Abstract

Traditional 'evolutionary' classifications of hominids are contrasted with some of the earliest cladistic approaches from the 1970-s (based exclusively on monophyletic groups), and the shortcomings of the former are discussed. Paraphyletic taxa are especially counterproductive and misleading, and translate also to severe problems with the concept of true 'fossil ancestors', of which some can be saved with a 'Popperian' argument about testability. These are specific aspects of what generally has been called 'metaphyly' which is also relevant for many famous hominid 'ancestors'. Several conventions for classifying in strictly cladistic ways are discussed, and sequencing of fossil (extinct) taxa is recommended to reduce the number of categories for ranking. It is acknowledged that molecular biologists, like Goodman, very early in the 1960-s proposed the relevant type of classification for living primates incl. Hominidae of an untraditional scope.

The basic units for classification are compared, biological, evolutionary and some phylogenetic 'species', and as the smallest unit in practical classification is suggested a 'rank free' unit called Least Inclusive Taxonomic Unit (=LITU), corresponding to the smallest diagnosable group, the relevance of which must be defended by each author from his perspective and/or purpose. Our choice has been LITU's at what we believe to be the relevant level for a 'historical' analysis or phylogeny, and thereby of greatest generality. Others may pick other levels of monophyletic groups in the hierarchy to suit their special purposes, e.g. a 'bio-species' level. LITU's have no rank, they are tentative, non-authoritarian and for discussion rather than for 'final decision' and are therefore at odds with the Linnaean hierarchy. We abandon the latter for non-Linnaean classification with a single name for monophyletic taxa, and addition of symbols according to strict conventions, such as age or 'life span' in m.y. (which can be translated to comparable 'rank'), status of the taxon (fossil/extinct, monophyletic, paraphyletic, 'ancestral' and/or uncertain). A classification of Primates is developed after these principles, as well as an especially detailed hominid classification of (nearly) all LITU's on our separate branch of the phylogenetic tree. A few new taxon names are created, and some controversial synonymies suggested, especially for some of the most famous socalled 'ancestors' named during the latest 25 years, and a new LITU ('species') is proposed to cope with the diversity within the socalled "afarensis" complex.

Key words: Classification, Cladistic, Non-Linnean, Hominidae, Fossil, Living.

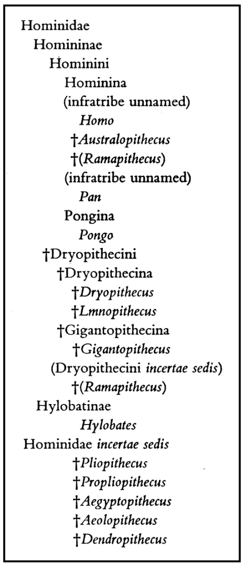
Progress in hominid classification: cladistic approaches

Niels Bonde & Bjarne Westergaard*

> «Identification or proposal of a (new) species in palaeontology (and biology) implies an hypothesis of a phylogenetic relationship» (Bonde, 1981)
>
> «The time dimension is notably significant in the assessment of phylogenetic relationships» (Schwartz *et alii*, 2001)
>
> «... the genus *Homo* should be recognized ... on the basis of an identifiably distinctive shift in adaptive strategies ...» (Wood in Schwartz *et alii*, 2001)

Introduction

We still believe the first quotation above is a sound statement concerning the frame in which taxonomic proposals should be understood. But we disagree with the other two quotations by the group concerned with "Systematics of Humankind", because such considerations as 'time' have only a very limited role in modern phylogenetic analysis (see 'ancestors', below), or the point made is a reversal to 'Simpsonian' or socalled 'evolutionary systematic' mumble and imprecision (e.g. 1959) long expected to be only of historical interest (Bonde, 1975: 312): 'shifts in adaptive strategies' fossilise poorly and are hardly proper characters to be used in a diagnosis of a taxon. Recall the quote by Darwin in a letter to Huxley: "In regard to classification and all the endless disputes about 'Natural System', ... 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, and will make the difference between analogy and homology clear. The time will come, I believe, though I will not live to see it, when we shall have very fairly true genealogical trees...". And in "The Origin" Darwin said: "On the view of characters being of real importance for classification, only in so far as they reveal descent, we can clearly understand why analogical or adaptive characters, although of the utmost importance to the wellfare of the being, are almost valueless to the systematist." (quoted by Goodman, 1975, here abbreviated).



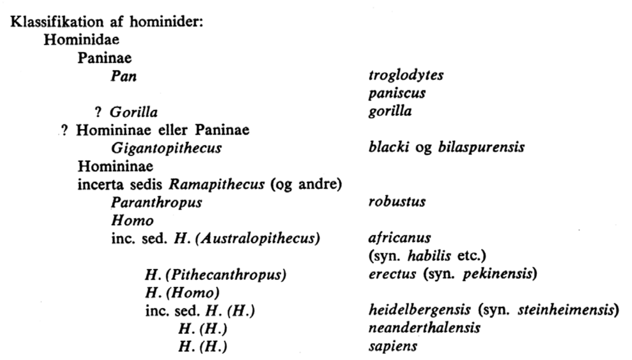
- Hominidae
  - Homininae
    - Hominini
      - Hominina
      - (infratribe unnamed)
        - *Homo*
        - †*Australopithecus*
        - †(*Ramapithecus*)
      - (infratribe unnamed)
        - *Pan*
      - Pongina
        - *Pongo*
    - †Dryopithecini
      - †Dryopithecina
        - †*Dryopithecus*
        - †*Lmnopithecus*
      - †Gigantopithecina
        - †*Gigantopithecus*
      - (Dryopithecini *incertae sedis*)
        - †(*Ramapithecus*)
  - Hylobatinae
    - *Hylobates*
- Hominidae *incertae sedis*
  - †*Pliopithecus*
  - †*Propliopithecus*
  - †*Aegyptopithecus*
  - †*Aeolopithecus*
  - †*Dendropithecus*

Fig. 1. Classification of hominids by Delson & Andrews (1975, Tab. III), part of the 'strict cladistic' classification (not preferred by any of them!).

'Genealogical', being phylogenetic or cladistic, classification of catarrhines, incl. hominids (Fig. 1), was first attempted by Delson & Andrews (1975) in the same volume as Goodman

---

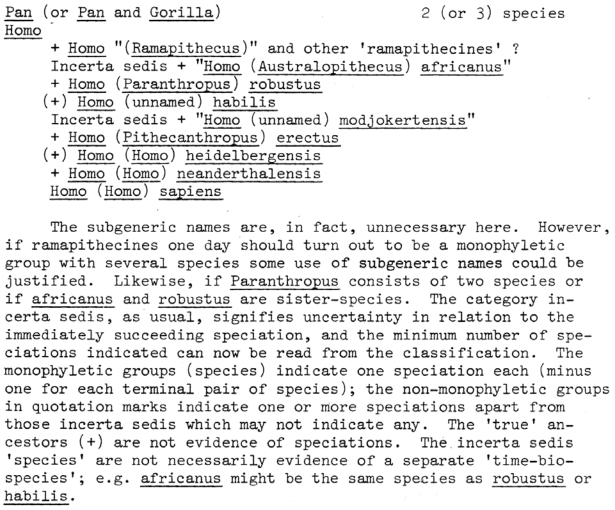
* Geological Institute, Østervoldgade 10, DK-1350 Copenhagen K, Denmark; nielsb@geol.ku.dk; b.westergaard@mail.dk



Klassifikation af hominider:

Hominidae	
Paninae	
Pan	*troglodytes*
	paniscus
? *Gorilla*	*gorilla*
? Homininae eller Paninae	
Gigantopithecus	*blacki* og *bilaspurensis*
Homininae	
incerta sedis *Ramapithecus* (og andre)	
Paranthropus	*robustus*
Homo	
inc. sed. *H. (Australopithecus)*	*africanus*
	(syn. *habilis* etc.)
H. (Pithecanthropus)	*erectus* (syn. *pekinensis*)
H. (Homo)	
inc. sed. *H. (H.)*	*heidelbergensis* (syn. *steinheimensis*)
H. (H.)	*neanderthalensis*
H. (H.)	*sapiens*

Fig. 2. Cladistic classification of hominids by Bonde (1976).



Pan (or Pan and Gorilla) 2 (or 3) species
Homo
+ Homo "(Ramapithecus)" and other 'ramapithecines' ?
Incerta sedis + "Homo (Australopithecus) africanus"
+ Homo (Paranthropus) robustus
(+) Homo (unnamed) habilis
Incerta sedis + "Homo (unnamed) modjokertensis"
+ Homo (Pithecanthropus) erectus
(+) Homo (Homo) heidelbergensis
+ Homo (Homo) neanderthalensis
Homo (Homo) sapiens

The subgeneric names are, in fact, unnecessary here. However, if ramapithecines one day should turn out to be a monophyletic group with several species some use of subgeneric names could be justified. Likewise, if Paranthropus consists of two species or if africanus and robustus are sister-species. The category incerta sedis, as usual, signifies uncertainty in relation to the immediately succeeding speciation, and the minimum number of speciations indicated can now be read from the classification. The monophyletic groups (species) indicate one speciation each (minus one for each terminal pair of species); the non-monophyletic groups in quotation marks indicate one or more speciations apart from those incerta sedis which may not indicate any. The 'true' ancestors (+) are not evidence of speciations. The incerta sedis 'species' are not necessarily evidence of a separate 'time-biospecies'; e.g. africanus might be the same species as robustus or habilis.

Fig. 3. The last of hominid classifications by Bonde (1977), totally sequenced for fossil groups, with its explanation from the text.

(above). The same, in which McKenna (1975) outlined a strictly cladistic classification for all mammals, naming almost every monophylogenetic group and therefore several new subgroups, such as Trechnotheria and Tribosphenida under Theria. At the same time the introduction was Simpson's sharpest attack (1975) on the classificatory implications of Hennig's 'phylogenetic systematics' (and on 'numerical taxonomy'). Eldredge & Tattersall (1975) also applied cladistics to hominid phylogeny.

Bonde's small Danish contribution (1976) on phylogeny and classification of hominids (Fig. 2) was made in desperation over the general lack of interest in phylogenetic systematics and precise methods for reconstruction of evolutionary history as demonstrated by most contributors to a large international meeting on human evolution in London spring 1975. Here most of the 'famous' palaeoanthropologists were gathered (see Bishop 1978) and 'Lucy' had just been found (Johanson *et alii,* 1978) but not yet described. In the public discussions only Bernard Wood and Peter Andrews seemed to be genuinely interested in better phylogenetic methods at that time. Both of them, and Delson and Tattersall, and a little later Stringer, have been in the forefront of revolutionising the phylogeny of 'Man', bringing the arguments and entire philosophy up to a modern standard leading into the present century. By 1976 at another London meeting Bonde used both the basal splits in mammalian phylogeny and extensively the evolution of hominids as a basis for many models of cladistic classifications (Bonde, 1977), and here invented some simple conventions for expressing precisely the known as well as the uncertain phylogenetic details in classifications (e.g. p. 792, fully sequenced and with all fossils included in *Homo*; Fig. 3; like in Wildman *et alii*, 2003).

Most of this was based upon ideas developed by Nelson in the early 1970-s (1971, 1972, 1974). Later Wiley explored such conventions in more detail, still trying to stay as close as possible to principles of Linnaean classification and the rules of nomenclature (Wiley, 1979; 1981). These two, by training, were ichthyologists like Farris was when he suggested a very unconventional way of cladistic classification (1976), which we shall briefly test below. He was among the very first also to explore the possibilities of developing quantitative cladistics (Farris *et alii*, 1970, continuing the approach of Kluge & Farris 1969) the methods which are now used routinely by reconstruction of phylogenies (see Kitching *et alii,* 1998).

We were then at a period 5-10 years after Hennig's major theoretical work on systematics (1966 – short review 1965), which in its American translation was the second and completely altered edition of his original German book from 1950. The aim of his 'phylogenetic systematic' philosophy –later by opponents called 'cladistics'– is to reflect the phylogeny in classification as precisely as possible. The philosophy and development of the methodology of cladistics have later been explored in several books and papers (Hennig 1969, 1975; Farris *et alii,* 1970; Farris, 1976, 1983; Nelson; 1970, 1994; Nelson & Platnick, 1981; Miles, 1973, 1975; Patterson, 1973, 1980, 1988; Bonde, 1975, 1977, 1987, 2001; Patterson & Rosen, 1977; Wiley, 1981; Ax, 1987; Forey *et alii,* 1992; Ridley, 1994; Smith, 1994; Kitching *et alii,* 1998).

Here we shall explore different ways of expressing in a cladistic classification what is known and not known about the phylogeny of a specific group like the hominids, as well as different ways of giving names to taxa, which all in principle should be strictly monophyletic groups. We also suggest ways of giving names to some few other sorts of groups and discuss the meaning and indication of taxonomic rank, as well as revealing some shortcomings of the Linnaean hierarchy.

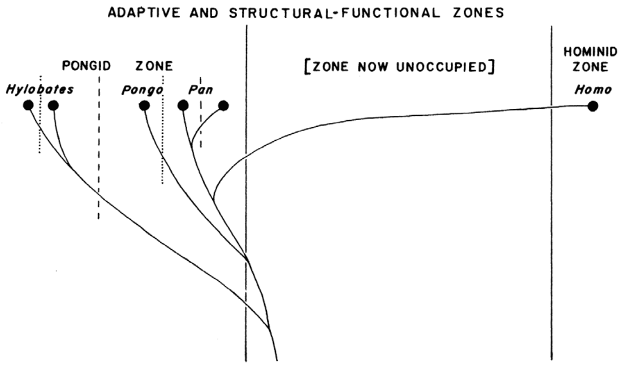


Fig. 4. Hominoid tree with 'adaptive zones' by Simpson (1963).

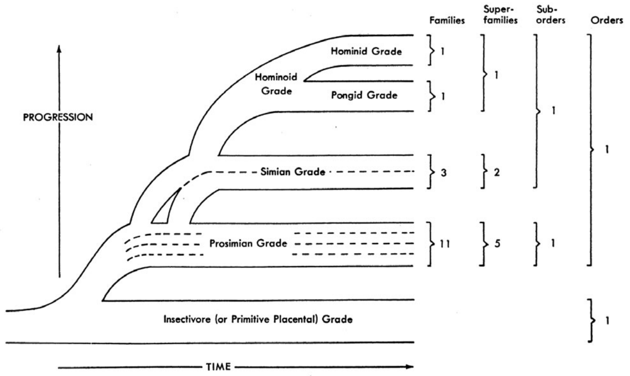


FIGURE 29. DIAGRAM OF GRADES IN THE PRIMATES AND THEIR RELATIONSHIP TO SOME TAXA

Fig. 5. Simpson's 'tree' (1961) and classification of primates using 'grades' and 'adaptive zones'.

Traditional classifications

All mammalian classifications have been under strong influence by the 'evolutionary' classification of Simpson (1945) in which he under hominoids maintained the paraphyletic "Pongidae" for the apes (even incl. *Australopithecus*) as opposed to Hominidae for *H. sapiens* (and close fossil relatives, *Pithecanthropus* and [the hoax] *Eoanthropus*). This arrangement of the recent forms was preserved in his taxonomic textbook (Simpson, 1961), where he spoke of the importance of adaptive changes to a different 'adaptive zone' (p. 215) for hominids as opposed to pongids. This was later elaborated, and he argued at length (1963) why he prefered using 'Pongidae' (incl. Hylobatinae, Dryopithecinae and Ponginae with *Pongo* and *Pan* [incl. *P. gorilla*]) as contrasted to Hominidae (at this time incl. *Australopithecus*) despite his new figures (5 and 6) showing *Pan* genealogically more closely related to *Homo* than to the other apes. He was keen pointing out that his fig. 5, "adaptive-structural-functional" dendrogram of "affinities" (our Fig. 4) is not a phylogenetic tree, none the less saying in the explanation, that "it is probable that divergences of lines showing affinities are topologically similar to the phylogenetic lineage pattern". And the same is shown in his "impressionistic and diagrammatic" tree (1963, Fig. 6). Simpson was very specific in arguing why *Pan* should not be included in the Hominidae (1975: 28; against Goodman 1975), despite claiming (p. 25) that "*Homo* is most closely allied to *Pan*. That conclusion ... is strongly supported by all new evidence ...". Unfortunately Simpson chose and argued for such grade classification also concerning the primates as a whole (1961: 212-16; our Fig. 5).

We emphasise these 'Simpsonian' conclusions because they were repeated by Mayr (1963a, b, below), who also (1969: 70-72, Fig. 4-5) reused Simpson's figure in his criticism of cladistics and gave as the only reason "To rank taxa according to branching points is nearly always misleading. It might necessitate, for instance, the inclusion of the African apes in the family Hominidae and their exclusion from the family Pongidae". Those two authors represented the 'authorities' of the day during the 1960's and part of the 70's, and Simpson was present at the 1974 symposium on 'Phylogeny of Primates' in his "illuminating presence and participation" (Luckett & Szalay, 1975: 3) to explain 'advances in... phylogenetic inference'. A meeting at which otherwise "There was a general endorsement of Hennig's method of cladistic analysis for the determination of branching sequences…" according to the editors (p. vi). A trend which was established first among fish-systematists and palaeontologists by 1972 (see Greenwood *et alii*, 1973; reviewed by Bonde, 1974).

Problems with paraphyletic groups

What then is wrong about such 'grade' classification (by Huxley explicitly meant to be a secondary type of classification, e.g. 1958, 1959), sometimes argued as an intension to express 'adaptive zones' (different 'niches') or 'evolutionary levels', and which employs paraphyletic groups ? As we will argue below, paraphyletic groups can sometimes be used under the condition, that they are marked (we suggest in quotationmarks "X"), and they are assumed to be preliminary left overs in a not yet completed analysis (e.g. at the 'primitive' end of a monophyletic group). The important thing is, that they should not be accepted as equivalent to monophyletic groups when engaged in further analyses. This means e.g. that they cannot be added to other groups in a diversity analysis, and they cannot be used in biogeographic analyses; further that they cannot even go extinct as a group, and they do not have a

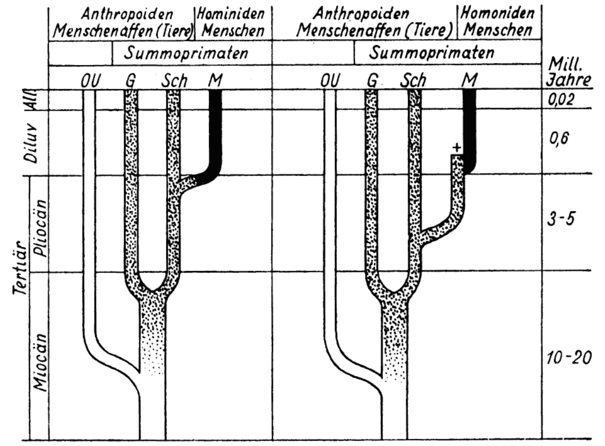


Abb. 129. Der gleiche Menschheitsstammbaum; links ohne, rechts mit ausgestorbenen Vorläufern

Fig. 6. 'Summoprimaten' for Homo and African apes by Weinert (1951) indicated on two phylogenetic trees, the one (right) with fossils included (+).

precise phylogenetic interrelationship with other groups. All of this because they constitute an incomplete historical group, an incomplete genome history –in short, they are rather useless, not to say meaningless. If they are not specifically marked as a warning, how should non-experts of certain systematic groups then know from the taxonomy how to avoid them?

As wastebaskets paraphyletic groups may sometimes be used, if marked as such, but in fact the worst thing about them is, that if they have been used as part of a classification, then there are relevant monophyletic groups, which cannot be recognised and named. The classical example again is hominoids; if apes are named as Pongidae (versus Hominidae for Man), then the relevant monophyletic group of Man plus chimps cannot receive a name, it cannot be talked about as a natural group under one term. The same counts for *Homo* plus *Pan* plus *Gorilla*, and in that way a lot of potential information remains hidden. Actually, it is not untill quite recently that these important groups have been named (as e.g. Hominini or Homininae or Hominidae) in the formal system, mainly due to molecular biologists such as Goodman (1962; 1963a, Fig.5, our Fig. 8; 1975, Tab. 4), who in the beginning was judged to be slightly, if not very, odd by classical systematists and anthropologists. Before that there had only been very unsuccessful attempts like that by Weinert (1951: 43) with his 'Summoprimaten' for gorilla, chimps plus Man (Fig. 6), which nobody else has used. Curiously, he argued in detail for the even closer relationship between chimps and Man (pp. 46-56), but he did not suggest a name for that important monophyletic group, which lately has been suggested even to be subsumed under one generic name, *Homo* (Goodman *et alii*, 1998, 1999; Wildmann *et alii*, 2003).

