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THE QUATERNARY BOUNDARY: 1.8 OR 2.6 MILLIONS YEARS OLD? CONTRIBUTIONS OF EARLY *HOMO*



Sandrine PRAT

ABSTRACT

The Quaternary, which is sometimes also termed the Anthropogene Period, often is linked to the beginning of humankind. But what exactly is the basis in the fossil hominin record for this link, in particular what is the early *Homo* evidence? Since 1999, debate concerning the definition of the genus *Homo* and the identification of its first members has intensified. At the centre of recent debates, there are four hypotheses: (1) all early *Homo* specimens belong to the same species: *Homo habilis sensu lato*; (2) the early *Homo* hypodigm is heterogeneous, two species could be defined: *Homo habilis sensu stricto* and *Homo rudolfensis*; (3) these species do not belong to the genus *Homo* but to the genus *Australopithecus*; or (4) it would be more appropriate to put the specimens of *Homo rudolfensis* into the genus *Kenyanthropus*. The earliest appearance of the genus *Homo* will differ depending upon the favoured hypothesis: 2.45 Myr (hypotheses 1 and 2); 1.9 Myr (hypothesis 3); 1.9 or 2.4 Myr (hypothesis 4, depending on the genus attribution for *habilis* (2.4 Myr if *Homo*; 1.9 Myr if *Australopithecus*)). Our study, based on palaeoanthropological data, is focused on the 2.6-1.6 Myr period. In this paper, we propose to review and assess knowledge of early *Homo* taxonomy in the context of the definition of the Quaternary boundary.

Key words: early *Homo*, cladistic, taxonomy, Quaternary.

RÉSUMÉ

LES LIMITES DU QUATÉNAIRE : 1,8 OU 2,6 MILLIONS D'ANNÉES? APPORTS DE L'ÉTUDE CONCERNANT LES PREMIERS REPRÉSENTANTS DU GENRE *HOMO*

Le Quaternaire est souvent considéré comme une période liée à l'apparition du genre *Homo* et marquée par la diversité de ses représentants, ce qui lui valu parfois d'être défini comme une période « Anthropozoïque ». Mais que nous indique vraiment le registre des hominidés fossiles et en particulier des premiers représentants du genre *Homo*?

La définition du genre *Homo* et l'identification de ces premiers représentants sont l'objet de nombreux débats depuis 1999. Quatre hypothèses sont actuellement débattues : (1) tous les spécimens appartiennent à un seul et même taxon : *Homo habilis* ; (2) deux espèces peuvent être identifiées dans ce groupe : *Homo habilis sensu stricto* et *Homo rudolfensis* ; (3) ces spécimens n'appartiennent pas au genre *Homo* mais au genre *Australopithecus* ; (4) les spécimens de l'espèce *rudolfensis* devraient être mis dans le genre *Kenyanthropus*.

L'émergence du genre *Homo* serait à 2,45 millions d'années (hypotheses 1 et 2) ; à 1,9 million d'années (hypothèse 3) ; à 1,9 ou 2,4 millions d'années (hypothèse 4, selon l'attribution de l'espèce *habilis*, au genre *Homo* (2,4 Ma), ou au genre *Australopithecus* (1,9 Ma)).

Nous exposons dans ce papier les problématiques actuelles et nos propres résultats (analyse cladistique) concernant l'émergence du genre *Homo* en Afrique, en les mettant en perspectives avec les différentes propositions concernant la limite du Quaternaire. Notre propos, basé sur les données paléanthropologiques, est centré sur la période allant de 2,6 à 1,6 millions d'années.

Mots clefs: *habilis*, *rudolfensis*, cladistique, taxinomie, Quaternaire.

1 - INTRODUCTION

The Quaternary, which is sometimes also termed the Anthropogene Period, often is linked to the beginning of humankind. The boundary of the Quaternary, thus, is connected strongly to the date of human origin. But how can you anatomically define the genus *Homo*? And, moreover, who are the first representatives of the genus *Homo*? Since 1999, debate is focused on this definition and on the date of the first occurrence of this genus.

What is exactly the evidence from the fossil hominin record? What information is provided by the hominin fossil bones, and, in particular, specimens of early *Homo*? These early *Homo* specimens are at the centre of major debates concerning the actual number of fossils and species; and the chronological boundaries of this taxon. Three questions can be proposed, who are the first specimens of early *Homo*, when is the first occurrence of the genus *Homo*, and what are the consequences for the determination of the inferior boundary of the Quaternary? We propose in this paper to A)

review and assess knowledge of the early *Homo* specimens; B) present our own approaches and results; C) discuss the identity of the first members of the genus *Homo* and the implications concerning the dating of the human origin and the Quaternary boundary (2.6 Myr or 1.8 Myr?).

