenoid process. 0 = very extended posteriorly; 1 = marginally extended backward; 2 = not extended posteriorly; 3 = tubercle (eg *H. sapiens*); 4 = not extended posteriorly or tubercle

65. does postglenoid process extend out beyond tympanic? 0 = doesn't overlap the tympanic; 1 = does overlap the tympanic; 2 = no postglenoid process or rudimentary process.

66. Profile of nasal saddle and nasal roof

1 = flat nasal bones
2 = slightly raised nasals, forming a curve
3 = nasals forming well-defined curve, ranging in size from medium to large
4 = deep angled nasal bones forming a 'pinched nose'

67. Relationship of rhinion to nasospinale

1 = nasospinale lies in front of rhinion
2 = nasospinale is on same plane as rhinion
3 = nasospinale lies behind rhinion

68. Condition of the *margo limitans*

1 = the *margo limitans* forms a sill
2 = *margo limitans* forms a smooth curve
3 = *margo limitans* includes a prenasal groove

69. The **condition of the *facies anterior* of maxilla and alveolar process**

1. = the *facies anterior* and alveolar process is inflated, puffy
2 = the *facies anterior* and alveolar process is well filled out
3 = the *facies anterior* and alveolar process is sunken
4 = the *facies anterior* and alveolar process forms a flat surface

70. presence of *jugum alveolar*
1 = there is no *jugum alveolar*
2 = the *jugum alveolar* forms a narrow ridge
3 = the *jugum alveolar* forms a broad and prominent ridge (width of 1+ premolar)

71. Presence of a *sulcus infraorbitalis* (i.e. under the infraorbital foramen)

1 =there is no *sulcus infraorbitalis*
2 = the *sulcus infraorbitalis is narrow*
3 = the *sulcus infraorbitalis is wide*

72. zygomaticoalveolar crest (ordered)

1= relatively straight
2 = curved
3 = forms an arc
4 = forms an arch

State 2 (curved) State 3 (arc) State 4 (arch)

73. Shape of naso-alveolar clivus
1 = naso-alveolar clivus is convex
2 = naso-alveolar clivus is flat
3 = naso-alveolar clivus is concave

74. Palate surface has low irregular crests or fine ridges arranged in more or less longitudinal direction.

1 = present
2 = absent

75. Location and direction of orifice of incisive canal

Character state:
1 = orifice of incisive canal is immediately posterior to incisors
2 = orifice of incisive canal is on a plane with canines
3 = orifice of incisive canal is on a plane with 1st premolar
4 = orifice of incisive canal is on a plane with 2nd premolar

76. Location of zygomatic arch

1 = the zygomatic arch runs below the Frankfurt horizontal
2 = the zygomatic arch runs at level of Frankfurt horizontal
3 = the zygomatic arch runs above the Frankfurt horizontal

77. Condition of the supraorbital margin

1 = the supraorbital margin is thick, rounded and not demarcated from roof of orbit
2 = the margin is thick with an edged crest not demarcated from roof of orbit
3 = the supraorbital margin is an edged crest demarcated from the roof of orbit
4 = the supraorbital margin is thin with an edged crest and demarcated from the roof of orbit

78. Condition of infraorbital margin of the orbits

1 = sharp high line dividing the floor of the orbit from the facial portion of the malar
2 = relatively rounded orbital margin but raised in relation to floor of the orbit
3 = pronounced rounding of the inferior **lateral** border which is leveled with the floor of the orbit (ie lower outside edge for half the lower edge of orbit is rounded but other half of lower orbit not rounded)

79. Character of superior fissure

1 = the superior fissure is small and round
2 = superior fissure is a slit-like lateral prolongation
3 = there is a strut dividing the fissure into 2

80. styloid process
1 = present; 2 = absent

81. tympanic trough
0 = absent; 1 = present
A coronally oriented long narrow trough along tympanic tube in basal view

82. **sagittal keeling on first half of parietal.**
0 = absent; 1= present

83. presence of external occipital crest
0 = absent; 1 = present

84. presence of glasseri fissure
0 = absent; 1 = present

85. supraorbital torus 0 = absent; 1 = present

86. tuberculum linearum
0 = absent; 1 = present

87. maximum cranial breadth
0 = at supramastoid region; 1 = at parietal region

88. superior-inferior length of nuchal dominates over superior-inferior length of occipital
0 = yes; 1 = no
Determined by comparing measurement for lambda-inion (occipital length) and measurement for inion-opisthion (nuchal length)

