Chapter 9 Hominid Diversity and 'Ancestor' Myths

Homo, H. sapiens, and Other Taxa from a Phylocladistic Viewpoint

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Abstract Many of the 'myths' of direct ancestors of 'all hominids' or of *Homo* or of *H. sapiens* and age of these 'ancestors' are shown to be 'false' or based on poor character analyses and/or suboptimal classifications and/or inconsequent choices of names of taxa. Ernst Mayr's devastating influence since 1950 on naming fossil hominids and therefore on comprehending their diversity is obvious. Recently, that is since mid 1990s, many more new taxa of fossil hominids have been found and named, and this has produced a much better appreciation of the prehistoric diversity, and has questioned and put into doubt, if not outright refuted, many of the traditional, often too simplified and adaptationistic scenarios (or 'just-so stories') about human evolution as evidenced by 'direct fossil ancestors'. The most famous of these, 'Lucy', is here named *Afaranthropus* (n. gen.) *antiquus* (Ferguson, 1984).

The diversity, classification, and age of fossils and the delimitation of taxa are obviously relevant also when speculating about the origin of such non-fossiliseable features of modern humans as (self)-consciousness, cognitive abilities, spoken language, early and simple tool making, wearing of clothes etc. As with the origin of such features as 'nakedness', large penis, certain immune systems and blood types, large female breasts, subcutaneous fat, and in fact also upright stance and walking, we can only be completely sure that these features originated somewhere before the last common stem-mother of living humans and after the split from chimpanzees – not a very precise indication: between 7 and 0.1 m.y.

When discussing the more precise level or stage in the phylogenetic tree, it becomes of utmost importance that we talk about the same taxa, and refer to the same groups designated by taxon names like *Homo* and *H. sapiens*. Here, it becomes clear that these names are not at all used in a consistent way, and also that most anthropologists and palaeontologists are not aware that both groups are completely arbitrarily delimited in the time dimension, as demonstrated by our analysis and

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conventions of non-Linnaean nomenclature (see the subtext to the classifications on the homepage [see p. 189]). To discuss a concept even as simple as the 'origin' or age of a taxon, one must make the cladistic distinctions between crown groups, stem groups and total groups, and taxon names attached to 'nodes', 'stems' or somewhere in between, namely to certain synapomorphic features ('key features' or 'adaptations'). Language and its origin will be discussed, and the relationship between early and primitive African languages compared with the tree of recent hominids based on MtDNA:

The complicated phylogenetic tree and the consequential (non-Linnaean) classification of hominids will be demonstrated, so that the diversity of hominids through time can easily be seen.

9.1 Introduction

Historically, the classification and evolutionary history of humans has been as 'minimalistic' as possible, presumably to reflect the uniqueness and unity of humans in a 'politically correct' way, also in respect of religious considerations. So apart from a period during early 20th century, when 'racial distinctions' were almost universally recognized and named, both living and fossil species and subspecies names have been kept at a minimum, grossly underestimating the 'true diversity'. Especially Ernst Mayr's renowned 1950 paper has had a devastating influence as a prohibition on recognizing new fossil hominid species. It is known that it took about four years between 1960 and '64 for L.S.B. Leakey and Ph. Tobias to agree on a new species name for Homo habilis due to the unwillingness to create new hominid species - Australopithecus africanus (not even necessarily A. robustus), Homo erectus, Homo sapiens and H. neanderthalensis (perhaps only as a subspecies of *sapiens*) then seemed to be a sufficient number of taxa to describe 'human diversity' through time. Later on (1963), Mayr did admit that recognizing the 'robust australopithecines' as a separate species A. robustus, was probably justified. He never understood or accepted that in that way both the genus Australopithecus and the subfamily Australopithecinae were un-natural (paraphyletic) groups. It is also known from Don Johanson (1990) that it took Tim White and him many discussions and consultations with Mayr before they decided to name Australopithecus afarensis in 1978 after the find of 'Lucy' in 1975. (Mary Leakey refused to be part of that paper, despite the fact that the type material from Laetoli, Tanzania, was primarily her findings, and White had worked for her - so Yves Coppens 'forced his way' into the paper very late, not to let the Americans run off with all the glory, as the original finds in the Afar region – and Ethiopia – were French [see Coppens, 1975] – see part of that story also in Tattersal [1995, p. 152]).

Admittedly, the four decades before Mayr's 'warning' had seen taxonomic names of fossil hominids being used almost like museum or field numbers with a pletora of generic and specific names. But only fairly recently, in the wake of many spectacular new finds, has it been more generally accepted that there are, in fact, quite a few recognizable human taxa, beginning perhaps with Michael Day's *Guides to Fossil Man* conservative, but gradually more diverse over the four editions from 1965 to 1986.

The aim of the present review is not only to expose the substantial diversity of fossil hominids, but also to disclose the many myths of 'hominid ancestors', especially of *Homo sapiens*, which have been published earlier – and which still occur at high frequency. Most of these postulates are poorly founded from a cladistic viewpoint – difficult as they must be, also from a general methodological viewpoint. Further, the influence this has on certain traditional ideas about the evolutionary history of 'soft' (non-fossiliseable) human features will be traced. Extremely good photos of most of the fossil specimens mentioned below have been published in natural size by Johanson and Edgar (1996), and likewise, continent by continent, by Schwartz and Tattersal (2002, 2003).

9.2 Classificatory Methods of Phylocladistics

Co-working with Bjarne Westergaard (who died 2008), I have developed a modern, non-Linnaean, 'phylocladistic' classification of all fossil and living 'hominids' (2004), taking into account all possible needs of a complete and precise system including taxonomic conventions for clades (monophyletic groups), paraphyletic groups, 'ancestors', metaphyly, uncertainties, doubts, lack of precise knowledge, fragmentary fossils, sequencing, subordination, and age. This is based on a rankfree, 'neutral' unit called LITU (Least Inclusive Taxonomic Unit) as the terminal taxon instead of the species, subspecies etc. of the traditional system (so it is the smallest recognizable group of individuals with some characteristic features – to be named as basal unit in the classification, and (usually) placed at the endpoints of the branches of the phylogenetic tree ('stem tree' – or at endpoints in the cladogram). A LITU is the smallest unit that can be given a differential diagnosis (characterization) and which is of historical (phylogenetic) relevance to be defended by the systematist. A taxon is a named group in the classification.

Hybridisation and other complications in terms of reticulate structures of relationships can be included if necessary. Naming of the taxa employs a single name for each taxon in lower case letters for LITUs and Capitalized for groups of LITUs (double names for hybrids). This is in contrast to the traditional Linnaean system and nomenclature where the basal unit is a species written in small case letters after a name of some genus (Capitalized – perhaps abreviated to just the first upper case letter), into which category any species has to be placed. F.ex. *Homo sapiens* or *H. sapiens* (usually written in *italics*). In the non-Linnaean system, there are no (absolute, Linnaean) ranks or categories (like genera, families etc.), because age of origin (or age span from 'origin' to extinction for fossil groups); can act as both relative and absolute 'rank' at the same time in a precise and relevant way, seen from a phylogenetic viewpoint. This classification is based on the simplest possible phylogeny (parsimony) which maximises, in a cladistic framework, the number of synapomorphies for all taxa (constituting their diagnoses) and optimises the number of characters used as synapomorphies (the mutual, derived features characterizing a taxon/group (Patterson, 1980)). It therefore seems difficult, if not impossible, to find a 'better' system in terms of the informations at hand which are the features analysed cladistically for the relevant (or known) groups of organisms.

The diversity of fossil 'hominids' (here Hominina) of our branch as separated from that of the chimps about 7 m.y. ago, is often grossly underestimated by palaeontologists and anthropologists. Here, we demonstrate that there are at least about 35–40 LITUs that can be distinguished among the known fossils (and several more are likely to be found in the future). And, as shown by DNA research and other molecular or physical anthropological analyses, there is also a historical structure among living humans (the LITU of crown group 'modern' *Sapiens* can apparently be subdivided into historically relevant groups, which in this case will be LITU-s incl. in the 'higher' taxon *Sapiens*).

This is certainly of significance for the analysis of language history which, already for decades, has been done by methodologies very similar, if not identical, to those of cladistics (and further similar to the much older techniques of 'textual critics' analysing the history of old manuscripts (Platnick & Cameron, 1977)). It is probably not just a coincidence that some of these ideas on historical analyses of languages and evolutionary history and the way to illustrate them by 'trees' can be traced back to the two colleagues and friends August Schleicher and Ernst Haeckel in the 1860s (1861 resp. 1866; the former sometimes considered father of historical linguistics, the latter inventor of numerous biological terms, among them 'phylogeny'), both directly inspired by Darwin's *Origin*, which has only one figure, a 'tree-like' diagram (1859).

Concerning nomenclature, the naming of the taxa, we have the cladistic problem of distinguishing so-called 'node-based' crown group taxa and apomorphy based ones from 'stem-based' taxa in a consistent way in the nomenclature for the classifications. I believe the only consequent and 'minimalistic' way of doing this is by naming only terminal taxa/LITUs, clades and crown-groups as far as possible. But what we tried to demonstrate in 2004 (Bonde & Westergaard – check home-page [see p. 189]) was that in practice you need rules also for naming other sorts of groups if you want to cover all known diversity of life. Namely, e.g. paraphyletic, metaphyletic and hybrid groups and 'ancestral' species/LITUs (see also Bonde, 2001). But we were not really consequential (2004) as we named some 'stem-based' groups (Queiroz & Gauthier, 1992), also recommended by the PhyloCode (Cantino & Queiroz, 2004 or newer edition), which is, in fact, unnecessary if not outright impossible.

Such stem-based groups originating at the very split from their living sister groups and comprising the very earliest parts of the said lineages – although they must have existed in the past – can never be satisfactorily and precisely indicated in the practical classification and nomenclature of known organisms. With a group which has fossils as well as recent forms present there will always be a certain 'total group' (a living crown group clade [Jefferies' term] combined with its fossil 'stem-group' [paraphyletic] of Hennig (1966) and together forming a clade – see

Queiroz and Gauthier (1992, 1994)). A total group contains a certain clade and the fossil(s) indicated by at least one synapomorphy to represent the first branch to split off from that clade. This, then, in practice constitutes the closest approximation to a truly 'stem-based' group. But this total group does not include the very earliest parts of the stem-lineage, because if such specimens were really found as fossils they would not show the relevant synapomorphy, or at least not in sufficiently high frequency. Those very earliest 'ancestral' fossils can only be classified as incerta sedis within the relevant higher crown group because one cannot show whether they belong just above or just below the relevant split (or 'speciation'), as I have repeatedly argued (1977, 1981, 2001 – see also Bonde & Westergaard, 2004). These supposed and very ideal 'ancestors' (morphotypes in Nelson's (1970) terminology), should they ever be found, which is entirely unlikely, they would form a paraphyletic or metaphyletic group anyway and can by no means be precisely classified (a general feature of organisms with only relatively 'primitive' or plesiomorphic characters). So no groups are in pratice really 'stem-based' (contra Queiroz & Gauthier and the PhyloCode); all groups/clades must be based on the earliest node ('speciation') within the group, unless in rare cases the earliest fossil can be assumed to be truely 'ancestral' and lie on the stem-branch itself. Concerning the positive possibility, in rare cases, of being able to indicate such 'actual ancestors', we disagree with most cladists, while many palaeontologists, especially micro-palaeontologists (who may believe they can dig the phylogeny right out of the ground or rather a drill hole) are willing to consider such possibilities - or even (far too) eager to do so. But surely, if somebody think they can identify 'real ancestors' they must have a possibility to precisely indicate that in a classification by certain conventions. And biologists should not believe that this is a problem only concerning fossils, because neontologists also need sometimes to classify taxa which look exactly like 'primitive ancestors' of other groups (usually their derived sister species) and therefore are, in fact, paraphyletic 'species' with no autapomorphy (e.g. diploid plants giving rise to tetraploids).

9.3 Diversity

The taxonomic diversity of fossil hominids in the restricted sense of being those fossils more closely related phylogenetically to living humans than to chimpanzees, is today realized to be much greater than believed fifty years ago. Many recent fossil discoveries surely contribute to that understanding but still there is, in many textbooks and semi-professional accounts (and a few professional ones), a reluctance to accept this diversity (e.g. Napier, 1975; Leakey, 1981; Winkler & Schweikhardt, 1982; Jones et al., 1992; Stringer & Gamble, 1993; Stringer & McKie, 1996; Lewin, 1999; Benton, 2005). And despite lots of beautiful photos of fossil hominids, the entire diversity is not really mapped by Johanson and Edgar (1996), and books like *Lucy* by Johanson and Edey (1990), and Leakey's *Homo* (1994) are not meant to cover everything. The others mentioned above comprise something like 15–20 taxa of hominids, while Bonde and Westergaard (2004) have 35–40 taxa (LITUs, 'species' or 'subspecies' – some 10 of them traditional chrono-species subdividing branches) as a minimum. But some of the simplifications in the most popular reviews (Tattersal, 1993 for the American Museum exhibit, Gore, 1997; Anon, 2004), and especially in those for kids, (e.g. Thomas, 1994; Ebbesen, 1990), are quite misleading.

But see also Schwartz (2004) about the recent trend of recognizing and naming many more fossil hominid taxa after this had been hampered for 30–40 years by Mayr's 1950 paper. The 'taxonomic activity' slowly increased by the descriptions of *H. habilis* (1964) and *H. ergaster* and 'Lucy' (1975, resp. 1978 – but these new species were discussed as very problematic, or were even neglected), and then it accellerated by the 1990s. Tattersal has rightly warned (1986) that if fossil diversity is not formally named then it will not be discussed – he even claims that subspecific names will be completely forgotten and that we underestimate the 'true' diversity anyway by only having hard parts. One reason is the tradition in palaeontology most often to discuss and to register at the generic level, and only rarely at the specific level (Treatise on Invertebrate Paleontology, Romer's 1966 Vertebrate Paleontology and younger followers; Cooper, 1970; Forey et al., 2004).