The traditional 'evolutionary' classifications could be like (nos. 1 & 2):

Superfam Hominoidea (1)	or alternatively Hominoidea (2)
Fam. Pongidae	Fam Hylobatidae *(Hylobates)*
Subfam Hylobatinae	Fam Pongidae *(Pongo, Gorilla, Pan)*
Subfam Ponginae	Fam Hominidae (*Homo)*
Fam Hominidae	

And if fossils were added, it would be as 'stem-pongids'/ '-pongins', e.g. an extinct subfamily, Dryopithecinae, under the Pongidae like (no. 3) by Simpson (1945):

Superfam Hominoidea (3)	or an alternative (4):
Fam Parapithecidae	Hominoidea
Fam Pongidae	Fam Hylobatidae
Subfam Hylobatinae	Fam Pongidae
Subfam Dryopithecinae	Subfam Dryopithecinae
Subfam Ponginae	Subfam Ponginae
Fam Hominidae	Fam Hominidae

Or in Leakey's version (1963) including fossils, completely sequenced :

Hominoidea (5)
Pongidae *(Pan, Pongo, Gorilla)*
Hylobatidae
Proconsulidae
Hominidae (incl *Australopithecus*)
Oreopithecidae
Incerta sedis: *Dryopithecus, Sivapithecus* etc.
(as Leakey does not accept 'Simpson's dustbin' Dryopithecinae).

From none of those classifications can the 'correct' (hypothesised) phylogeny be derived, even though some would claim, that phylogeny has been build into the classification, or refer to Simpson's ideal from 1961: the classification is 'consistent' with phylogeny. No, it is not, it is in contradiction, because the supposed 'great distance' between *Homo* and the apes has been expressed by giving *Homo* far too high rank (as a separate family). A viewpoint which can only be justified as anthropocentric. (As an illuminating expression of this type of 'artistic', evolutionary, adaptationistic babble we can do no better than refer to Simpson's paper from 1959 on classification, repeated 1961: 205-220). And nowhere can *Homo* and *Pan* (or *Pan* + *Gorilla*) be seen to be each others closest relatives, because the paraphyletic "Pongidae/-inae" has been used. The latter may be referred to as 'non-human honinoids' or simply 'apes'.

As to the 'stem-group' Dryopithecinae, it was traditionally used as something from which all the groups classified after it (say here within Hominoidea) were derived, and these derived groups were under Simpson's definition (1961, also from Beckner, 1959) called 'minimal monophyletic' ; heavily criticised by Bonde 1977: 757-762), because they were supposedly derived from a group (Dryopithecinae) of the same or lower rank. How this rank of that stemgroup was decided, was rarely touched upon, and neither was the evidence given, why it should be a group at all. In such cases it might have been justified by claiming that the differences between the few fossil genera in the group were so small that it 'only deserved' rank of subfamily (in an analogous way it was claimed, that Man was so different from the apes that he 'deserved' to be recognised as a distinct family).

These were the type of arguments used by Mayr (1950), when he as the expert systematist 'taught' the anthropologists, that all of their fossil hominids, incl. *Australopithecus*, ought to be subsumed into one genus *Homo:* "not ... unequivocal claim for [generic] separation". A viewpoint he revised in 1963b (p. 631), when he had learnt that this was probably too restrictive, and *Australopithecus* was anyway so different from *Homo,* that this 'justified' its own generic name because of the differences in brain size. This was further supported by an adaptationist argument, that Man had entered "so completely different a niche that generic separation is definitely justified". This despite his claim that "the Australopithecines do not have a single character or combination of characters that would clearly disqualify them from the main line of human evolution". And the "Australopithecines" [? formal subfamily] only contained one genus, *Australopithecus* (including *Paranthropus*, although he p. 629 described it as "a specialized ... sideline diverging farther than *Australopithecus* from the human type"). The earliest stage of more advanced hominids he called (presumably vernacular) "The Pithecanthropines" though arguing that all should be classified as *Homo*. And the entire discussion of hominid evolution he began by accepting the division in Pongidae and Hominidae (1963b: 624), talking about the "branching of the hominid from the pongid line (speciation)", despite claiming (p. 628) that "(Goodman 1962) proves conclusively that the third alternative is correct", namely that "the hominid line branched off from the line of African apes ... at a comparatively recent date, long after the pongid line had split into an Asiatic ... and an African ... branch" (see Fig. 8, below).

Mayr's meaning had profound influence on the palaeoanthropologists, who for decades hardly dared name a new species, let alone a new genus. So Leakey and Tobias had a hard time discussing among themselves and convincing others about the justification for *Homo habilis* (Leakey *et alii,* 1964). As late as in 1978 some young anthropologists consulted Mayr about the new form 'Lucy' and her 'allies', and were allowed to give it a separate specific name as *Australopithecus afarensis*, but not a new generic name (Johanson, White *et alii,* 1978), which even at that time would clearly have been appropriate. However by now *Australopithecus* was generally used as a 'catch all' primitive stemgroup as by Mayr (see above) –clearly paraphyletic– but if one did not even recognise that concept, no problem appeared.

In conclusion: To extract precise phylogenetic information from a classification, all taxa should as far as possible be strictly monophyletic; that is, a taxon must include all known descendants of a common ancestor. Consequently only cladistic classifications are really informative. Another advantage by cladistic classifications derived by a parsimony method (Farris, 1983), is that by that treatment of the character analyses, all taxa will be maximally characterised, and all characters will be optimally used as synapomorphies to characterise the groups (Patterson, 1980). A byproduct is, that the implied phylogeny is as simple as possible, indicating as few changes on the tree as possible ('Occam's razor').

Conventions and cladistics

From a classificatory viewpoint it is worth noting, that the above classifications (1-5) demonstrate the use of both of the 'resources' available in a hierarchy, namely the usual 'subordination' where every group is divided into two subgroups of same rank (no. 1), or 'sequencing' within every group (as nos. 2 and 5) with more than two subgroups of same rank at every level, or a mixture of the two methods (in nos. 3 and 4); further that Leakey (no. 5) also used the *incerta sedis* to signal uncertainty about the placement of some genera. Those three conventions are usually the only ones employed in a Linnaean hierarchy. Subordination into two subgroups often does not signal two sistergroups, see nos. 1 & 4. Sequencing has often been used to indicate, that there was no firm idea about the precise interrelationship of the subgroups classified at the same level (like no. 5), but mostly the order of the succession did not mean much (it might be made alphabetically, or sometimes there might be an idea about those subgroups mentioned first as the most 'primitive', a principle difficult to use in a precise way, and the opposite seems to be the idea e.g. in at least part of Delson's [2000] classification).

Nelson (1974) explored the possibilities of these three devices in phylogenetic classifications also including fossils (usually marked with a dagger, or with + like by Bonde, 1977; see Fig. 3). Nelson showed that sequencing could be used to show either uncertainty or (if *inc. sed.* was used for that) one could use sequencing instead of subordination to reduce the need of many intermediate ranks between two different categorical levels. The latter only called for a convention, that every mentioned group in a sequence is sistergroup to all following below it in the same sequence. So if a family is sequenced into several subfamilies, then that rank needs not be divided into tribes, subtribes etc. (but the obligatory genera obviously have to be named, as do species). One can also use sequencing of living groups at the same level to mean uncertainty, while sequencing of fossil groups (marked +) means successive sistergroups as just mentioned, to avoid that fossil groups force lots of intermediate ranks in between those of the recent groups. This also has the advantage, that all the fossil groups can be removed without any consequence for the classification of the living groups –the reasoning being, that in general there are more uncertainties around the precise placement of fossils, so these should usually not have influence on the system of the living (Bonde, 1977: 786).

By the same reasoning Patterson & Rosen (1977) suggested a category 'Plesion' exclusively for such fossil taxa, which could be sequenced under living taxa so that the latter would not be affected by the removal of all the fossils. In our model of hominid classification (below) this is the case, all the fossils can be considered plesions, that is taxa with no formal rank (or taxa of the 'same rank' as their closest recent relative). Patterson & Rosen (1977) also scrutinised several other ways of classifying fossils either with the recent organisms or separate from them, and disqualified several models. Bonde (1977) presented some models of cladistic classifications using hominids as the most detailed examples and exploiting the possibilities of including 'true ancestors' marked in a specific way (as [+], Fig. 3). Wiley (1978, 1981) specified in even greater detail simple conventions for cladistic classifications, which kept the system as close as possible to a Linnaean hierarchy, but still allowed the phylogenetic relationships to be read directly from the classification. Forey (1992) gave a short review of these classificatory techniques and conventions.

Most of the cladistic papers mentioned here stick to the convention, which also Hennig (1966) took to be most obvious, namely that sistergroups are given same rank (at least the recent ones –plesions can be excepted), because they have the same origin and age. A logical consequence of this is Hennig's suggestion (1966), that categorical rank should be determined or, in fact, defined by age as the only non-arbitrary measurement of such rank. All other methods, e.g. by diversity ('size' of the taxon) or by 'evolutionary level' or degree of specialization or 'adaptive level' (a sort of 'grade') seem to be difficult to apply (Ereshefsky, 2001)or simply very subjective (often anthropocentric) –clearly what Simpson meant by 'art' in classification (e.g. 1961). The epitome of 'subjectivity' for many seems to be the often cited authoritarian statement concerning the rank of species by Regan (1926: 75): «A species is… in the opinion of a competent systematist, sufficiently definite to entitle it… to a name». Much depreciated by Ghiselin (1997: 118), but it might be seen in a more positive light as an invitation among 'competent systematists' to discuss and disclose their needs in terms of a biological unit, which suits their specified purposes (Bonde, 2001: 50).

Contrary to Hennig and the above mentioned cladists, Farris (1976) has devised conventions for classifying fossils with recent animals, according to which sistergroups do not usually have the same rank, because the rank is measured by the elapse of time since the initial diversification of the group, not since the origin of the group as in Hennig's system. For extinct groups the rank is measured as 'lifespan' from the diversification to the extinction. As sistergroups are obviously still classified together in a taxon, it is necessary to have a convention so that subordinated under a taxon, the sistergroup with the lower rank should be written down first (if not, it would be misunderstood as a subgroup of its own higher ranking sistergroup). Farris did not want to use sequencing, only subordination, therefore he also devised a method for generating intermediate names of categorical ranks *ad infinitum*, so that the prefixes sub-sub-super-etc. -family rank alone from the prefix combination can be evaluated as higher or lower than some other intermediate rank –an extraordinarily tedious and precise algorithm, which we doubt will ever be seriously used. Bonde (1981, 2001) has, however, demonstrated the possibilities of subdividing (time-) biological species into sub-sub-groups of *H. sapiens* (Fig. 7).

For recent groups the effect of Farris' method is that under a taxon the latest diversified sistergroup will always be listed first. For extinct sistergroup taxa the one with the shortest 'lifespan' is listed first. One advantage of his system is that it eliminates 'empty' higher categories, e.g. in monotypic taxa such as Hylobatidae in the traditional system having only one subordinated taxon, *Hylobates*, and Ponginae with only one genus *Pongo*. The example will show this with Hominidae to include all the larger apes and sistergroup relation indicated by the same indentation:

Hominoidea:
- *Hylobates*
  - *H. (Symphalangus)* (1 sp.)
  - *H. (Hylobates)* (div. spp.)
- Hominidae
  - *Pongo pygmaeus* (1 sp.)
  - Homininae
    - *Gorilla* (div. spp.)
    - Hominini
      - *Homo sapiens* (1 sp.)
      - *Pan* (2 spp., one with subspp.)

Estimating the age of diversification for a single species (or rather a 'least inclusive taxonomic unit', LITU, see below) is meaningless, so a single undivided lineage has no time-depth to indicate rank and must be listed first as a subgroup. For more diverse groups the age of differentiation (or the last common ancestor) can be calculated either by the 'molecular clock' or by finding fossils to estimate the (minimum) age of a lineage and thereby of a node of the tree. In groups where neither fossils nor molecular data are available, one could divide into equal parts for the number of nodes the (minimum) age calculated from the first outgroup with such data available. In this way it would be equivalent to belief in the regular 'molecular clock'.

Molecular biology and classification

Molecular biologist Morris Goodman already in the early sixties (1962, 1963a, 1963b; Fig. 8) concluded from immunologic data on serum proteins that African apes and humans are closely related. The evidence was accepted by Simpson (1963, 1975, above), but did not change his view on hominoid classification. Later on mitochondrial DNA data resolved this trichotomy, with chimps and man being sistergroups, and gorillas the next branch (e.g. Ruvolo, 1997). Following the Hennigian tradition this has prompted Goodman and his group (Goodman *et alii*, 1998, 1999; Wildman *et alii,* 2003) to propose strictly cladistic classifications of

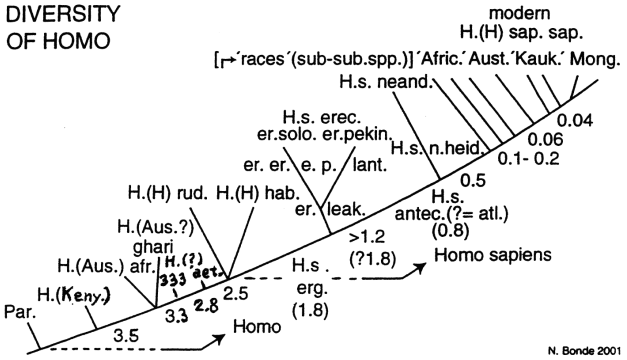


Fig. 7. Diversity of Homo. Diagram (tree) of the diversity of part of our lineage from Bonde (2001), corrected for the English translation (demonstrating the difficulty sometimes of translating between a tree and a classification, so Homo 333 group and 'H. aethiopicus' (= aet) had to be inked in). H. sapiens as a 'time-bio-species' as old as near 2.5 m.y., and Homo over 3.5 m.y. old as incl. Kenyanthropus (= Keny), and as sistergroup to Paranthropus (= Par). Numerous sub-sub-...spp. indicated, e.g. H. sapiens erectus pekinensis lantaniensis as a chrono-sub-etc.; 'er. leak' = OH9 as an 'ancestral' sub-sub-sp.; two modern 'races' as paraphyletic: 'name'. This is a consequence of using 'time-bio-species'. afr = africanus; 'Afric' = (Sub-Saharan) Africans; antec = antecessor; atl = atlanticus; Aus = Australopithecus; Aust = Australians; e = er = erec = erectus; erg = ergaster; hab = habilis; heid = heidelbergensis; 'Kauk' = Caucasians; leak = louisleakeyi; Mong = Mongolians; n = nead = neanderthalensis; p= pekin = pekinensis; rud = rudolfensis; s = sap = sapiens.

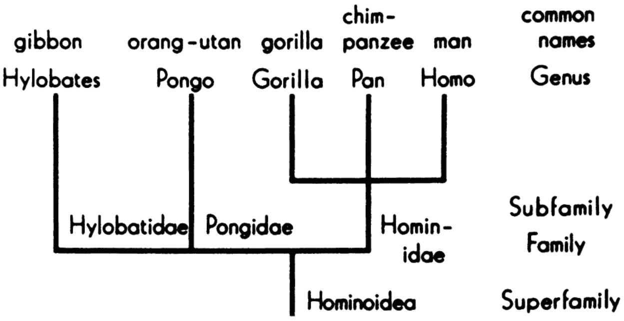


Fig. 8. Part of Goodman's diagram and classification of hominids (1963a), entirely cladistic (no subfamilies in this part of the diagram).

primates. Using Hennig's (1966) idea of ranking clades by their absolute age, and estimates from the molecular clock, genus *Homo* so embraces chimps as a subgenus, *Homo (Pan)*, in addition to subgenus *Homo (Homo)*! –A logical consequence that would certainly not be favoured by evolutionary taxonomists like Mayr (1963b) and Mayr & Ashlock (1991), still looking for gaps, adaptive zones and grades as a basis for (generic) ranking.

Stemspecies and ancestors

The possibility of actually finding a fossil stemspecies prompted Hennig (1966) to refute classifying fossil and recent organisms in the same system, because from a certain phylogenic systematic viewpoint an ancestor is 'equivalent' to all of its descendants. Others like Crowson (1970) agreed, and Løvtrup (1975) followed up denying the very possibilty of classifying fossils, an extreme position criticised by e.g. Bonde (1977).

The problem of classifying ancestors appears totally imaginary to many cladists. They argue that actual fossil ancestors can in practice never be identified (Forey, 1982; 1992). This is because an ancestor, by definition, has only plesiomorphic characters as compared to its descendants, and therefore can only be classified with uncertainty (as *incerta sedis*, see Nelson, 1974). Being only relatively plesiomorphic –that is posessing no autapomorphic features to characterise itself– an ancestor is what Nelson (1970) called 'morphotypic'. In a cladistic framework an ancestor (comprising more than one specimen) can, in fact, not truely be shown to constitute a proper group. It is clearly paraphyletic (or 'metaphyletic', see below) and all proper groups or taxa have to be demonstrably monophyletic.

Bonde (1977 –expanded 2001: 44-46) agreed that in general these 'morphotypic' groups cannot be demonstrated to be 'ancestral'. But although most cladists disagree, he also claimed, that in certain cases the hypothesis of some fossils as 'directly ancestral' is indeed 'scientific', that is testable (possible to refute by observations, the demarcation of 'science' by Popper, e.g. 1972), while the only alternative hypothesis possible, that of being in a sistergroup position (a side branch on the phylogenetic tree) is not so clearly testable, at least not by observations on the fossils themselves concerned.

The case of this socalled 'fossil ancestor' occurs when (as seen in a framework of a certain accepted phylogeny) the fossils in question are fullfilling two demands (Fig. 9): 1) They have features intermediate between two reconstructed morphotypes, namely that of the 'last common ancestor' (lca) of the group they are claimed to be ancestral to, and the 'lca' of the latter group plus its sistergroup; 2) These 'intermediate' fossils are also older than all known members of the supposed descendant group. When testing this hypothesised 'ancestral position' on the tree, it may be refuted by finding (perhaps in better fossils of the 'same sort') one or more specialisations (autapomorphies) not expected for that ancestor; or finding even older fossils of the descendant group. The alternative 'side branch' position can never be contradicted by finding new features of the fossil group concerned or by age comparisons. In fact, this sistergroup position can be refuted only if changing the entire accepted phylogenetic frame and/or the evaluation of certain characters as plesiomorphic in stead of apomorphic. In addition the 'ancestral position' may be said to be a simpler phylogenetic hypothesis at the level of the phylogenetic tree, in

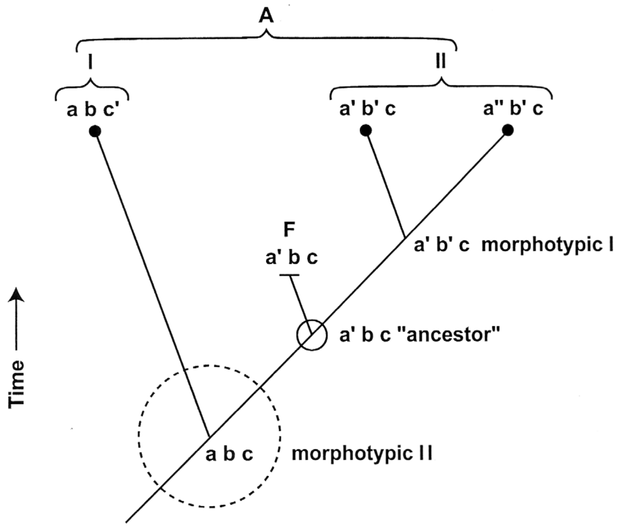


Fig. 9. The ancestor problem on a phylogenetic tree: Morphotypic ancestors impossible to place precisely, while the fossil, F, is a possible true “ancestor”, at least more testable than the alternative sistergroup position (simplified from Bonde, 1977). a, b, c plesiomorphic features; a, a’, a” a morphocline towards more apomorphic; in the circle, a and c have not yet changed to a’ resp. c’, so a morphotypic fossil (with a, b, c) can be placed in any position within the circle.

as much as the position as ‘ancestor’ implies one cladogenetic event less based on the same data (Bonde, 1977, 2001).

One should note, that this disagreement between cladists mainly exists because some only accept discussing phylogenies in terms of interrelationships and cladograms, which depict only sistergroup relationships (‘ancestry’ is irrelevant). Others, however, are willing to discuss phylogenies also in terms of phylogenetic trees, where ancestral positions are relevant. Admittedly, discussing in terms of trees elevates the level of abstraction (Tattersal & Eldredge, 1977; Bonde, 1984), as it adds assumptions about time dimension and evolution, with the consequence that tests of the entire phylogenetic hypothesis are less transparent than tests of cladograms (Bonde,1984).

Metaphyly and uncertainty

Some further aspects of the problems with ‘fossil ancestors’ were explored by Bonde (1996) using the most famous of all ‘ancestors’, namely *Archaeopteryx*, and this lead to realisation of some typical features of such ‘ancestral groups’. One feature was the need to discuss different categories of ‘taxa’/groups in terms of the ‘data’ from which they are recognised as elaborated by Archibald (1994). The groups in question are socalled ‘metataxa’, which are taxa not known to be either mono- or paraphyletic. This was an expansion to higher classificatory categories upon Donoghue’s concept metaspecies (1985) for groups of organisms with no autapomorphies (that is exactly like ‘ancestors’ as *A. lithographica** –the star signifies metaspecies) or with conflicting apomorphies leading to polytomies in a cladogram, like morphotypic ‘ancestors’ would also do. Metataxa can be considered intermediate as category between monophyletic and clearly paraphyletic groups (Archibald, 1994), and the uncertain relationship of metataxa can be called ‘metaphyly’ (Fig. 10).