89. foramen magnum
0 = round; 1 = oval

APPENDIX 3: MANDIBULAR CHARACTER STATES

1. Lower dental arcade 1. long and narrow 2. short and wide	**12. Gonal region in lateral view** 1. thicker than ramus 2. same thickness as ramus 3. thins towards posterior margin
2. Lower dental arcade 1. broadly curved at front 2. tightly curved 3. square shaped	**13. Gonal region** 1. flares outwards 2. flares outwards with marked lateral flexion (may have channelling) and external rim 3. flares inwards 4. no flaring
3. Symphyseal region (ordered) 1. mental protuberance (chin) present 2. no mental protuberance and vertical 3. no mental protuberance and retreats	**8 14. Mandibular foramen** 1. laterally depressed 2. circular
4. Symphyseal keel 1. present 2. absent	**15. Mandibular foramen** 1. directed posteriorally 2. directed upwards
5. Subalveolar depression 1. present 2. absent	**16. Internal coronoid pillar** 1. present 2. absent
6. Mental foramen (ordered) 1. present under M1 2. present under P2 3. anterior to P1	**17. Coronoid process (ordered)** 1. higher than mandibular condyle 2. same height as mandibular condyle 3. lower than mandibular condyle
7. Posterior marginal tubercles 1. well defined 2. weak 3. absent	**18. Sygmoid notch** 1. 'V' shaped 2. 'U'shaped
8. Mandibular corpus 1. taller anteriorly than posteriorly 2. taller posteriorly 3. uniform height 3. uniform height	**19. Mylohyoid groove** 1. long 2. short
9. In lateral view, anterior margin of ramus 1. lies behind last molar (retramolar space) 2. lies anterior to last molar	**20. Post-incisal plane (ordered)** 1. vertical 2. inclined slightly 3. inclined markedly

10. Anterior notch (swelling) on anterior surface of ramus 1. present 2. absent	**21. Digastric fossa** 1. deep 2. deep and separated by tubercle 3. shallow 4. shallow and separated by tubercle 5. absent
11. Gonal region 1. smooth 2. rugose 3. has pterygoid tubercles	**22. From below, symphyseal region** 1. thickest at molars/on lateral edges 2. Uniformly thick 3. Thickest at midline
23. Submandibular fossa 1. long 2. short 3. absent	**32. Torus lateralis superior** 1. absent 2. narrow 3. broad 4. very broad and bulbous
24. Submandibular fossa 1. absent 2. narrow 3. broad 4. very broad and bulbous	**33. Origin sulcus extramolaris** 1. lingual edge M2 or M3 2. central posterior edge of alveolus at M3 3. no sulcus extramolaris
25. Sublingual fossa 1. present 2. absent	**34. Mental foramen** 1. single (both sides) 2. double (either side) 3. multiple
26. Sigmoid notch deepest 1. centrally 2. towards coronoid 3. towards condyle	**35. Anterior marginal tubercles** 1. absent 2. weak 3. marked **36. inferior transverse torus** 1. present 2. absent
27. Torus marginalis 1. present 2. absent	
28. Muscle scarring on ramus 1. absent 2. minimal 3. marked	

29. Mylohyloid ridge
1. narrow superior/inferiorly 2. bulbous superior/inferiorly 3. absent
30. Sulcus extramolaris
1. narrow 2. wide 3. very wide
31. Lateral prominence greatest below
1. M_1 2. M_2 3. M_{2-3} 4. M_3