Admittedly, the trend in the decades before the mentioned period had been using the taxonomic names rather like museum collection numbers, which had created a plethora of names for what was just variations within the natural taxonomic units or species. Understandably, a certain reduction of the names of 'units' and of small and 'blind' collateral branches on the family tree has to be made for pedagogical reasons in the more popular accounts, but it is much less acceptable in professional reviews of our evolutionary history. It has, in the past, created a totally misleading picture of human phylogeny with profound consequences for ideas about the evolution of specific features both in the skulls and the post-cranium with implications for 'soft parts', functional anatomy, behaviour, and palaeoecology.

The most 'simple' and extreme idea, the so-called 'single species hypothesis' (e.g. Brace & Ashley Montagu, 1965; Wolpoff, 1968, 1980 - 'dogmatic' according to Tattersal, 1995 – later called 'ludicrous'), was upheld in certain anthropological 'schools' even until about thirty-five years ago (see Tattersal, 1995, pp. 127ff). Only the finds of robust australopithecines in the same deposits in Kenya as much more Homo-like fossils (Leakey, 1976; Leakey & Walker, 1976) put a final stop to this idea (or nearly so). It visualised the entire evolution of humans since the split from chimps as just one ('biological') species lineage ascending through time - albeit divided into successive 'species' (or chronospecies) for 'practical' or stratigraphic reasons, or because of intuitive ideas of important 'adaptive shifts' (Simpson, 1959, 1961). Similar adaptationistic arguments repeated as late as 1999 by B. Wood & Collard – but after the jubilee year of Darwin we should rather recall his remarks in a letter to T.H. Huxley 'In regard to classification I believe it ought ... to be simply genealogical ... I think it ultimately will, ... for it will clear away an immense amount of rubbish about the value of characters, The time will come, I believe, when we shall have very fairly true genealogical trees ...' [quoted by Goodman, 1975, here much abbrieviated with my emphasis]). Perhaps the 'time has come' to stop adaptationistic story telling about 'key characters'?

So finally, in 1975–76, it had been 'proved' that there were at least two human lineages, one a 'robust australopithecine' (Paranthropus spp.) and another much more *Homo*-like. The latter much later caller *H. (Pithecanthropus) rudolfensis*. and the age of these at Koobi Fora/'East Rudolph' is between $1\frac{1}{2}$ and 2 m.y. (at the time mistakenly dated to be about 1 m.y. older). The relative ages between the South African cave localities themselves, Sterkfontein, Swartkrans, Kromdrai and Makapansgat was not well known at that time, and neither was their ages as compared to those of East Africa, and the age of the Taung locality for the type Australopithecus africanus was entirely uncertain. So phylogenetic (or possible ancestor-descendant relations) were very uncertain, although it was generally assumed that the 'gracile' A. africanus (comprising also Plesianthropus) was older than the 'robust' forms (Paranthropus), but many only recognized one genus, Australopithecus, for them all (also classified as a separate subfamily, Australopithecinae, which Simpson [1945] in his famous classification of mammals included in his family Pongidae for the apes !). Robinson (1956, 1972, and with Broom, 1952) always stressed the latter's name for the 'robust' forms, *Paranthropus*, as a very distinct taxon, but despite the supposed age-relations he preferred some unknown 'robust' australopithecine as ancestral to both Australopithecus and Homo (1972), in the same spirit as Weidenreich (1946) deriving later humans from 'giants'. The few branches of the phylogenetic tree I showed in 1989 (from a 1987 meeting) was even beyond the tradition at that time (but Groves excellent 1989 book appeared just after that with many more taxa). Figure 9.1 shows the diversity presented in a recent Danish Encyclopedia.

9.4 Australopithecus – An Old Homo

The rather old Australopithecus africanus (between 2 and 3 m.y. (Delson, 1988) in S-Africa) was a problem: To some, it was a variant of (or a more primitive species grading into) the 'robust' australopithecines (e.g. Johanson & White, 1979 – an older idea that it was just the females (Brace, 1967) had been abandoned (Birdsel, 1975, pp. 263ff, Tattersal, 1995, pp. 128ff)). To others, it was only a very primitive Homo (Robinson, 1956, 1972; Bonde, 1976, 1977, pp. 790–791) based mainly on the postcranial skeleton, but also on some skull features which was repeated by many analyses (Groves, 1991; Tattersal, 1995). This problem remained later because to some, A. africanus was clearly related to Paranthropus (Rak, 1983; Wood, 1992) wavering), while to Groves (1989, 2001; Olson, 1985; Lockwood & Tobias, 1999; Robinson, 1972) and to myself (1976, 1989, 2001; Bonde & Westergaard, 2004) africanus is clearly a Homo, based on several synapomorphies, but very primitive. Remember though, that before much was known about the chronology of the South African caves (Taung, Sterkfontein, Makapansgat), and under influence of Weidenreich's Apes, Giants and Man (1946), Robinson (1972) also thought that we were derived from 'giants'/large apes in a transformation series over robust Paranthropus via Australopithecus (= primitive Homo) to more advanced and smaller *Homo* (today we know that the trend in size is the opposite).

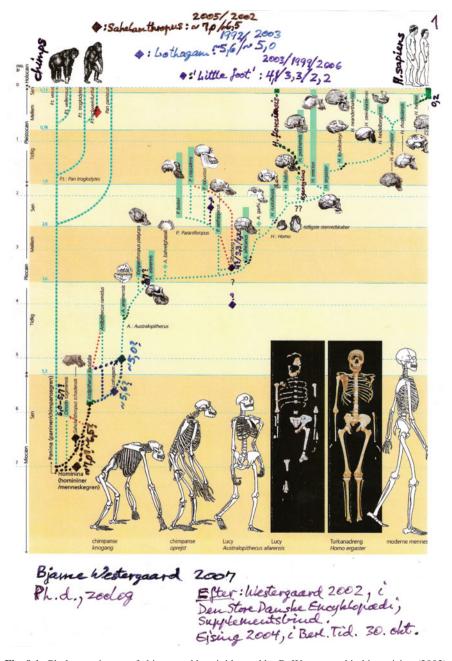


Fig. 9.1 Phylogenetic tree of chimps and hominids used by B. Westergaard in his revision (2002) of 'Human evolution' in 'Den Store Danske Encyclopedi' (Large Danish Encyclopedia) suppl. vol., and here with his further revisions and remarks added by hand. Used also by Bonde and Hoeg (2008) in their obituary on Bjarne W. in Yearbook of Danish Natural History Society after he had been murdered in Jan. 2008

Some have suggested that *africanus* could be common ancestor of both the robust and the *Homo* lineages (Day, 1965). The latter is refuted by finds of *Paranthropus* such as the 'Black skull' (WT 17000 (= West Turkana – Walker et al., 1986) – which should probably not be referred to the species *aethiopicus*, as the holotype jaw of this taxon, *Paraustralopithecus aethiopicus*, from Omo region, South Ethiopia (Arambourg & Coppens, 1968) has too small molar teeth (Groves, 1991); he refers it to an old *Homo* as *H. aethiopicus*). Its age is 2.5 m.y., that is, older than the youngest *africanus* (Thackeray et al., 2000) inclusive the holotype, 'Dart's baby' (Dart, 1925; Delson, 1988). The proper name for the 'black Skull' is *P. walkeri* by Ferguson (1989 – and see Groves (1991, pp. 254)).

This immediately makes a great difference for the age of *Homo*. In the first model, the oldest *Homo* is almost 2.5 m.y. (the so-called *H. habilis* and/or *H. rudolfensis* – see Leakey, 1994; Kimbel et al., 1996). In the second model, *Homo* must be much older, as some *africanus* from Makapansgat are probably a little over 3 m.y. old (Delson, 1988; Clarke. 1988).

9.5 The 'Robust' Paranthropus

This again implies that the sister group, Paranthropus (see Tobias, 1967; Grine, 1988; Groves, 1991), must have the same age within the clade Parhomo, named (by Bonde & Westergaard, 2004) for this combined Homo-Paranthropus group. But have 'robust' fossils that old ever been found? Usually, *Paranthropus* is also recorded as about 2.5 m.y. old, e.g. the age of the 'Black Skull' (WT 17000, socalled 'A. aethiopicus', Walker et al., 1986; Kimbel et al., 1985 – disqualified above). But there is apparently an even more primitive *Paranthropus*, a fragmentary skull from Sterkfontein reconstructed by Clarke (1988) with concave face and the large molars, but no parietal crest, and even more primitive by being rather prognath and with much larger canines and incisors (not named – should, however, be critically compared with A. garhi of approximate same age (White et al., 1999; see below), which also has very large molars, and lacks a parietal crest). This is the same age as A. africanus from this locality, about $2\frac{1}{-3}$ m.y. But some records are almost always forgotten (at least not mentioned): In the lower part of the Omo section (Shungura Fm.), two very large deciduous molars have been found with an age about 2.9 m.y. (Coppens, 1975; Groves, 1991, p. 195), and it is quite likely they represent *Paranthropus*. And one should recall that at the beginning when hominids were found in the Afar region (Johanson & Taieb, 1976; Coppens, 1977; Taieb et al., 1976), the diversity of species was supposed to be two or three hominids, and some researchers later on thought that the so-called 'first family' at locality 333 represented early, robust australopithecines (e.g. Olson, 1985) – now known to have an age of 3.22 m.y. (Walter & Aronson, 1982). And it is sometimes indicated that there might be 'robust' types in Makapansgat (Tobias, 1989, but cf. Clarke, 1985 – originally called A. prometheus by Dart, 1948, now A. africanus), perhaps of a similar age over 3 m.y. In fact, the ideas of some people were that there was more than one taxon in most of the South African cave localities.

9.6 Our Stem-Mother 'Lucy'

Over the next few years after the find of the skeleton 'Lucy' (40% preserved, very little skull but the lower jaw) this very variable 'sample' over 3 m.y. old from the Afar region (Senut, 1978; Johanson & Taieb, 1976) was said to be more than one species (one Homo-like, one like A. africanus acc. to Johanson (1978), but a few month later considered the same taxon as known from jaw fragments from Laetoli in the Olduvai Gorge, Tanzania (White, 1977), half a million years older). This taxon was a new species called Australopithecus afarensis, but with the holotype jaw from Tanzania (Johanson, White, & Coppens, 1978). This will create eternal confusion, and this despite Coppens' (1977) demonstration that the lower dentition, especially the premolars are quite different in 'Lucy' (much more primitive, Coppens' gracile 'pre-Australopithecus' (e.g. 1994)), and the AL (= Afar Locality) 333 sample is more robust and advanced, Homo-like. These and other differences are said by White (1985; Kimbel, White, & Johanson, 1985; Johanson & White, 1979) to be bridged by intermediate forms in the samples, or they may be considered sexual differences. But this seems highly dubious, especially for the elbow and knee joints (Senut, 1978, 1980; Tardieu, 1979; Senut & Tardieu, 1985; both students of Coppens), as well as the heelbone and ankle (Stern & Susman, 1983; Susman et al., 1985). This 'taxon', as usual when White is involved, is claimed to be the ancestor of all younger hominids (White et al., 1981, 2009 – it is a remarkable incidence that one single person can, many times, find something so extremely rare as 'direct fossil ancestors' - and make other people believe it). It has become enormously popular, nicknamed as it is, from the Beatles' song (Johanson & Edey, 1981), and mostly palaeoanthropologists – surprisingly – seem to accept this taxon, of which even the name is not appropriate, as it should be *Praeanthropus africanus*, the name of the first hominid fragment found at Laetoli/Garusi in the 1930s (see Bonde & Westergaard, 2004; Strait et al., 1997). Below follows more on Lucy's bipedality and the controversy around her 'walking style', as well as problems with the famous foot prints in Laetoli, and the 'name-business'.

'Lucy', age 3.18 m.y. (Walter & Aronson, 1982) and some other Afar fossils constitute another, much more primitive species, dubbed Homo antiquus by Ferguson (1984) with the famous skeleton as holotype. But although it is far too primitive to be a member of *Homo*, it still has not received a proper generic name (in the Linnaean tradition), but is just called nov. gen. antiquus by Bonde & Westergaard (2004). To provoke a discussion of this important and primitive taxon (which due to its too young age is not ancestral to any other taxon/group, whether it has known autapomorphies or not, but must be a 'blind' side branch) this new generic name will here be proposed as Afaranthropus (Afar after this important region where Lucy's species so far seems to be endemic) with type species A. antiquus (Ferguson, 1984). The diagnosis of both genus and the single species can be taken as the character combination from Groves' analysis (1991, p. 223 fig. C and features favouring this cladogram C from the scheme p. 224) - despite the not so convincing autapomorphies for a proper cladistic characterization. The relatively long pubis might, however, be one more specialization creating a 'true' clade for 'Lucy' and her kin (Fig. 9.2). Discussion and synonomies by Groves (1991, pp. 249–251) as gen. indet.

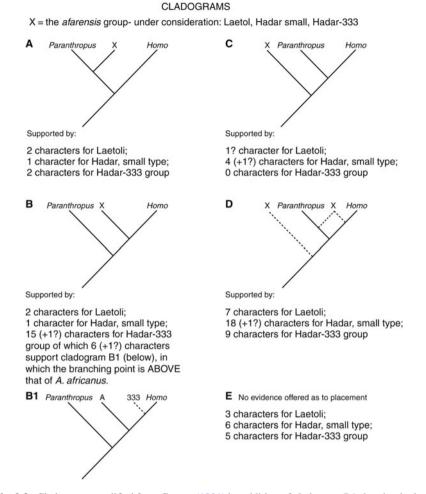


Fig. 9.2 Cladograms modified from Groves (1991) by addition of cladogram B1 showing in detail the position of *Homo hadar* Bonde and Westergaard (2004; = 333). Homo in the other diagrams comprises *Australopithecus africanus* (as a primitive member). x is that one of the three subdivisions of the polyphyletic '*Au.*' *afarensis*, which is tested in the resp. diagram. So B and B1 support inclusion of AL 333 fossils in *Homo*, while C indicates that 'Lucy', now *Afaranthropus antiquus* (Ferguson, 1984) is most primitive. For the Laetoli sample (incl. type of '*Au.*' *afarensis*) two charaters weakly favour each of the cladograms A and B, but overall similarity is with the primitive *Au. africanus* (acc. to Groves), so it can best be placed with some uncertainty as an early member of that lineage. This is very important, because this implies a minimum age ca. 3.7 m.y. for the split between *Homo* and *Paranthropus*, meaning that both of those lineages are nearly 4 m.y. old. If the Laetoli sample is part of *Australopithecus* (s. s.), then it can – as *Au. africanus* is occupied – retain the name *Au. afarensis* (unfortunately), but if not, then the name shifts back to *Praeanthropus africanus* with the Garusi maxilla as type specimen (and *afarensis* as synonym)

antiquus. We (Bonde & Westergaard, 2004) disagree with Groves concerning the much older Lothagam and Tabarin mandibles, they can certainly not be included in the same species as Lucy, as they are even more primitive, the former named *lothagamensis* by us and the latter *praegens* by Ferguson (1989 – see further below under *ramidus*, p. 167).