2 - THE DEFINITION OF EARLY *HOMO*: A REVIEW

2.1 - THE DEFINITION OF EARLY *HOMO*

Since discovery of the first specimens attributed to *Homo habilis* in the Olduvai Gorge in 1959, and subsequent definition of *Homo habilis* by Louis Leakey, John Napier and Phillip Tobias in 1964, no consensus has been achieved on allotting specimens to early *Homo*. In order to accommodate *H. habilis* into the genus *Homo*, Leakey and collaborators were forced to modify the definition of the genus *Homo* proposed originally by Le Gros Clark (1955). Specially, they reduced the lower end of the cranial capacity range from 900 cm³ to 600 cm³.

Forty-seven dental, thirty-one cranial, twenty-one mandibular and twenty-four postcranial fragments have been allocated to this taxon (Prat, 2000; Prat *et al.*, 2005). These specimens have been discovered in Ethiopia (Hadar, Omo), Kenya (East Turkana, West Turkana, Chemeron), Tanzania (Olduvai), Malawi (Uraha) and the Republic of South Africa (Sterkfontein, Swartkrans, Drimolen) (fig. 1).

Since the middle of the 80's, phylogenetic and taxonomic studies of the genus *Homo* have progressed considerably in a series of steps. Some are the direct result of discovery of new specimens (OH 62, OH 65 at Olduvai Gorge (Tanzania); UR 501, Uraha (Malawi); AL 666-1, Hadar (Ethiopia)). Others result from

reinterpretations of existing anatomical features and the development of new methods and analyses (cladistics, bootstraps technique, 3D coordinate data, and geometric morphometry...).

Recent studies have been conducted, on the one hand, to re-examine the taxonomic validity and composition of the species *habilis* (e.g. specimen diversity representing one or two species), and on the other hand, to discuss the attribution of this species (or these species) to the genus *Homo*. Four hypotheses have been proposed:

(1) all specimens belong to the same species: *Homo habilis sensu lato*.

For some authors (Howell, 1978; Tobias, 1978, 1991, 2003; Blumenshine *et al.*, 2003), all specimens belong to one species: *Homo habilis*. In these authors, metric and morphometric differences between the specimens can be interpreted as an intra-specific variability. They argued that *Homo habilis* is a polymorphic species evolutionarily between *Australopithecus africanus* and *Homo erectus*. For example, the masticatory apparatus is more reduced compared with the australopithecines, but less reduced compared to *Homo erectus*, and the face is less prognathic than the former and more prognathic than the latter. *Homo habilis* exhibits increased brain size and development of the cranial vault relative to australopithecines, but less of an increase than observed in *Homo erectus*.

(2) two species could be defined: *Homo habilis sensu stricto* and *Homo rudolfensis*.

Others researchers (Stringer, 1986; Chamberlain & Wood, 1987; Lieberman *et al.*, 1988; Wood, 1991, 1992; Rightmire, 1993; Lieberman *et al.*, 1996; Prat, 1997, 2000) do not support the retention of a single taxon. They argue that the degree of variation within *Homo habilis sensu lato* is too large relative to what can be justified for a single taxon. Different parameters have been studied: morphology, endocranial volume, sexual dimorphism, and degree and pattern of variation of the cranio-facial measurements. This point of view is the current consensus opinion, but it is important to note that the specimens included in these species differ according to the authors. A majority of the distinctive traits are located on the face. For example, *Homo rudolfensis* exhibits a greater absolute size of the brain case, a face that is widest in its mid-part, complex roots and large crowns, and a powerful masticatory apparatus.

(3) the species *habilis* and *rudolfensis* do not belong to the genus *Homo* but to the genus *Australopithecus*.

For many years, the criteria used to allocate species to *Homo*, and those proposed by Leakey and colleagues to define the genus *Homo* (Leakey *et al.*, 1964), have been considered insufficient or inappropriate. In 1999, Bernard Wood and Mark Collard proposed alternative criteria for defining the genus *Homo*. Wood and Collard (1999 a, b) suggested that the definition of the genus should follow both the evolutionary systematic method of classification and the cladistic criteria.

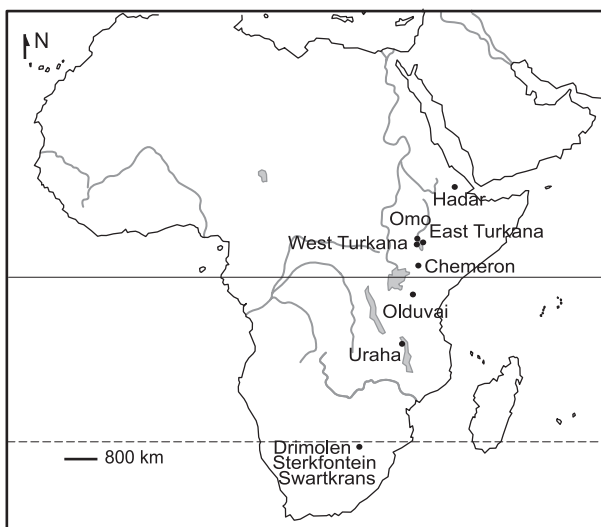


Fig. 1: Map of distribution of early *Homo* specimens.