APPENDIX 4. CRANIAL CLADISTIC DATA

DATA THESIS post LB1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	H. rhodesiensis	1	0	1	0	1	2	1	2	1	2	0	0	0	0	1	1	1	0	1	0	1	0	?	?	?	?	0
2	Sangiran 4	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	?	?	1	1	2	1	2	0	1	0
3	Sangiran 2	?	1	?	?	?	?	?	?	0	1	1	0	0	0	1	1	1	0	?	0	1	2	0	?	0	?	0
4	Trinil	0	1	?	0	?	?	1	?	0	1	1	1	0	?	1	?	1	1	0	0	1	2	0	1	0	1	?
5	Sangiran 17	1	0	0	0	0	2	1	?	0	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1	0
6	H. erectus	0&1	0&1	0	0	0	2	1	?	0	1	1	0&1	0	0	1	1	1	0&1	0&1	0&1	1	1&2	0&1	1&2	0&1	1	0
7	ATD6-15 + 6-69	0	0	?	?	?	?	1	?	0	0	2	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?
8	Ceprano	1	1	1	1	0	1	0	2	1	1	1	?	?	0	1	1	1	?	0	1	1	1	1	?	0	2	1
9	Daka	1	0	1	1	0	1	1	1	1	2	0	0	0	1	1	1	1	0	1	1	1	0	0	?	0	1	0
10	Bodo	0	1	1	1	2	1	1	2	1	1	1	1	0	0	?	?	1	?	0	?	?	?	?	?	?	?	?
11	KNM-ER 3883	1	0	1	0	0	2	2	2	1	0	2	0	0	0	1	1	1	0	0	0	1	0	1	1	?	3	0
12	KNM-ER 3733	1	0	1	0	0	2	2	2	1	2	1	?	0	0	1	1	1	0	0	0	1	2	1	2	1	1	0
13	KNM-WT 15000	0	0	?	?	?	?	1	?	0	0	2	0	0	0	?	?	1	0	0	0	1	0	1	1	0	1	0
14	KNM-OL 45500	2	0	1	0	2	2	2	2	0	0	2	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
15	OH9	1	0	1	1	0	2	1	0	1	0	2	?	?	?	?	?	1	0	?	0	1	1	0	?	?	1	0
16	SK 847	?	0	?	0	?	?	2	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	D2280	0	1	1	1	0	2	2	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	2	0	3	1
18	D2282	2	0	?	1	0	2	?	1	1	0	2	1	0	1	0	0	1	0	?	0	1	1	?	1	0	0	?
19	D2700	0	0	0	1	2	2	2	1	?	1	0	1	0	0	0	0	1	0	1	0	1	1	0	1	0	1	?
20	Dmanisi	0&2	0&1	0&1	1	0&2	2	2	1	1	0&1	&1&	1	0&1	0&1	0&1	0&1	1	0	1	0&1	1	1	0&1	1&2	0	&1&	1
21	H. habilis	1	0&1	0&1	0&1	0	1&2	1	2	0	0	2	0	0	0	0&1	1	1	0	0	0	1	0	0&1	?	?	0&1	0
22	H. floresiensis	1	0	?	?	?	1	1	?	0	1	?	?	0	0	2	1	1	0	0	0	0	1	1	2	1	1	0
23	A. africanus	1	1	0&1	0&1	1	2	0&1	1	0	0	2	0	0	0	1	?	1	?	0	?	1	1	?	?	0	?	?
24	H. sapiens	0	0	0&1	1	0&1	0	0	4	0	0	2	0	0	0	0&1	1	0	0	0	0	0&1	0	0&1	1	0	0&1	0
25	P. troglodytes	2	1	0&1	0&1	1	2	2	1	1	0	2	0	0&1	0&1	0	?	?	0	0	0	0&1	1	0&1	1	0	1	1
26	Gorilla	2	0&1	0	0	?	2	2	1&3	0&1	0	2	0	0	0	2	1	?	0	0	0	1	2	1	?	0&1	1	1
27	KNM-ER 1813	1	1	1	1	0	1	1	2	0	0	2	0	0	0	1	1	1	0	0	0	1	0	1	?	?	1	0
28	OH24	1	0	0	0	0	2	1	?	?	0	2	0	0	0	0	1	?	?	?	0	1	?	0	?	?	0	0