These are the 'gracile' or 'small' Afar fossils distinguished by Groves plus a rather large palate (showing that not all antiquus are small) which was used for the reconstruction of the skull of 'A. afarensis' (Kimbel & White, 1980; Kimbel et al., 1984), often supposed to be the skull of 'Lucy', although almost all of the other parts are from H. hadar, AL 333 (only small fragments of the braincase were found with the type skeleton of Lucy). Therefore important parts of the usual reconstructions of 'Lucy' are misleading; also the fingers and toes are from the AL 333 sample (none found with Lucy). And this likewise counts for the claim by Lovejoy (1988, also Johanson, Lovejoy et al., 1982) and others, that Lucy had a striking gait, almost *exactly* like modern humans. This must be wrong, as the shape and 'flare' of the pelvis is different from the modern condition, and so is the relative length and the shape of the femoral neck and the pubis (critique also by Stern & Susman, 1983; Susman et al., 1985). So the muscles must have worked at least in a slightly different way, and furthermore her body proportions are unlike ours, making it extremely unlikely that she would have walked *exactly* like us. This mistake seems repeated by White and his team (2009), where 'A. afarensis' is supposed to be a 'very modern biped' compared with its 'direct ancestor', A. ramidus (this actually constitutes two mistakes, or something unknown).

This controversy is reviewed in some detail by Cherfas (1983), incl. some aspects of the Laetoli footprints and who made them, a problem later treated by Anderson (1983) also in New Scientist, and Hay and Leakey (1992). Stern and Susman (1983) as well as Senut and Tardieu (1985) have demonstrated that the small specimens in the Afar area, like Lucy, and the larger ones like those from AF 333 are characteristically different concerning the postcranium, all with reference to mobility and ability for climbing and walking. In all cases, comparing elbows, knees, ankle joints and heelbones shows that the 'small' sample (Lucy) is much more ape-like, and the large specimens much more *Homo*-like. Lucy has retained many primitive features connected to climbing abilities, and she could well walk upright also, although not exactly a striding gait like modern humans, but probably with a slight bend in hips and knees. The large specimens were better adapted for walking on the ground. Lucy also had relatively long arms compared to the legs like in apes, while this measure is unknown for the larger specimens. Lucy has an unicuspid lower anterior premolar somewhat like apes, while the larger jaws tend to have a high inner cusp on that premolar like in man. Although male gorillas live more on the ground than the females which are more frequently climbing, it seems impossible to explain these differences just as sexual dimorphism; it is much more likely to be species differences between primitive Afaranthropus antiquus and the more Homo-like AL 333 - the same pattern which appeared from Groves' analysis of some different characters. And the two species are usually not found together on the same locality. The Lucy

skeleton is from a higher member of the local formation with an age like 3.18 m.y., while the AL 333 sample is from the member immediately below with age 3.22 m.y. (Walter & Aronson, 1982). The Laetoli sample with the type of *afarensis* is a much older third species, its proper name being *Praeanthropus africanus* (above under Lucy).

9.7 Very Early Homo

The only profound cladistic analysis of this mess is that by Groves (1989, 1991 – and I have seen no valid arguments against it – those by White (e.g. 1985) seem so biased towards his original idea of one taxon that they are very difficult to use). Groves found to his own surprise, when the nearly 30 characters differing between the three localities/samples were analysed, that the 'robust first family' (AL 333) was quite advanced and Homo-like (Coppens, 1994; Senut & Tardieu, 1985 agree). This taxon even has several synapomorphies with *Homo* which are not found in the slightly younger Australopithecus africanus (Fig. 9.2). Recently, Westergaard and I (2004) have created a name, *Homo hadar* (or homo-hadar, non-Linnaean – see Groves, 1989, 1991, p. 260, where he almost implied this name in the headline) for this important taxon, the earliest, 3.22 m.y. old, representative for the Homo lineage (as distinct from *Paranthropus*) with the incomplete skull AL 333–45 as holotype (face lacking, but a juvenile one is known (see e.g. Olson, 1985; Johanson & Edgar, 1996), comparable to the type of A. africanus ('Dart's baby' of 1925)). We also indicated autapomorphies as diagnosis for H. hadar as a true clade using features listed by Groves. See a detailed discussion of this species ('unnamed') of Homo by Groves (1991, pp. 260–263). At loc. 333 (where now over 250 bones of the so-called 'first family' have been found) a recent find of a foot bone, metatarsal 4, has indicated – as expected from the heel and ankle – that the foot of this Hadar hominid is very Homolike, and it indicates an arch in the foot like in modern humans (Ward et al., 2011), and therefore a human-like gait. This is clearly different from the condition indicated by the ankle of the more primitive skeleton of Lucy (Af. antiquus – see above under Lucy), although this is not the point made by the authors (incl. Johanson, Lucy's finder).

It appears that no-one has criticized and refuted the distribution of characters used by Groves (1991), so here his conclusion which now and then is confirmed, is as just shown, and many implications follow: AL 333 is a very early representative of the *Homo* lineage in East Africa – exactly like the Leakey family used to predict but now apparently will not admit, or even mention in a book on the origin and evolution of *Homo* (R. Leakey, 1994). So, unfortunately the traditional story told about these important fossils from Afar, also in the textbooks (e.g. Benton, 2005), is quite misleading, and it should clearly be revised and the taxonomy rectified.

These unexpected findings concerning AL 333 have several important implications:

- (1) There must be representatives of the more primitive *Homo (Australopithecus) africanus* somewhere of at least the same age, probably somewhat older.
- (2) Also, an early member of the robust *Paranthropus* lineage (sister group to *Homo*) must exist somewhere in Africa, over 3 m.y. old. Perhaps the so-called 'Little Foot' skeleton from Sterkfontein, S-Africa is of relevance here, because it clearly has a strong parietal crest and is rather prognath. Its age is said to be about 3.3 m.y. (Clarke, 2002) from an old 'pocket' in the limestone cave. Could it be the predicted old *Paranthropus*?
- (3) Clearly, there is sufficient 'unknown' space in Central and Western Africa to accommodate such ancient species – almost nothing is known of fossiliferous layers of the right age in these regions.
- (4) The large and slightly younger skull from Afar, AL 444-2, ca. 3 m.y. old said to be the largest 'australopithecine' skull known, at least widest in the eye region (Kimbel et al., 1994 nicknamed 'Boy of Lucy'), could rather be an advanced male of *H. hadar*, a species different from 'Lucy'. The former's relationship with the so-called 'advanced or primitive' (?) '*Australopithecus'*, *A. garhi* (White et al., 1999) suggested as more '*Homo*-like', but with big molars has not been thoroughly investigated (see below under 'Stem-mothers').
- (5) The Laetoli sample from Tanzania of age 3.6 m.y., incl. the holotype lower jaw LH 4 of Australopithecus afarensis (Johanson et al., 1978 - a most peculiar and unfortunate choice combining name and type, see Johanson & Edey, 1981; Tattersal, 1995, p. 152) is of more uncertain relationship. It was said by Groves (1991) to be 'most similar' to A. africanus. In that case, it could be the early *africanus* relative predicted above (under point 1), and one could argue that it should preserve its specific name, but as *Homo (Australopithecus)* afarensis. The nomenclature is more complicated, however: The Laetoli sample has always been considered just one single specific taxon (despite debate on who made the famous footprints). Therefore it comprises the first hominid fragment found in that locality in the 1930s, the so-called 'Garusi maxillary' (Kohl-Larsen & Reck, 1936), which was first named Meganthropus africanus. It was later considered unlikely to represent this Javanese 'genus', and was therefore referred to a new genus Praeanthropus (see the story in Strait et al., 1997). Accordingly, if the Laetoli sample is not believed to belong to Australopithecus, then its proper name is Praeanthropus africanus (syn. A. afarensis) as also used e.g. by Bonde & Westergaard (2004) - in our non-Linnaean nomenclature, however, it should be just one name, e.g. praeanthropus, for that terminal taxon/LITU.
- (6) The relationship of that rather primitive species and others with ages around 3–4 m.y. like 'Australopithecus' anamensis (Ward et al., 2001 clearly not a Homo (Australopithecus) sensu stricto) and Kenyanthropus (Leakey et al., 2001) and 'A.' bahrelghazali, a lower jaw from Tschad (Brunet et al., 1996), should obviously be cleared up. Our suggestion (Bonde & Westergaard, 2004) is shown in the tree and classification below, but note: without implying the reasonable splitting of praeanthropus (= afarensis) into three different taxa.

9 Hominid Diversity and 'Ancestor' Myths

- (7) An even more critical analysis would probably have a sequence of advancing sister groups: *lothagamensis* (Bonde & Wesytergaard, 2004), *anamensis*, *kenyapithecus*, *antiquus*, (which are more primitive than) *praeanthropus*, *bahrelghazali* below the split between *Paranthropus* and *Homo* (combined in the clade Parhomo by Bonde & Westergaard, 2004), but with the latter two 'species' possibly interchangeable with the Parhomo stem (indicated as *sedis mutandis*, of uncertain and interchangeable interrelationship). And as the faces and ear regions are unknown or very little known for all of the last three 'species', their relationship with the characteristic, flat-faced *kenyanthropus* skull may seem quite uncertain too. The AL 333 sample should be removed from the *praeanthropus/afarensis* group together with a few slightly older Afar specimens, they all clearly seem to belong in the *Homo*-lineage, though not as the most primitive members (see comments above).
- (8) 'Lucy' (= Af. antiquus) is by no means the stem-mother/ancestor of all later hominids, like it is most often presented by the 'White-Johanson group' (e.g. Johanson & White, 1979 now separated for good? Kimbel et al., 1984, White et al., 2009) and by the popular press. She (if it is not a male cf. Schmid, 1983) is quite primitive, but simply too late in the stratigraphy, and therefore must be an old, extinct side branch of the phylogenetic tree.
- (9) This entire 'story' has great consequences for estimates of the (minimum) age of the *Homo* lineage more than 3.2 m.y. or maybe more than 3.6 m.y., if *praeanthropus* is really closest to *H. [Australopithecus] africanus*, while the modern 'tradition' mostly claims about 2¹/₂ m.y. (e.g. Leakey, 1994; Kimbel et al., 1996), based on the earliest finds of *H. rudolfensis* and/or *H. habilis*, two taxa which Wood & Collard recently (1999a, 1999b) would even relegate to 'Australopithecus' for entirely 'adaptationistic' reasons, making *Homo* less than 2 m.y. old. It will, however, be indicated below that quarrels about these ages and the boundaries of the 'genus *Homo*' are completely arbitrary. They have, as usually employed, no 'precise meaning' at all, but are consequences of sub-optimal classifications and often adaptationistic decisions about so-called 'key-characters'. In fact, the same counts for our own 'species', *Homo sapiens*!
- (10) It should be absolutely obvious, that the traditional names and terms for *Australopithecus* and Australopithecinae (both incl. 'gracile' and 'robust' forms, and perhaps even older, more primitive taxa) are paraphyletic or polyphyletic concepts of no use in a consequent (natural) phylogenetic classification. Even in the vernacular form, 'australopithecines' can only be imprecise and spread confusion. This is entirely neglected by many prominent palaeoan-thropologists like Berger et al. (2010) referring the clearly *Homo*-like new species *sediba* to a very 'broad' *Australopithecus* (incl. from (a broad) *afarensis* to *boisei*). This despite a phylogenetic analysis clearly showing *sediba* to be sister group of *Homo* (from *habilis* to (a broad) *erectus*) in the cladogram (fig. S 3 in Supp. Mat homepage), because all the derived features are held in common with *Homo* while similarities with *Australopithecus* clearly are in 'primitive' characters (cf. Berger's diagnosis of *sediba* and table 1). His analysis also supports *A. africanus* as the next sister group, that is, as a more

primitive *Homo*, as argued above. The same 'broad *Australopithecus*' also incl. *anamensis* is used explicitly by White et al. (2009 – in the thematic issue on *Ardipithecus* in *Science* – see p. 165), and in many of their texts they employ such 'grade groups' which are obviously paraphyletic and cannot be discussed in a precise way concerning relationships and phylogeny.

9.8 Stem-Mothers, 'Australopithecus' and Australopithecines

So much for 'stem-mothers' like 'Lucy' or 'Australopithecus' afarensis, or for her 'Boy' AL 444-2, or for 'ancestors' like the 'first family', H. hadar (AL 333), a neat little 'social group' (Radosevich & Retallack, 1988; Tattersal, 1989), or species like 'Australopithecus' anamensis, none of which can convincingly be shown to be the closest relatives of Australopithecus africanus, the type species of this 'genus' (Dart, 1925). All of this makes the 'taxa' or groups Australopithecus (also with A. garhi from Ethiopia included [White et al., 1999]), and the subfamily Australopithecinae ('australopithecines') utterly paraphyletic. The 'genus' is almost polyphyletic as Kenyanthropus is excluded. This means nonsensical 'non-groups' of which one cannot speak precisely of neither phylogenetic relationships, their characteristic traits, nor literal extinction (see Bonde, 1975, 1977, 1981; Patterson, 1980). It appears extremely unfortunate that some modern anthropologists (Cela-Conde & Altbara, 2002) have tried to revive this counter-productive 'subfamily'. Perhaps even worse, Wood & Collard (1999a, 1999b) and Carbonell & Bermudez de Castro (2004) expand this 'group' by including some primitive species of Homo like habilis and rudolfensis in 'Australopithecus' because of their presumed 'lack of certain key adaptations'. As Patterson argued (1980) it is difficult/impossible to characterize something by features it does not have - this creates 'non-groups' (paraphyletic).

There are so many myths and so much propaganda around this supposed 'taxon' ('*Au. afarensis*'), and the genus *Australopithecus* that it is very difficult for even professional (palaeo)anthropologists to disentangle.