Fig. 1 : Carte de répartition des fossiles attribués aux premiers représentants du genre *Homo*.

Genus names should correspond to both grades and clades (fig. 2). According to their criteria, a genus is a group of species that are related more closely to one another than to species assigned to another genera (cladistic interpretation) occupying an ecological situation, or adaptive zone, that is different from that occupied by the species of the genus in question (evolutionary systematic interpretation) (Wood & Collard, 1999 a).

They tested whether or not the genus *Homo* (including both *Homo habilis* and *Homo rudolfensis*) is monophyletic and adaptively coherent. For them, all the species within genus *Homo* must share a functionally coherent adaptive strategy with *H. sapiens* rather than with other genera (e.g. *Australopithecus*). But the species *habilis* and *rudolfensis* present an australopith-like pattern rather than a modern human-like pattern for body mass (relatively low), body shape (interpreted in terms of thermoregulation as being better suited to a relatively closed environment), locomotion (combination of terrestrial bipedalism with proficient climbing), morphology of the jaws and teeth, development and brain size (Wood & Collard, 1999b). Moreover, the genus *Homo* is monophyletic, in the spirit of Wood and Collard, only if the species *habilis* and *rudolfensis* are excluded. Therefore, they proposed that *habilis* and *rudolfensis* should be placed in the genus *Australopithecus* as *Australopithecus habilis* and *Australopithecus rudolfensis*, respectively (Wood & Collard, 1999 a, b).

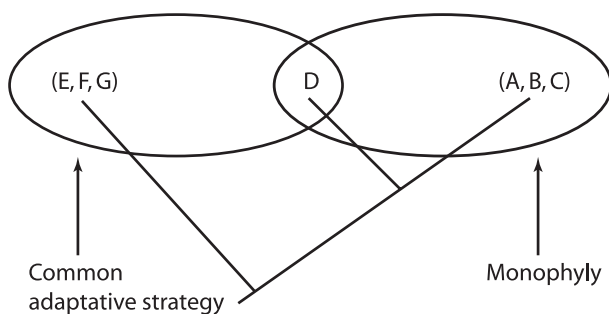


Fig. 2: Definition of a genus according evolutionary systematic (left) or cladistic (right) criteria (after Wood & Collard, 1999 b).

Fig. 2 : Définition du genre selon les méthodes de classification évolutionniste (à gauche) ou les méthodes cladistiques (à droite) (d'après Wood & Collard, 1999 b).

(4) it would be more appropriate to put *Homo rudolfensis* into the genus *Kenyanthropus*.

More recently, in 2001, Meave Leakey and colleagues described a new species they termed *Kenyanthropus platyops*. For them, this new species has close affinities (especially in its facial morphology) with KNM-ER 1470, which is the holotype specimen of *Homo rudolfensis*. Thus, while the transfer of this species to the genus *Australopithecus* has been recommended by others (see preceding point), it would be more appropriate to put *rudolfensis* into genus

Kenyanthropus (Leakey *et al.*, 2001 p. 439). No genus attribution for *habilis* is mentioned by these authors.

2.2 - GEOGRAPHICAL AND CHRONOLOGICAL SETTING

All *habilis* and *rudolfensis* specimens have been discovered in Ethiopia, Kenya, Tanzania, Malawi and the Republic of South Africa. Dating of these specimens, in particular those of the East Turkana region in Kenya have been at the heart of many controversies between 1970 and 1989. Indeed, these dating are linked to those of the associated tuffs. For example, the KBS tuff, which delimited the top of the upper Burgi Member, has been dated to 2.44 +/- 0.03 Myr by Fitch and Miller in 1970. But the review of the isotopic and magnetostratigraphic dating evidence demonstrates that the KBS is dated to 1.88 +/- 0.02 Myr (Feibel *et al.*, 1989), or 1.87 +/- 0.02 Myr (McDougall & Brown, 2006). Some specimens ascribed to *rudolfensis* (e.g. KNM-ER 1470, ER 1801, ER 1802) and *habilis* (e.g. ER 3735 and the fossil from Area 123 (ER 1501, 1502, 1813)) are below the KBS tuff. This implies that during the 70's and 80's, these early *Homo* specimens were considered older than 2.5 Myr, but after the review of Feibel *et al.* (1989) their dates were revised to 1.8-1.9 Myr. Moreover, it must be noted that the stratigraphical position and dating of the fossils from Area 123 (in which some are allocated to *habilis*) are still debated (Gathogo & Brown, 2006). Indeed, for Gathogo and Brown, these fossils belong to the KBS member rather than the upper Burgi Member, as proposed by Feibel *et al.*, 1989. These specimens are placed relative to the airfall KBS tuff and the lower Ileret Tuff, which have been dated to 1.87 +/- 0.02 Myr and 1.53 +/- 0.01 Myr respectively (McDougall & Brown, 2006). Their stratigraphic revisions result in age estimates between 1.53 and 1.75 Myr for the fossils from Area 123 whereas they were believed to be between 1.65 and 1.9 Myr in age (Gathogo & Brown, 2006, p. 478).