This ‘ancestral’ *Archaeopteryx* (as used e.g. by Paul, 2002) turns out in reality to be composed of different taxa, at least three, perhaps four, of which the interrelationships and relationship to the taxon Aves (living crowngroup birds) is unknown (a polytomy in the cladogram). So *Archaeopteryx* in the broad textbook sense is that category of metataxa called a mixotaxon (Archibald, 1994; Bonde, 1996), in which only some of the subgroups (species) can indeed be characterized by autapomorphies. And admittedly the ‘group’ is recently often divided into several genera (Elzanowski, 2002; Bonde, 1996), but at least two species, *lithographica* and *bavarica*, are generally retained in the mixotaxon *Archaeopteryx*** (marked by two stars).

Now, what is the significance of this for hominids ? The situation is somewhat similar concerning the ‘ancestor’ *Australopithecus*, which as a stemspecies, *A. africanus**, is a metaspecies, and in a ‘broad’ generic sense *“Australopithecus”* including *anamensis*, *‘afarensis’*, *bahrelghazali* and *garhi*, and sometimes even the ‘robust’ forms (appropriately classified as *Paranthropus*) is simply a paraphyletic mess. *Australopithecus* is also a metataxon, and if it includes only *africanus* and the ‘robust’ forms and the interrelationship between these two “Australopithecines” and *Homo* remains uncertain, and if *A. africanus* is considered morphotypic, then *Australopithecus*** is a mixotaxon, like *Archaeopteryx*** forming a polytomy. If the reason for this trichotomy is a conflict of characters, however, then it would be an ambitaxon (Archibald 1994) and marked as such, *Australopithecus**** . So some of the very popular ‘taxa’ in anthropology are rather dubious constructs, as indicated also by Bonde (2001), see Fig. 7, where the mixotaxon is at the level of subgenus *H. (Australopithecus)*** including *A*** *garhi* and its uncertain relation to *H (Homo)*. It is unfortunate that Wood and Collard (1999a, 1999b) recently have used *“Australopithecus”* in an even broader sense to include also *habilis* and *rudolfensis,* normally referred to *Homo*, making *Australopithecus* even more undiagnostic and useless.

In the genus *Homo* similar problems cannot occur, unless a fraction, say a ‘broadly defined’ *erectus* (like by e.g. Rightmire 1994, Delson 1997, and Stringer’s fig. a, 2003) is placed in its own subgenus, *H. (Pithecanthropus),* comprising also *heidelbergensis* and some morphotypic form like the African *ergaster*. A procedure which has actually been implied often enough by some of the multiregionalists and others operating with the term ‘pithecanthropines’ (an old French tradition continued by Lumley e.g. 1982; and see Mayr’s 1963 discussion, above). As opposed to this it is our intention below to use *Pithecanthropus* in a cladistic frame, where it is not an ‘ancestral’ metataxon.

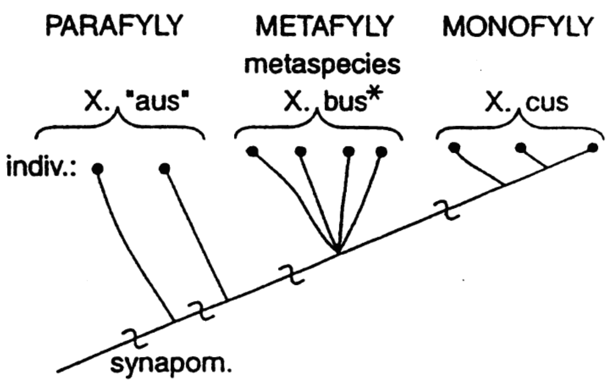


Fig. 10. Mono-, meta- og parafyli (from Bonde, 2001; Archibald, 1994). Indiv. = individual organisms; synapom. = synapomorphy.

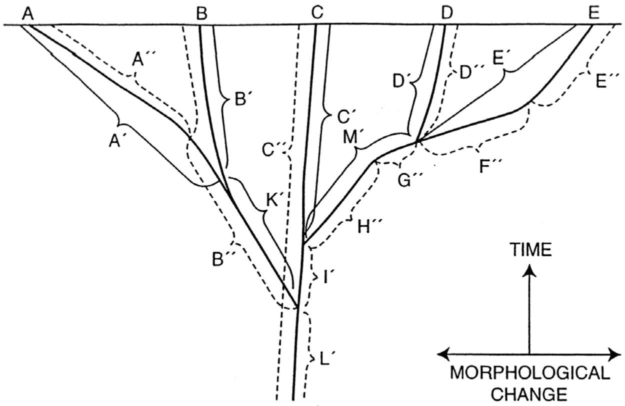


Fig. 11. Limitations of 'species' in the time dimension: A-E are living 'bio-species'; A' – M' are Bonde's 'time-bio-species' delimited by nodes ('speciations') like by Hennig; A'' – H'' are Simpsonian 'evolutionary species' or 'chrono-species', some times like E'' – I'' they should rather be called 'chrono-sub-species', and these can in fact be used as LITU's, which in this case are fossil, but not truely extinct. From Bonde, 1981, 2001.

Species and LITU

The literature on species concepts is vast as it is one of the few biological topics that have been interesting to philosophers and some other scientists outside biology/palaeontology. Among all this a tiny fraction concerns the socalled 'palaeontological species problem', taking into account the extension of species in the time dimension (Fig. 11). Some aspects of this has been treated by Bonde (1975, 1977, 1981) and Westergaard (1989) focusing on fossil hominids as examples, and has recently been reviewed in some detail by Bonde (2001) with some new suggestions for the science of species ('speciology'). Larger treatments of species are e.g. Ereshefsky (2003, 1992), Gould (2002), Wheeler & Meier (2000), Avise (1999), De Queiroz (1999, 1998), Ghiselin (1997), Mayden (1997), Cracraft (1997, 1983), Kimbel & Martin (1993), DeQueiroz & Gauthier (1992), Nelson (1989), Tattersall (1986), Wiley (1981), Cracraft & Eldredge (1979), and many of the older papers reprinted by Slobodnikoff (1976). The palaeontological species problem got a diverse treatment in Sylvester-Bradley (1956), but only few people besides Simpson, Wiley, Bonde and Gingerich have treated this seriously.

Mayr throughout his carreer has defended the 'biological species concept' (e.g. 1963, 2000) understanding species as reproductive units isolated from other such units, a concept which does not really take time into account (and obviously cannot be applied to asexual organisms –profound criticism by Bonde, 2001). Most biologists probably use this or a very similar concept (e.g. Hennig, 1966), and palaeontologists mostly imagine, that biological species can be seen as time transects of a 'similar' unit sliding through time (e.g. in Sylvester-Bradley, 1956; Gingerich, 1979). But this concept is of very limited practical use for palaeontology, and Simpson (1951, 1961) tried to improve this situation by his 'evolutionary concept' in the definition of which the aspect of time and history figured prominently. It has never been accepted by Mayr, but was defended and modified by Wiley (1981). Bonde (1977: 781) tried to reconcile his 'time-bio-species' corresponding –like Hennig's species concept– to internodes of the phylogenetic tree (Fig. 11), with Simpson's (1961) evolutionary species by a slight modification of the latter's definition as a 'lineage separate from others' concerning the meaning of his qualification, "with its own evolutionary role and tendencies". If the 'role' is its unique phylogenetic position and the 'tendency' is towards coherence, then the delimitations in the time dimension would be the same for the two concepts, namely at the nodes.

Wiley (1978, 1981) also defended Simpson's 'evolutionary species' by modifying the same few qualifying words to "evolutionary tendency and historical fate", but neither Simpson nor Wiley gave a precise suggestion for the species limitation in time, and 'evolutionary tendency' is as vague as 'role' (critique in Bonde, 1981; 2001: 41). Wiley (1979, 1981) specified in much greater detail than Bonde (1977, 1981) conventions for classifying in a precise cladistic way with very little violation of the Linnaean hierarchy and the nomenclature rules. But contrary to Hennig and Bonde he allowed an 'ancestral species' to transcend a speciation (split in a tree, Fig. 11) and keep the same name afterwards if unchanged morphologically/genetically –something appealing to palaeontologists and, in fact, demanded by traditional nomenclature rules. Seen from a theoretical cladistic viewpoint this is illogical in terms of degree of phylogenetic relationship, because the two 'parts' of the surviving 'ancestor' do not have the same relation to the rest of the system, and are therefore 'different' on these basic cladistic terms (Bonde, 1981). But in practical classification it works easily by a convention (not permissible in the Linnaean hierarchy), that the name of this ‘ancestor’ be repeated at two different levels in the classification (Wiley, 1979) –that is, if one is willing to classify phylogenetic trees as demonstrated below.

In the detailed discussions by Wiley (1981), DeQueiroz & Gauthier (1992), Christoffersen (1995), Mayden (1997), DeQueiroz (1999), and Bonde (2001) it is argued, that the theoretically most ideal and generalised species concept is the ‘evolutionary’ one understood as a lineage concept and a ‘unit’, which comprises all the other concepts as ‘special purpose cases’ (Mayden, 1997; DeQueiroz, 1999), which in a certain way are complementary to each other (Bonde, 2001). But this ideal unit is non-operational, giving no criteria for recognising an ‘evolutionary species’, so in practical classification one needs a much smaller unit as the basic unit or ‘terminal taxon’ in the system (Bonde, 2001). Here the different ‘phylogenetic species’ come into play as discussed by Mayden, DeQueiroz, and in detail in Wheeler & Meier (2000). Christoffersen (1995) and Bonde (2001) agreed that the proper unit would probably be the ‘smallest recognisable or diagnostic’ unit as argued by Cracraft (1983, 1997). Such small units could be defended also in palaeontology – contrary to Bonde (1981) and Hennig – as subdivisions of internodes of the phylogenetic tree; that is corresponding to ‘chrono(-sub-)species’ (Bonde 1981, 2001) if recognisable within a lineage (Fig. 11, 12). These are then the ‘least inclusive taxonomic units’, LITU’s (Pleijel & Rouse 2000, 2003), of the palaeontologists to be given a name – and here, as well as in neontology, it must depend on the purpose of the scientific study, just how small units it is reasonable to name.

With DNA techniques we know that it is now possible to distinguish/recognise most individual organisms, so in principle the individual could be the LITU or terminal taxon (and remember that in palaeontology some single unique fragmentary fossils are in fact each the sole representatives of some taxa) –the individual organisms as terminal units have been suggested by Vrana & Wheeler (1992). At this level (unless it concerns asexual organisms) the structure of the descent relationships is a network, not a hierarchy, and for most (palaeo-) biological studies it is probably groups at the interface or borderline between the net and the hierarchy, which are most relevant as the basic units given names in the classification– but every scientist must argue his case and accept, that for some other purposes the relevant units may be at another level in the hierarchy. The final and uniform system is –with our present knowledge of the diversity of life– not such an apparently easy goal to day, as many of us thought/hoped a few decades ago. However, with computed and well resolved hierarchies (trees or cladograms) it should in the future be possible to compare different levels in the hierarchies rather easily, to detect patterns of relevans to e.g. ‘biospecies-level’ and ‘deme-level’, as measured against the basic ‘smallest diagnostic unit’ or LITU. The striking differences in treatment of “species” in different subdisciplines of biology (say zoology and botany) will then be quite apparent.

The LITU’s we have chosen to name below are small recognisable groups of fossils with a minimum of variation, and which in most cases can be recognised by proper autapomorphies. Some few are, however, possible ‘ancestors’ or metataxa without unique specialisations, and they have been properly marked as such, while only few are paraphyletic ‘leftovers’ awaiting further analyses. Characters of LITU’s are supposed to be homologous, inherited from a commen ancestor, which means that the discovery of named LITU’s being polyphyletic necessitates a reevaluation. In this sense, hypotheses of LITU’s also imply hypotheses of phylogenetic relationships (Bonde, 1981, first quotation, above), and our units/LITU’s are chosen because of their presumed historical relevans. This is because ‘history’ or phylogeny is the one aspect which encompasses all the others, is of greatest generality (Hennig, 1966), and therefore should be precisely expressed in the biological system according to cladistic philosophy and its methodology of parsimony analyses, which implies the fewest extra assumptions (Farris, 1983).

Modern (non-Linnaean) cladistics.

The shortcomings of classification based on the Linnaean hierarchy (see e.g. Ereshefsky, 2002; Haerlin, 1998, 2001, 2003; Pleijel, 1999), with its subjective and little informative ranking, can be eliminated giving up this tradition. In the following classifications of primates and hominids, LITU’s are given a single ‘name’ (as proposed by Bonde already 1977 [p. 784] for ‘species’ to be consistent with cladistics) beginning with lower case letter, whereas groups of LITU’s are recognised by ‘Names’ with upper case first letters, as suggested by Pleijel & Rouse (2000, 2003). Other than this the name does not signify any rank. 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 LITU’s is shown by subordination of their names in boldface, while totalgroups (marked: Name$_a$) 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 (as in Fig. 3).

Informal ranks of recent crowngroups can be provided by their absolute age in million years in brackets: (m-number), 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 (Name$_a$): 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 novum*, 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 (Least Inclusive Taxonomic Unit) usually corresponds to the smallest recognisable socalled 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.

Below is our classification of primates (cf. the more detailed classifications by Shoshani *et alii* [1996] and Delson [2000] with Plesiadapiformes included, ranks for all groups and all fossil genera and living subgenera listed, but in both with sequencing indicating only uncertainty and no rule for the succession of names, and *Pan* left as uncertain in Homininae by Delson). Some fossils mentioned (see Hertwig, 2002) are in paraphyletic stemgroup positions; for recent taxa cf. Groves (2001). Our classification is much more elaborate for hominids, especially as (almost) all fossil relatives on the lineage to sapiens are classified according to our phylogenetic model (tree, Fig. 12).

Details of hominin taxa

In the following, a cladistic evaluation (outgroups being African apes) of listed hominid LITU's (numbered 1 to 34) and necessary clades is performed to specify important common derived characters (synapomorphies: s) and unique specialisations (autapomorphies: a). These are used as arguments for the phylogenetic relationships presented in our tree (Fig. 12), and our classification below. Relatively plesiomorphic LITU's (or parts of LITU's) are boldly proposed as 'ancestors', if their fossils are older than those of their descendants. 'Names' are given in inverted commas, as they are not yet proper taxon names provided with symbols of convention. The traditional names (as species or subspecies) are given in brackets, paraphyly being indicated by quotation marks.

1. 'orrorin' (*Orrorin tugenensis*); s: relatively small upper canine compared to apes, human-like proximal femur with long neck, but still chimplike cortical bone?; a: thick tooth enamel (Senut *et alii*, 2001; Wong, 2003).
2. 'sahelanthropus' (*Sahelanthropus chadensis*); s: apical wear of canines, smaller upper canine, lower canine with distal bulge; a: very thick browridge, rather vertical face (Brunet *et alii*, 2002).

- Primatesa
  - ?+ altiatlasius inc. (60)
  - **Primates** (m63)
    - Strepsirrhinia
      - "+ Adapiformes" (55-8)
      - **Strepsirrhini** (m50)
    - Haplorrhinia
      - "+ Omomyida" (55-30)
      - **Haplorrhini** (m58)
        - Tarsiusa
          - + xanthorhysis (50)
          - **Tarsius** (m6) [?12 LITU's]
        - Simiia
          - "+ Parapithecida" (36-33)
          - **Simii** (m40)
            - Platyrrhinia
              - + branisella (26)
              - **Platyrrhini** (m25)
            - Catarrhinia
              - "+ Propliopithecida" (36-33)
              - **Catarrhini** (m25)
                - Cercopithecidaa
                  - "+ Victoriapithecida" (21-12)
                  - **Cercopithecida** (m15)
                - Hominoidaa
                  - + morotopithecus mut. (21)
                  - **Hominoida** (m18)
                      - **Hylobatida** (m8) [?28 LITU's]
                    - Hominidaa
                      - + Dryopithecus inc. (12-9)
                      - **Hominida** (m14)
                        - Pongoa
                          - + Sivapithecus (13-7)
                          - **Pongo** [?3 LITU's] b
                        - Homininaea
                          - ?+ samburupithecus inc. (9.5)
                          - **Homininae** (m7)
                            - **Gorillini** [?4 LITU's, one is gorilla] b
                            - **Hominini** (m6)
                                - **Pan** (m3)
                                  - paniscus b
                                  - **Troglodytia** (m1.5) b
                                    - Troglodyti
                                      - troglodytes
                                      - schweinfurthii
                                    - Veri
                                      - verus
                                      - vellerosus
                              - Homininaa [/Sapiensa] (?6.5)
                                - sapiens b,g

3. ‘kadabba’ (“*Ardipithecus ramidus” kadabba*); s: mesial shoulder on lower canine (Haile-Selassie, 2001). Problem: the included toe bone is c. 0.5 m.y. younger and found c. 20 km apart from the rest, so may not represent the same LITU.
4. ‘ardipithecus’ (“*Ardipithecus ramidus” ramidus*); s: less sharp lingual cusps on lower M3, distal tapering of upper M3, lower canine not mesiodistally-to-distobuccally compressed; a: reduced lower P4 with single root, shortened basis of braincase (Haile-Selassie, 2001; White *et alii*, 1994; Wood, 1994). Perhaps a synonym of *Homo antiquus praegens* Ferguson 1989, from Tabarin, Kenya.
5. ‘lothagamensis’ (new name of new LITU); s: thicker enamel on broader lower M1, more robust mandibular corpus (Haile-Selassie, 2001; Leakey & Walker, 2003).
6. ‘anamensis’ (*”Australopithecus” anamensis*); s: more high-crowned molars with thick enamel; a: pointed upper canine with low mesial and distal bulges (Ward *et alii*, 2001).
7. ‘kenyanthropus’ (*Kenyanthropus platyops*); s: smaller canines, smaller lower lateral incisors?, less parallel rows of cheek teeth, less wear differential?, mandible with less sloping symphysis, no subalveolar hollowing?, mental foramen opens anterior/superior?, brain sligthly bigger than chimp? (some of the traits with question marks may belong to ‘praeanthropus’ and its sistergroup); a: flat middle face, rounded tooth rows with smaller front and anterior cheek teeth (Leakey *et alii*, 2001).
8. ‘praeanthropus’ (*”A. afarensis” ?*); s: large modern ear opening (Leakey *et alii*, 2001). This taxon possibly includes two or even three groups (LITU’s), of which the older from Laetoli with the type specimen was dubbed *Praeanthropus africanus* (Weinert/Senürek –see Strait *et alii*, 1997). The much younger forms (perhaps two, mostly accepted as sexual dimorphism) from Afar region has ‘Lucy’ as type of (n. gen.) *antiquus* Ferguson (1984), which in several details (canines, diastemata, elbow, knee and ankle joints) appears more primitive than the Afar 333 sample. Groves (1989) surprisingly showed that the Afar 333 group was most likely an early *Homo* relative (n. sp.), more advanced than *H. (Australopithecus) africanus.* (Discussion below).
9. ‘bahrelghazali’ (*”A.” bahrelghazali*); a: more vertical mandibular symphysis, three-rooted lower P3 and P4 (Brunet *et alii*, 1996). L.H.-24 from “*afarensis*” has three-rooted lower P3 (White *et alii*, 2000).

   Clade ‘Parhomo’ (new name); s: no ridge on distal radial joint surface (Richmond & Strait, 2000), indicating no knuckle walking; includes clades ‘Paranthropus’ (a: very large masticatory complex with e.g. combined occipito-temporal crests and concave face; Grine, 1988) and ‘Homo’ (a: more modern brain, less postorbital constriction).
10. ‘aethiopicus’ (*Paranthropus aethiopicus*) – socalled ‘Black Skull’, WT 17000, and more fragmentary fossils; s: robust skull and cheek teeth, male with long prominent sagittal crest, small front teeth (but still prognath), hyperthick enamel. The name ‘aethiopicus’ may not be appropriate, as the type specimen of *Paraustralopithecus aethiopicus* appears to have too small teeth (Groves [1989] considered it an early ‘Homo’). The relation to another even more primitive and prognath, robust “*Australopithecus*” skull from Sterkfontein bed 4 (Clarke 1985a), about the same age, but with larger canines and incisors, have not been discussed (not incl. here as LITU). The ‘Little Foot’ skeleton, c. 3.3 m.y., from Sterkfontein (Clarke, 2002) may be the oldest ‘robust’ form (see below, 14).
11. ‘robustus’ (*P. robustus*); s: flat less prognath face, anterior pillars (Rak, 1983).
12. ‘crassidens’ (*P. crassidens / robustus*); s: molarised milk premolars (Grine, 1985; 1988), more vertical face; a: squared face with very strong pillars (Rak, 1983).
13. ‘boisei’ (*P. boisei*); a: hyperrobust skull, large, rather vertical face, very large molars, reduced anterior pillars (Rak, 1983; Lieberman, 1999). The smaller socalled ‘females’ may belong to another taxon (see Groves, 1989).