Recently a still more unlikely, if not outright impossible, 'ancestor story' has been published by *Science* (Berger et al., 2010). Based on two new skeletons with skulls found in the Malapa Cave in Transvaal, S. Africa not far from the famous sites in the Sterkfontein Valley, a new species of *Australopithecus* is described and named *Au. sediba*, although it is pointed out that it has several derived *Homo*-like features not found in any other *Australopithecus* (see above point 10). Despite it is made clear in this way that this species is most closely related to *Homo*, it is still referred to *Australopithecus* anyway because of a number of primitive features they have in common (symplesiomorphies) – exactly the type of arguments which cannot create a classification with natural (monophyletic) groups, and therefore cannot contribute to the reconstruction of phylogeny or evolutionary history (presumbly the aim of such a paper).

9.9 Anthropologists, Ancestors, Adaptations and Annoyances

Now this has been known as a methodological fact for nearly fifty years since Hennig's book *Phylogenetic Systematics* (1966), so how come that some 'scientists' today can be completely ignorant of that, and how can that be accepted by reviewers of professional journals? Is it really impossible to convey such simple and logical biological methodology to anthropologists – or don't they care? Wood's & Collard's idea (1999) of moving some of the most primitive species of *Homo* over to *Australopithecus* would have the same effect, namely creating an even more useless paraphyletic taxon, '*Australopithecus*'. How come that they can propose such meaningless taxa without giving any reasonable 'explanation' but traditional, unfounded Simpsonian, adaptationalism? Lacking a supposed 'adaptation' (or belonging in a certain 'adaptive niche') is no character to be used in in taxonomy, systematics or phylogeny reconstruction – it is pure fantasy, 'just-so stories' of the most useless sort in an empirical science (cf. also under *ramidus*). Having supposed functional 'adaptations' is interesting, it just has nothing to do with classifications (Bonde, 1984a).

So what is the possible 'motivation' for such choice? In Berger's case, apparently, it has to do with being an (almost) 'ancestor', while everybody inclusive the authors themselves can see that this is not really the case – but this can be 'sold' to the journalists, media, and publishers of *Science* (same motivations for White, Johanson et al. concerning 'afarensis', ramidus etc). Here, 'Au.' sediba is obviously not an ancestor of *Homo*, because it is (even in the most favourable model) about 0.5 m.y. too young with its age of 1.8–1.9 m.y. There are early *Homo* (rudolfensis or habilis) about 2.5 m.y. old – in reality even much older *Homo* (see above), and Berger claims 'It is not possible to establish the precise phylogenetic position to the various species assigned to early *Homo*'.

If this were really what we know about *sediba*, then it should be classified as *incerta sedis* (or *sedis mutandis*), as *H. sediba inc. sed.*, at level with and sequensed with *H. rudolfensis*, *H. habilis* and the taxon of 'higher' *Homo* (*georgicus, ergaster, erectus, sapiens* etc.), and all of these would be *inc. sed.* So clearly, *sediba* is just another 'dead end', something Berger admits by stating that it 'represents a candidate ancestor of the genus [*Homo*], or a sistergroup to a close ancestor that persisted for some time after the first appearance of *Homo*' (precise meaning? *Science News*, 2010). If this is what Berger knows, then why not convey that information to the readers of the scientific paper and to the public, instead of relegating *sediba* to that mess of '*Australopithecus*' as traditionally (mis-)used? Then, on the other hand, *Au. africanus* is also just another primitive relative of *Homo* (as opposed to *Paranthropus*), and *H. hadar* from AL 333 is just a little more advanced (see above), so the real job would be putting *sediba* in a more precise phylogenetic relationship with all of these early members of the *Homo*-branch.

The interesting fact about *H. sediba* may well be that it could be near sympatric with *Homo* sp. (*?habilis*) from Sterkfontein, age between $1\frac{1}{2}$ and 2 m.y., and/or the *Homo* sp. from Swartkrans lower horizon, Mb 1, originally called *Telanthropus capensis*, a mandible and a fragmentary part of a face. This is said by Groves (1991,

p. 239) to be 'indistinguishable from the 3733 taxon', which he classified as *Homo* sp. (unnamed) with the beautiful skull ER 3733 (ER = E of L. Rudolf = L. Turkana) implied as the type. This skull was later, by Zeitoun (2000), made the type specimen of *H. turkanensis* but it is by many people (incl. Bonde & Westergaard (2004)) referred to *H. ergaster* and considered an adault skull of age ca. 1.8 m.y. corresponding to the juvenile skeleton, 'Turkana boy' WT 15000, from the area W of L. Turkana which is roughly contemporaneous with the type jaw of *H. ergaster*, ER 992 (Groves & Mazak, 1975), age ca. 1.6 m.y.

Another 'Australopithecus' which is in a similar way said to be 'Homo-like' is Au. garhi (White et al., 1999) from Ethiopia, mentioned above, and also attempted by its authors to be 'sold' as ancestral to Homo. This is yet another 'taxon' which may be a mix of two different taxa from two localities: The skull appears 'primitive' and has very large check teeth, while the femur may be more advanced and Homo-like, but is from another nearby locality, so it could easily represent another taxon. Checking the list of characters described from the skull, most are very Australopithecus africanus-like, and very little, in fact, seems to point towards Homo. Its age is about $2^{1}/_{2}$ m.y., possibly just a little older than the oldest skull fragments and tools traditionally referred to Homo (e.g. H. rudolfensis of 2.3 m.y.).

9.10 The *ramidus* Story – Our 'Roots'?

This everlasting story of 'famous ancestors' can easily be expanded with both recent and more ancient examples. From the front cover of Nature: the 'oldest ancestor' of everything human, the so-called Australopithecus ramidus (White et al., 1994 referring to 'our roots'), age ca. 4.5 m.y. from Middle Awash in Ethiopia. It was shown, however, already in the invited commentary to the paper by Wood (1994), that this species was too specialized in the skull base to be ancestral to all later 'hominids' (and thus implicitly should not have been referred to Australopithecus). In fact, it was not at all our successful 'ancestor', but rather the oldest human 'failure', a blind side branch. In our model of the phylogeny (Bonde & Westergaard, 2004 and below) even a long 'dead end', as the older Lothagam mandible (age about 5 m.y.) appears to have more advanced corpus and molars (we gave it a new LITU name, lothagamensis). Curiously, Nature allowed White et al. to publish the generic name Ardipithecus as a 'correction' to the original paper shortly after in 1995- well, somebody or several, including editors and reviewers, had made mistakes - presumably selling more issues that week with that front page and getting, in the long run, more quotations (like here).

Worse, even the specific name is dubious, as the new fossils from Ethiopia were not properly distinguished from the so-called 'Tabarin mandible' of about same age from North Kenya (Bonde & Westergaard, 2004) which Ferguson had already (1989) named as a subspecies, *Homo antiquus praegens* (in his opinion closely related to 'Lucy'), so *ramidus* is perhaps synonymous with *praegens* (for nomenclature it makes no difference that the latter was suggested as a subspecies – Johanson (1996) also vaguely indicates that *ramidus* and *praegens* may be the same species, and so does Tattersal (1995)). Perhaps this 'scientific story' is what Feyerabend (1975) means by 'anything goes' as a piece of propaganda for 'anarchistic science' against methods.

But seen from a phylogenetic perspective, the example *Ardipithecus* grew even more ridiculous as Haile-Selassie (2001) published some much older fossils from Ethiopia, with an age more than 5.5 m.y., as a 'subspecies' *A. ramidus kadabba*. As the new 'subspecies' (presumably in the traditional sense of chrono(-sub-)species, like in Simpson (1961) as modified by Bonde (1981, 2001)) clearly has a more primitive dentition than the original *A. ramidus ramidus*, this makes both the genus and species of *A. ramidus* paraphyletic, because the type-subspecies is more closely related to 'higher hominids' (see Fig. 9.3).

We simply classified this LITU as *kadabba*, noting that as described it lacks autapomorphies, and therefore cannot be distinguished from a 'true ancestor'. Because it is so fragmentary, this really does not mean much – and this counts to an even higher degree for the probably slightly younger LITU *lothagamensis*, a lower jaw fragment likewise without its own specializations.

As a curiosity, the single toe bone referred to this new 'subspecies' *kadabba* as the sole argument for its upright stance is about 0.5 m.y. younger than the type series of fossils – and obviously may quite likely belong to another taxon, as there are no points of comparisons. See also the nice and fanciful reconstructions in Lemonick and Dorfman (2001).

And 'curiosities' do not stop here, because White et al., Suwa et al., Lovejoy et al., etc. with an introduction by Gibbons (all 2009 in Science) have finally completed the long awaited and secretive task of describing the fragile partial skeleton referred to A. r. ramidus (found 1994, the year of description of the type material by White et al. in Nature). It is now claimed that this skeleton and its limbs and their proportions show that proper 'hominids' never went through a stage of knuckle walking like chimps, although this seemed indicated by the detailed anatomy of some hand-bones of both 'afarensis' and the older 'A.' anamensis (Strait et al., 1997 – and the latter would imply a simple refutation of the supposed 'joint advanced feature' or synapomorphy, knuckle walking, in only chimps and gorillas). So we are not so closely related to chimps, it is argued in the 'popular press' and internet by its commentaries. How all that can be concluded from this remarkable skeleton (more complete than 'Lucy') beats me. But apparently, every published fossil hominid has to imply some sort of 'sensational news' (for reasons of publicity and funding, presumably, and ranking of publications from the 'group', department or institute or the journal - it is a competitive world, especially after Reagan and Thatcher). And it is getting worse with revised university legislation all over Europe, and enormous cuts in the state support to teaching and basic research, so we can expect more 'ancestors' and other 'sensations' in near future (see below).

Furthermore, the entire set of papers in *Science* are performed in an unusually adaptationistic style. In the conclusion by White et al. concerning 'paleobiology of early hominids', the word 'adaptive' is mentioned about ten times (adaptive shifts, plateaus, phases etc.). The entire narrative has the character of 'just-so stories' with the arguments not very convincing. The late Steve J. Gould would have made fun of this, presumably in one of his essays (see Gould & Lewontin, 1972). Why should such 'stories' be necessary, however interesting they may seem to some 'evolutionists'? I hoped they had died out more quickly after Simpson (e.g. 1961, 1976). Is it really informative with all these detailed scenarios where almost none of the arguments can be strictly tested? They are just fictitious, (science?) fictions, poems, if you wish. Lovejoy (2009) is even working within a framework of 'adaptive suites', said to be 'semiformal, largely inductive algorithms that causally interrelate fundamental characters that may have contributed to an organisms total adaptive pattern'. Does this mean that we now have to know, which characters are 'fundamental', and what is the 'total adaptive pattern'? Because one of the rationales behind this thematic issue of *Science* was the Darwin anniversary, and Darwin is quoted in almost every paper, I should like again to point to the quotation above (section on 'diversity') from the great hero about 'the immense amount of rubbish about the value of characters' - and to leave this as a warning.

9.11 Homo Ancestor Habilis?

So much for our 'oldest ancestor' ramidus – out on a limb – and we could go on with earlier and important examples: Homo habilis from Tanzania was considered an almost 'ideal ancestor' for the younger Homo spp. when it was described in 1964 (Leakey, Tobias, & Napier, 1964) and for about twenty-five years, when finally Groves' analyses (1989, 1991) showed that it has too narrow premolars, a specialization which prevents it from being an entirely convincing 'ancestor'. The proper, detailed description came in 1991 by Tobias (most of these Olduvai fossils found around 1960). And even here there has been, right from the beginning, some doubts whether the oldest specimens from Olduvai 'Lower Bed 1', like the type mandible, OH 7 (Olduvai Hominid 7, incl. parietal and postcranial fragments like the famous 'manipulative' hand supposed to be from the same young individual the foot OH 8 is not from habilis, but more likely P. boisei), and the younger specimens (skulls, one with lower jaw) from the upper 'Bed 1' and bottom of 'Bed 2', are really the same taxon. And further, whether the fine skull ER 1813 from the East side of Lake Turkana, N. Kenya (ER = East Rudolf, the older German colonial name of the lake), found in the 1970s and of about the same age as the type (1.8–1.9 m.y.) also belongs in that taxon (see e.g. Rightmire 1993 contra Wood, 1992). ER 1813 has also been referred to H. ergaster, and the youngest habilis specimens were said to be more '*erectus*-like' (which they hardly are, but perhaps ergaster like).

This mess leaves us with a not so 'ideal ancestor'. The phylogenetic tree (Fig. 9.3) shows that in this time interval between $1\frac{1}{2}$ m.y. and 2 m.y. the diversity of hominids was at its peak with about a dozen taxa worldwide, but only two outside of Africa, namely *Homo (Pithecanthropus) erectus* on Java and *H. georgicus* in SE-Europe. The remaining forms were living in Africa, and if Zeitoun's two new species (2000) from East Turkana are included, then about 7 of them lived more or less at the same time in the East African Rift valley – how to explain that in ecological and 'adaptationistic' terms?

9.12 H. ergaster – A 'True Ancestor'? – And the 'Flores Dwarf' or Hobbit

The next ancestral 'grade' on the ladder towards modern man is *H. ergaster*, mainly from Koobi Fora, East Turkana, age ca. 1.5–1.9 m.y. (the type mandible ER 992 youngest). And as can be seen on our tree, in our analysis we find it very difficult, even with the inclusion of the very excellent skull and skeleton of the 'Turkana Boy' (WT 15000; WT = West Turkana) from West of the lake (as by Westergaard & Bonde, 1986; Wood, 1992), to distinguish this taxon from an ideal ancestor of all the younger *Homo* spp. – so we classify it partly as an 'ancestor' by dividing it into two similar parts and repeat it twice in the classification. And this taxon should probably not be treated under the name *H. erectus* (or 'African *erectus*') as done by Leakey (1994 and his TV-series, Walker & Leakey, 1993; Bräuer, 1994; Rightmire, 1990, 1998), a name of an apparently characteristic taxon from East and SE-Asia which is somewhat more specialized (Bonde, 1976, 1977; Andrews, 1984; Groves, 1991; Wood, 1994; Anton, 1997; Anton et al., 2002). And it may turn out to be nearly just as old on Java (about 1.7 m.y. (Schwisser et al., 1994), but perhaps more likely only a little more than 1.5 m.y. (Larick et al., 2001)). Note, though, that Zeitoun's detailed cladistic analysis (2000) based on a large number of measurements from all the relevant skulls (each of them used as a 'terminal taxon' in the analysis), surprisingly placed WT 15000 in the middle of Asian *Pithecanthropus*, although it seems to lack the more evident specialisations of the 'proper' Asian *erectus* skulls (claimed by Walker & Leakey (1993) to be due to its young age, perhaps 9–10 y. in the midst of changing its milk-canines). Also analyses by Rightmire and Bräuer (cit. above) found no obvious differences between the African and Asian samples (see illustrations in Schwartz & Tattersall, 2003). Zeitoun also found that the adult skulls ER 3733 and 3883 are not adults of the same form as WT 15000, but represent two more primitive taxa, each characterized by almost a score of autapomorphies (specializations). Accordingly, he gave them two new separate species names, e.g. 3733 = Homo turkanensis (not used in Bonde & Westergaard, 2004), thereby indicating even more diversity between 1.5 and 2 m.y. Also Groves (1991) has 3733 as a separate taxon (unnamed).