In the beginning of the 90's, additional fieldwork in Malawi, Kenya and Ethiopia, led to the discovery of new specimens of *habilis* and *rudolfensis* at 2.3-2.4 Myr. Therein, they provide new data for the chronological framework of these species. However, across Africa, few cranial specimens allocated to early *Homo* are known from this time period. They are represented by the temporal bone KNM-BC 1, recovered at Chemeron, Kenya, 2.4 Myr (Hill *et al.*, 1992; Sherwood *et al.*, 2002); the mandible UR 501 from Uraha, Malawi, ca. 2.45 Myr (2.3-2.5 Myr) ascribed to *Homo rudolfensis* (Schrenck *et al.*, 1993; Bromage *et al.*, 1995); the maxilla AL 666-1 from Hadar, Ethiopia, 2.33 +/- 0.07 Myr, allocated to *Homo aff. H. habilis* according to the morphology of the palate and the alveolar region (Kimbel *et al.*, 1996); and teeth from the Omo basin, Ethiopia, 2.3-2.4 Myr (Suwa *et al.*, 1996). More recently, in the Lokalalei complex site in West Turkana (Kenya), a first molar, dated to 2.34 +/- 0.05 Myr also has been allocated to early *Homo* (Prat

et al., 2005). Thus, the chronological distribution is circa 2.45-1.85 Myr for *rudolfensis* and 2.4-1.6 Myr for *habilis*.

3 - THE DEFINITION OF THE GENUS *HOMO*: ANOTHER PERSPECTIVE

Concerning the taxonomic position of the early *Homo* specimens, we have proposed another point of view (Prat, 2000, 2004, 2005) based on a cladistic analysis of twenty-two original Plio-Pleistocene specimens.

3.1 - MATERIAL AND METHODS

Cladistic analysis is the method of choice for reconstructing the relationships among species, when it can be assumed that the phenotype is an efficient safe proxy for genetic affinity.

Because no consensus concerning the hypodigm of the species *Homo habilis* has been achieved, our analysis is **based on specimens, not on species** to define the Operational Taxonomic Unit (OTU). Indeed, because the aim of our analysis is to understand and define this species, the creation of an OTU based on the species would have been a circular reasoning. This approach with the specimen as OTU has been used by Capparo (1997), Zeitoun (2000), Prat (2000), Asfaw *et al.* (2002) and Gilbert *et al.* (2003). Our study, therefore, differs from prior studies concerning early *Homo* phylogeny, where the OTU is defined by the species (Skelton *et al.*, 1986; Skelton & McHenry, 1992; Lieberman *et al.*, 1996; Strait *et al.*, 1997; Strait & Grine, 2004).

For our analysis, the trait list comprises 122 cranial features. This list and the definition of the traits are derived both from our own observations (Prat, 2000) and a compilation list of various other studies (Chamberlain & Wood, 1987; Lieberman *et al.*, 1996; Skelton *et al.*, 1986; Skelton & McHenry, 1992; Strait *et al.*, 1997; Stringer, 1987; Tobias, 1991; Zeitoun, 2000).

We scored features on original material (see illustration in Prat, 2000, 2004, 2005). Outgroup taxa used in the present analysis are mature specimens of *Pan* and *Gorilla*. This included twenty-five males and twenty-five females of *Pan* (*Pan paniscus*, *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthi*) and fifteen males and fifteen females of *Gorilla* (*Gorilla gorilla gorilla*, *Gorilla gorilla beringei*, *Gorilla gorilla graueri*). All specimens are from the Musée Royal d'Afrique Centrale de Tervuren (Belgium) and the Powell Cotton Museum (United Kingdom).

The ingroup includes 22 original hominin specimens in the first analysis, and 23 specimens (the same specimens plus KNM-WT 40 000, holotype of *Kenyanthropus platyops*) in the second one. These specimens represent the most preserved accessible Plio-Pleistocene specimens. This fossil sample is comprised of original

cranial specimens discovered in Ethiopia, Kenya, Tanzania, and Republic of South Africa. For KNM-WT 40000, data were obtained from the literature. Specimens from Hadar (Ethiopia), AL 666-1 (Kimbel *et al.*, 1996), and from the Olduvai Gorge, OH 65 (face and palate), described by Blumenshine and colleagues (Blumenshine *et al.*, 2003), are not included in this study because their data come from the literature, and their condition is judged too fragmentary.