    Clade ‘Homo’ is characterised by many features (see ‘australopithecus’, and Groves 1989), and here has a minimum age of 3.2 m.y. as *A. africanus* is included (c. the same if Afar 333 is incl. as *H*. n.sp. [ibid.]). An odd fact, that R. Leakey does not accept this, although very old ‘Homo’ would seem to ‘be water on the family mill’ (1994, Fig. 2.4).
14. ‘australopithecus’ (*A. africanus*); s: less postorbital constriction, more modern braincase and brain (Lockwood & Tobias, 1999; Richmond, 2000), more angled ‘step’ into the nasal opening; a: anterior pillars (Rak, 1983). A very problematic taxon, almost morphotypic, but already by Robinson (1956, 1972) considered an early ‘Homo’, also due to his interpretation of the Sts 14 pelvis (now supposed to be the same individual as the skull Sts 5, Thackeray *et alii*, 2002) and Groves’ (1989) analysis confirmed this relationship (favoured also by Bonde, 1976). Here provisionally accepted as one taxon with a very long lifespan, 1.2 m.y.; suspicious because the earliest from Makapan (originally *A. prometheus*) with plesiomorphic flat palate (Tobias 1989) are slightly more robust than the younger from Sterkfontein (original name *Plesianthropus transvaalensis*); and the very late age of Stw 53 (recently removed from ‘habilis’ because of anterior pillars and similarity to Stw 5, as female and male, Thackeray *et alii*, 2000), 2 m.y. is quite problematic. The older part could be ancestral to more advanced ‘Homo’, but is also complicated by the find in Sterkfontein of the ‘Little foot’ skeleton (c. 3.3 m.y., Clarke, 2002), which though still ‘on the rocks’ is said to be more robust, ‘Paranthropus’-like (Clarke in TV spot, 2001; in that case the ‘Paranthropus’ ‘ghost lineage’ would disappear –but see further discussion below).
15. ‘garhi’ (“*A.” garhi*); s: longer femur?; a: very large teeth (White *et alii*, 1999). Also a problematic taxon; type skull may be more plesiomorphic than *A. africanus*, while the

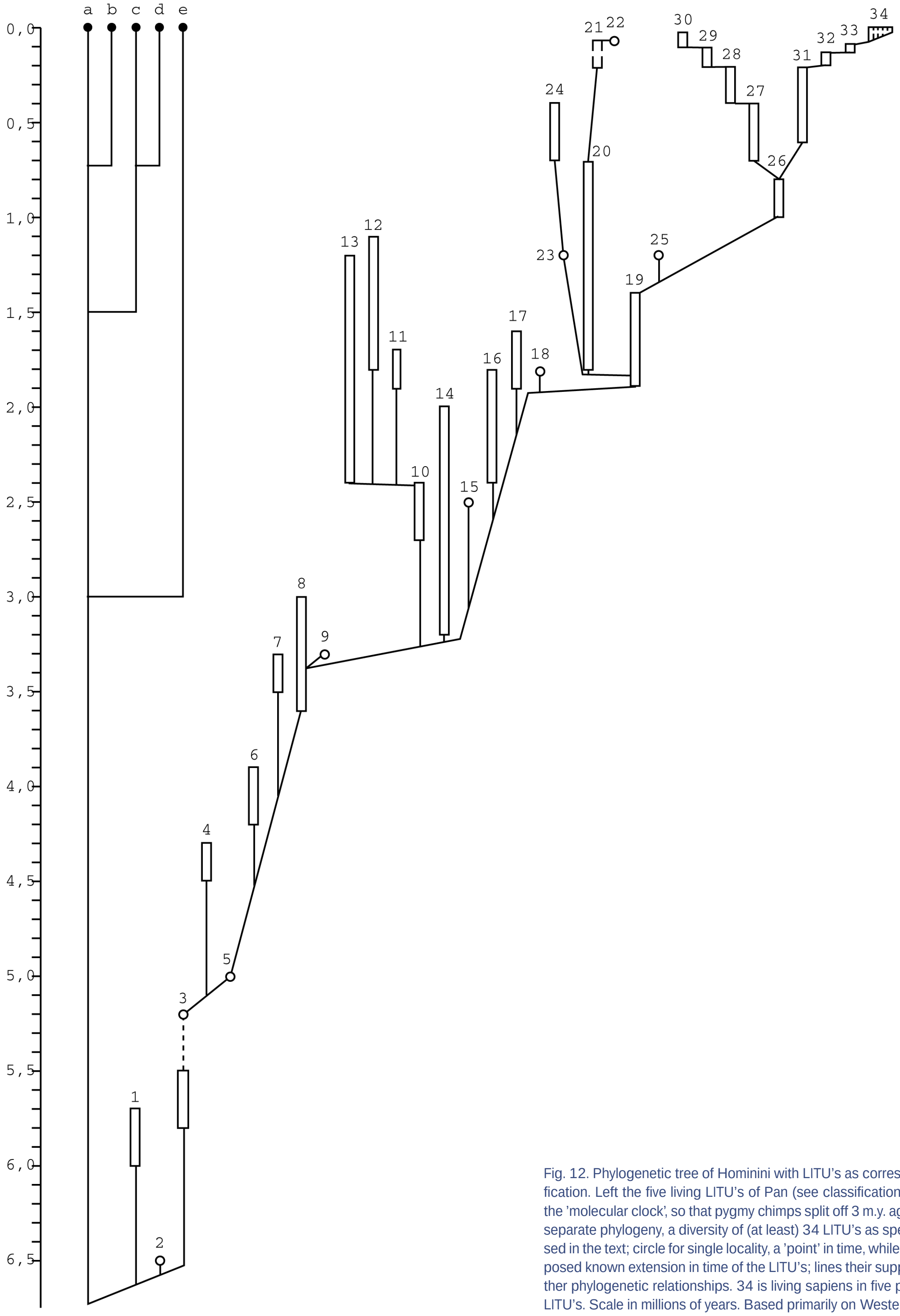


Fig. 12. Phylogenetic tree of Hominini with LITU's as corresponding to our classification. Left the five living LITU's of Pan (see classification above), split ages by the 'molecular clock', so that pygmy chimps split off 3 m.y. ago. Right branch is our separate phylogeny, a diversity of (at least) 34 LITU's as specified and characterised in the text; circle for single locality, a 'point' in time, while bars indicate the supposed known extension in time of the LITU's; lines their supposed 'ancestry' or rather phylogenetic relationships. 34 is living sapiens in five possible subgroups or LITU's. Scale in millions of years. Based primarily on Westergaard (2002).

postcranial skeletons with longer femurs come from a nearby locality and could belong to another LITU.

16. ‘rudolfensis’ (*Homo rudolfensis / habilis*; Alexeev 1986, Wood 1991); s: bigger brain; a: flat face with smaller front teeth. Incl. Hadar maxilla (c. 2.3 m.y.) because it has broader premolars than ‘habilis’ (but see Kimbel *et alii*, 1996).
17. ‘habilis’ (*H. habilis*, see Tobias, 1991); s: smaller more modern cheeck teeth; a: very narrow premolars; reduced body size with shorter legs? (Richmond *et alii*, 2002; but impossible to measure femur length, see White *et alii*, 1999). Incl. OH 65 because it has smaller cheek teeth than ‘rudolfensis’ (but see Blumenschine *et alii*, 2003). Problematic relations between the type material and other, younger skulls in Olduvai, and presumed ‘habilis’ at Koobi Fora (Stringer, 1986; Wood, 1992; Rightmire, 1993) and skull Stw 53 from Sterkfontein bed 5 (see above, 14).
18. ‘georgicus’ (*H. georgicus / ergaster*); s: transitory morphology between ‘rudolfensis’/’habilis’ and ‘ergaster’; a: robust male lower jaw ? (Gabounia *et alii*, 2002). Problematic variation; may be first LITU to leave Africa (there are, however, possibly primitive stone tools at 2.2 m.y. in Central Massif, Fr.), and perhaps a synonym of *H. erectus wushanensis* (Wanpo *et alii*, 1995).
19. ‘ergaster’ (*H. ergaster / erectus*); s: more modern postcranial skeleton, bigger size. Incl. the famous ‘Turkana Boy’ (refered to *‘ergaster’* by Westergaard & Bonde, 1987), continously misnamed *‘erectus’* by many (Walker & Leakey, 1993 –referred to 3 taxa by Zeitoun, 2000). Perhaps incl. *Telanthropus*. A very morphotypic probable ‘ancestor’. But the late part of ‘ergaster’ really belongs to a younger clade, ‘Euhomo’, below, and also includes the type jaw of *H. ergaster* (Groves & Mazák, 1975), and may be a ‘surviving ancestor’ of all more advanced *Homo*. The entire ergaster lineage (19) could (Bonde, 1981; 1989; 2001) be the beginning of one ‘time-bio-species’, *H. sapiens* (with e.g. the *erectus* group –here ‘Pithecanthropus’– and neanderthals as strings of geographic subspecies at different time sections). African and Asian skulls, see Schwartz & Tattersall (2003).

Clade ‘Pithecanthropus’ (*H. erectus*); s: prominent continuous ‘straight’ supraorbital torus, marked angular and occipital tori, thick tympanic plate, very thick skull and limbbones etc. (see Andrews, 1984).

Clade ‘Javanthropus’: Accretion Model with three soloensis stages, see descriptions in Anton *et alii* (2002), Baba *et alii* (2003); contra Zeitoun (2000).

20. ‘erectus’: Djetis and Trinil fossils, ‘Java Man’. Note that the earlier forms have been named as separate taxa: *erectus, modjokertensis, dubius*, *robustus*, and the gorilla-sized *Meganthropus* jaws (Weidenreich, 1946; Koenigswald, 1960), mostly seen as sexual dimorphism; cf. variation in 18) ‘georgicus’. (Very few possible stone tools known).
21. ‘erectus’-‘soloensis’: Sambungmacan 1-4, sharing characters with both ‘erectus’ and ‘soloensis’.
22. ‘soloensis’: Ngandong fossils, ‘Solo Man’; a: increased brain size, thicker bones (Santa Luca, 1980).

Clade ‘Sinanthropus’: two stages/LITU’s; a: flat orbital roof; see descriptions in Wu & Poirier (1995).

23. ‘lantianensis’: Lantian skullcap; ‘Lantian Man’.
24. ‘pekinensis’: Chenjiawo mandible (?), Zhoukoudian fossils, Hexian skull (?); ‘Peking Man’; a: bigger brain, incipient forehead, supraorbital sulcus.

Clade ‘Euhomo’ (new name): late ‘ergaster’ and its sistergroup; s: slightly smaller cheek teeth? Incl. WT 15000, the ‘Turkana Boy’, and type jaw ER 992 (see Groves & Mazák, 1975); morphotypic. Groves (1989) also included ER 1813 (1.9 m.y.), but this is more likely a ‘habilis’.

25. ‘louisleakeyi’ (*H. erectus / ergaster*), OH9; s: brain a little enlarged, thick continuous, not ‘straight’, supraorbital torus, wide occipital torus; a: prominent supraorbital and occipital tori (Rightmire, 1990; Klein, 1999).
26. ‘antecessor’ (*H. antecessor / erectus*); s: slightly bigger brain, vertical sides of skull, thick double-arched browridges. Incl. Atapuerca GD (Arsuaga *et alii*, 1999), Daka (Asfaw *et alii,* 2002, Manzi *et alii,* 2003), Bouia (Abbate *et alii,* 1998), Ceprano (Manzi *et alii,* 2001; named *H. cepranensis*, Mallegni *et alii,* 2003), ?Salé, ?Ternifine. Perhaps a synonym of *H. mauritanicus* (see Arambourg, 1954).

Clade ‘Neandertalia’: Accretion Model with four neandertal stages, see description in Dean *et alii* (1998). European fossils are described in Schwartz & Tattersall (2002).

27. ‘heidelbergensis’ (*H. heidelbergensis*), ‘early pre-neandertals’; s: slight taurodonty?, no fossa canina and receding cheek bones; incl. Mauer, Arago, Petralona. For ages see Czarnetzki *et alii* (2003).
28. ‘steinheimensis’ (*H. heidelbergensis*), ‘pre-neandertals’; s: incipient globular skull, suprainiac fossa, protruding midface, retromolar space; incl. Steinheim, Swanscombe, Bilzingsleben, Vértesszöllös, Reilingen, Atapuerca SH (Arsuaga *et alii,* 1997; Aguirre, 1998).
29. ‘aniensis’ (*H. neanderthalensis*), ‘early neandertals‘; s: increased brainsize, bunning, globular skull, reduced mastoid process, taurodonty; incl. Saccopastore, Ehringsdorf, Biache 1, La Chaise Suard, most of Krapina, ?Tabun, ?Gibraltar.
30. ‘neanderthalensis’ (*H. neanderthalensis*), ‘classic neandertals’, see Trinkaus (1983), historical Trinkaus & Shipman (1993); a: quite characteristic with very large and long globular skull with large sinuses, large rounded piriform aperture in strongly protruded midface with slightly enlarged incisors, characteristic scapula, pubes and short distal limb segments; most extreme in western Europe, cline towards east (Vandermeersch 1989); burials and Mousterien tools; perhaps ‘jewellery’ (Arsuaga, 1999). Very likely a different biospecies (and gamospecies?) from ‘sapiens’ (Caramelli *et alii,* 2003; Harvati, 2003).

Clade ‘Sapientia’: Accretion Model with four sapiens stages (Bräuer, 1989). a: with brain enlargement, more vertical sidewall tending towards widest high in temporal region. For estimates of ages see McBrearty & Brooks (2000).

31. 'rhodesiensis' (*H. heidelbergensis / rhodesiensis*), 'early archaic sapiens'; incl. Kabwe, Saldanha, Bodo, Ndutu, ?Salé, ?Narmada, ?Dali, ?Jinniushan (Stringer, 2002; 2003); s: bigger brain, more modern, rather vertical face, robust but modern postcranial skeleton (Rightmire, 1996).
32. 'helmei' (*H. heidelbergensis / rhodesiensis*), 'late archaic sapiens'; incl. Florisbad, Singa, Djebel Irhoud, Ngaloba, Eliye Springs, Omo 2, Herto (White *et alii,* 2003; Stringer, 2002, 2003); s: bigger brain (but still long skull and markedly flexed occipital), sloping forehead, reduced browridges, smaller face. Synonym of *H. s. idaltu* White *et alii* (2003). Herto skull BOU-VP-16/1 is e.g. similar to Djebel Irhoud 1 and Singa; though like Singa slightly advanced towards 'palestinus' in skull hight and brain size, it is not considered sufficiently different for a separate LITU.
33. 'palestinus' (*H. sapiens*), 'early modern sapiens'; incl. Skull, Quafzeh, Omo 1, Mumba, Klasies; s: slightly bigger, but shorter brain, more vertical forehead, slighly more reduced browridges, more or less well-developed chin.
34. 'sapiens' (recent *H. sapiens*),'late modern sapiens'; a: more gracile body, near vertical face and forehead, diminutive browridges, typical chin. Border Cave skull (c. 70 kyr ?) is suggested to belong to African branch; Australian Mungo 3 is redated to c. 40 kyr (Bowler *et alii,* 2003); Swabian Jura Aurignacien c. 40 kyr (Conard & Bolus, 2003); Zhoukoudien Upper Cave c. 30 kyr with perhaps a few mongoloid features (Wu & Poirier, 1995). New World humans not known to be older than c. 12 kyr, whether the oldest were mongoloid or not is a moot question -cf. e.g. the 'Kennewick Man' – see Gonzales *et alii* (2003).

As shown at the end, **sapiens** may perhaps alternatively be divided into several recent LITU's, establishing its own recent crowngroup, **Sapiens**, wherein LITU's here are sequenced following DNA relationships (Cavalli-Sforza, 1989; Stringer, 2002; Cann & Wilson, 2003); see also the discussion on sapiens subgroups or geographic 'races' by Bonde (2001) and Bennike & Bonde (1992). Then the total clade changes name from Homininaa to Sapiensa. Most fossils are sequenced, and their successive monophyletic groups are not named. Instead they can be referred to as 'name et a' : Clade of LITU and its sistergroup. Ex.: (+) lothagamensis* et a: clade of hominids with thicker enamel, adapted for savannah hard food processing; **australis** et a: clade of modern man emigrated from Africa.

Not strictly testable (morphotypic) ancestors: (+) praeanthropus* (perhaps polyphyletic), (+) ergaster* (1.9-1.8), (+) ergaster* (1.8-1.4)(?), (+) antecessor*, while other 'ancestors' are more testable according to discussion above by being 'intermediate'. In cladogram terms the non-testable 'ancestors' constitute tricho- or polytomies.

	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. antiquus) 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)
21	+) erectus-soloensis* (?0.2-?0.08)
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)]

On some recent 'namedropping'

We observe that in recent times a number of people have been particularly unfortunate naming new fossil hominin taxa – often of great fame – which are very likely to be synonyms of older taxa names. White has been involved with many of these cases, lately naming the 'new' palaeosubspecies, *Homo sapiens idaltu* (White *et alii,* 2003) from Ethiopia, which appears not to be clearly differentiated from forms just slightly more primitive than 'anatomical modern sapiens' (AMS), such as African skulls from Jebel Irhoud, Singa, Omo 2, Ngaloba and Florisbad (Clarke 1985b), which have been named by the epithet *helmei* (*Homo helmei*, Dreyer, 1935 for the Florisbad skull). These are more advanced than Bodo, Saldanha and Kabwe (*H. s. rhodesiensis*), but more primitive than AMS, Omo I, Quafzeh and Skhul (*H. s. palestinus*), and the age of the Herto fossils also correspond to the *'helmei* group', c. 0.2 – 0.13 m.y. Therefore we synonymise *idaltu* under (+) helmei* (ancestral metataxon).

Johanson, White *et alii* (1978) formally named the widespread fossils (both in time and geography) from Laetoli, Tanzania and Hadar in the Afar region as *Australopithecus afarensis*, unfortunately picking a fossil from Laetoli as the type specimen. As mentioned above it appears to be a heterogenous sample, perhaps covering three taxa, and the first Laetoli (Garusi) hominid fragment found by Kohl-Larsen in the 1930's had already been named *Praeanthropus africanus*. Only by classifying the samples under the paraphyletic group *"Australopithecus"* was it possible to disqualify this name, because the type species of *Australopithecus* was also named *africanus* by Dart in 1925. The Garusi maxillary fragment has always been considered the same taxon as *afarensis*. If the samples from the Afar region are distinguishable from the Laetoli fossils, the former require different name(s), and the one available is *antiquus* by Ferguson (1984), appropriately with 'Lucy', the most primitive form (Coppens' [1994] "Pre-Australopithecus"), as type specimen.

Groves (1989) argued that the largest Afar sample, AL 333 (and others) represents a primitive *Homo*, more advanced than *H. (A.) africanus,* and therefore it needs a new ('specific') name. We here propose *Homo hadar* n. sp. (in our modern cladistic terminology the LITU should rather be 'homo-hadar') with the adult, incomplete skull AL 333-45 as type specimen (by Kimbel *et alii*, 1984 combined with material likely to be from another taxon into the very popular 'skull of Lucy'), and all AL 333 and 333-w specimens (list in Johanson *et alii*, 1978) and AL 400-1a as hypodigm. The diagnosis in traditional sense consists of the character combination in Groves' Table 7.2 (1989), especially those apomorphic features (marked B1) which indicate its position as a *Homo* more advanced than *A. africanus*. To distinguish it from more advanced *Homo*, one only needs consider many of those 'primitive' characters –as far as they count for the 333 samples– claimed by Johanson *et alii* (1978), Johanson & White (1979), Kimbel *et alii* (1985 –especially concerning the type specimen), and White (1985–teeth), and which constitute the evidence for their eternal statements that *"afarensis"* (our + praeanthropus*) is the 'ancestor' of all later hominids. But recall that Groves' analyses (1989: 223) showed no characters of 'homo-hadar' to be more primitive than *Paranthropus* or *Homo*. From a cladistic viewpoint, however, it is more difficult to establish whether 'homo-hadar' is a proper clade or perhaps just a metataxon/ -'species', without autapomorphies to characterise it. We here tentatively suggest that the rather strong occipital crest and the combined lateral occipito-temporal crests are such autapomorphies (developed convergently with 'Paranthropus'), and the first two features in Groves' Table 7.2 (1989) show the same pattern. Perhaps some features of the nasals of the juvenile skull 333-105 have a similar status (shown by Olson, 1985). This may indicate that 'homo-hadar' is an extinct proper clade (named + homo-hadar) with a (cladistic) diagnosis including at least those four traits first mentioned. We note that this may have consequences for the evaluation of the 'Little Foot' skeleton from Sterkfontein, which has about the same age and is said to show *Paranthropus*-like features (see above) –could it be + homo-hadar?

We hope that this will force our colleagues to discuss more seriously the heterogeneity of the *"afarensis"* samples and the analyses and suggestions by Groves (1989) and many others critical of this immensely popular taxon. That *"afarensis"* should be just one taxon, as usually accepted, would seem unlikely both on morphological, geographical and stratigraphic considerations. We find it significant that the later find of the best preserved skull of *"afarensis"*, AL 444-2 (the socalled 'Boy of Lucy'), the youngest specimen of these samples, in several measurements is the largest "australopithecine" skull known (Kimbel *et alii,* 1994) – to us, that might well 'smell' of early *Homo* – and Ferguson (2001) refers it to *A. africanus* (- but A.L. 333-45 to a pongid!).