DATA THESIS post LBI		28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
1	H. rhodesiensis	0	0	0	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	2	1	1	1	1	2	2	1	1
2	Sangiran 4	?	?	0	?	0	0	1	0	?	0	0	0	1	0	0	1	1	?	2	?	1	2	1	2	2	1	1
3	Sangiran 2	1	1	0	1	0	1	1	0	?	0	0	0	1	?	1	1	0	1	2	?	0	1	1	?	?	?	1
4	Trinil	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	Sangiran 17	1	1	0	1	0	1	0	0	1	2	0	0	1	?	1	1	1	1	?	1	1	1	1	2	2	2	1
6	H. erectus	1	1	0	1	0	0&1	0&1	0	1	0&2	0	0	1	0	1	1	0&1	1	2	1	0&1	1&2	1	2	2	1&2	1
7	ATD6-15 + 6-69	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Ceprano	1	0	0	0	0	1	1	0	1	2	0	0	?	?	?	1	1	1	0	0	0	2	1	2	1	?	1
9	Daka	1	0	0	1	0	0	0	0	?	0	?	0	1	2	1	1	0	1	0	1	1	2	1	?	?	1	2
10	Bodo	1	0	?	?	?	?	?	?	?	?	?	1	?	?	1	1	?	1	0	0	0	0	?	?	?	?	0
11	KNM-ER 3883	0	0	0	1	0	0	0	0	1	2	1	0	1	2	1	1	1	0	1	1	1	1	1	2	?	2	1
12	KNM-ER 3733	1	0	1	1	0	0	1	0	1	1	0	0	1	0	1	2	?	0	2	1	1	1	1	2	2	2	1
13	KNM-WT 15000	1	1	0	1	0	0	0	0	1	1	1	0	1	0	1	1	0	0	2	1	1	0	1	2	1	2	1
14	KNM-OL 45500	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	1	?	2	1	1	0	?	2	0	?	1
15	OH9	1	0	1	?	1	0	1	1	1	2	0	1	1	0	1	0	1	1	1	1	1	1	1	2	2	1	2
16	SK 847	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	?	0	?	1	?	2	1	2	2	2	0
17	D2280	1	0	1	1	0	0	0	1	1	2	0	1	1	1	0	0	?	1	0	1	1	1	?	1	1	2	1
18	D2282	1	0	1	1	0	0	?	?	?	?	?	1	1	1	1	0	?	?	?	1	1	?	?	1	1	?	1
19	D2700	1	0	1	1	0	0	0	0	?	?	?	0	1	1	1	0	?	?	0	0	0	?	?	1	?	1	0
20	Dmanisi	1	0	1	1	0	0	0	0&1	1	2	0	0&1	1	1	0&1	0	0	1	0	0&1	0&1	1	?	1	1	1&2	0&1
21	H. habilis	1	0	1	1	1	0	0	0	1	2	1	0	0&1	0	1	1	0	0	2	1	0&1	1&2	1	2	2	2	1
22	H. floresiensis	1	0	0	1	1	0	1	0	1	1	0	0	1	1	0	2	0	1	2	1	1	0	1	1	0	1	1
23	A. africanus	1	0	1	1	1	1	0	?	?	0	0	0	0	?	1	0	0	1	2	?	1	0	1	1	0	2	0
24	H. sapiens	0	0	0	0&1	0&1	0	0	0	1	2	0	0	1	1&2	0	1	1	1	0&1	0	1	0	0	2	0&1	1&2	2
25	P. troglodytes	0&1	1	0	0&1	1	0	0	1	0	2	0	0	0&1	0	0&1	0&1	0	0&1	2	1	0	0	1	?	0	0&1	0
26	Gorilla	0	1	0&1	1	0	0	1	0	0&1	1&2	0	0	1	0&1	0	0	1	?	2	1	0&1	2	1	1	1	2	0
27	KNM-ER 1813	1	0	1	1	1	0	0	0	1	2	1	0	0	?	1	1	0	0	2	1	0	1	1	2	2	2	1
28	OH24	1	?	1	?	?	0	?	0	?	?	?	0	1	0	?	1	?	0	?	1	1	2	?	?	?	2	1