All 122 traits have been used independently to maximize information. Furthermore, an effort was made to eliminate characters that redundantly describe the same underlying morphological feature. Dental data have been excluded in this analysis because many specimens are edentulous. Moreover, since cranial capacity has been estimated for only a small number of specimens in the sample, it was excluded as well.

Character polarity has been determined by rooting the out-group. The polymorphism is coded as multiple states (0/1, 0/2, 0/1/2) with the polymorphism option of the Paup 3.1 software (Swofford, 1993). Quantitative characters were coded using the method proposed by Thiele (1993) ($xs = ((x - \min) / (\max - \min))^n$; $n =$ maximum number of ordered states allowable by the algorithm used (32 for PAUP), after a logarithmic transformation of data). Data have been computed in a non-arbitrary way in order to avoid any preconceived phylogenetic hypothesis. The most parsimonious trees have been obtained using the heuristic algorithm with the options "general, starting trees, stepwise addition and branch swapping". These trees are presented with their length, their consistency index, and their retention index. These indices measure the relative amount of homoplasy. Consistency index (CI) is calculated as the minimum possible tree-length divided by the observed tree-length (Farris, 1989). If there is no homoplasy in a tree, then its observed length equals the minimum tree-length, and the CI equals one. If homoplasy is present, then the CI is less than one. Retention index (RI) is calculated by subtracting observed tree-length from maximum possible tree-length, and then dividing this value by the difference between maximum and minimum lengths (Archie, 1989; Farris, 1989).

3.2 - RESULTS

- *Homo* / *Australopithecus*

Three equally parsimonious trees have been obtained using all option analyses (« general, starting trees, stepwise addition or branch swapping ») based on 122 unordered cranial characters, which were taken on 22 mature fossil individuals. A consensus tree (fig. 3) has been constructed based on topologies of all trees. The length of this tree is 431 steps with a consistency index of 0.452 and a retention index of 0.431.

The result of the analysis suggests the existence of two monophyletic groups: the *Homo* clade defined at node A and the *Australopithecus* clade defined at node B. The *Homo* clade is defined by (((((KNM-ER

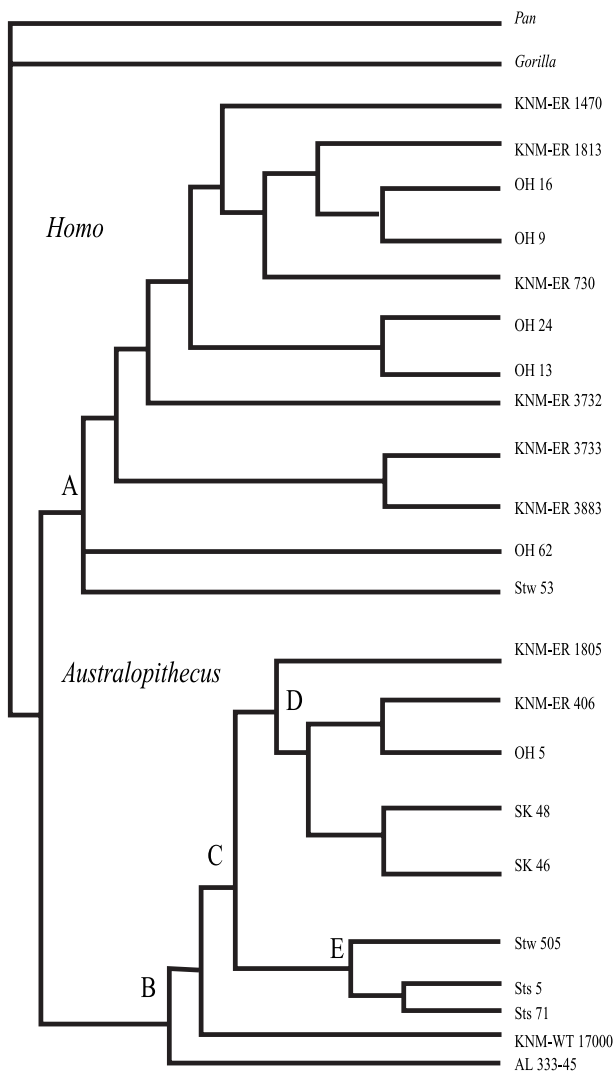


Fig. 3: Most parsimonious cladogram. Consensus tree, 122 traits, 22 mature specimens (L= 421 steps, IC = 0.452; IR= 0.431).