White *et alii* (1994) named our 'oldest ancestor' *Australopithecus ramidus* from Middle Awash along the same river, but in age nearly 4.5 m.y. Well, it was quickly realised, that it was not really our direct and successful ancestor (despite Nature's front page), even in the commentary by Wood (1994), but rather the first known hominid failure and extinction, and it (appropriately!) received a new generic name as a specialised 'dead end', *Ardipithecus*, published very unusually as a "correction" in Nature. But worse, it has not been shown convincingly to be different from the Tabarin lower jaw fragment of about the same age from northern Kenya. And this fossil already had received a name *praegens* (as *H. antiquus praegens* by Ferguson, 1989), supposed to be the same 'species' as Lucy but distinct subspecifically. So the proper name for the Aramis sample is possibly *praegens* (also in Tattersal, 1995). But White *et alii* (1994) attempted to disqualify the Tabarin jaw as a 'name bearer', type specimen, by suggesting it as a *nomen dubium* because of the fragmentary state, and even to disqualify it also in the future, should more Tabarin fossils be found to show near identity with the Aramis sample! (Did referees really accept that?). As seen above, we also 'like' 'ardipithecus' best, but is that sufficient reason?

And further, by 2001 *"Ardipithecus"* was made paraphyletic by the inclusion of a new and much older socalled subspecies *kadabba* of *A. ramidus* (Haile-Selassie, 2001), because the original *ramidus* is more advanced than its 'new subspecies' (see above). And the indicated 'bipedalism' of *kadabba* was based on an isolated toe bone much younger than the type material.

So we perceive the outline of a strategy, which generates nice front pages of Nature and Science, naming 'new ancestral' taxa, while if they cannot really be told apart from some earlier named samples, it is attempted to disqualify these earlier findings. Also the *H. helmei* fossils were disqualified on two lines as "inadequate" and "too fragmentary" because of state of preservation, in stead of doing the proper comparisons. But in this case these fossils are really substantial parts of skulls, not just jaw fragments, so what is next to be disqualified for a headline? From the viewpoint of nomenclature, a new taxon can only be established, if the items –here fragmentary fossils– are demonstrated to be different from other named samples –this was not properly done.

Another unfortunate 'misuse' of a name is Wood & Collard's (1999a, 1999b) return to Simpsonian adaptationism by stating that + rudolfensis and + habilis are too 'australopithecine'-like in adaptive strategies to be included in genus *Homo*. We see no reason for making the genus *Australopithecus* even 'more paraphyletic', when the delimitation of genus *Homo* from a cladistic viewpoint is in fact arbitrary –any branching point would do. We prefer to include LITU's 'down to' the next well diversified, undoubted clade (+ Paranthropus), so adding +garhi and +australopithecus (and perhaps + homo-hadar) to the clade Homo, while 'australopithecus' can never be monophyletic with 'habilis' and 'rudolfensis' included. Neither is *"Australopithecus"* monophyletic in the 'new taxonomic proposal' by Cela-Conde & Altaba (2002), who back up behind Wood and refer "*A.*" to a likewise paraphyletic subfamily (the classic "Australopithecinae" –not a 'redefinition' as claimed). They further create a paraphyletic mess of *"Praeanthropus"* in its own subfamily to cover all more primitive 'hominids', but an *inc. sed. Ardipithecus* –all based upon an entirely essentialistic and adaptationistic 'genus concept'.

It appears obvious that within the traditional, Linnaean systematics with formal ranks it is from the molecular biologists like Goodman *et alii* (1998, 1999), Wildman *et alii* (2003) and Shoshani *et alii* (1996) that any renewal of the taxonomy will come, not from the (palaeo-)anthropologists, a field that still suffers under an old Simpsonian burden of muddy adaptationism.

Conclusions

From our cladistic viewpoint all problems of the (palaeo-) biological classifications revolve around exploring phylogenetic relationships (see our first quotation above), which should as precisely as possible be reflected in the classifications. Not only should they reflect what we think we know, but preferably they should also reflect our ignorance or doubts. This can be achieved if the appropriate units are discovered and selected, and if their relationships are analysed and synthesised in the relevant, precise and consistent way by a cladistic parsimony method. When realising that there are many ways of expressing the phylogenetic relationships in a classification, it clearly becomes important to establish some conventions by which such relationships and the resulting classifications can be communicated as simple as possible to other people. One goal therefore is not having a proliferation of names and (misleading) categories (Ereshefsky, 2001), but at the same time retain means by which all the taxa can be unequivocally compared.

It is obvious that systematisation of the total diversity of life will require a huge amount of names if all the relevant groups shall be characterised. This is here limited by sequencing most fossil groups (as 'plesions') with no formal rank, while still making it possible to compare and communicate about all the monophyletic taxa (at least easily in writing) by attaching simple symbols and ages, here used as informal ranks. LITU's are completely free of ranks, which means that one can discuss interesting questions about different sorts of 'species' in relation to these LITU's. And should somebody like to further subdivide or combine our 'terminal taxa' they are free to argue for that –there are no sacrosant levels (like the traditional species and genus categories) in our hierarchy, we have just chosen a level at which we feel sure there is an interesting history to pursue. We have exposed our reasons for accepting these monophyletic taxa, as well as some necessary metaphyletic ones (some of which may in fact be 'real ancestors') –and a few paraphyletic ones to be rectified by others.

To achieve as detailed classifications as possible, with maximum information content, we need bold hypotheses of phylogenetic relationships based on available evidence, later to be tested, refined and/or changed with new fossil information. And we therefore deplore the new trend that some scientists do not dare commit themselves to state precise and testable models of relationships in terms of trees or cladograms, like e.g. Wood (2002) and Tattersall (2003).

Frankly, we believe an approach as presented here is the proper way of looking at a modern, non-authoritarian systematic science, which should be open for discussions and problem solving, in line with suggestions by Haerlin (2001, 2003), not for decisive or empty statements. This should open for an era in biological systematics in which 'stability' is not necessarily the highest goal, but rather the intelligent dialogue exposing the 'state of the art' of our knowledge –and lack of the same.

Acknowledgments

We thank colleagues Drs. P.K.A. Jensen, E. Thomsen, both Aarhus University, Per Christiansen, Zoological Museum, J. Høeg and the late K.G. Wingstrand, Zoological Institute, and P. Makovicky, now Chicago, for numerous discussions about cladistics, classifications and hominids; NB thanks P. Forey and the late C. Patterson, London, P. Tassy and P. Janvier, Paris, G. Nelson (now Melbourne) and his New York colleagues for similar discussions – not that any of them necessarily endorse all our viewpoints. We are thankful to Drs M. Laurin & V. Zeitoun, Paris, P. Andrews, London, J. Tattersall, New York and J. Richter, Copenhagen, for critical comments on our MS; we also thank C. Hagen for the new drawings, and O.B. Bertelsen (both Geological Institute) for a poster on this topic presented September 2003 at Symp. Vert. Pal. Comp. Anat. in Oxford by NB. BW thanks I. & C. Westergaard for help and support. NB thanks for the invitation to participate in this large project in honour of Dr. E. Aguirre, we have both been fortunate to meet him decades ago, and one of us has visited Atapuerca guided by Dr. J.L. Arsuaga. Financial support to NB to join several meetings on hominid evolution, and in 2002 a visit to Zhoukoudian guided by colleagues from Beijing, has come mainly from his institute.

Bibliography

Abbate, E.; Albianelli, A. *et alii* (1998): ”A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea”. *Nature*, 393: 458-460.

Aguirre, E. (1998) (Ed.): *Atapuerca y la evolución humana*. Fundación Ramón Areces. Madrid.

Alexeev, V.P. (1986): *The origin of the human race*. Progress Publishers. Moscow.

Andrews, D. (1984): ”An alternativ interpretation of the characters used to define *Homo erectus*”. *Courier Forschungsinstitut Senkenberg*, 69: 167-175.

Antón, S.C.; Márquez, S. & Mowbray, K. (2002): ”Sambungmacan 3 and cranial variation in Asian *Homo erectus*”. *Journal of Human Evolution*, 43: 555-562.

Arambourg, G. (1955): “A recent discovery in human palaeontology: *Atlanthropus* of Ternifine (Algeria)”. *American journal of Physical Anthropology*, 13: 191-202.

Archibald, J.D. (1984): “Metataxon concepts and assessing possible ancestry using phylogenetic systematics”. *Systematic Biology*, 43: 27-40.

Arsuaga, J.L. (1999): *El collar del neandertal. En busca de los primeros pensadores*. Ediciones Temas de Hoy. Madrid.

–; Martínez, I. *et alii* (1997): ”The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study”. *Journal of Human Evolution*, 33: 219-281.

Asfaw, B.; White, T. *et alii* (1999): ”*Australopithecus garhi*: a new species of early hominid form Ethiopia”. *Science*, 284: 629-635.

–; Gilbert, W.H. *et alii* (2002): ”Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia”. *Nature*, 416: 317-319.

Avise, J.C. (1999): *Phylogeography. The history and formation of species*. Harvard University Press. Cambridge.

Ax, P. (1987): *The phylogenetic system. The systematization of organism on the basis of their phylogenies*. Wiley-Interscience. New Nork.

Baba, H.; Aziz, F. *et alii* (2003): ”*Homo erectus* calvarium from the Pleistocene of Java”. *Science*, 299: 1384-1388.

Bennike, P. & Bonde, N. (1992): ”Physical anthropology and human evolution in Denmark and other Scandinavian countries”. *Human Evolution*, 7, 2: 69-84.

Bishop, W.W. (1978) (Ed.): *Geological background to fossil man*. Scottish Academic Press. Edinburgh.

Blumenschine, R.J.; Peters, C.R. *et alii* (2003): ”Late Pliocene *Homo* and hominid land use from Western Olduvai Gorge, Tanzania”. *Science*, 299: 1217-1221.

Bonde, N. (1974): “Review: Interrelations of fishes”. In P.H. Greenwood, R.S. Miles & C. Patterson (Eds.) 1973: *Systematic Zoology*, 23: 562-569.

– (1975): “Origin of “higher groups”: Viewpoints of phylogenetic systematics”. *Colloque international CNRS*, 218: 293-324.

– (1976): “Nyt om menneskets udviklingshistorie (News of Man’s evolutionary history)”. *Geol. Soc., Denmark, Årsskrift for 1975*: 19-34.

– (1977): “Cladistic classification as applies to vertebrates“. In M.K. Hecht, P.C. Goody & B.M. Hecht (Eds.): *Major patterns in vertebrate evolution*: 741-804. Plenum Press. New York.

– (1981): “Problems of species concepts in palaeontology“. *Inter. Sympos. Concpt. Meth. Paleo.*, Barcelona: 19-34.

– (1983): “Human palæontology: de seneste frem- og tilbageskridt”. *Dansk geol. Foren., Årsskrift for 1982*: 67-79.

– (1984): “Functional anatomy and reconstruction of phylogeny”. In E. Bufftaut, J.M. Mazin & E. Salmon (Eds.): *actes du symposium paléontologique G. CUVIER, MONTBELIARD*: 11-26.

– (1989): “*Erectus* and *neanderthalensis* as species and subspecies of *Homo* with a model of speciation in Hominids”. In G. Giacobini (Ed.): *Hominidae: Proceedings of the 2^{nd} International Congress of Human Paleontology*: 205-208. Editoriale Jaca Book. Milan.

– (1996): “The systematics and classificatory status of Archaeopteryx”. *Mus. North. Arizona Bull.*, 60: 193-199.

– (2001): “L’espece et la dimension du temps”. *Biosystema 19 (Systematique et Paleontologie)*: 29-62. (Eng. transl. available from NB).

Bowler, J.M.; Johnston, H. *et alii* (2003): “New ages for human occupation and climatic change at Lake Mungo, Australia”. *Nature*, 421: 837-840.

Brunet, M.; Beauvilain, A. *et alii*: “*Australopithecus bahrelghazali*, une nouvelle espèce d’Hominidé ancien de la région de Koro Toro (Tchad)”. *C.R. Acad. Sci. Paris*, 322, série II a: 907-913.

–; Guy, F. *et alii* (2002): “A new hominid from the Upper Miocene of Chad, Central Africa”. *Nature*, 418: 145-151.

Bräuer, G. (1989): “The ES-11693 hominid from West Turkana and *Homo sapiens* evolution in East Africa. In G. Giacobini (Ed.): *Hominidae: Proceedings of the 2^{nd} International Congress of Human Paleontology*: 241-245. Editoriale Jaca Book. Milan.

Campbell, B. (1963): “Quantitative taxonomy and human evolution”. In S.L. Washburn (Ed.): *Classification and Human Evolution*: 50-74. Methuen & Co. Ltd. London.

Cann, R.L. & Wilson, A.C. (2003): “The recent African genesis fo humans”. *Scientific American*, 13, Special Edition: 54-61.

Caramelli, D.; Lalueza-Fox, C. *et alii* (2003): “Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans”. *PNAS*, 100: 6593-6597.

Cavalli-Sforza, L.L. (1989): “The last 100,000 years of human evolution: the vantage points of genetics and archaeology”. In G. Giacobini (Ed.): *Hominidae. Proceedings of the 2^{nd} International Congress of Human Paleontology*: 401-413.

Cela-Conde, C.J. & Altaba, C.R. (2002): “Multiplying genera versus moving species: a new taxonomic proposal for the family Hominidae”. *South African Journal of Science*, 98: 229-232.

Christoffersen, M.L. (1995): “Cladistic taxonomy, phylogenetic systematics, and evolutionary ranking”. *Systematic Biology*, 44: 440-454.

Clarke, R.J. (1985a): “*Australopithecus* and early *Homo* in southern Africa”. In E. Delson (Ed.): *Ancestors: The hard evidence*: 171-177. Alan R. Liss, Inc.. New york.

– (1985b): “A new reconstruction of the Forisbad cranium, with notes on the site”. In E. Delson (Ed.): *Ancestors: The hard evidence*: 301-305. Alan R. Liss, Inc. New York.

– (2002): “Newly revealed information on the Sterkfontein Member 2 *Australopithecus* skeleton”. *South African Journal of Science*, 98: 523-526.

Conard, N.J. & Bolus, M. (2003): “Radiocarbon dating the appearance of modern humans and timing of cultural innovations in Europe: new results and new challenges”. *Journal of Human Evolution*, 44: 331-371.

Coppens, Y. (1994): “East side story: the origin of humankind”. *Scientific American*, May: 62-67.

Cracraft, J. (1983): “Species concepts and speciation analysis”. *Current Ornithology*, 1: 159-187.

– (1997): “Species concepts in systematics and conservation biology – an ornithological viewpoint”. In M.F. Claridge, H.A. Dawah & M.R. Wilson (Eds.): *Species. The Units of Biodiversity*: 325-339. Chapman & Hall. London.

– & Eldredge, N. (1979): *Phylogenetic analysis and paleontology*. Columbia university Press. New York.

Crowson, R.A. (1970): *Classification and biology*. Heinemann Educational Books. London.

Curnoe, D. (2001): “Early *Homo* from southern Africa: a cladistic perspective”. *South African Journal of Science*, 97: 186-190.

Czarnetzki, A.; Jacob, T. & Pusch, C.M. (2003): “Palaeopathological and variant conditions of the *Homo heidelbergensis* type specimen (Mauer, Germany)”. *Journal of Human Evolution*, 44: 479-494.

Dean, D., Hublin, J.-J. *et alii* (1998): “On the phylogenetic position of the pre-Neandertal specimen from Reilingen”. *Journal of Human evolution*, 34: 485-508.

Delson, E. (1997): “One skull does not a species make”. *Nature*, 389: 446-447.

– (2000): ”Classification of Primates”. In E. Delson, I. Tattersall *et alii* (Eds.): *Encyclopedia of Human Evolution and Prehistory*. Garland. New York.

– & Andrews, P. (1975): ” Evolution and interrelationships of the catarrhine primates”. In P.W. Luckett & F.S. Szalay (Eds.): *Phylogeny of the primates. A multidisciplinary approach*: 405-446. Plenum Press. New York.

de Queiroz, K. (1998): “The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommandations”. In D.J. Howard & S.H. Berlocher (Eds.): *Endless forms: species and speciation*: 57-78. Oxford University Press. Oxford.

– (1999): “The general lineage concept of species and the defining properties of the species category”. In R.A. Wilson: *Species. New interdisciplinary essays*: 49-89. MIT Press. Massachusetts.

– & Gauthier, J. (1992): “Phylogenetic taxonomy”. *Annu. Rev. Ecol. Syst.*, 23: 449-480.

Donoghue, M.J. (1985): “A critique of the biological species concept and recommandations for a phylogenetic alternative”. *Bryologist*, 88: 172-181.

Dreyer, T.F. (1935): “A human skull from Florisbad, Orange free State, with a note on the endocranial cast, by C.U. Ariëns Kappers”. *Konink. Akad. van Wetensch. te Amsterdam, Proceedings*, 38: 3-12.

Eldredge, N. & Tattersall, I. (1975): “Evolutionary models, phylogenetic reconstruction, and another look at homind phylogeny”. In F.S. Szalay (Ed.): *Approaches to primate paleobiology. Contributions to primatology,* 5: 218-242. S. Karger. Basel.

Elzanowski, A. (2002): “Archaeopterygidae (Upper Jurassic of Germany)”. In L.M. Chiappe & L.M. Witmer (Eds.): *Mesozoic Birds*: 129-159. University California Press, Berkeley.

Ereshevsky (1992): *The units of evolution: Essays on the nature of species*. MIT Press. Cambridge.

– (2001): *The poverty of the Linnaean hierarchy. A philosophical study of biological taxonomy*. Cambridge University Press. Cambridge.

Farris, J.S. (1976): “ Phylogenetic classification of fossils with recent species”. *Systematic Zoology*, 25: 271-282.

– (1983): “The logical basis of phylogenetic analysis”. *Advances in Cladistics*, 2: 7-36.

–; Kluge, A.G. & Eckardt, M.J. (1970): “A numerical approach to phylogenetic systematics”. *Systematic Zoology*, 19: 172-189.

Ferguson, W.W. (1984): “Revision of fossil hominid jaws from the Plio/Pleistocene of Hadar, in Ethiopia including a new species of the genus *Homo* (Hominoidea: Homininae)”. *Primates*, 25: 519-529.

– (1989): “Taxonomic status of the hominid mandible KNM-ER TI 13150 from the Middle Pliocene of Tabarin, in Kenya”. *Primates*, 30: 383-387.

– (1999): “Taxonomic status of the skull A.L.444-2 from the Pliocene of Hadar, Ethiopia”. *Palaeont. afr.*, 35: 119-129.

Forey, P.L. (1982): “Neontological analysis versus palaeontological stories”. In K.A. Joysey & A.E. Friday (Eds.): *Problems of phylogenetic reconstruction*: 119-157. Academic Press. London.

– (1992): “Fossils and cladistic analysis”. In P. Forey, C.J. Humphries *et alii*: *Cladistics. A practical course in systematics*: 124-136.

Gabounia, L., de Lumley, M.-A. *et alii* (2002): ”Découverte d’un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie)”. *C. R. Palevol.*,1: 243-253.

Ghiselin, M.T. (1997): *Metaphysics and the origin of species*. State University New York Press. Albany.

Gingerich, P.D. (1979): “The stratophenetic approach to phylogeny. Reconstruction in Vertebrate paleontology”. 41-77. In J. Cracraft & N. Eldredge (Eds.).

Gonzalez, S., Jiménez-López, J.C. *et alii* (2003): “Earliest humans in the Americas: new evidence from México”. *Journal of Human Evolution*, 44: 379-387.

Goodman, M. (1962): “Immunochemistry of the primates and primate evolution”. *Annuals of the New York Academy of science*, 102: 219-234.

– (1963a): “Man’s place in the phylogeny of the primates as reflected in serum proteins”. In S.L. Washburn (Ed.): *Classification and human evolution*: 204-234. Methuen & Co. Limited. London.

– (1963b): ”Serological analysis of the systematics of recent hominoids”. *Human Biology*, 35: 377-436.

– (1975): ”Protein sequence and immunological specificity: their role in phylogenetic studies of primates”. In P.W. Luckett & F.S. Szalay (Eds.): *Phylogeny of the primates. A multidisciplinary approach*: 219-248. Plenum Press. New York.

–; Porter, C.A. *et alii* (1998): “Toward a phylogenetic classification of Primates based on DNA evidence complemented by fossil evidence”. *Molecular Phylogenetics and Evolution*, 9: 585-598.

–; Page, S.L. *et alii* (1999): “Primate phylogeny and classification elucidated at the molecular level”. In S.P. Wasser (Ed.): *Evolutionary theory and processes: Modern perspectives, papers in Honour of Eviatar nevo*: 193-211. Kluwer Academic Publishers. The Netherlands.

Gould, S.J. (2002*): The Structure of Evolutionary Theory*. Belknap Press, Harvard. 1433 pp.

Greenwood, P.H.; Miles, R.S. & Patterson, C. (1973) (Eds.): *Interrelationships of fishes*. Academic Press. London.

Grine, F.E. (1985): “Australopithecine evolution: the deciduous dental evidence”. In E. Delson (Ed.): *Ancestors: the hard evidence*: 153-167. Alan R. Liss. New York.

– (1988) (Ed.): *Evolutionary history of the “robust” australopithecines*. A. de Gruyter. New York.