	ATA THESIS post LBI	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
1	H. rhodesiensis	3	2	2	1	0	1	0	2	0	2	1	2	3	1	3	1	1	2	1	2	3	2	1	?	1	1	0
2	Sangiran 4	?	?	?	?	2	1	1	2	1	2	0	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	0
3	Sangiran 2	?	?	?	1	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
4	Trinil	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5	Sangiran 17	3	2	2	1	1	1	1	1	1	2	0	4	1	2	1	1	?	?	2	2	3	1	1	2	?	1	0
6	H. erectus	3	2	2	1	1&2	0&1	1	1&2	1	2	0	4	1	2	1	1	?	?	2	2	3	1	1	2	?	1	0
7	ATD6-15 + 6-69	?	?	?	?	?	?	?	?	?	?	?	?	?	1	3	1	1	4	2	2	1	?	3	?	?	?	?
8	Ceprano	2	?	2	1	1	1	0	?	0	2	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0
9	Daka	3	2	1	1	2	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0
10	Bodo	?	?	?	0	1	1	?	2	1	2	0	3	1	2	1	1	2	1	2	2	1	?	1	3	1	?	?
11	KNM-ER 3883	2	2	1	1	2	0	0	1	1	1	1	2	?	?	?	?	?	?	?	?	?	?	2	3	2	?	1	0
12	KNM-ER 3733	2	2	1	1	2	0	0	1	1	1	2	2	1	2	2	1	?	3	1	2	1	1	3	2	?	1	0
13	KNM-WT 15000	2	1	1	2	0	0	0	?	1	4	0	?	1	2	3	1	3	2	1	2	1	1	3	3	?	1	1
14	KNM-OL 45500	2	1	1	1	2	1	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
15	OH9	2	1	1	1	2	1	0	1	0	4	1	4	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
16	SK 847	2	?	1	?	?	1	?	2	1	2	?	?	?	?	3	2	?	?	2	2	3	1	4	2	?	1	?
17	D2280	?	1	1	1	1	1	0	1	1	3	1	3	?	?	?	?	?	?	?	?	?	?	3	?	?	1	0
18	D2282	?	?	?	0	0	?	0	?	?	?	?	?	1	2	?	3	?	3	1	2	3	1	?	1	?	?	0
19	D2700	?	1	?	1	1	0	0	0	1	4	1	?	1	2	3	3	3	3	1	?	?	1	3	1	?	1	1
20	Dmanisi	?	1	1	0&1	0&1	0&1	0	0&1	1	3&4	1	3	1	2	3	3	3	3	1	2	3	1	3	1	?	1	0&1
21	H. habilis	3	0&1	1	1	0	0&1	0	1	1	2	1	?	1	1&2	4	1	2	2	2	2	?	?	3&4	1	?	1	0&1
22	H. floresiensis	3	1	1	1	0	1	0	?	0	1	2	?	1	2	3	3	3	2	2	1	4	1	3	2	?	1	1
23	A. africanus	3	1	1	?	0	1	?	0	0	2	1	1	1	2	4	1	3	1	2	2	3	1	4	2	?	1	0
24	H. sapiens	2	0&1	2	2	1&2	1	0&1	2	1	2	1	&3&	1&2	1	3	1	1	3&4	2&3	2	1&2	1&2	3&4	1&2	1&2	1	0
25	P. troglodytes	1&2	0&1	1&2	0	0	0&1	0	?	0&1	4	0	4	1	2&3	3	1	2	1	2	2	1&2	?	2&4	1	3	1	0
26	Gorilla	1	0	0	0	0	0	0	&1&	0	4	0	4	1	2	3	1&2	3	1	2&3	2	2	?	1	2	1&3	1	0
27	KNM-ER 1813	3	1	1	?	0	0	0	1	1	2	1	?	1	1	4	1	2	2	2	2	?	?	3	1	?	1	0
28	OH24	3	0	1	1	0	1	0	1	1	2	?	?	1	2	4	1	?	?	2	2	?	?	4	1	?	1	1

DATA THESIS post LB1		82	83	84	85	86	87	88	89
1	H. rhodesiensis	0	1	0	1	?	0	?	1
2	Sangiran 4	1	1	1	?	1	0	0	?
3	Sangiran 2	1	?	0	?	?	0	?	1
4	Trinil	1	1	?	?	1	0	?	?
5	Sangiran 17	1	1	1	1	1	0	0	?
6	H. erectus	1	1	0&1	1	1	0	0	1
7	ATD6-15 + 6-69	0	?	?	0	?	?	?	?
8	Ceprano	?	1	0	1	?	?	?	?
9	Daka	1	1	0	1	0	0	1	1
10	Bodo	1	?	?	1	?	?	?	?
11	KNM-ER 3883	0	1	0	1	1	0	1	?
12	KNM-ER 3733	0	1	0	1	1	0	1	?
13	KNM-WT 15000	0	1	1	?	1	0	0	1
14	KNM-OL 45500	?	?	?	1	?	?	?	?
15	OH9	?	1	1	1	?	0	?	?
16	SK 847	?	?	0	?	?	?	?	?
17	D2280	1	1	1	1	1	0	?	?
18	D2282	?	0	?	1	1	0	?	0
19	D2700	1	1	1	1	1	0	1	1
20	Dmanisi	1	0&1	1	1	1	0	1	1
21	H. habilis	0	0&1	0	1	0	0	1	0
22	H. floresiensis	0	1	0	1	1	0	1	1
23	A. africanus	0	?	?	1	?	0	?	?
24	H. sapiens	0	0&1	1	0	0&1	1	1	1
25	P. troglodytes	1	1	0	1	0&1	0	0	?
26	Gorilla	1	1	0	1	0	0	?	1
27	KNM-ER 1813	0	1	0	1	0	0	1	?
28	OH24	?	?	?	1	0	?	?	0