The Caucasian finds from Dmanisi of an age about 1.7 m.y. are very '*ergaster*-like', perhaps even slightly more primitive, and the three good skulls seem quite variable, but they have all been dubbed *H. georgicus* (Gabounia et al., 2002; Vekua et al., 2002; Balter & Gibbons, 2000).

Anyway, the oldest part of *H. ergaster* (represented by a skull like ER 3733 in Bonde & Westergaard, 2004 and the classification below) could in principle, perhaps, be ancestral to all later *Homo* (but cf. again Zeitoun, 2000 placing it on a 'long sidebranch' as *H. turkanensis* and ER 3883 also on the next higher, long, specialised sidebranch). The younger part, incl. ER 3883, WT 15000 and the type jaw, ER 992, perhaps cannot be such common ancestors, because being of too young ages to be stem-forms of *Pithecanthropus*. However, they may be ancestral to the line towards neanderthals and sapients (the 'Euhomo' of Bonde & Westergaard, 2004).

And in this connection it should be mentioned that the controversial 'Hobbit' or Flores dwarf, *H. floresiensis* from a large cave on Flores, Indonesia (Brown et al., 2004; Morwood et al., 2005) including one buried skeleton about 18000 y. old and not much over 1 m tall, has a skull as primitive as this '*ergaster*-level'. This implies an age for this line of small *Homo* as more than $1\frac{1}{2}$ m.y., and a very long 'ghost lineage'. This might indicate the earliest migration 'out of Africa'. Including it in the modern *H. sapiens* as abnormal or pathological dwarf seems out of the question as indicated by several studies of both skull and feet (Falk et al., 2005, 2007; Jungers & Baab, 2009), despite claims to the contrary (Martin et al., 2006; Obendorf et al. 2007; Oxnard, 2010 – first stated by the Indonesian palaeoanthropologist T. Jacob in newspapers and television, see Jacob et al., 2006).

The hope of finding ancient DNA in these very recent fossils from layers only about 12000 to ?28000 years old unfortunately seems to have faded away, because DNA cannot be preserved in such warm and humid conditions. It would have been very interesting to have a 'molecular clock' estimate of the approximate age of *ergaster, georgicus* or *erectus/Pithecanthropus* lineages. There are very old tools on Flores (Morwood et al., 1998) and the 'Hobbit' is sometimes 'associated' with these without any shred of evidence, and the tools seem too large anyway for that small human. They are about 0.8 m.y. old and the most interesting about them is clearly, that someone must have been crossing a reasonable stretch of water and the 'Wallace Line' to reach Flores even during the lowest water level during a glaciation – so that someone knew how to sail already at that date or before! (The world's oldest known boats are those from the Mesolithic Ertebölle culture in Denmark, only 7–8000 y. old). The passage to Australia, where the oldest fossil *Homo* are 50–60000 y. old (and not dwarfs) also runs through Flores and across the continental shelf known as 'Sahul Land' when dry during hard glaciations.

9.13 The 'erectus Stage' – En Route Towards Sapiens?

The '*erectus* group' – by Bonde and Westergaard (2004) revived as clade Pithecanthropus (Dubois, 1892, and first used by Haeckel as a hypothetical '*P. alalus*', the 'apeman with no language' (1866)) – is another classical 'mistake' as ancestor of *H. sapiens* (and Neanderthals). An almost universal claim some 40–60 years ago (e.g. Weidenreich, 1946; Day, 1965, textbooks like Romer, 1966; Carroll, 1987; Trinkaus & Shipman, 1992; Benton, 2005 wavering a little, and all popular literature, even today) – only old Louis Leakey strongly contradicted this (1963; Leakey & Goodall, 1969) and found his own *H. habilis* a better candidate, and therefore moved *erectus* out as a sidebranch. This placement seemed rather obvious when looking at the many characteristic specializations in the faces of both Java- and Peking-man (Bonde, 1976, 1989; Andrews, 1984; Wood, 1992, 1994 contra Rightmire, 1990 – Bonde & Westergaard revived the relevant older names *Javanthropus* and *Sinanthropus* for these two subclades).

Many seemed to have greatly favoured calling their pet-fossils by this popular 'ancestral name', such as Lumley (1982) for the 'Tautavel man' from Arago Cave – it seemed to be more interesting to have a 'true *erectus* ancestor' (perhaps for funding reasons?) rather than just another ancient Neanderthal, of which there are so many in France (the Arago skull and face and jaws have but one possible advanced feature in common with Pithecanthropus, all other similarities are 'primitive' symplesiomorphies). Likewise R. Leakey also 'hung his hat' on the well known 'ancestor H. erectus' for his pet skulls from Koobi Fora, ER 3733 and 3883. (Walker & Leakey, 1978; Leakey, 1994 – but see critique by Groves, 1991). And later H. erectus was used also for the even better find, the 'Turkana boy' from Nariokotome, WT 15000 (Walker & Leakey, 1993). But as mentioned above, it appears to lack the specializations of the face and skull and limp bone thickness of typical Asian Pithecanthropus (but cf. Zeitoun [2000] who referred those three specimens to as many different taxa!), and we prefer to classify them as a possible 'ancestor', H. ergaster, like most people do today (Westergaard & Bonde, 1987; Tattersal, 1995; Schwartz & Tattersal, 2003; Wood, 1992). Recall that Wood, in his huge monography on the Koobi Fora fossils (1991), was not allowed by the editor R. Leakey even to mention the name *ergaster*! The reason being that Leakey was furious over the publication of the name by Groves & Mazak (1975 – see comments and excuse by Groves (1991, p. 197)). By now it is fair to state that H. ergaster is a much more acceptable 'human ancestor' than erectus. The latter, on the other hand, with its youngest and most specialized representative, the Solo man, H. (P.) soloensis, now dated as less than 50000 y., has therefore become a late contemporaneous human with 'modern' H. sapiens in the far East, and presumably also with the 'primitive dwarf' H. floresiensis.

Therefore all the nonsense about an *erectus-sapiens* transition and what this implies of shifts in 'adaptations' etc. (Weidenreich, 1946; Campbell, 1963; Day, 1965; Romer, 1966; Rightmire, 1990; Wu & Poirier, 1995) is now utterly outdated – it never took place. The African *ergaster* and the equally old and enigmatic finds from Dmanisi in Caucasia of Georgia (Europe's oldest hominids, about 1.7 m.y.) called *H. georgicus*, with its great variation between the three skulls (Gabounia et al., 2000, Vekua et al., 2002; Balter & Gibbons, 2000) should rather be in focus of our 'ancestral interests'. They may hold the keys to the first (or second?) 'out of Africa', at least that migration which created Neanderthals and the line towards modern man (see also Stringer, 2002, 2003). There is also a partial skeleton associated with one skull and many other limb bones (Lordkipanidze et al., 2007). The skeleton is small like the skulls, which have cranial capacities between 600 and 780 cc., that is, in the range of *H. habilis*. Despite some variation between the three skulls, they are recognized as belonging to one species, and this is most similar to *H. ergaster* from E-Africa.The common 'stem lineage' of the neanderthals and

the modern groups (dubbed Neanderthalia and Sapientia in Bonde & Westergaard, 2004) may well lie close to such fossils as *H. antecessor*, 0.8 m.y. from Atapuerca in N-Spain (Carbonell et al., 1995; Bermudes de Castro et al., 1997, 1999 – and recently a fragmentary lower jaw, provisionally referred to the same species, and stone tools have been found at a lower level, age 1.1-1.2 m.y. (Carbonell et al., 2008)) and H. cepranensis, 0.9 m.y. old from Italy (Mallegni et al., 2003). And these may represent the same 'species' on the other side of the Mediterranean, e.g. the Algerian Ternifine (Thigenif) skull and jaw, Atlanthropus mauretanicus' (Arambourg, 1963) and/or from Morocco the Salé skull, all claimed to be more than 0.5 m.y. old (Hublin, 1985 – if only one taxon, it should be named *H. mauretani*cus). The OH 28 skull from Olduvai may also be a candidate. The 1 m.y. old skull of Eritrea may also be of interest here (Abbate et al., 1998), as well as an Ethiopean skull of about same age (Manzi et al., 2003), but the interrelationships of those skulls and the older finds have never been satisfactorily analysed (cf. Rightmire, 1990, who referred the earlier African finds to '*erectus*'), although it should be obvious, that it is among those fossils from Europe and/or Africa we might find the ancestors of Neanderthals and ourselves. Great potential of the Mediterranean region. But in N-Europe there were people already 0.7 m.y. ago, as wittnessed by their flint tools from SE-England (Parfitt et al., 2005). In Denmark the oldest tools may be derived flints from sediments of the last interglacial in S-Jutland (Holm, 1996), but of a type (if they are tools at all) most similar to Tayacien and Clactonian in France and UK, earlier dated to the previous interglacial about 0.25 m.y., but now supposed to be around 0.4 m.y. old. The northernmost occurrence of stone tools is probably 'The Cave of the Wolf' in Finland, said to be from the last interglacial, ca. 130000 y (Pettitt & Niskanen, 2005; Schultz, 2010). All of those tools must have been made by Neanderthalia.

9.14 Neanderthal and Sapient 'Ancestors'?

Can we ever expect to find such actual 'ancestors'? We believe it is not entirely impossible (Bonde & Westergaard, 2004), and that both the neanderthal and sapient lineages may show reasonable examples of such 'ancestral fossils' in an accretion model with about four stages (chronospecies) om each limb. Both lineages during the latest half a million years or more seem to have been separated and living in different geographic regions, some of them under quite different ecological regimes (Stringer & Gamble, 1993; Stringer & McKie, 1996; Trinkaus & Shipman, 1992; Trinkaus, 1983; Foley, 1987; Arsuaga, 1999; Schwartz & Tattersall, 2002). This age of the split seems to agree reasonably well with the ancient DNA evidence (Krings et al., 1997, 2000), and to be older than that indicated by traditional morphology often citing the neanderthal lineage as being about 0.3 m.y. (Tattersal's fossil record diagram 1995, partly also Stringer & McKie's diagram) and that of Homo sapiens as being about 0.13 m.y. (Stringer & Gamble, 1993, fig. 28), and Winkler and Schweikhardt (1982) take pre-neanderthals only back to ca 0.1 m.y. but pre-sapients (in Europe) ca. twice as long. But both of the latter ages are clearly misleading seen from a cladistic viewpoint (Bonde & Westergaard, 2004), as the

socalled Homo heidelbergensis incl. its type specimen, the 'Heidelberg jaw' from Mauer has a few neanderthal specialisations in the dentition (e.g. size of dentition, weak taurodonty), the Petralona skull from N-Greece and the Arago face from S-France lack a 'fossa canina' like the neanderthals, and they likely represent the very early and primitive part of the neanderthal lineage, a clade we in 2004 dubbed 'Neandertalia' (see, Schwartz & Tattersal, 2001 about European fossils - earlier the *heidelbergensis* was seen as a possible 'ancestor' of both neanderthals and sapients - Bonde, 1976, 1977, 1981; Stringer, 1984, 1985; Groves, 1991). This lineage can now be 'followed through time' from the Heidelberg and perhaps the Petralona fossils being about 0.6–0.7 m.y. in an 'accretion model' of successive ancestors via 'steinheimensis' (e.g. from Steinheim, Swanscombe, Reilingen (Dean et al., 1998) and Atapuerca SH (Arsuaga et al., 1997)). Not all the features of all the fossils will entirely follow the 'model', the Steinheim skull e.g. seem to have a fossa canina like sapients, and it has been used as an argument for two lineages in Europe. I once used this as an indication for possible gene flow between the two lineages when arguing, that they might be just 'subspecies' seen from a 'time-bio-species' viewpoint (Bonde, 1989) resulting in a 'hybrid' like the Steinheim skull with both fossa canina and the Neanderthal mark of a suprainiac fossa at the back of the skull (Hublin, 1988).

9.15 Homo and H. sapiens???

Within *Homo* and *H. sapiens* as generally used, there is a problem part of which to day is based on 'political correctness' (as expressed by Gould (1977) and Ghiselin (1997) and many others who do not want to be framed as 'racists'). This means acc. to the above two, that one ought not scientifically discuss the possible valid subdivisions of our own species and e.g. map their history, because such might have to do with discrimination – or rather some others might misuse it for purpose of racial discrimination. Knowing how much interest there is in the populations for following the history of their own family or 'ethnic group' or population, and the relevans of 'ethnic' medicine, this is a very peculiar constraint to impose on the scientists. Should scientists be censored because of a possibility of 'misuse' of their results, then physics and chemistry could shut down immediately. And biology, computer science, sociology and economics could follow soon.

Because of this legitimate interest in population history, your own 'roots', and the possibilities given by modern genetic techniques, it is worth pointing out that the pattern of relationships does not follow the boundaries of the traditional 'races' based on skin colour, shape of hair and other very superficial features. Many of these features can often be explained by selection pressure from the local environment and climate.