Fig. 3 : Arbre de consensus strict des trois arbres les plus parcimonieux se rapportant à 122 caractères crâniens non ordonnés et 22 spécimens fossiles adultes (L = 421 pas, IC = 0,452, IR = 0,431).

1470((KNM-ER 1813(OH 16, OH 9))KNM-ER 730))(OH 24, OH 13)KNM-ER 3732)(KNM-ER 3733, KNM-ER 3883))OH 62) Stw 53) at node A by six unambiguous characters: asymmetrical shape of the postglenoid process, uniform petrous crest, articular eminence with two joint areas (angle superior to 90°), angle between the articular eminence and the preglenoid planum (parallel with clade C), medial position of the parietal prominence, and presence of an anterior nasal spine.

The *Australopithecus* clade is defined, at node B, by (((((KNM-ER1805((KNM-ER406,OH5)(SK48,SK46))) (Stw505(Sts5,Sts71)))KNM-WT17000)AL333-45) by four unambiguous characters. The synapomorphies are anterior position of the foramen magnum relative to the bi-tympanic line, presence of temporal crests and presence of a sagittal crest (on the anterior part of the bregma-lambda arch) with a moderate expansion. The sagittal crest is not observed in *Pan*. This trait is only observed in some *Gorilla* specimens (on 35% of females,

43% of males; 70% of adult overall). The presence of a sagittal crest is influenced to a greater extent by the anatomical age rather than by the sex of the individuals (Prat & Thackeray, 2001).

- *Homo / Kenyanthropus*

The new cladistic analysis (fig. 4) includes data from the description of the new Kenyan specimen KNM-WT 40000, the holotype of the species *Kenyanthropus platyops*. Results indicate that the following specimens: KNM-ER 730, 1470, 1813, 3732, 3733, 3883, OH 9, 16, 13, 24, 62, Stw 53, belong to the clade *Homo* (defined at node A). In other words, these specimens are not linked with *Kenyanthropus platyops* (KNM-WT 40000).

The consensus tree of the two most parsimonious trees has a length equal to 442 steps with a consistency index of 0.442 and a retention index of 0.431. Synapomorphies at node A are a flat glabellar region in *norma lateralis*, a lateral postorbital depression, absence of a sagittal crest, a weak development of the supramastoid crest, no junctions between the mastoid and supramastoid crests, an uniform petrous crest, a canine region independent of the piriform aperture, no lateral prominence of the zygomatic bone, the inferior part of the orbital region posteriorly located relative to the superior part and nasal bone eversion.

It is worth noting in this analysis both that, KNM-WT 40000 is linked neither with *Homo* nor *Australopithecus* specimens, and that, with the introduction of this specimen, *Australopithecus* becomes paraphyletic. New analyses based on the cast or on the original specimen of KNM-WT 40000, instead of the data derived from existing studies in the literature, are required.

4 - DISCUSSIONS AND CONCLUSIONS

4.1 - WHO ARE THE FIRST MEMBERS OF THE GENUS *HOMO*?

Cladistic analysis indicates that the specimens KNM-ER 1470, KNM-ER 1813, KNM-ER 3732, OH 24, OH 62 and Stw 53 belong to the genus *Homo* rather than the genus *Australopithecus* (fig. 3). Furthermore, KNM-ER 1470 is not grouped with KNM-WT 40 000 (fig. 4), holotype of *Kenyanthropus platyops*, as was proposed by Leakey *et al.*, 2001.

The *Homo* genus is monophyletic even if the specimens of the species *habilis* and *rudolfensis* are included (Prat, 2000, 2004, 2005). These results have been confirmed by other analyses (e.g. Strait & Grine, 2004), but contrast with additional studies (e.g. Wood & Collard, 1999 a, b) that use the same methodological approach (cladistic analysis). For the latter authors, the earliest species of *Homo* is *ergaster*. They also argued (Wood & Collard, 1999 a, b; Wolpoff, 1999) that an important change in terms of body proportions, brain