Groves, C.P. (1989): *A Theory of human and primate evolution*. Clarendon Press. Oxford.

– (2001): *Primate taxonomy*. Smithsonian Institution Press. Washington.

– & Mazák, V. (1975): “An approach to the taxonomy of the Hominidae: gracile Villafrancian hominids of Africa”. *Casopis pro Mineralogii Geologii*, 20: 225-247.

Haile-Selassie, Y. (2001): “Late Miocene hominids from the Middle Awash, Ethiopia”. *Nature*, 412: 178-181.

Haerlin, M. (1998): “Taxonomic names and phylogenetic trees”. *Zool.Scripta*, 27: 381-390.

– (2001): “Towards a new biological taxonomy – let us give up the Linnaean hierarchy!” *Zool. Scripta*, 30: 337-339.

– (2003): “Taxon names as paradigms: the structure of nomenclatural revolutions*”. Cladistics*, 19: 138-143.

Harvati, K. (2003): “The Neanderthal taxonomic position: models of intra- and inter-specific craniofacial variation”. *Journal of Human Evolution*, 44: 109-132.

Hennig, W. (1950): *Grundzüge einer Theorie non phylogenetischen Systematik*. Berlin.

– (1965): “Phylogenetic systematics”. *Ann. Rev. Entomol.*, 10: 97-116.

– (1966): *Phylogenetic systematics*. University of Ilinois Press. Urbana.

– (1969): *Die stammesgeschichte der Insekten*. Senkenberg Naturf. Ges. Frankfurt a.M. (1981: *Insect Phylogeny*. Wiley. New York).

– (1975): “Cladistic analysis ro cladistic classification?: A reply to Ernst Mayr”. *Systematic Zoology*, 24: 244-256.

Hertwig, W.C. (2002): *The primate fossil record*. Cambridge University Press. Cambridge.

Huxley, J.S. (1958): “Evolutionary processes and taxonomy, with special reference to grades”. *Uppsala Univ. Årsskr*., 1958, 6: 21-39.

– (1959): “Clades and grades”. *Syst. Assoc*, 3: 21-22.

Johanson, D.C.; White, T.D. & Coppens, Y. (1978): “A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa”. *Kirtlandia*, 28: 1-14.

–; Taib, M. *et alii* (1978): “Geological framewkork of the Pliocene Hadar Fromation (Afar, Ethiopia) with notes on palaeontology including hominids”. In W.W. Bishop (Ed.): *Geological background to fossil man*: 549-564. Scottish Academic Press. Edinburgh.

– & White, T.D. (1979): “A systematic assessment of early African hominids”. *Science*, 202: 321-330.

Kimbel, W.H.; White, T.D. & Johanson, D.C. (1984): “Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull”. *American Journal of Physical Anthropology*, 64: 337-388.

–; – & – (1985): “ Cranio-dental morphology of the hominids from Hadar and laetoli: evidence of “*Paranthropus*” and *Homo* in the mid-pliocene of eastern Africa ?”. In E. Delson (Ed.): *Ancestors: the hard evidence*: 120-137. Alan R. Liss. New York.

–; Johanson, D.C. & Rak, Y. (1994): “The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia”. *Nature*, 368: 449-451.

–; Walter, R.C. *et alii* (1996): “Late Pliocene *Homo* and oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia”. *Journal of Human Evolution*, 31: 549-561.

– & Martin, L.B. (1993): *Species, species concepts, and primate evolution*. Plenum Press. New York.

Kitching, I.J.; Forey, P.L. *et alii* (1998): *Cladistics.The theory and practice of parsimony analysis*. Oxford University Press. Oxford.

Klein, R.G. (1999): *The human career. Human biological and cultural origins*. The University of Chicago Press. Chicago.

Kohl-Larsen, L. & Reck, H.(1936): “Erster Ueberblick über die Jung-diluvialen Tier und Menschenfunde. Dr. Kohl-Larsen‘s im Nordöstlichen Teil des Njarasa-Grabens (Ostafrika)”. *Geologische Rundschau*, 27: 401-441.

Koenigswald, G.H.R. v. (1960): *Die Geschichte des Menschen*. Springer-Verlag. Berlin.

Leakey, L.B.S. (1963): “East African fossil Hominoidea and the classification within this super-family”. In S.L. Washburn (Ed.): *Classification and human evolution*: 32-49. Methuen & Co. Limited. London.

Leakey, R. (1994): *The origin of humankind*. Weidenfeld & Nicolson. London.

Leakey, M.G. & Walker, A.C. (2003): “The Lothagam hominids”. In M.G. Leakey & J.M. Harris: *Lothagam: The dawn of humanity in eastern Africa”*: 249-257. Columbia University Press. New York.

–; Spoor, F. *et alii* (2001): “New hominin genus from eastern Africa shows diverse middle Pliocene lineages”. *Nature*, 410: 433-440.

Lieberman, D.E. (1999): “Homology and hominid phylogeny: Problems and potential solutions”. *Evolutionary Anthropology*, 7: 142-151.

Lockwood, C.A. & Tobias, P.V. (1999) “A large male hominin cranium from Sterkfontein, South Africa, and the status of *Australopithecus africanus*”. *Journal of Human Evolution*, 36: 637-685.

Lumley, H. de (1982) (Ed.): *Origine et Evolution de l’homme*. Labo. Prehist. Mus. de L’Homme, Paris.

Løvtrup, S. (1975): “On phylogenetic classification”. *Acta Zool. Cracov.*, 20: 499-523.

Malegni, F.; Carnieri, E. *et alii* (2003): “*Homo cepranensis* sp. nov. and the evolution of African-European Middle Pleistocene hominids”. *C.R. Palevol.*, Paris, 2: 153-159.

Manzi, G.; Mallegni, F. & Ascendi, A. (2001): “A cranium for the earliest europeans: Phylogenetic position of the hominid from Ceprano, Italy”. *PNAS*, 98: 10011-10016.

–; Bruner, E. & Passarello, P. (2003): “The one-million-year-old *Homo* cranium from Bouri (Ethiopia): a reconsideration of its *H. erectus* affinities”. *Journal of Human Evolution*, 44: 731-736.

Mayden, R.L. (1997): “A hierarchy of species concepts: the denouement of the saga of the species problem”. In M.F. Claridge, H.A. Dawah & M.R. Wilson (Eds.): *Species. The units of biodiversity*: 381-424. Chapman & Hall. London.

Mayr, E. (1950): “Taxonomic categories in fossil hominids”. *Cold Spring Harbour Symp. Quant. Biol*., 15: 109-118.

– (1963a): “The taxonomic evaluation of fossil hominids”. In S.L. Washburn (Ed.): *Classification and human evolution*: 332-346. Methuen & Co. Limited. London.

– (1963b): *Animal Species and Evolution*. Belknap Press, Harvard.

– (1969): *Principles of systematic zoology*. McGraw-Hill. New York.

– (2000): “The biological species concept”. In Wheeler, Q.D. & Meier, R. (Eds.), Ch. 2, 7, 12.

– & Ashlock, P.D. (1991): *Principles of systematic zoology*. McGraw-Hill, Inc. New York.

McBrearty, S. & Brooks, A.S. (2000): “The revolution that wasn’t: a new interpretation of the origin of modern human behavior”. *Journal of Human Evolution*, 39: 453-563.

McKenna, M.C. (1975): “Toward a phylogenetic classification of the Mammalia”. In W.P. Luckett & F.S. Szalay (Eds.): *Phylogeny of the primates. A multidisciplinary approach*: 21-46. Plenum Press. New York.

Miles, R.S. (1973): “Relationships of acanthodians”. In Greenwood, P.H. *et alii* (Eds.).

– (1975): “The relaionships of the Dipnoi”. *Coll. Int. CNRS*, 218: 133-148.

Nelson, G.J. (1970): “Outline of a theory of comparative biology”. *Systematic Zoology*, 19: 373-384.

– (1971): “’Cladism as a philosophy of classification”. *Systematic Zoology*, 20: 373-376.

– (1972): “Phylogenetic relationship and classification”. *Systematic Zoology*, 21: 227-231.

– (1974): “Classification as an expression of phylogenetic relationships”. *Systematic Zoology*, 22. 344-359.

– (1989): “Species and taxa: systematics and evolution”. In D. Otte & J.A. Endler (Eds.): *Speciation and its consequences*: 60-81. Sinauer, Sunderland.

– & Platnick, N. (1981): *Systematics and biogeography. Cladistics and vicariance*. Columbia University Press. New York.

Olson, T.R. (1985): “Cranial morphology and systematics of the Hadar Formation hominids and “*Australopithecus” africanus*”. In E. Delson (Ed.): *Ancestors: the hard evidence*: 102-119. Alan R. Liss. New York.

Patterson, C. (1973): “Interrelationships of holosteans”. 233-305 in P.H. Greenwood *et alii.*

– (1980): “Cladistics”. *Biologist*, 27: 234-240.

– (1988): “Homology in classical and molecular biology”. *Mol. Biol. Evol*., 5: 603-625.

– & Rosen, D.E. (1977): “Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practise of classifying fossils”. *Bull. Amer. Mus. Nat. Hist*., 158: 81-172.

Paul, G.S. (2002): *Dinosaurs of the Air*. Johns Hopkins Univ. Press, London.

Pleijel, F. (1999): “Phylogenetic taxonomy, a farewell to species, and a revision of Heteropodarke (Annelida, Polychaeta, Hesionidae)”. *Syst. Biol*., 48: 755-789.

– & Rouse, G.W. (2000): “Least inclusive taxonomic unit: a new taxonomic concept for biology”. *Proc. R. Soc., London B*, 267: 627-630.

– & – (2003): “Ceci n’est pas un taxon: names, clades, and phylogenetic nomenclature”. *J. Zool. Syst. Evol. Res.*, in press.

Popper, K.R. (1972): *Objective Knowledge. An Evolutionary Approach*. Oxford Univ. Prtess, Oxford.

Rak, Y. (1983): *The australopithecine face*. Academic Press. New York.

Regan, C.T. (1926): ”Organic evolution”. *Report Brit. Assoc. Advanc. Sci.*, 1925: 75-86.

Richmond, B.G. (2000): “Primate and human evolution at the 1999 meeting of the American Association of Physical Anthropologists”. *Evolutionary Anthropology*, 8: 159-161.

– & Strait, E.S. (2000): “Evidence that humans evolved from a knuckle-walking ancestor”. *Nature*, 404: 382-385.

–; Aiello, L.C. & Wood, B.A. (2002): “Early hominin limb proportions”. *Journal of Human Evolution*, 43: 529-548.

Ridley, M. (1994): *Evolution*. Blackwell Scientific Publications. Boston.

Rightmire, P.G. (1990): *The evolution of Homo erectus: Comparative anatomical studies of an extinct human species.* Cambridge university Press. Cambridge.

– (1993): “Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region”. *American Journal of Physical Anthropology*, 90: 1-33.

– (1996): “The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene?”. *Journal of Human Evolution*, 31: 21-39.

Robinson, J.T. (1956): “The dentition of the Australopithecinae”. *Transvaal Museum Memoir*, 9.

– (1972): *Early hominid posture and locomotion*. University of Chicago Press, Chicago.

Ruvolo, M. (1997): “Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets”. *Molecular Biology and Evolution*, 14: 248-265.

Santa Luca, A.P. (1980): “The Ngandong fossil hominids. A compareative study of a Far Eastern *Homo erectus* group”. *Yale University Publications in Anthropology*, New Haven 78: 1-175.

Schwartz, J.H.; Collard, M. & Cela-Conde, C.J. (2001): “Systematics of ”humankind”. *Evolutionary Anthropology*, 10: 1-3.

– & Tattersall, I. (2002, 2003): *The human fossil record 1 & 2; Europe resp. Asia & Africa*. Wiley-Liss. New York.

Senut, B.; Pickford, M. *et alii* (2001): “First hominid from the Miocene (Lukeino Formation, Kenya)”. *C. R. Acad. Sci. Paris, Sciences de la Terre et des planètes*, 332: 137-144.

Shoshani, J. ; Groves, C.P. *et alii* (1996): “Primate phylogeny: morphological vs molecular results”. *Molecular Phylogenetics and Evolution*, 5: 102-154.

Simpson, G.G. (1945): “The principles of classification and a classification of mammals”. *Bull. Amer. Mus. Nat. Hist*., 85: 1-350.

– (1951): “The species concept”. *Evolution*, 5: 285-298.

– (1959): “The nature and origin of supraspecific taxa”. *Cold Spring Harbour Symp. Quant. Biol*., 24: 255-271.

– (1961): *Principles of animal taxonomy*. Columbia University Press. New York.

– (1963): “The meaning of taxonomic statements”. In S.L. Washburn (Ed.): *Classification and human evolution*. Methuen & Co. Limited. London.

– (1975): “Recent advances in methods of phylogenetic inference”. In W.P. Luckett & F.S. Szalay (Eds.): *Phylogeny of the primates. A multidisciplinary approach*: 3-19. Plenum Press. New York.

Slobodnikoff, C.N. (1976) (Ed.): *Concepts of species*. Benchman Papers on Systematic and Evolutionary Biology, 3.

Smith, A.B. (1994): *Systematics and the fossil record: documenting evolutionary patterns*. Blackwell Scientific Publications. Oxford.

Strait, D.S.; Grine, F.E. & Moniz, M.A. (1997): “A reappraisal of early hominid phylogeny”. *J. Hum. Evol*., 32: 17-82.

Stringer, C.B. (1986): “The credibility of *Homo habilis*”. In B. Wood, L. Martin & P. Andrews (Eds.): *Major patterns in primate and human evolution*: 266-294. Cambridge University Press. Cambridge.

– (2002): “Modern human origins: progress and prospects”. *Phil. Trans. R. Soc. Lond.* B, 357: 563-579.

– (2003): “Human evolution: out of Ehtiopia”. *Nature*, 423: 692-695.

Sylvester-Bradley, P.C. (1956): *The species concept in palaeontology*. Syst. Assoc. Publ. 2. London.

Thackeray, J.F.; Loth, S.R. *et alii* (2000): “Comparison of Sts 5 (‘Mrs Ples’) and Stw 53 (‘Early *Homo*’) from Sterkfontein, South Africa”. *South African Journal of Science*, 96: 21.

–; Gommery, D & Braga, J. (2002): “Australopithecine postcrania (Sts 14) from the Sterkfontein Caves, South Africa: the skeleton of ‘Mrs Ples’?”. *South African Journal of Science*, 98: 211-212.

Tattersall, I. (1986): “Species recognition in human paleontology”. *Journal of Human Evolution*, 15: 165-175.

– (1995): *The fossil trail*. Oxford University Press. New York

– (2003): “Once we were not alone”. *Scientific American*, 13, Special Edition: 20-27.

– & Eldredge, N. (1977): “Fact, theory, and fantasy in human paleontology”. *American Scientist*, 65: 204-211.

Tobias, P.V. (1989): ”Hominid variability, cladistic analysis and the place of *Australopithecus africanus*”. In G. Giacobini (Ed.): *Hominidae: Proceedings of the 2^{nd} International congress of Human Paleontology*: 119-127. Editoriale Jaca Book. Milan.

– (1991): *Olduvai Gorge. Vol. 4. The skulls, endocasts and teeth of Homo habilis*. Cambridge University Press.

Trinkaus, E. (1983): *The Shanidar Neandertals*. Academic Press. New York.

– & Shipman, P. (1993): *The neandertals: changing the image of mankind*. Alfred A. Knopf. New York.

Vandermeersch, B. (1989): In G. Giacobini (Ed.): *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology*. Editoriale Jaca Book. Milan.

Vrana, P. & Wheeler, W. (1992): “Individual organisms as terminal entities: laying the species problem to rest”. *Cladistics*, 8: 67-72.

Walker, A. & Leakey, R. (1993) (Eds.): *The Nariokotome Homo erectus skeleton*. Harvard University Press. Cambridge.

Wanpo, H.; Ciochon, R. *et alii* (1995): “Early *Homo* and associated artefacts from Asia”. *Nature*, 378: 275-278.

Ward, C.V., Leakey, M.G. & Walker, A. (2001): “Morphology of *Australopithecus anamensis* from Kanapoi and Allia bay, Kenya”. *Journal of Human evolution*, 41: 255-368.

Weidenreich, F. (1946): *Apes, giants and man*. University of Chicago Press. Chicago.

Weinert, H. (1951): *Stammesentwicklung der Menschheit. Die Wissenschaft*. Vieweg & Sohn. Braunschweig.

Westergaard, B. (1989): ”A new species concept: Cladospecies (and cladosubspecies). Pluralistic realism and biotaxonomy: A radical solution to classification exemplified by hominids”. In G. Giacobini (Ed.): *Hominidae: Proceedings of the 2^{nd} International Congress of Human Paleontology*: 71-74. Editoriale Jaca Book. Milan.

– (2002): “Menneske. Menneskets evolution”. In *Den Store Danske Encyklopædi. Danmarks Nationalleksikon*. Supplement: 437-439. Gyldendal. Copenhagen.

– & Bonde, N. (1987): “Menneskets afstamning – synspunkternes udvikling”. In N. Bonde, J. Hoffmeyer & H. Stangerup: *Naturens historie fortællere bd. 2. Udviklingsideens historie. Fra Darwins syntese til nutidens krise*: 288-320. G.E.C. Gad. Copenhagen.

Wheeler, Q.D. & Meier, R. (Eds.) (2000): *Species condepts and phylogenetic theory. A debate.* Columbia University Press. New York.

White, T.D. (1985): “The hominids of Hadar and Laetoli: and element-by-element comparison of the dental samples”. In E. Delson (Ed.): *Ancestors: the hard evidence*. Alan R. Liss. New York.

–; Suwa, G. *et alii* (2000): ”Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ehtiopia”. *American Journal of Physical Anthropology*, 111: 45-68.

–; Asfaw, B. *et alii* (2003): ”Pleistocene *Homo sapiens* form Middle Awash, Ethiopia”. *Nature*, 423: 742-747.

Wildman, D.E.; Uddin, M. *et alii* (2003): ”Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpansees: Enlarging genus *Homo*”. *PNAS*, 100: 7181-7188.

Wiley, E.O. (1978): “The evolutionary species concept reconsidered”. *Systematic Zoology*, 27: 17-26.

– (1979): “An annotated Linnean hierarchy, with comments on natural taxa and competing systems”. *Syst. Zool*., 28: 308-337.

– (1981): *Phylogenetics. The theory and practice of phylogenetic systematics*. John Wiley and Sons. New York.

Wong, K. (2003): “An ancestor to call our own”. *Scientific American*, 13. Special Edition: 4-13.

Wood, B. (1991): *Koobi Fora research project 4. Hominid cranial remains*. Clarendon Press. London.

– (1992): “Origin and evolution of the genus *Homo*”. *Nature*, 355: 783-790.

– (1994): “Taxonomy and evolutionary relationships of *Homo erectus*”. *Courier Forschungsinstitut Senckenberg*, 171: 159-165.

– (2002): “Who are we?”. *New Scientist*, 26 October: 44-47.

– & Collard, M. (1999a): “The human genus”. *Science*, 284: 65-71.

– & – (1999b): “The changing face of genus *Homo*”. *Evolutionary Anthropology*, 8:195-207.

Wu, X. & Poirier, F.E. (1995): *Human evolution in China. A metric description of the fossils and a review of the sites.* Oxford University Press. New York.

Zeitoun, V. (2000): “Revision de l’espece *Homo erectus* (Dubois, 1893)”, *Bull. Mem. Soc. Anthrop*., Paris, N.S. 12: 1-200.

Symbol. Sp. Ch. 9. (N Bonde). **Extra Refs., annotated**. Hominid diversity. (10 pp)

A large number of references especially concerning the reconstruction of the phylogenetic tree from **Bonde & Westergaard 2004** are not repeated here, but are available as a pdf of B&W 04 on the homepage of the book/publisher as well as on NB's homepage at Copenhagen University. In the same way this list of 'extra references' is linked as a pdf to both homepages.

Anon 2004 Human. (Dorling Kindersley, London). [Dan: Mennesket – illustreret opslagsværk. (Forlag Aktium, Danmark) 2005].

Anton, S. 1997 Developmental age and taxonomic affinity of the Modjokerto child, Java, Indonesia. Amer. J. Phys. Anthropol. 102, 497-514.
[Also Swisher, C.C., Curtis, G.H. et al. 1994 Age of the earliest known hominids in Java, Indonesia. Science 263, 1118-1121].

Arambourg, C. 1963 Le gisement de Ternifine, II. L'*Atlanthropus mauretanicus*. Arch. Inst. Paléont. Hum., Mém. 32, 37-190.
[Also 1955 A recent discovery in human paleontology: *Atlanthropus* of Ternifine (Algeria). Amer. J. Phys. Anthropol. 13, 191-202].

Arambourg, C. & Coppens, Y. 1958 Découverte d'un australopithecien nouveau dans les gisements de l'Omo (Ethiopie). South Afr. J. Sci., Freb issue, 58-59. [*A. aethiopicus*]

Asfaw, B., White, T. et al. 1999 *Australopithecus garhi*: A new species of early hominid from Ethiopia. Science 284, 629-635. [Referred in text as White et al. 1999]

Balter, M. & Gibbons, A. 2000 A glimpse of humans first journey out of Africa. Science 288, 948-950. [Also 2002 Were 'Little People' the first to venture out of Africa ? Science 297, 26-27; criticisme in J. Hawks' weblog 2007:
http://johnhawks.net/weblog/fossils/lower/dmanisisi/dmanisi_postcrania_nature_2007.html].