Such features and measurements of skulls (skull indices by the Swede Retzius in 1842), body shapes, height etc are classical parametres to characterise the human 'races' in the 19th century. These already had Linnaean names since his first small edition of 'Systema Naturae' (1735), namely classified under *Homo sapiens* ('know yourself') as *Europaeus* ('white'), *Americanus* (red), *Asiaticus* (yellowish)

and Africanus (black). They were re-named shortly after 1800 by the Germann Blumenbach, based on his huge collection of skulls from all over the world. He added the Malaysian race, and he chose to call the white race 'caucasicus', because he had such a 'perfectly' beautiful female skull from Caucasia. From this type he thought the other races were developed by degeneration (today still believed by the 'Watchtower' sect in their propaganda material). This was a sort of 'evolutionary theory' also held by the great French naturalist Buffon (1749) concerning human races, and in 1766 he expanded that concept to all animals – but such changes are confined within a species. Here it is also worth noticing that his pupil Lamarck when describing the first proper evolutionary theory in 1809, exposed the idea that humans were derived from the most perfect ape, the chimpanzee (orang-utan was less perfect, and gorilla unknown), which as such was on its way to greater perfection, the general trend of changes (that is evolution) in all lines. Lamark's general trend towards higher organisation has in modern times been taken up in theories about orthogenesis, often as evolution aiming at a 'higher goal' (e.g Teilhard de Chardin (1955)).

A refinement much later was mapping of such features as blood types, they did not follow the limits of the traditinal 'races', although Coon (1962) tried to apply the traditional race-concepts to a lot of different physical anthropology and compared with available fossils. His results were not very successful, and they were expressed in a 'multiregional model' (see below) of local, isolated, parallel development from fossil '*erectus*-like' forms, which were not very obviously related to their postulated, modern *H. sapiens* 'descendants'. And he had very few 'negroid' fossils to illustrate his claim, that the 'negroes' were the last ones to cross the 'boundary' between modern *H. sapiens* and their *erectus* forrunners although postulating that such took place all over the old world. Neither did the mapping of certain genes or other genetic markers (Bodmer & Cavalli-Sforza, 1976; Lewontin, 1982) have obvious success, and no consistent pattern appeared.

But the research on the diversity of human mitochondrial DNA (MtDNA) since 1987 (Cann et al.) indicated a picture (if a constant molecular clock is assumed) of origin of modern humans in Africa, where the largest population differences are found, and then spread to Eurasia. The last common ancestor of all living humans was calculated at roughly 200000 \pm 100000 y., and the exodus from Afrika about half that old. This picture was quickly backed up by Stringer & Andrews (1988) based on fossil distribution through time. Our 'stemmother'in Africa was dubbed the 'mitochondrial Eve' or 'African Eve' (Brown [1990] on the background and research history), and the early results and some controversies are reviewed by Johanson (1996), and Stringer and McKie (1996). Although reasonable criticisme of the original research and its methodology quickly came up, it turned out that most subsequent studies more or less confirm the general pattern, then called 'out of Africa' (Vigilant et al., 1991; Wilson & Cann, 1992; Horai et al., 1995), but the timing changed quite a bit. Search for 'Adam' based on Y-chromosomes gave a shorter time frame (Hammer, 1995), one study a very young common ancestor, less than 50000 y. And some studies of nuclear DNA also gave rather short ranges of time, about 100000. The age estimates have mostly been handled as if they gave

the 'origin' as the age of the last common ancestor (LCA) of all living humans. But one should realise that all these calcultions probably rather give the age of a certain change in the genome, one or more mutations, and the 'African Eve' is more likely a position along the stem of our group somewhere before the split of the LCA. So these ages are maximum ages for the LCA, that could be much younger. And this is probably the case, and the agreement today lies somewhere between 100000 and 50000 y. for our LCA. This is apparently in agreement with the few relevant fossils of early, but entirely anatomical 'modern' people – none of these are over 40000 y. old (such as the Niah skull on Borneo), apart from earliest Australians perhaps 50–60000 y. The whole 'out of Africa' is treated in detail by Stringer and McKie (1996) in the book 'African Exodus'.

Certain rare mutations can characterize large groups of the living humans, and they have been mapped especially for sequences of haplotypes in the 'genographic project' by Wells (2002), so that by now the migrations both within and out of Africa can be followed in great detail because of a relatively small number of very rare and characteristic mutations. This is not in focus of this review, but can also be picked up in textbooks by Molnar (1998), Jobling et al. (2004), and in Denmark in excellent books by Jensen (2004, 2008) explaining the genetic background.

But how much do we know about the fossil record of even late Pleistocene hominids? Well, The 'Hobbit', *Homo floresiensis*, turned up in very young layers a few years ago, an entire skeleton of a completely unknown and very primitive branch of the phylogenetic tree (Brown et al., 2003). A neanderthal was recently identified from MtDNA in a bone fragment from southern Sibiria, and now another bone fragment, an isolated finger bone about 40000 y. old from the Denisova Cave in the Altai Mountains in S-Sibiria turns out to be a completely unknown type of hominid based upon its MtDNA, which show marked differences from both neanderthals and the *sapiens* lineage (Krause et al., 2010 – but clearly a neanderthal acc. to E. Willerslev, pers. comm. 2011). So big are the said difference that the new Denisova hominid should be the sister group of neanderthals plus sapients, and its origin can be calculated to about 1 m.y. ago, if the split between neanderthals and modern man was about 0.5 m.y. ago. With the new and very precise sequence methods, we are likely to encounter other surprises in the near future, and recalling the surprising find of the Hobbit such may come even from the palaeontological front.

9.16 Age and Limits of *H. sapiens*

What about our own species, presumably the most thoroughly surveyed species in the world? Is some agreement possible around this 'important species'? Apparently not – and from a cladistic viewpoint not at all. First, there are two competing models of the origin and evolution of our species, the 'multiregional model' and the 'out of Africa' or 'replacement model' mentioned above.

The multiregional model is vividly defended by only a few, like Wolpoff (1980, 1984), Thorne and Wolpoff (1992). This model derives living *H. sapiens* in parallel locally on all continents of the Old World from *H. erectus* stages, in some areas

like Europe and the Middle East via a neanderthal stage, and with only little influence from other regions. Some hybridization is not excluded, but it is used as an explanation for the parallel development towards the more advanced *H. sapiens* in all regions, as 'well adapted' genes and traits are spread over the continents outcompeting the less favourable. From a biological species viewpoint where a species is a group of interfertile organisms isolated (concerning reproduction) from other species, then it is clear that one consequence of the model is that *H. sapiens* and *H. erectus* are actually the same species, just gradually changing through time (anagenesis or phyletic evolution), so there is no use for two names. And neanderthals form a subgroup of that species also. Wolpoff has also argued for this, and one could then easily subdivide this 'species' into chronosubspecies, one slowly replacing the other through time.

Unless one wants to follow such a scheme all the way back to the beginning of life (in a truely Lamarckian model of great numbers of parallel lines with the same evolutionary tendencies, eternal orthogenesis), then this will have to stop somewhere - but where? Well, earlier than about 2 m.y. there are only human fossils in Africa, so in some way it will presumably have to start there with a migration out of the contient after that date, and this corresponds well to the oldest fossils in Europe, H. georgicus, and the oldest Java populations, in both areas very 'erectus-like' and about 1.7 m.y. old., so this will also become the age of *H. sapiens* sensu lato. If this is not upheld, and the transition from erectus to sapiens-like occurs between species at different ages in different regions, then the question of the age of H. sapiens is troublesome. The downside of this model, apart from the age problem, is from a cladistic viewpoint the excessive parallel evolution, which is very un-parsimonious: the same shift occurring many times. In a cladistic model or reconstruction of the phylogeny, one would use the mutual derived/advanced features as potential synapomorphies showing that all *H* sapiens individuals are more closely related to each other than to any *H. erectus* lacking these traits, and this would imply that *erectus* became truly extinct (not just technically that the name stopped to apply).

In that way we are suddenly in the alternative 'model of replacement' and, as we saw, there has to be at least one out-of-Africa event ca. 2, m.y. ago. This model operates, however, with several migrations from Africa, and it is especially the last one or last few ones that are in focus when speaking of *H. sapiens*. As seen above, the genetic results seem to clearly confirm an 'out of Africa' model, and that modern type *H. sapiens* originated say 50000–200000 y. ago in (E-)Africa and from there expanded to the rest of the world replacing more archaic populations on the way. And from a genetic viewpoint, there seems not to be much evidence of mixing with the local, archaic populations (or there may be few characteristic genes that have been lost in our populations).

The replacement model avoids excessive parallel evolution and is therefore more simple and satisfactory from a cladistic methodological viewpoint, but this does not necessarily mean that it is the 'true' description of the history. It could also be better expressed in a system of natural groups of phylogenetic relationships (monophyletic or clades). In this model, the age of *H. sapiens* (or the subspecies *H. s. sapiens* depending on the reproductive relation to the neanderthals and the late *erectus*) is not so troublesome, if one can agree on how to define and recognise its origin. Is

that when it finally split up into the first two subgroups still living today, or is it when our lineage split away from our sister(?sub-)species neanderthalensis (that is, a stem-definition)? Or is it somewhere in between?

The first definition from the point of diversification (the end of last common ancestor) would give a minimum age about 50–60000 y (the age of oldest representative from a subgroup, in this case australians which are said to be 50–60000 y. old). If the age corresponds to the split from neanderthals, then this is around, possibly over, 0.5 m.y. And if we pick one specific character or a functional character complex somewhere in between, then the age of the oldest fossil with that specific feature indicates a minimum age. Unfortunately, palaeontogists nearly always select the latter definition and point to a 'key character', in this case perhaps a chin and/or a vertical forehead, or if we could find a good indication, perhaps something like spoken language (perhaps of a certain complexity?) – and in this way we could quarrel from now to eternity without ever being able to agree upon the 'relevant' character. This is why a simple question about age can simply not be answered before we agree about some conventions.

In this way, both the inclusiveness and the age of *H. sapiens* is uncertain and completely arbitrary. We may give reasonably precise upper and lower limits, here minimum 60000 y and maximum ca. 0.5 m.y., but what you see in the textbooks and papers is something like ca. 0.2 m.y. (for the Kibish 1 fossil from Kenya), and before that it was ca 0.13 m.y. because that was the supposed age of those sediments found with the oldest so-called 'anatomically modern man'. And this is actually a misnomer, because it has too large eyebrow ridges (*tori supraorbitales*) for 'modern man', which can really not be traced further back than to 40–60000 y.

Exactly the same uncertainty counts for genus *Homo* or any other taxon in the system, it is completely arbitrary where the taxonomist chooses to 'cut off' the group, so all ages are completely arbitrary. This is why our system (Bonde & Westergaard, 2004) indicates only (minimum-)ages of splits in the tree, so that a group has the minimum age of the oldest fossil of its subgroups. And this age can also replace Linnaean rank, both relative and absolute at the same time. So here the age of *H. sapiens* is (40-) 60000 y., and 0.5 m.y. is the age of the (unnamed) group embracing *H. sapiens* (and Sapientia) and the sister group Neanderthalia, indicated by the oldest fossil, the Heidelberg jaw of the latter subgroup (ca 0.5–0.6 m.y.) – or from molecular biology, ancient DNA and the molecular clock (Krings et al., 1997 – here giving about the same result). We suggested that both ages be indexed: Sapientia + Neanderthalia: 0.5–0.6 m.y.; m: 0.5 m.y. (m: for molecular age).

How old then is *Homo*? Well here one consequent way of doing it would be all the way down to the split from chimps 6–7 m.y. ago – and actually some of the molecular biologists have recently suggested including chimps in *Homo* (Wildman et al., 2003). In this way, the split age within *Homo* would be 6–7 m.y. (molecular age probably a little less?). We have however, arbitrarily, decided to delimit *Homo* at the major extinct sister clade, the 'robust' *Paranthropus*, both lineages members of the clade Parhomo. The oldest fossil giving the minimum age in the phylogenetic model here is then '*afarensis'/praeanthropus* ca 3.7 m.y. on the *Homo*-line, and if this is not acceptable, then *H. hadar* ca. 3.4 m.y will indicate the minimum age (all

fossils on the *Paranthropus* line are younger). We could have chosen another rather large sister group as 'cut off', namely *Pithecanthropus*, giving quite a different result (between $1\frac{1}{2}$ and 2 m.y.). If so the traditional system would need a lot of new generic names for branches between *Pithecanthropus* and *Paranthropus*.

9.17 Evolution of 'Soft' Traits: Language

Only one example will be presented concerning 'non-fossilisable' features, and as this is about the 'Symbolic species', then it has to be about language. How can we judge the origin of spoken language, and is there a reasonable way of estimating its age? There must be a phylogenetic framework, and we here have one model based on fossils, but with some corners confirmed by molecular biology and clocks, such as the split-ages mentioned above. Here, an interplay between a well known phylogenetic model, that of the 'African Eve' theory, and a much less known model of all languages made by the old Polish historical linguist, R. Stopa in his hunt for the origin of the Indo-European language which also brought him to Africa.

The model by Vigilant et al. (1991) gave a tree of the interrelationships of modern populations based on MtDNA and with chimps as outgroup (the latter is important; the first model on 'Eve' by Cann et al. (1987) did not have an outgroup). The structure of Vigilant's model is approximately as follows: large difference between Pan and Homo, difference that can be translated to age spans, if the age of the split between the two groups can be estimated. (Had bonobo, P. paniscus, been incl. in the study, it should split away from the other chimps about halfway out the branch). All the sapient populations, of which many are from Africa (as opposed to Cann's study), are close together at the beginning of the *Homo* clade with only very small differences between them. The structure of their interrelationship is so that just about the dozen of branches first to split off are all from Africa, so these branches are long with relatively big differences between them, when compared to the closely packed branches at the top of the stem, whch are all from outside Sub-Saharan Afrika. Some of the very first groups to split off are some pygmees and !Kung-San people and several of the next branches are Bantu speaking people, then comes the rest of Africa and the rest of the world.

Stopa's studies in his books on the evolution of languages (1972, 1979) and his short review of his theory (1973) indicate that he finds 4–5 major levels in the early evolution of languages, and he translates many expressions/'sentences' between these levels of increasing complexity. In the 1972 book, Stopa analysed the African languages and compared them with Arabic and Indo-European on the one hand, and with 'Bushman' on the other side to see how sounds, clicks, phonemes and also body language (gesticulation) transforms from one language to the others.