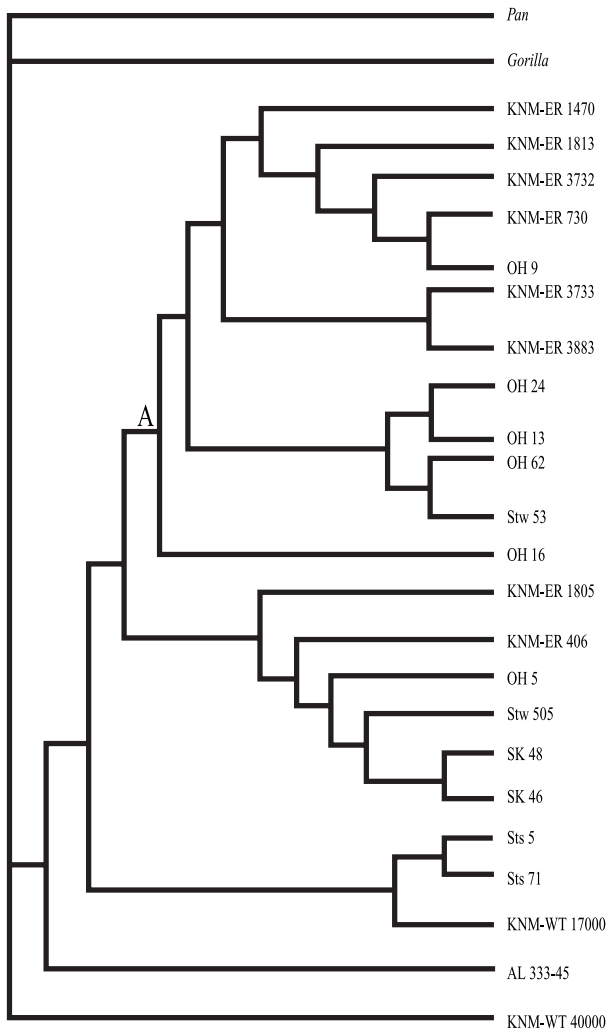


Fig. 4: Most parsimonious cladogram. Consensus tree, 122 traits, 23 mature specimens (L= 442 steps, IC = 0.442; IR= 0.431).

Fig. 4 : Arbre de consensus strict des deux arbres les plus parcimonieux se rapportant à 122 caractères crâniens non ordonnés et 23 spécimens fossiles adultes (L = 442 pas, IC = 0,442, IR = 0,431).

size and facial morphology occurs between *habilis/rudolfensis* and *ergaster* (referred as early *Homo sapiens* by Wolpoff (1999)). However, one specimen from Dmanisi (D2700) exhibits facial morphology and brain size approximating those associated with *Homo habilis* (Vekua *et al.*, 2002). Thus, any discussion about substantial morphological change between *habilis* and *ergaster* requires further examination of the Dmanisi specimen.

Moreover, it is important to note the existence of a methodological problem in comparing different cladistic results. Differences between tree topology could be due to species attribution of specimens or to the traits included in the analyses. For example, allocation, for example, of the Kenyan specimen KNM-ER 1805 to the species *Homo habilis* has some important consequences for the character state assignment of this species. Indeed, “presence of a sagittal crest and presence of a temporo-nuchal crest” are coded “yes” for *habilis* (Skelton & McHenry, 1992, p. 321; Strait *et al.*, 1997, p. 26), simply because of the inclusion of KNM-ER 1805 in this species (for temporo-nuchal

crest « the *H. habilis* state assignment is based on KNM-ER 1805 », Strait *et al.* 1997, p. 69). However, if we do not consider KNM-ER 1805 to be the average male *Homo habilis* (Prat, 2002), then these traits are coded « no » and all topology of the consensus tree can be modified.

Concerning significance of the morphological traits used in the comparative and cladistic studies, it is essential to test whether the traits are homologous (Lieberman, 1999; Lockwood & Fleagle, 1999) or independent [i.e. not functionally- or structurally-related (Skelton & McHenry, 1998; Strait & Grine, 1998; Strait, 2001)]. It is also important to exclude non-informative diagnostic traits (Capparos, 1997). Moreover, it is important to test whether the traits are related to developmental age or to sex-specific characteristics of the specimen (Prat, 2000; Prat & Thackeray, 2001). Indeed, numerous traits, that distinguish the two groups in this study, much less others (Lieberman *et al.*, 1996; Strait *et al.*, 1997), could be related to the sex-specific characters or to the age of the specimen. Re-examination of the significance of traits is necessary for all comparative and phylogenetic studies.

4.2 - IMPLICATIONS FOR DATING THE FIRST OCCURRENCE OF THE GENUS *HOMO*

The four main hypotheses concerning taxonomic allocation of early *Homo* (cf. *supra* paragraph 2.1. and 2.2.) have some important implications for dating the earliest occurrence of the genus *Homo*.

The appearance of genus *Homo* is at:

- 2.45 Myr for hypothesis 1 (all the specimens belong to the same species *Homo habilis sensu lato* (fig. 5a)) and hypothesis 2 (two taxa can be distinguished in genus *Homo*: *Homo habilis sensu stricto* and *Homo rudolfensis* (fig. 5b)). Our results are in accordance with the latter hypothesis;
- 1.9 Myr for hypothesis 3 (the two species *habilis* and *rudolfensis* do not belong to genus *Homo*, but belong instead to genus *Australopithecus* (fig. 5c)). *Homo ergaster* and the Dmanisi specimens (Gabunia & Vekua, 1995; Gabunia *et al.*, 2000; Vekua *et al.*, 2002; Lordkipanidze *et al.*, 2005) are the first members of the genus *Homo*, at 1.9 Myr. Dates of *Homo ergaster* in Africa are between 1.45 to 1.9 Myr, with majority of specimens dated between 1.45 and 1.65 Myr, if we refer to the new age estimations of the specimens from Koobi Fora (Gathogo & Brown, 2006; Brown *et al.*, 2006).
- 1.9 Myr or 2.4 Myr for hypothesis 4 (it would be more appropriate to put *rudolfensis* into the genus *Kenyanthropus* (fig. 5d)). According to the genus attribution of the *habilis* specimens, the first appearance of genus *Homo* is at 2.4 Myr if *habilis* is allocated to *Homo* genus or at 1.9 Myr if *habilis* is allotted to *Australopithecus* genus.