Benton, M. 2005 Vertebrate Palaeontology. 3rd ed. (Chapman & Hall, London).

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.
[Also Balter, M. 2010 Candidate human ancestor from South Africa sparks praise and debate. Science 328, 154-155; Dirks, P.H.G.M., Kibili, J.M. et al. 2010 Geological setting and age of *Australopithecus sediba* from Southern Africa; Fischman, J. 2011 Halvt abe halvt menneske. Nat. Geogr., Danmark 2011 (8), 74-87 (Eng: Half ape half man. Nat. Geogr., Sept. 2011)].

Bermudes de Castro, J.M., Arsuaga, J.L., Carbonell, E. et al. 1997 A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to neandertals and modern humans. Science 276, 1392-96. [on *Homo antecessor* from Gran Dolina, Atapuerca; see also Carbonell et al., below]

Bermudes de Castro, J.M., Carbonell, E. & Arsuaga, J.L. (eds.) 1999 The Gran Dolina site: TD6 Aurora Stratum (Atapuerca, Burgos, Spain). J. Hum. Evol. 37 (special issue), 309-700.
[Also Carbonell et al., below]

Birdsell, J.B. 1975 Human Evolution. 2nd ed. (R. McNally College Publ. Co, Chicago)

Bodmer, W.F. & Cavalli-Sforza, F.F. 1976 Genetics, Evolution and Man. (Freeman,San Francisco).
[Also Cavalli-Sforza 1991 Genes, peoples and languages. Sci. Amer. 265 (5), 72-78].

Bonde, N. 1984b Primitive features and ontogeny in phylogenetic reconstructions. Vidensk. Meddr. Dansk Naturhist. Foren. 145, 219-236. (Also Patterson 1983, below).

Bowler, P.J. 1986 Theories of Human Evolution: A Century of Debate, 1844 – 1944. (J. Hopkins Univ. Pr., Baltimore)

[See also Bowler, P.J. 2003 Evolution, the History of an Idea. (Univ. Calif. Press, Berkeley); Bonde, N., Hoffmeyer, J. & Stangerup, H. (eds.) 1996 Naturens historiefortællere. Udviklingsideens historie, vol. 1 & 2. 960 pp. (2nd ed., Gad, København). In Danish: Nature's Story-tellers. History of Evolutionary Ideas. 1st eds. 1985 & 1987; rev. by Ph. Janvier 1988 in The Linnean 1988, 50-52].

Brace, C.L. 1967 The Stages of Human Evolution. 116 pp (Prentice Hall, Englewood Cliffs, NJ); 5th ed 1995, 371 pp. [Also Brace, C.L. 1971 Atlas of Fossil Man. (Holt, Rinehart, Winston, New York); 1997 One human line, two million years. Natural Hist. 106 (8), 5-6]

Brace, C.L. & Montagu, A. 1965 Man's Evolution: An Introduction to Physical Anthropology, (2nd ed. 1977: Man's Evolution: An Intro to Biological Anthropology). [Both Brace and Montagu were strongly against the concept of 'race', e.g. Montague, A. 1942 Man's Most Dangerous Myth: The Fallacy of Race (6th ed. 1998); 1999 (ed.) Race and IQ (Oxf. Univ. Pr., 2nd ed); Brace 1964 A non-racial approach to the understanding of human diversity, p. 103-52 in Montagu (ed) The Concept of Race. (Free Pr. Glencoe, New York); Brace et al. 1971 (eds) Race and Intelligence; 2005 Race is a Four Letter Word. (Oxf.Univ.Pr.,N.Y.)]

Bräuer, G. 1994 How different are Asian and African *Homo erectus*? Courier Forschungsinst. Senckenberg 171, 301-31 8.

Broom, R. & Robinson, J.T. 1952 Swartkrans Ape-Man: *Paranthropus crassidens*.Transvaal Museum Mem. 6, 1-123. [Also Grine, F.E. (ed.) 1988 Evolutionary History of the Robust Australopithecines. (de Gruyter, New York); Keyser 2000 under

Brown, M.H. 1990 The Search for Eve. (Harper & Row, New York). [Dan: Jagten på Eva. Spektrum, København].

Brown, P., Sutikna, T., Morwood, M.J. et al. 2004 A new small-bodied hominid from the Late Pleistocene of Flores. Nature 431, 1055-1061. (Describing *Homo floresiensis* n.sp.). [Mispr. 2003]

[Agreeing: Lahr, M.M. & Foley, R. 2004 Palaeoanthropology: Human evolution writ small. Nature 431, 1043-1044; Argue, D. et al. 2006 *Homo floresiensis*: microcephalic, pygmoid, *Australopithecus* or *Homo* ? J. Hum. Evol. 51, 360-374; Tocheri, M.W. et al. 2007 The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. Science 317, 1743-1745; Baab, K.L. & McNulty, K.P. 2008 Size, shape and asymmetry in fossil hominins: The status of the LB1 cranium based on 3-D morphometric analysis. J. Hum. Evol. (doi:10.1016/j.jhevol.2008.08.011), and below Falk, D. et al. 2005, 2007, and Morwood, M.J. et al. 2005. Contra: Culotta, E. 2006 Skeptics seek to slay the 'Hobbit', calling Flores skeleton a modern human. Science 313, 1028-1029; Jacob, T. et al. 2006, Martin, R.D. et al. 2006, Obendorf, P.J. 2007, and Oxnard et al. 2010, all below, and Hershkovitz, I. et al. 2007 Comparative skeletal features between *Homo floresiensis* and patients with primary growth hormon insensitivity (Laron syndrome). Amer. J. Phys. Anthropol. 134, 198-208; Weber, J. et al. 2005 Comment on 'The brain of LB1, *Homo floresiensis*'. Science 310, 236b].

Buffon, G.L.L. de 1749 Histoire naturelle de l'homme. Histoire naturelle générale et particuliere (Buffon & Daubenton) vol. 3. (Imprim. Royale, Paris).

Buffon, G.L.L. de 1766 De la dégeneration des animaux. Ibid. vol. 16.

[Also Sloan, P. 1986 From logical universals to historical individuals. Buffon's idea of biological species. In Anon (ed.) Histoire du Concept d'Éspèce dans les Sciences de la Vie. (Fondation Singer-Polignac, Paris)].

Cann, R.L., Stoneking, M. & Wilson, A.C. 1987 Mitochondrial DNA and human evolution. Nature 325, 31-36. [Also Wilson & Cann 1992, below]

[Cf. Semino, O. et al. 2000 The genetic legacy of Paleolithic *Homo sapiens sapiens* in extant Europeans: A Y chromosome perspective. Science 290, 1155-59; Tashian, R. & Lasker, G. (eds.) 1996 Molecular Anthropology: Towards a New Evolutionary Paradigm. Molec. Phylog. Evol. 5 (1, Special issue), 1-285; Stringer & Andrews 1988, and Horai et al. 1995, below].

Cantino, P.D. & Queiroz, K. de 2004 The PhyloCode. [Check internet for new editions]

Carbonell, E. & Bermudes de Castro, J.M. 2004 Atapuerca, perdidos en la colina. La historia humana y cientifica del equipo investigador. 446 pp. (Destino, Barcelona).

Carbonell, E., Bermudes de Castro, J.M. et al. 1995 Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). Science 269, 826-830.

[Also Carbonell, E., 1999 The TD6 lithic industry from Gran Dolina, Atapuerca (Burgos, Spain): Production and use. J. Hum. Evol. 37, 653-693; Bower, B. 2009 Europe's oldest stone hand axes emerge in Spain. Science news, web ed. Sept 2, 2009 referring Scott, G. & Gibert, L. from Nature Sept. 3, 2009].

Carbonell, E., Bermudes Castro, J.M. et al. 2008 The first hominin of Europe. Nature 452, 465-469.

[Also Carbonell, E. & Rodríguez, X.P. 2006 The first human settlement of Mediterranean Europe. C. R. Palevol 5, 291-298; Rosas, A. et al. 2006 The 'Sima del Elefante' cave site at Atapuerca (Spain). Estudios Geol. 62, 327-348; Pares, J.M. et al. 2006 Matuyama age lithic tools from the Sima del Elefante site, Atapuerca (northern Spain). J. Hum. Evol. 50, 163-169].

Clarke, R.J. 1988 A new australopithecine cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In Grine, F.E. (ed.) The Evolutionary History of the Robust Australopithecines, 285-92. (de Gruyter, New York)

[Also Keyser, A.W. 2000 The Drimolen skull: the most complete australopithecine cranium and mandible to date. S. Afr. J. Sci. 96, 189-193 (*P. robustus*, probably famale) – and sequel Keyser et al. 193-197 about the geology of the site]

Coon, C.S. 1962 The Origin of Races. (J. Cape, London). [See also Coon, C.S. 1965 The Living Races of Man. (J. Cape, London); and under Brace & Montagu, above, and Gould, below].

Cooper, G.A. 1970 Generic characters of brachiopods. Proc. N. Amer. Paleont. Conv., C, 194-263.

Coppens, Y. 1975 Évolution des hominids et de leur environnement au cours du Plio-Pleistocène de la basse Vallée de l'Omo en Ethiopie. C.R. Acad. Sci., Paris 281, sér. D, 1693-1696.

Coppens, Y. 1977 Évolution morphologique de la prémière prémolaire inférieure chez certains primates supérieurs. C. R. Acad. Sci., Sér. D, Paris, 1299-1302. [Contra Johanson, White, Coppens 1978, below]

Dart, R.A. 1925 *Australopithecus africanus*: the man-ape of South Africa. Nature 115, 195-199.

Dart, R.A. 1948 The Makapansgat proto-human *Australopithecus prometheus*. Amer. J. Phys. Anthropol. 6, 259-284. [Cf. Brain, C.K. 1981 The Hunters or the Hunted? (Chicago Univ. Press)]

Darwin, C.R. 1859 The Origin of Species by Means of Natural Selection: Or the Preservation of Favoured Races in the Struggle for Life. (John Murray, London). [Dan: Arternes Oprindelse ved naturlig selektion. 1st ed. transl. by J. Madsen 2009 (Statens Naturhistoriske Museum, Københavns Universitet). 6th ed. 1872; 5th ed. 1869 transl. by I.P. Jacobsen 1871/1872 Arternes Oprindelse, 1-2 (København). Also Browne, J. 2006 Darwin's Origin of Species, a Biography (Atlantic Books, London); and 2002 & 2003 Charles Darwin, vol. 1 & 2 (Pimlico, London); Desmond, A. & Moore J. 1991 Darwin. (M. Joseph, London); Ridley, M. 2006 How to Read Darwin. (W.W. Norton, New York); Young, D. 2007 The Discovery of Evolution. (2nd ed., Cambridge Univ. Press); Ruse, M. & Richards, R.J. (eds.) 2008 The Cambridge Compagnon to 'Origin of Species'. (Cambr. Univ. Pr.)].

Delson, E. 1988 Chronology of South African australopith site units. In F.E. Grine (ed.) Evolutionary History of the "Robust" Australopithecines, 317-324. (A. de Gruyter, New York).

Dubois, E. 1894 *Pithecanthropus erectus*, eine menschenähnliche Übergangsform aus Java. (Landesdruckerei, Batavia). [Misprint 1892 – see also Theunissen, B. 1988 Eugéne Dubois and the Ape-Man from Java. (Kluwer Acad., Dortrecht)]

Ebbesen, C. 1990 Danmarks oldtid, bd. 1, Octo, 80 pp, København (Dan: Antiquity of Denmark).

Falk, D. et al. 2005 The brain of Homo floresiensis. Science 308, 242-245. [Cf. Brown et al. 2004]

Falk, D., Hildebolt, C., Smith, K. et al. 2007 Brain shape in human microcephalics and *Homo floresiensis*. Proc. Nat. Acad. Sci. USA 104, 2513-2518. (Cf. refs. under Brown et al. 2004, above)

Forey, P.L., Fortey, R.A. et al. 2004 Taxonomy and fossils: a critical appraisal. Phil.Trans.R.Soc. Lond. B 359, 639-653. [Also Forey, P.L. 2005 Naming the World: Is there anything left of Linnaeus? Proc. Calif. Acad. Sci., Ser. 4, 56, Suppl. I, No. 17, 182-195; contra Cantino & Queiroz]

Gabounia, L., Vekua, A. et al. 2000 Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting and age. Science 288, 1019-25.

[Also Gabunia & Vekua 1995 Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. Nature 373, 509-512; Vekua, A., Lordkipanidze, D., Rightmire, G.P. et al. 2002 A new skull of early *Homo* from Dmanisi, Georgia. Science 297, 85-89; see Balter & Gibbons, above; further Lordkipanidze, D. et al. 2005 The earliest toothless hominid skull. Nature 434, 717-718; Rightmire, G.P., Lordkipanidze, D. & Vekua, A. 2006 Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisis, Republic of Georgia. J. Hum. Evol. 50, 115-141; Lordkipanidze, D. et al. 2006 A fourth hominin skull from Dmanisi, Georgia. Anat. Rec. 288A, 1146-1157; Lordkipanidze, D. Jashashvili, T. et al. 2007 Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature 449, 305-310 – severe criticisme by J. Hawks 2007: http://johnhawks.net/weblog/fossils/lower/dmanisi/dmanisi_postcrania_nature_2007.html].

Gibbons, A. 2009a A new kind of ancestor: Ardipithecus unveiled. Science 326, 36-40; 2009b Habitat for humanity. Ibid. p. 40; 2009c The view from Afar. Ibid. 41-43. (Intro to thematic issue, see below Lovejoy et al., Suwa et al. and White et al., all 2009, Science 236 no. 5949).

Gore, R. 1997 The most ancient Americans. Nat. Geographic Oct. 1997, 92-99.

[Cf. Bahn, P.G. 1993 50,000-year-old Americans of Pedra Furada. Nature 362, 114-115, referring Ph.D. thesis by F. Parenti 1993 Le gisement quaternaire de la Toca do Boqueiráo da Pedro Furada (Piaui, Bresil) dans le contexte de la préhistoire américaine. 4 vols. École Hautes Études en Science Sociale, Paris, and Bahn 1997 Bridge to the past. Nature 385, 128-129 reviewing F.H. West (ed.) 1996 American Beginnings: The Prehistory and Paleoecology of Beringia. (Univ. Chicago Press)].

Gould, S.J. 1977 Why we should not name human races – A biological view. *In* Ever Since Darwin, 231-236. (Burnett Books; and Penguin,New York 1978).

[Also the punctualistic essay on Laetoli and *H. habilis*, 'Bushes and ladders in human evolution'. Ibid. 56-62. (Both originally in Natural History Mag., Amer. Mus. Nat. Hist., New York). On race, see under Brace, above].

Gould, S.J. & Lewontin, R.C. 1979 The spandrels of San Marcos and the Panglossian paradigm. Proc. Roy. Soc. London, Ser. B 205, 581-598. [Misprinted 1972 & 1978]

[Also Gould 1976 Ladders, bushes, and human evolution. Natural History 85 (4), 24-31].

Häckel, E. 1866 Generelle Morphologie der Organismen. 1-2. (Reimer, Berlin).

[Also 1868 Natürlische Schöpfungsgeschichte. (10th ed. 1902 – The History of Creation 1892 Appleton, New York), and 1874 Anthropogenie oder Entwicklungsgeschichte des Menschen, 730 pp. (4th ed. 1891, 906 pp. Engelmann, Leipzig)].

Hammer, M.F. 1995 A recent common ancestry for human Y chromosomes. Nature 378, 376-8.

Hay, R.L. & Leakey, M.D. 1992 The fossil footprints of Laetoli. Sci. Amer. 246 (2), 50-57.
[Also papers in Coppens, Y. & Senut, B. (dir.) 1991 Origine(s) de la Bipédie chez les Hominidés. Colloque Internat. Fond. Singer-Polignac 1990. Cahiers de Paléontol. (CNRS) incl. Deloison, Y.: Les australopitheques marchaient-ils comme nous ? Pp. 177-186; Tuttle, R.H. et al.: Laetoli footprint trails and the evolution of hominid bipedalism. Pp. 187-198; Day, M.: Bipedalism and prehistoric footprints. Pp. 199-213; White, T. & Suwa, G. 1987 Hominid footptints at Laetoli: Facts and interpretations. Amer. J. Phys. Anthrop. 72, 485]

Holm, J. 1996 The earliest settlement of Denmark. In Larsson, L. (ed.) The Earliest Settlement of Scandinavia. Acta Archaeol., Lund 24. [Hamburgian culture – but older tools in Holm 1987 Primitive flint i Vejstrup Ådal. Årbog Svendborg & Omegns Mus. 1987, 8-16 (in Danish)]

Horai, M. et al 1995 Recent African origin of modern humans revealed by the complete sequences of Hominoid mitochondrial DNA. Proc. Nat. Acad. Sci. 92, 532-536.

Hublin, J.J. 1978 Le torus occipitaltransverse et les structures associées: evolution dans le genre *Homo*. These es Sci. Nat., Univ. Paris VI, 176 pp. [See under Stringer 1985, below]

Hublin, J.J. 1985 Human fossils from the North African Middle Pleistocene and the origin of *Homo sapiens*. In Delson, E. (ed.) Ancestors: The Hard Evidence, 283-288. (Liss, New York).

Hublin, J.J. 1988 Caractères derivés de la region occipito-mastoidïenne chez les néandertaliens. In Otte, M. (ed.) L'Homme de Néandertal, vol. 3: L'anatomie, 67-73.

Jacob, T., Indriati, E. et al. 2006 Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. Proc. Nat. Acad. Sci. USA 103, 13421-13426. (Cf. refs. Under Brown et al. 2004, above).

Jensen, P.K.A. 2004 Da mennesket blev menneske. (Gyldendal, København). [Danish: When Man became Man]. (2nd ed 2007)

Jensen, P.K.A. 2008 read: 2006 Mennesket – den genetiske arv. (Aarhus Univ. Forlag). [Danish: Humans – the genetic inheritance; also Jobling et al. 2004, Molnar 1998, both below]

Jobling, M.A. et al. 2004 Human Evolutionary Genetics: Origins, Peoples and Diseace. (Garland Science, New York)

Johanson, D.C. 1978 Early African hominid phylogenesis – A re-evaluation. Nobel Symposium, Karlskoga. Royal Swedish Academy of Science, 8 pp. [Also Johanson, D.C. 1989 The Current status of Australopithecus. In Giacobini, G. (ed.) Hominidae. Proceedings of the Second International Congress of Human Paleontology, 77-96 (Jaca Book, Milano); White, T. & Johanson, D.C. 1989 The hominid composition of Afar locality 333: Some preliminary observations. In Giacobini (ed.), Ibid., 97-101]

Johanson, D.C. 1996 The strategy of paleoanthropology: Early African hominids. Yearbook Phys. Anthropol. 39, 1-10.

Johanson, D.C. 1996 Face-to-face with Lucy's family. Nat. Geogr. Mag. 189 (3), 96-117.
[Also Johanson & O'Farrell, K. 1990 Journey from the Dawn: Life with the World's First Family. (Villard Books, New York). Critique: Day, M.H., Leakey, M.D. & Olson, T.R. 1978 On the status of *Australopithecus afarensis*. Science 207, 1102-1103; Tobias, P.V. 1980 *"Australopithecus afarensis"* and *A. africanus*: Critique and an alternative hypothesis. Palaeont. Afr. 23, 1-17; and cf. Coppens 1977, below].

Johanson, D.C. & Edey, M. 1981 Lucy: The Beginning of Humankind. (Simon & Schuster, New York).

[Also Johanson & Shreeve, J. 1989 Lucy's Child: The Discovery of a Human Ancestor. (William Morrow, New York), and Johanson, Johanson, L. & Edgar, B. 1994 Ancestors: In Search of Human Origins. (Villard Books, New York), and 'Lucy's Baby'. Nat. Geogr. Sep. 21, 2006, and Alemseged, Z., Spoor, F. et al. 2006 A juvenile early hominin skeleton from Dikika, Ethiopia. Nature 443, 296-301, and Wood, B. 2006 A precious little bundle. Ibid. 278-281].

Johanson, D.C. & Taieb, M. 1976 Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. Nature 260, 293-297.

Johansen, D.C., Lovejoy, C.O., Kimbel, W. & White, T. 1982 Pliocene hominid fossils from Hadar, Ethiopia. Amer. J. Phys. Anthropol. 57 (4), 373-427.

Johanson, D.C., Lovejoy, C.O., Kimbel, W. et al. 1982 Morphology of the Pliocene partial hominid skeleton (A.L., 288-1) from the Hadar Formation, Ethiopia. Amer. J. Phys. Anthropol. 57, 403-51. [Cf. Schmid, P. 1989 How different is Lucy ? In Giacobini, G. (ed) Hominidae. (Jaca Books, Milano), 109-114].