APPENDIX 5. MANDIBULAR CLADISTIC DATA

MANDIBLES THESIS DA		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	KNM ER 992	?	?	2	?	2	2	2	3	2	1	2	?	4	?	?	?	?	?	?	?	?	?	1	2	2	?	1
2	KNM WT 15000	2	2	2	1	2	3	2	3	2	1	1	?	4	?	?	1	1	2	2	2	4	3	1	2	2	1	?
3	Tigenif 3	2	2	2	1	2	3	1	3	2	1	1	?	4	?	?	1	1	2	2	2	4	3	1	2	?	3	1
4	Tigenif 2	2	2	?	1	2	3	3	3	2	1	1	?	4	?	?	?	?	?	?	2	4	3	1	2	?	?	1
5	Tigenif 1	2	2	2	1	2	2	2	3	2	?	?	?	4	?	?	?	1	2	2	2	?	3	1	2	?	?	1
6	D211	2	2	2	1	2	3	1	?	?	?	?	?	?	?	?	?	?	?	2	3	3	2	?	?	?	?	1
7	D2600	1	2	2	1	2	3	1	1	2	1	?	?	?	?	?	?	1	?	2	?	3	2	?	?	?	1	1
8	D2735	2	2	2	1	2	3	3	1	2	1	?	?	?	?	?	?	?	?	?	?	3	2	?	?	?	?	?
9	Zhoukoudian P696	2	2	2	2	2	1	3	1	2	1	3	?	2	?	?	1	2	2	?	1	5	2	2	2	?	2	2
10	Zhoukoudian P695	2	1	2	2	2	1	3	1	2	1	1	?	2	?	?	1	2	1	?	2	4	2	3	?	?	2	1
11	H sapiens 1	2	1	1	1	1	3	3	1	2	1	2	?	1	?	?	1	1	2	2	1	4	1	1	1	?	1	1
12	H sapiens 2	2	1	1	1	1	2	3	1	2	1	2	?	1	?	?	1	1	2	2	1	3	1	1	1	?	1	2
13	Gorilla	1	3	3	2	2	2	1	1	2	2	1	?	4	?	?	1	1	2	1	3	4	1	3	?	2	2	1
14	LB1/2	2	1	3	2	2	3	3	1	2	2	1	3	2	?	1	2	1	2	2	2	4	3	3	1	?	3	1
15	LB6/1	2	1	3	2	2	3	3	1	2	?	1	1	2	?	?	?	1	?	2	1	3	3	3	?	?	3	1
16	Sangiran 9	1	2	?	?	2	2	?	1	2	?	?	?	?	?	?	?	?	?	1	2	?	1	?	?	?	?	1

MANDIBLES THESIS DA		28	29	30	31	32	33	34	35	36
1	KNM ER 992	?	2	2	1	4	1	?	1	1
2	KNM WT 15000	1	?	2	?	?	2	2	1	1
3	Tigenif 3	1	1	2	4	3	3	?	1	1
4	Tigenif 2	1	?	2	1	3	?	1	1	1
5	Tigenif 1	1	1	1	1	1	1	1	1	1
6	D211	?	?	2	1	3	2	2	1	1
7	D2600	3	?	2	1	?	1	1	1	1
8	D2735	1	?	2	1	2	1	1	1	1
9	Zhoukoudian P696	1	1	1	2	3	3	1	1	1
10	Zhoukoudian P695	1	1	1	4	2	3	1	1	1
11	H sapiens 1	1	1	4	1	2	1	1	2	2
12	H sapiens 2	1	1	4	1	2	1	1	2	2
13	Gorilla	1	3	2	1	1	1	1	1	1
14	LB1/2	2	2	2	2	2	2	2	1	1
15	LB6/1	2	2	?	2	?	2	2	1	1
16	Sangiran 9	?	?	2	1	2	1	?	1	1

APPENDIX 6. Broken Hill (Kabwe) site plan

The Rhodesian or Broken Hill cave shortly after the discovery of the skull. (After The London Illustrated News.)