Bushman (Khoisan) language appears to be the most 'primitive' (explained at length 1972, pp. 35 ff. and 1979, pp. 17–20), but also quite complicated and full of dental clicks and other sounds with the lips, as well af gesticulation when speaking. Words are very short, just one consonant and one vowel, can often mean several things, sentences very short, of one word or repeats of the same word, and there are

no abstract words, only concrete ones. Counting goes one, two, three = many, and general terms are missing, such as 'to eat', there is only a word for eating something specific like meat, and no word for fruit, only words for concrete fruits.

But the most interesting aspect is his direct comparison (rather 'translations') of a number of expressions by chimps and Bushmen in different categories like 'calls connected with food', warning signals, calls for help, calls to partner of the other sex, cries of pain, laughter, and a sound when looking through the other chimps fur (for lice etc). These he describes (1972, pp. 34–35) as 23 calls ('words') of chimps and similar words of Bushmen, and in a large scheme pp. 50–57 comparing the 'chimp language' with six different Bushman languages.

These chimpanzee words he got exclusively from Yerkes' primate laboratory from the observations of Miss Blanche Learned (very suitable name) as published in a book by Yerkes and Learned in 1925. And there is indicated the number of observations for each utterance, most of them have been observed 100–300 times. I have checked this source, and admit that I had difficulties finding this exact 'list of words' or utterances. But never mind, in the 1979 book he expands the comparative schemes (pp. 100–103) as a 'dictionary' running from chimpanzee words to Bushman, then West Sudanic, and lastly Bantu, and in other parts of the books the 'translation' is continued to the level of other African languages + Hamitic + Indo-European.

The little summary of his linguistic studies (1973) and speculations about the origin of languages is interesting, because he tries to reconstruct the structure of a 'proto-language' between those of chimps and of Bushmen, the language of 'Homo fossilis' as he calls it. And finally, in the appendix, he characterises four levels of 'languages', the first being from animals, just sounds, no proper language, the second Bushmen, Hottentots, Zulu-Kafirs etc., the third Bantu, Hamites, some Caucasian and American (probably Na-Dene), and the fourth Europe, Asia, Australia, Oceania. He specifies the structure and how they are being spoken, how sounds are combined, and their cultural background like hunter-gatherers, fishermen, herdsmen, agriculture and trade. And further he specifies, for each group of sounds/languages, how they are produced in terms of form and function of the sounds. This is clearly a grade system going from 'primitive'/original to different levels of advancement.

If such a grade-scheme should be translated into a cladistic scheme of relationships, it would show the following pattern: animals (here of relevance Chimps) as sister group of the remaining groups combined. Within these Bushman-Hottentot sister group to the two advanced groups, Bantu + Hamites etc and the rest of the world. This pattern of relations is exactly included in the relationships based on MtDNA: Chimps – Bushmen – Bantu – rest of the world.

That these two completely independent and entirely different analyses should give the same result can hardly be coincident. It must be significant, and one would predict that the language of neanderthals would be like the reconstruction for the missing level, that of 'Homo fossilis'. Neanderthals do fit into the scheme based on DNA, but how to test the level of their actual language will presumably be difficult.

As to very early or very late origin of modern people's type of languages, I tend to believe it is fairly late, that is, an origin within the last million of years, but before we split away from neanderthals ca 0.5 m.y. ago, because the latter with their very large brains must have had a rather advanced language as well, but probably no more advanced than that of Bushmen. As the latter split off between 50000 and 100000 y. ago, the evolution of languages was probably very slow until humans rather quickly spread all over the world, also accellerating the pace of linguistic evolution. But language probably did not evolve very suddenly and full fledged as some linguists (e.g. Chomsky) seem to believe, with complicated grammar and everything from the beginning. Such does not exist in Bushman language and could well be something developed within the last 30–40000 y. in the Late Palaeolithic when almost all other sorts of people had gone extinct: erectus, almost the neanderthals, and rather soon the Flores dwarfs leaving us alone to chat.

That there has literally been a sort of 'proto language', a 'mother tounge'.or 'Ursprache' is quite obvious from the genetic research, because this points to some sort of rather recent bottleneck (less than 0.1 m.y.) with a population less than 10000 people as 'founders' for all living people. So whatever sort of languages there may have existed at that time, only that from one little group survived and evolved untill today. The mother tounge is something many linguists look upon with much scepticism, and some believe that the different recent language groups are so different that they must have originated separately. This is pure nonsense, even if languages way back originated several times independently, then there still is a common mother tounge for all the living languages – and it must be possible to reconstruct some aspects of it by cladistic methods.

One should remember that historical linguistics has actually employed cladistic methods or something very close to that for longer than the biologists (Platnick & Cameron, 1977), and that this has been based on a tradition from 'textual critics', the reconstruction of the history of old manuscripts and books, which have been copied from each other – a method several hundred years old. So surely the linguists have encountered all the same difficulties and controversies over 'ancestors', primitive features, classifications and the like. And there have been many attempts to reconstruct language evolution, not the least for Indo-European languages. Stopa's is a brave attempt to establish an overview of all languages and their common origin. Cavalli-Sforza et al. (1989) compared their tree based on genetic data for the world population with an evolutionary tree of all languages. They were satisfied with the match, but in reality the language tree was not sufficiently resolved to be very informative, as half of its groups were single branches of uncertain relationship, and therefore these groups could fit almost any other tree, so I believe the test failed, or was not very convincing. Stopa's language relations and their congruence with the MtDNA tree is much more significant, but should be specified in more detail.

How far back one can trace other features connected with language is much more uncertain. People have looked at brain endocasts for traces of symmetry and Broca's area and believe they can observe the latter 'bump' in *Homo rudolfensis*, ca. 2 m.y. ago, but whether this is really significant for location of a center for speach and has anything to do with an association center is very doubtful. Other 'soft' features which have no way of connecting directly or indirectly to the skeleton are clearly even worse to reconstruct from the fossils, and one will have to go to another

abstraction level like supposed social relations or tool making to get a faint and very unsecure idea of language, conciousness and the like. But here is a 'free playground' for adaptationists and their 'just-so stories'.

9.18 Discussion

The proper phylogenetic framework establishing the 'simplest' relationship between the relevant groups based on analyses of their features (what else?) is essential for understanding the evolutionary history of man and his relatives inclusive the many fossils, be they 'complete', fragmentary or just scraps. Here the relationships, the phylogenetic tree, is based on cladistic methods, meaning that only shared, derived traits (synapomorphies; concerning morphology, molecules, behaviour etc.) count as evidence for close phylogenetic relationship. Another demand or ideal convention of this evolutionary philosophy here called 'phylocladistics' is that in phylogenetic systematics the 'natural' classification should portray these relationships (the 'tree of life') as precisely as possible and comprise taxa (named groups), be they mono-(holo-)phyletic, paraphyletic, metaphyla, ancestral, hybrids or of another biologically relevant sort, which may be expressed in a hierarchy.

Such classification and the corresponding evolutionary tree have to be the basis for speculations about the evolution of both the features on which the tree is based (most often morphology and molecules) and other features, e.g. 'soft' parts, development, genetics, 'adaptations', functional anatomy (e.g. upright stance and walking), behaviour, ecology, 'change' (evolutionary rates and 'kinds'), abilities for tool making, types of communication (language etc.) and conciousness, rituals, religions etc. That is, all these 'exotic' phenomena which most anthropologists seem to be mainly interested in, the origin of 'key adaptations', the 'real biological evolution', not just the dry bones or dull molecules (an exception to the 'dullness' seeming to be such genes from ancient DNA by which we can reconstruct features such as colours, earwax etc. of a 'fossil' organism, in case a 4000 years old inuit – see Nielsen et al., 2010).

So what are the relations between all these interesting features and phenomena and the phylogenetic tree and ditto hypotheses – and the 'data' upon which the latter is based? Here, it appears that closest to the 'data', the traits, features or characters is the simplest cladogram (or cladograms) as a symbol or a mapping of the distribution of features which employs as many of these as possible as synapomorphies (characterization of groups, clades, taxa), and therefore makes the groups maximally characterized (meaning that as many as possible generalisations can be made about these taxa; this is actually the reason why we use classifications at all – see e.g. Patterson, 1980; Nelson & Platnick, 1981; Bonde, 1984a). The 'data' here are put in quotes because they depend on hypotheses of homology (some sort of 'evolutionary sameness'), and are not just raw and 'objective' facts.

When a certain cladogram among several, perhaps many, possible ones is preferred, then that one can be transformed into a phylogenetic tree, implying the minimum number of changes of features on the tree, by adding some assumptions like time, and that the groups are 'blood related' in terms of 'nearness of common ancestry' that is one aspect, the cladistic one, of evolution (which some of us would consider a 'discovered fact' about nature), that features change along the branches of the tree, which is another aspect called 'phyletic evolution', and perhaps also that some taxa may be 'ancestral' to others (Bonde, 1977, 2001).

In general, many trees will be possible as corresponding to a certain cladogram, e.g. by just changing the timing of the splits a little (most of them are fossil based minimum ages anyway), or by changing position of sister groups (the sister clades of the tree may all be turned 180 degrees or interchanged), but these are insignificant banalities.

There are more principal differences between the possible trees when there are polytomies in the cladogram (expressing uncertainties) because for any trichotomy four different trees are 'equally good' (or possible), and this number increases alarmingly at multi-splits in the cladogram (Platnick, 1977; Patterson, 1980). From the tree (or rather from a characterstate tree) one or several precise classifications may be made which are 'isomorphic' with the tree, if certain conventions are obeyed (and disagreement can obviously exist concerning such conventions).

Should a certain phylogenetic tree ('stem tree'; or just a few of them) be preferable, then this may be seen as a model of the evolutionary history, and then further assumptions can be added about, say, economizing principles and functional anatomy implying certain behaviour and perhaps ecology. These phenomena can be 'mapped' onto the tree with implications for certain changes along the branches (or rather between the splits assumed to be 'speciations'). And even further assumptions can be added, if necessary, such as believing that these changes were 'adaptive', and stories about why some branches were more successful than others which died out, may be reconstructed. By asking and 'answering' these many 'why' questions (and not just 'how') by selecting preferred models among several possible, one presumably approaches the ideal of a complete 'evolutionary scenario'.

Now a characteristic feature of this 'layered' scientific process adding more and more assumptions about the world ('Nature') seem to be that, if controversies should rise about different models, the many extra assumptions make it very difficult to perform a precise test. Actually, it is only at the level of the cladogram that simple and precise tests based on 'data' can be carried out (more and/or 'better' characters by outgroup method = congruence among characters, which is really not a test against 'Nature'; or even closer to observable data by comparing with ontogeny [Patterson, 1983; Bonde, 1984b]).

Even at the next level of abstraction, that of the 'stem tree', so many extra assumptions have been added to make it less transparent what should be tested in case of evaluating two different models (trees), because a number (or all) of the assumptions might be wrong (presuming that the cladistic analyses at the lower level were all right). It is easy to see that the more assumptions, the further away from the 'data' and the more complicated the tests – if they are possible at all. Increasing the levels of abstraction evidently decreases the possibilities for precise tests. What may seem, instead, to increase when raising the level of abstraction is the tendency to use teleological explanations, as shown in my schematic diagram from 1984a. The more 'why' questions, the more 'purposefulness' – and probably more 'anthropocentrism'. This is the reason why S. J. Gould called the adaptive scenarios 'just-so

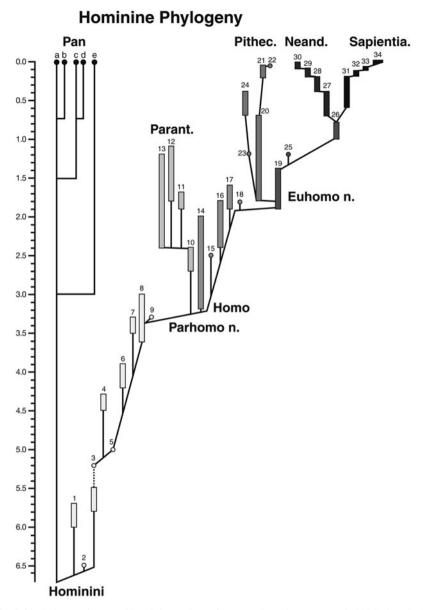


Fig. 9.3 Phylogenetic tree of hominins and Pan from Bonde and Westergaard (2004), but shaded version, based on characters and arguments in that paper, which is linked as pdf with the many references to the publisher's and N. Bonde's homepages – see p. 189. This tree is isomophic with the 'phylocladistic', non-Linnaean classification in Fig. 9.4

Fig. 9.4 Phylocladistic, non-Linnaean classification of Hominina corresponding to the phylogenetic tree in Fig. 9.3, and with conventions explained by Fig. 9.5. From Bonde and Westergaard (2004) Homininaa [/Sapiensa] (?6.5) 1 + orrorin (6.0 - 5.7)2 + sahelanthropus (?6.5) 3? (+) kadabba* (5.8-?5.2) 4 + ardipithecus (?syn. praegens) (4.5-4.3) 5? (+) lothagamensis* nov. (?5.0) 6 + anamensis (4.2-3.9)7 + kenyanthropus (3.5-3.3) 8 (+) praeanthropus* (syn. afarensis) (3.6-?3.3) 8 + praeanthropus* (syn. antiquua) mut. (?3.3-3.0) 9 ?+ bahrelghazali mut. (? 3.3) Parhomo nov. mut. (3.2) + Paranthropus (2.7-1.1) 10 +) aethiopicus* (2.7-2.4) 11 $+ robustus^{*} (1.9-1.7)$ 12 + crassidens (1.8-1.1) 13 + boisei (2.4-1.2) Homo (3.2) 14 + australopithecus (3.2-2.0) 15 + garhi (2.5) 16 + rudolfensis (2.4-1.8) 17 + habilis (1.9-1.6) 18 + georgicus (?syn. wushanensis) (1.8) 19 (+) ergaster* (1.9-1.8) + Pithecanthropus (1.8-?0.08) + Javanthropus (1.8-?0.08) 20 +) erectus* (1.8-0.7) +) erectur-soloensis* (?0.2-?0.08) 21 22 + soloensis (?0.08) + Sinanthropus (1.2–0.4) 23 +) lantianensis* (1.2) 24 + pekinensis (0.7-0.4) Euhomo nov. (1.8) 19 (+) ergaster* (1.8-1.4) 25 + louisleakeyi (1.2) 26 (+) antecessor* (?syn.mauritanicus) (1.0-0.8) + Neandertalia (0.7-0.03;m0.6) 27 +) heidelbergensis* (0.7-0.4) 28 +) steinheimensis* (0.4–0.2) 29 +) aniensis* (0.2-0.1) 30 + neanderthalensis (0.1-0.03) b Sapientia (0.6) 31 (+) rhodesiensis* (0.6–0.2) 32 (+) helmei* (syn. idaltu) (0.2-0.13) 33 (+) palestinus* (0.13-0.09) 34 sapiens (?0.07) b,g [/Sapiens (m0.1-0.2) b,g 34.1 afer (?0.07) 34.2 australis (0.04) 34.3 europaeus (0.04) 34.4 asiaticus (?0.03) 34.5 americanus (0.01)]

LITU's from traditional monotypic genera are given the genus name to save the species name for any later subdivisions.