Jones, S., Martin, R.D. & Pilbeam, D. 1992 The Cambridge Encyclopedia of Human Evolution. (Cambridge Univ. Press, New York).

Kant, I. 1793 Kritik der Urteilskraft.

[Also Kant, I. 1797 (1996) The Metaphysics of Moral. (Cambridge Univ. Press, Cambridge)].

Kimbel, W.H. & White, T. 1980 A reconstruction of the adult cranium of Australopithecus afarensis. Am. J. Phys. Anthropol. 52, 244-50. [Cf. Ferguson, W.W. 1987 Reconstruction and reevaluation of the skull of *Homo antiquus* (Hominoidea: Homininae) from Hadar. Primates 28, 377-391; Schmid, P. 1989 How different is Lucy ? In Giacobini, G. (ed.) Hominidae. 109-114. (Jaca Books, Milano)]

Krings, M., Stone, A. et al. 1997 Neandertal DNA sequences and the origin of modern humans. Cell 90, 19-30.

[Krings et al. 1999 DNA sequence of the mitochondrial hypervariable region II from the Neandertal type specimen. Proc. Nat. Acad. Sci. 96, 5581-86 – and below].

Krings, M., Capelli, C. et al 2000 A view of Neandertal genetic diversity. Nature Genetics 26, 144-146.

[Also Green, E.R. et al. 2010 A draft sequence of the Neandertal genome. Science 328, 710-22; Höss, M. 2000 Neanderthal population genetics. Nature 404, 453-54]

Lamarck, J.B. 1809 Philosophie zoologique. 2 vols. (Dentu, Paris). [Amer: The Zoological Philosophy, 1984. 1 vol. (Univ. Chicago Press, Chicago) – with essays by Burckhardt and Hull].

Larick, R., Ciochon, R.L. et al. 2001 Early Pleistocene 40Ar/39Ar ages for Bapang Formation hominins, Central Java, Indonesia. Proc. Nat. Acad. Sci. 98 (9), 4866-4871.

Leakey, L.B.S. & Goodall, V.M. 1969 Unveiling Man's Origins. (Methuen, London).

Leakey, R. 1981 The Making of Mankind. (M. Joseph, London).

[Also Leakey 1994 The Origin of Humankind. (Basic Books – Danish transl. 1995 Menneskeslægtens oprindelse. Munksgaard/Rosinante, København)]

Lemonick, M.D. & Dorfman, A. 2001 One giant Stepp for mankind. Time July 23, 46-53. (On *A. ramidus kadabba* – see Haile-Selassie, Y. 2001 Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412, 178-181).

Lewin, R. 1999 Human Evolution. (Blackwell Science, New York). [See also 1998: Principles of Human Evolution. (Blackwell, Malden, MA). 1993: The Origin of Modern Humans. (Sci. Amer. Library, New York). 1987: Bones of Contention: Controversies in the Search for Human Origins.

(Simon & Schuster, New York), and 1988: In the Age of Mankind: A Smithsonian Book of Human Evolution. (Smithsonian Books, Wash. D.C.)].

Lewontin, R.C. 1982 Human Diversity. (Scientific American Library, New York).

Linnaeus, C. 1735 Systema Naturae. (Theodorum Haak, Lugduni).

Lovejoy, C.O. 1988 Evolution of human walking. Sci. Amer. 256 (5), 118-125.

Lovejoy, C.O. 2009 Reexamining human origins in the light of Ardipithecus ramidus. Science 326, 74-74e8. (See Gibbons 2009, above).

Lovejoy, C.O., Suwa, G. et al. 2009 The great divide: Ardipithecus ramidus reveals the postcrania of our last common ancestors with African apes. Science 326, 100-108. And: L, S, et al. 2009 The pelvis and femur of Ardipithecus ramidus: The emergence of upright walking. Ibid. 71-71e6. (Cf. Gibbons 2009, above, and White et al. 2009, below).

Martin, R.D., MacLarnon, A.M. et al. 2006 Flores hominid: new species or microcephalic dwarf ? Anat. Rec. A 288, 1123-1145. (Cf. refs. under Brown et al. 2004, above).

Mayr, E. 1963 The taxonomic evaluation of fossil hominids. In S.L. Washburn (ed.) Classification and Human Evolution, 332-346. (Methuen, London). [Diff. from Mayr 1950, in Bonde & W. 2004]

Molnar, S. 1998 Human variations: Races, Types and Ethnic Groups. (6th ed.; paper 2005, Pearson, New York). [Also Jobling et al. 2004, above; on race under Brace & Montagu, above]

Morwood, M.J., O'Sullivan, P.B. et al. 1998 Fission track ages of stone tools and fossils on the east Indonesian island of Flores. Nature 392, 173-176. (Ages ca. 0.8 – 0.9 m.y.).

[Cf. also O'Sullivan, P.B., Morwood, M. et al. 2001 Archaeological implications of the geology and chronology of the Soa basin, Flores, Indonesia. Geology 29 (7), 607-610. (Same age); Jensen, G. et al. 2010 Hominins on Flores, Indonesia, by one million years ago. (doi:10.1038/nature08840) in Nature (Age of tools a bit older)].

Morwood, M.J. et al. 2005 Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. Nature 437, 1012-1017. (Cf. refs. under Brown et al. 2004, above).

[Also Morwood, M.J., Soejono, R.P. et al. 2004 Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature 431, 1087-1091; Brumm, A., Aziz, F. et al. 2006 Early stone technology on Flores and its implications for *Homo floresiensis*. Nature 441, 624-628].

Napier, J.R. 1975 Primate Locomotion (Oxford Univ. Press, Oxf.). [Also 1972 The Roots of Mankind (Smithsonian Books, Wash. DC); 1982 The Origins of Man (McGraw Hill, New York)]

Nielsen, R. et al 2010 (see **Rasmussen** et al 2010)

Obendorf, P.J., Oxnard, C.E. & Kefford, B.J. 2007 Are the small human like fossils found on Flores human endemic cretins ? Proc. R. Soc., B (doi:10.1098/rspb.2007.1488), 10 pp. [Cf below]

Oxnard, C., Obendorf, P.J. & Kefford, B.J. 2010 Post-cranial skeletons of hypothyroid cretins show a similar anatomical mosaic as *Homo floresiensis*. PloS ONE, 2010; 5 (9): e 130 18 (doi:10.1371/journal.pone.0013018). [Further under Brown et al. 2004, above]

Parfitt, S.A. et al. 2005 The earliest record of human activity in northerne Europe. Nature 438, 1008-1012. [Cf also Schultz 2010 below]

Patterson, C. 1983 How does phylogeny differ from ontogeny? Brit. Soc. Developm. Biol., Sympos 6, 1-31. (See also Bonde 1984b, above).

Pettitt, P. & Niskanen,M. 2005 Neanderthals in Susiluola Cave, Finland, during the last interglacial period. Fennoscandia Archaeologica XXII, 79-87. [See Schultz 2010, below. Cf. Pavlov, P., Svendsen, J.I. & Indrelid, S. Human presence in the European Arctic nearly 40,000 years ago. Nature 413, 64-67; Parfitt et al. 2005, above; in America (Alaska): Bhanoo, S.N. 2011 Child's bones are earliest human remains found in the Arctic Region. New York Times Feb 25 referring B.A. Potter et al. in Science Feb 26 – see also Gore 1997, above, and Rasmussen, Li et al. 2010, below].

Platnick, N. 1977 Cladograms, phylogenetic trees and hypothesis testing. Syst. Zool. 26, 438-442.

Platnick, N. & Cameron, H. 1977 Cladistic methods in textual, linguistic and phylogenetic analysis. Syst. Zool. 26, 380-385.

Queiroz, K. de & Gauthier, J. 1992 Phylogenetic taxonomy. Ann. Rev. Ecol. Syst. 23, 449-480.

Queiroz, K. de & Gauthier, J. 1994 Toward a phylogenetic system of biological nomenclature. Trends Ecol. Evol. 9, 27-31. [Also Cantino & Queiroz, above]

Radosevich, S.C. & Retallack, G.J. 1988 Paleoecology of hominids from the site Al333, Hadar, Ethiopia. Abstract. Amer J. Phys. Anthrop. 75 (2), 258

[Also Radosevich et al. 1992 Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. Amer. J. Phys. Anthrop. 87, 15-27]

Rasmussen, M., Li, Y. et al. 2010 Ancient human genome from an extinct Palaeo-Eskimo. Nature 463, 757-762. [Ref. by mistake as Nielsen et al 2010]

Rasmussen, M., Guo, X. ..... Willerslev, E. (*in toto* 60 aut.) 2011 An arboriginal Australian genome reveals separate human dispersals into Asia. Science 334, 94-98.

Retzius, G. 1842 Om Formen af Nordboernes Cranier. Förh. Skandinav. Naturforsk. 3, Stockholm, 1-45. [On the shape of the skulls of the Nordic Race].

Rightmire, P.G. 1998 Evidence from facial morphology for similarity of Asian and African representatives of Homo erectus. Amer. J. Phys. Anthropol. 106, 61-85.

Schleicher, A. 1861-62 Compendium der vergleichenden Grammatik der indogermanischen Sprachen.

Schleicher, A. 1863 Die Darwinische Theorie und die Sprachwissenschaft.

Schultz, H.-P. 2010. The Susiluola cave site in Western Finland – Evidence of the northernmost Palaeolithic settlement in Europe. In Burdukiewics, J.M. & Wisniewski, A. (eds.) Middle Palaeolithic Human Activity and Palaeoecology. New Discoveries and Ideas. Internat. Conf. Wroclaw 22-24 June 2006. Acta Univ. Wratislaviensis No. 3027, Studia Archeologiczne XLI Wroclaw 2010, 47-67.

Schwartz, J.H. 2004 Issues in hominid systematics. (Ref as Bonde & Westergaard 2004). Zona Arqueologica Num. 4, Vol III, 360-371.

Schwisser et al. 1994 (see **Swisher** et al. 1994)

Senut, B. 1978 Contribution à l'étude de l'humérus et de ses articulations chez les Hominidés du Plio-Pleistocène. These de Doctorat de 3éme cycle (Paléontologie Humaines de l'Université Pierre et Marie Curie). Paris.

Senut, B. 1980 New data on the humerus and its joints in in plio-pleistocene hominids. Coll. Anthropol. 4, 87-93.

[Also Coppens, Y. & Senut, B. (ed.) 1991 Origine(s) de la Bipédie chez les Hominidés. Cahiers de Paléoanthropologie, CNRS, Paris].

Shreeve, J. 2010 The evolutionary road. National Geographic, 218 (1), 34-67. (On *A. sediba*).

Simpson, G.G. 1976 The complete paleontologist? Ann. Rev. Eart Planet. Sci. 1976, 1-13.

Stopa, R. 1972 Structure of Bushman and its Traces in Indo-European. Polska Akad. Nauk – Oddzial W Krakowie, Prace Komisji Orientalistycznej 10, 217 pp.

[Modern analyses: Lieberman, P: 1984 The Bi ology and Evolution of Language. (Harvard Univ. Press, Cambridge); Gramkrelidze, T.V. & Ivanov, V.V. 1990 The early history of Indo-European languages. Sci. Amer. 262 (3), 82-89; Ross, P.E. 1991 Hard words. Sci. Amer. Apr. 1991, 70-79; Wright, R. 1991 Quest for the Mother Tongue. The Atlantic 267 (4), 39-68; Pinker, S. 1994 The

Language Instinkt. (W. Morrow, New York); Noble, W. & Davidson, I. 1996 Human Evolution, Language and Mind. (Cambridge Univ. Press); Mithen, S. 1996 The Prfehistory of Mind. (Thames & Hudson, London); Deacon, T.W. 1997 The Symbolic Species: The Co-evolutoion of Language and Brain. (Norton, New York); Lai, C.S.L. et al. 2001 A for-head domain gene is mutated in a severe language and speech disorder. Nature 413, 519-523; Buckley, C. & Steele, J. 2002 Evolutionary ecology of spoken language: co-evolutionary hypotheses are testable. J. Anthropol. Archaeol. 7, 412-457].

Stringer, C. 1984 Human evolution and biological adaptation in the Pleistocene. In Foley, R. (ed.) Hominid Evolutioin and Community Ecology, 55-84. (Acad. Press, London).

Stringer, C. 1985 Middle Pleistocene hominid variability and the origin of Late Pleistocene humans. In Delson, E. (ed.) Ancestors: The Hard Evidence, 289-295. (Liss, New York).

[Also 1990 The emergence of modern humans. Sci. Amer. 263 (6), 68-74; 2002 (ref. in Bonde & Westergaard 2004); Stringer, C. & Mellars, P. (eds.) 1989 The Human Revolution. Behavioural and Biological Perspectives in the Origins of Modern Humans. (Edinburgh Univ Press); Aitken, M., Stringer, C. & Mellars, P. (eds.) 1993 The Origin of Modern Humans. And the Impact of Chronometric Dating. (Princeton Univ. Press, New Jersey); Smith, F.H. & Spencer, F. (eds.) 1984 The Origins of Modern Humans: A World Survey of the Fossil Evidence. (Liss, New York); Akazawa, T. et al. (eds.) 1992 The Evolution and Dispersal of the Modern Humans in Asia. (Hokusen-sha, Tokyo); Tattersal, I. 1997 Out of Africa again … and again? Sci. Amer. 276 (4), 46-53; Straus, L.G. & Bar-Yosef, O. 2001 Out of Africa in the Pleistocene: an introduction, p. 1-3 (to a thematic issue) in Quaternary International vol. 75; Stringer, C., Barton, R. & Finlayson, C. 2000 Neanderthals on the Edge. (Oxbow Books, Oxford); Crow, T.J. (ed.) 2002 The Speciation of modern *Homo sapiens*. (Oxford Univ. Press, Oxford); Finlayson, C. 2004 Neanderthals and Modern Humans: An Ecological and Evolutionarty Perspective. (Cambridge Univ. Press, Cambridge); Manica, A., Amos, W. et al. 2007 The effect of ancient population bottlenecks on human phenotypic variation. Nature 448, 346-348; Grine, F.E. et al. 2007 Late Pleistocene human skull from Hofmeyr, South Africa, and modern human origins. Science 315, 226-229; Vandermeersch, B. & Maureille, B. (eds.) 2009 Les Néandertaliens: Biologie et Culture. (CTHS, Paris); Hublin, J.J. 2009 The origin of Neandertals. P N A S USA (www.pnas.org/content/106/38/16022)].

Stringer, C. & Andrews, P. 1988 Genetic and fossil evidence for the origin of modern humans. Science 239, 1263-1268.

[Also Andrews, P. & Stringer, C. 1989 Human Evolution: An Illustrated Guide. (Cambridge Univ. Press, New York and Cambridge); Stringer, C. & Andrrews, P. 2005 The Complkete World of Human Evolution. (Thames & Hall, London); Mellars, P. 2006a Going east: New genetic and archaeological perspectives on the modern human colonization of Eurasia. Science 313, 796-800; 2006b Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. Proc. Nat. Acad. Sci. USA 103, 9381-9386].

Susman, R.L., Stern, J.T. & Jungers, W.L. 1985 Locomotor adaptations in the Hadar hominids. In Delson, E. (ed.) Ancestors, the Hard Evidense, 184-192. (Liss, New York).

Suwa, G., Asfaw, B. et al. 2009 The Ardipithecus ramidus skull and its implications for hominid origins. Science 326, 68-68e7. (See Gibbons 2009, above).

Swisher, C.C. et al. 1994 The age of the earliest known hominids in Java, Indonesia. Science 263, 1118-1121.

[Cf. Swisher, Rink, W.J. et al. 1996 Latest *Homo erectus* of Java: Potential contemporaneity with *Homo sapiens* in southeast Asia. Science 274, 1870-1874; Swisher, Curtis, G. & Lewin, R. 2000 Java Man. (Univ. Chicago Press); Larick, R., Ciochon, R.L. et al. 2001, above]

Taieb, M., Johanson, D.C. et al. 1976 Geological and palaeontological background of Hadar hominid site, Afar, Ethiopia. Nature 260, 289-293

Tardieu, C. 1979 Analyse morpho-functionelle de l'articulation du génou chez les primates: application aux Homonidés fossils. These de Doctorat de 3ème cycle (Paléontologie Humaine) de l'Université Pierre et Marie Curie, Paris.

Tattersal, I. 1993 The Human Odyssey. Four Million Years of Human Evolution. (Prentice Hall, New York).

[Also Tattersal & Schwartz, J. 2000 Extinct Humans. (Westview Press, New York); Tattersal, I. et al. 2005 The Human Fossil Record. 4 vols. (Wiley, New York)].

Teilhard de Chardin, P. 1955 Le phénomène humain (Seuil, Paris). [1959 The Phenomenon of Man (1965 paperback); Danish: Fänomenet menneske 1960; 1999. The Human Phenomenon (Sussex Acad., Brighton, UK)]

Thomas, H. 1994 L'Homme avant l'Homme, le scenario des origines. (Gallimard, Paris).

Thorne, A. & Wolpoff, M.H. 1992 The multiregional evolution of humans. Sci. Amer. April, 28-33. [See Wolpoff, below].

Trinkaus, E. & Shipman, P. 1992 The Neandertals. 455 pp. (Vintage, New York).

Walker, A. 1976 *Australopithecus, Homo erectus* and the single species hypothesis. Nature 261, 572-4.

Walker, A. & Leakey, R.E. 1978 The hominids of East Africa. Sci. Amer. 239 (2), 44-56.

Walker, A., Leakey. R.E. et al. 1986 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322, 517-522.

[Also Ferguson, W.W. 1989 A new species of the genus *Australopithecus* (Primates: Hominidae) from Plio/Pleistocene deposits west of Lake turkana in Kenya. Primates 30, 223-232 naming WT17000 as type of *A. (=Paranthropus) walkeri* n.sp.]

Walter, R.C. & Aronson, J.L. 1982 Revision of the K/Ar ages for the Hadar hominid site, Ethiopia. Nature 296, 122-127.

[see also W & A 1993 Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. J. Hum. Evol. 25, 229-240; Walter, R.C. 1994 Age of Lucy and the first family: Single crystal 40Ar/39Ar of the Denen Dora and lower Kada Hadar Members of the Hadar Formation, Ethiopia. Geology 22, 6-10; Kimbel, W., Walter, R.C., Johanson, D., Aronson, J.L. et al. 1996 Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. J. Human Evol. 31 (6), 549-561]

Ward, C.V., Kimbel, W.H. & Johanson, D.C. 2011 Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. Science 331 (6018): 750 DOI: 10.1126/science. 1201463. [Also Science Daily Feb. 11, 2011].

Westergaard, B. & Bonde, N. 1986 misprint for 1987 [in Bonde et al. (eds) Naturens Historiefortällere, vol. 2 – see above under Bowler, and refs in Bonde & Westergaard 2004]

White, T. 1977 New fossil hominids from Laetoli, Tanzania. Am. J. Phys. Anthropol. 53, 197-230.

White, T. et al 1999 [*Australopithecus garhi*] – see Asfaw, B., White, T. et al. 1999

White, T. & Suwa, G. 1987 Hominid footprints at Laetoli: facts and interpretations. Amer. J. Phys. Anthropol. 73, 485-515.

White, T., Johanson, D. & Kimbel, W. 1981 Australopithecus africanus: Its phyletic position reconsidered. S. Afric. J. Sci. 77, 445-470.

White, T., Asfaw, B. et al. 2009 *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326, 75-86. (See Gibbons 2009, above).
Wilson, A.C. & Cann, R.L. 1992 The recent African genesis of humans. Sci. Am. 266 (4), 22-27.
Winkler, E. & Schweikhardt, J. 1982 Expedition Mensch. Streifzüge dursch die Anthropologie. 326 pp. (Ueberreuter, Wien)
Wolpoff, M.H. 1968 'Teleanthropus' and the single species hypothesis. Am. Anthrop. 70, 477-493.
Wolpoff, M.H. 1971 Competitive exclusion among Lower Pleistocene hominids: The single species hypothesis. Man 6, 601-614.
Wolpoff, M.H. 1984 Modern *Homo sapiens* origins: A general theory of hominid evolution involving the fossil evidence from East Asia. In F.H. Smith & F. Spencer (eds.) The Origin of Modern Humans: A World Survey of the Fossil Evidence, 411-483. (Liss, New York).
[Also Wolpoff, M.H. 1989 Multiregional evolution: The fossil alternative to Eden. In Mellars, P. & Stringer, C. (eds.) The Human Revolution, 62-108. (Princeton Univ. Press, NJ); Wolpoff et al. 1994 The case for sinking *Homo erectus*: 100 years of *Pithecanthropus* is enough. Cour. Forschungsinst. Senckenberg 1721, 341-361; Wolpoff, M.H. Hawks, J & Caspari, R. 2000 Multiregional, not multiple origins. Amer. J. Phys. Antrhropol. 112, 129-136; Wolpoff 1996 Human Evolution. McGraw Hill, New York); Thorne & Wolpoff 1992, above, contra Stringer].
Wood, B. 1994 The oldest hominid yet. Nature 371, 280-281. [Ad White et al. 2004]
Yerkes, R. & Learned, B. 1925 Chimpanzee Intelligence and Its Vocal Expressions. (Baltimore).

[Correction of some misprints etc are also linked to Bonde homepage at his institute]