The classification of recent crowngroups and LITUs (Least Inclusive Taxonomic Units) is shown by subordination of their names in boldface, while totalgroups (marked: Name¢) with names of fossils (marked: +) mostly sequenced can easily be included or removed.

Paraphyletic groups are problematic and should be avoided, but can temporarily be classified by marking them with quotation marks. Significantly, a paraphyletic fossil group ("+ Name") may as a stemgroup not be extinct.

Informal ranks of recent crowngroups can be provided by their absolute age in million years in brackets: (mnumber), as suggested by Westergaard (1989), and calculated by the molecular clock by Goodman *et alii* (1998, 1999).

Ages of fossils (here taken from Hertwig, 2002), giving minimum ages of taxa, are also put in brackets: (number), and informal ranks of extinct groups may be defined as their (minimum) time span (Farris' suggestion from 1976).

Further conventions are as follows; (?number): uncertain age; crowngroup (Name): last common ancestor and all its known descendants for a monophyletic group or clade of recent taxa; totalgroup (Nameø): crowngroup with addition of all known fossils from its paraphyletic stemgroup (usually not named), demarcated by recent diversification point and branch to recent sistergroup; ?+: fragmentary fossil of uncertain status; (+): possibly ancestral LITU (or part of LITU), where fossils are older than fossils from its recent descendant groups; +): same for extinct descendant groups; *; metaphyletic (plesiomorphic) LITU; syn.: synonymous name; inc: *incerta sedis*. taxon with uncertain relationships; mut.: *sedis mutandis*. taxon being included in an unresolved polytomy; nov: *nomen norum*, new name; b: taxon being a biological species ('biospecies'), isolated by internal reproductive isolation mechanisms; g: taxon being a gamogenetic species ('gamospecies'), integrated by gene flow (see Westergaard, 1989); a LITU usually corresponds to the smallest recognisable so-called phylogenetic species ('phylospecies'). With adequate conventions, it would also be possible to classify these different 'pluralistic' levels of species and hierarchies (Westergaard, 1989). Sistergroups are indented the same distance.

Fig. 9.5 Explanation of the conventions used for the classification Fig. 9.4. From Bonde and Westergaard (2004, pp. 46–47). Further in the pdf linked to the homepage, see p. 189

stories' (Gould & Lewontin, 1978). And philosopher I. Kant would presumably say (1795), that this is because our minds prefer such explanations, so we never see the world 'as it is'.

9.19 What Can Be Known About Hominid Evolution?

Clearly the evolution of the characters which were used in reconstructing the tree (Fig. 9.3) can be followed in detail: There are from 1 to 6 characters mentioned as synapomorphies for each group among the nearly 40 taxa, say three as a mean, giving about 120 features. And to these should be added a few autapomorphies for each terminal taxon, about two for each of these 35, giving another 70, that is in toto nearly 200 changes of characters. Of these, between 40 and 50 are on the line from the split from chimps to the last common ancestor of modern humans. So the change of these skeletal features can obviously be followed from split to split, but to discover the sequence of new traits between the splits among these up to 6 changes demands discovery of more 'intermediate' fossils with their specific combinations of features.

Concerning most of the 'soft' and other interesting features mentioned above in which we believe ourselves to be different from chimps, and which cannot directly be seen in fossils or be firmly correlated to skeletal traits, when did they occur? This is the issue of when did language originate, or 'hairlessness', or tool making or self-consciousness (Linnaei most important character for *H. sapiens*) or big female breasts or a big penis or association of certain centres in the brain.

The most precise that can be said is that it happened somewhere between the two splits just mentioned above, the origin of our lineage and the diversification of modern humans – that is, between about 7 and 0.1 m.y. ago, not a very precise result. And there is even a tendency to discover more and more of these 'human characteristics' in some chimps, meaning that their origin was most likely before our split from the chimps (e.g. tool making, self-conciousness – and may be even 'language', although not a 'spoken' one, but see Stopa, 1972, 1979, and above). Sophistication of tool making can only be followed in detail if we can make sure which taxon most likely made the tools from a certain deposit – and then, as always with fossil finds, they only give a minimum age of features and thereby have no direct association with tools. At the 'low level' within modern humans, the evolution of languages can be seen in a similar light and symbolized by evolutionary trees e.g. by the historical linguist Schleicher (1861, 1863, directly inspired by Darwin's 'tree of life', 1859) – and further inspiring his friend Haeckel (from 1866 the 'world champ' in phylogenetic trees). That the methods behind such trees in phylogenetic systematics and historical linguistics are almost identical was shown by Platnick and Cameron (1977).

9.20 Conclusion

The diversity of fossil hominid taxa is a lot larger than usually appreciated. Here is demonstrated a phylogenetic tree with 35–40 units/LITUs of fossil hominids and a corresponding 'phylocladistic' and non-Linnaean classification. The data and arguments for this recontruction is from Bonde and Westergaard (2004 – and can be seen as link from the homepage, also presenting the many references to the data background, which are not repeated here). Some few taxa are accepted as possible 'ancestors' and are placed on the branches not as terminal taxa (this seems to be in conflict with most other cladists). Therefore, it is a phylogenetic tree, elevated at least one abstraction level above a cladogram. Many other myths about 'direct ancestors' in the traditional phylogeny of hominids, such as Lucy, *Australopithecus afarensis, Ardipithecus ramidus/praegens, Australopithecus africanus, 'Au.' garhi, 'Au.' sediba, Australopithecus* in general, *Homo habilis,* and *H. erectus* are all shown not to be such 'ancestors' as claimed by their authors and many others.

Trying to trace the origin of the Indo-European languages, the Polish linguist R. Stopa has done a formidable study of the African languages, especially the Sub-Saharan ones and those of the Bushman tribes. In several books and large papers (1972, 1973, 1979) he has established that the Bushman languages are the most

'primitive' in the world characteristic with a large number of click and lip sounds, gesticulations and a very simple structure of the language, sentenses and words, lack of abstractions and no grammar. By comparing with other African languages, he has established a grade system of increasing complexity from Bushman languages over Bantu (which still has some clicks) to other African languages, Hamitic, and Indo-European languages. And interestingly, he claims he can directly translate from utterances by chimps to the equivalent expressions in the Bushman languages. The pattern of his hierarchical evolutionary model, chimp – Bushman – Bantu – other African languages plus the rest of the world, if interpreted in cladistic terms, can directly be compared with the model of relationships between the world populations based on MtDNA. Thus it becomes evident that the branching structure of the two models is exactly the same, which can hardly be a coincidence, so the two models confirm each other, and human language originated from ape utterances. This proves the utility of precise cladistic models of interrelationships, and the very complicated human family tree should be a warning against making very rash decisions about adaptationistic scenarios. The diversity of early humans in Africa was very high, especially in the interval between $1\frac{1}{2}$ and 2 m.y. ago with about a dozen forms living at the same time worldwide, 10 of these in East and South Africa, 7 of them in the East African Rift valley at the same time.

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References

- A large number of references especially concerning the reconstruction of the phylogenetic tree from Bonde and Westergaard (2004) are not repeated here, but are available on the homepage of the publisher (http://extras.springer.com) as well as on NB's homepage (www.Institut.Geografi. Geologi.ku.dk/emeritus/Niels.Bonde) as link to a pdf. A long list with the remaining literature is also placed with a link on the homepage.
- Anderson, I. (1983). Who made the Laetoli footprints? New Scientist, May 12, 1983, 373.
- Berger, L. R., de Ruiter, D. J., et al. (2010). Australopithecus sediba: A new species of Homo-like australopith from South Africa. *Science*, 328, 195–204.
- Bonde, N. (1977). Cladistic classification as applied to vertebrates. In M. K. Hecht, et al. (Eds.), Major patterns invertebrate evolution (pp. 741–804). New York: Plenum.
- Bonde, N. (1984a). Functional anatomy and reconstruction of phylogeny. In E. Buffetaut, et al. (Eds.), Actes du Symposium Paléontologique Georges Cuvier, Montbeliard, France 1982 (pp. 11–26). Imprim. Commune Montbéliard.

- Bonde, N. (1989). Erectus and neanderthalensis as species or subspecies of Homo, with a model of speciations in hominiods. In G. Giacobini (Ed.), *Hominidae. Proceedings of the 2nd international congress of human paleontology* (pp. 205–208). Milan: Jaca Book.
- Bonde, N. (2001). L'éspéce et la dimension du temps. Biosystema, vol. 19. Systématique et Paléontologie –2001, 29–62.
- Bonde, N., & Hoeg, J. T. (2008). Bjarne Westergaard, 25.05.1948–29.01.2008. Da.Naturhist. Foren., Yearbook 2007/2008, pp. 83–88.
- Bonde, N., & Westergaard, B. (2004). Progress in hominid classification: Cladistic approaches. Micselanea a E. Aguirre, Ill, Paleoantropologia, pp. 36–57. Zona Arquelogica, Num. 4, (Museo Arquelogico Regional).
- Brown, P., Sutikna, T., et al. (2004). A new small bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, 431, 1055–1061.
- Carroll, R. (1987). *Vertebrate paleontology and evolution* (pp. 277–285). New York: W.H. Freeman and Co.
- Cavalli-Sforza, L. L., et al. (1989). Reconstruction of human evolution: Bringing together genetic, archaeological and linguistic data. PNAS USA, 85, 602–606.
- Cherfas, J. (1983). Trees made man upright. New Scientist, 97(1341), 172-178.
- Coon, C. (1962). The origin of races. London: J. Cape.
- Day, M. (1965). Guide to fossil man (4th ed., 1986). New York: Cassell.
- Feyerabend, P. (1975). Against methods. London: Methuens.
- Foley, R. (1987). Another unique species. New York: Wiley.
- Gibbons, A. (2009). Ardipithecus ramidus: The view from Afar. Science, 326, 41-43.
- Groves, C. P. (1991). A theory of human and primate evolution. New York: Oxford University Press.
- Haile-Selassie, Y. (2001). Late Miocene hominids from the Middle Awash, Etiopia. *Nature*, 412, 178–181.
- Johanson, D., & Edey, M. (1990). Lucy, the beginnings of humankind. London: Granada.
- Johanson, D., & Edgar, B. (1996). From Lucy to language. London: Weidenfeld & Nicolson.
- Jungers, W., & Baab, K. (2009). The geometri of hobbits: *Homo floresiensis* and human evolution. *Significance*. DOI: 10.1111/j.1740-9713.2009.00389.
- Krause, J., Qiaomei, F., et al. (2010). The complete mitochondrial DNA genome of an unknown hominin from southern Sibiria. *Nature*. DOI: 10.1038/nature08976.
- Leakey, L. B. S., Tobias, P., & Napier, J. (1964). A new species of the genus Homo from Olduvai Gorge. *Nature*, 202, 5–9.
- Leakey, R., & Walker, A. (1976). Australopithecus, Homo erectus and the single species hypothesis. Nature, 261, 572–574.
- Pettitt, P., & Niskanen, M. (2005). Neanderetals in Susiluola Cave, Finland, during the last interglacial period. *Fennoscandia Archaeologica, XXII*, 79–87.
- Romer, A. S. (1966). Vertebrate paleontology. Chicago: University of Chicago Press.
- Schmid, P. (1983). A reconstruction of the skeleton of A.L. 288-1 (Hadar) and its consequences. Folia Primatol, 40, 283–306
- Senut, B., & Tardieu, C. (1985). Functional aspects of Plio-Pleistocene hominid limb bones: Implications for taxonomy and phylogeny. In E. Delson (Ed.), *Ancestors: The hard evidence* (pp. 193–201). New York: A.R. Liss.
- Stern, J. T., & Susman, R. L. (1983). The locomotor anatomy of Australopithecus afarensis, American Journal of Physical Anthropology, 60, 279–317.
- Stopa, R. (1973). Hominization. Journal of Human Evolution, 2, 371–378.
- Stopa, R. (1979). Clicks, their form, function and their transformation or how our ancestors were gesticulating, clicking and crying. Acta Scient. & Litterar. 561, Universitas Iagellonica., Krakow.
- Stringer, C., & Gamble, C. (1993). In search of the Neanderthals. London: Thames & Hudson.
- Stringer, C., & McKie, R. (1996). *African exodus. The origin of modern humanity*. London: Cape. Tattersal, I. (1995). *The fossil trail*. New York: Oxford University Press.

- Tobias, P. V. (1967). The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei. Olduvai Gorge 2. Cambridge: Cambridge University Press.
- Vekua, A., Lordkipanidze, D., et al. (2002). A new skull of early Homo from Dmanisi, Georgia. Science, 297, 85–89.
- Vigilant, L., Stoneking, M., et al. (1991). African populations and the evolution of human mitochondrial DNA. *Science*, 253, 1503–1507.
- Wells, S. (2002). The journey of a man. A genetic odyssey. London: Penguin.
- White, T., Asfaw, B., et al. (2009). Ardipithecus ramidus and paleobiology of early hominids. Science, 326, 75–86.
- White, T. D., Suwa, G., & Asfaw, B. (1994). Australopithecus ramidus, a new species of early hominid from Aramia, Ethiopia. *Nature*, 371, 306–312.
- White, T. D., Suwa, G., & Asfaw, B. (1995). Australopithecus ramidus, a new species of early hominid from Aramia, Ethiopia. *Nature*, 375, 88.
- Wolpoff, M. H. (1980). Paleoanthropology. New York: Knopf.