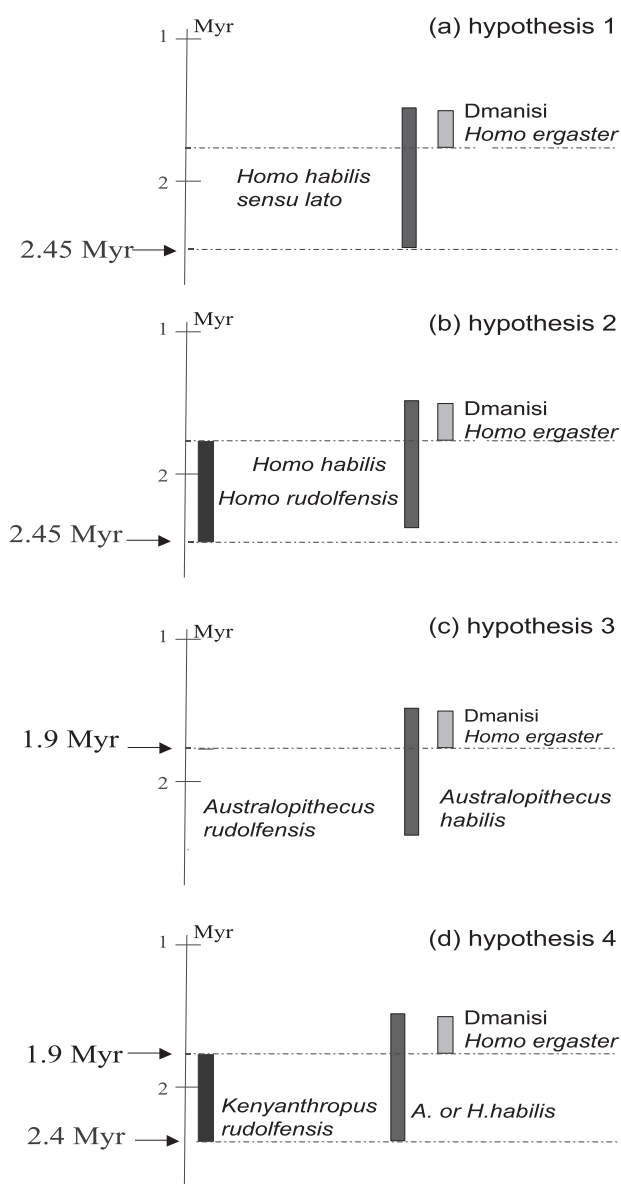


Fig. 5: Hypotheses concerning the first appearance of genus *Homo*.
 a) 2.45 Myr, one species; b) 2.45 Myr, two species, hypothesis selected in this article; c) 1.9 Myr; d) 1.9 or 2.4 Myr.
 Fig. 5 : Hypothèses concernant l'émergence du genre *Homo*.
 a) 2,45 Ma, une espèce ; b) 2,45 Ma, deux espèces, hypothèse retenue dans cet article ; c) 1,9 Ma ; d) 1,9 ou 2,4 Ma.

4.3 - IMPLICATION FOR THE DEFINITION OF THE QUATERNARY

Our prior results based on morphological and metric comparisons (Prat, 1997, 2000, 2004), as well as this current cladistic analysis (*cf. supra*), emphasize, on the one hand, that two species could be distinguished and defined *habilis* and *rudolfensis*, and on the other hand, that they belong to genus *Homo*. This implies an earliest appearance for the genus *Homo* at or before 2.45 Myr.

This date corresponds to a major climatic event (at 2.6 Myr) as well as the earliest known stone tools. Indeed, the earliest known occurrence of stone tools is at

2.3-2.6 Myr with the stone tools assemblages from Gona, Ethiopia (Roche & Tiercelin, 1977; Semaw *et al.*, 1997), and with the first knapping site (Lokalalei 2C; Roche *et al.*, 1999). Early *Homo*, present in this time period, could be a good candidate from knapping this lithic assemblage. But the presence of other species such as *P. aethiopicus* and *A. garhi* ought not to be ignored (Prat *et al.*, 2005). Concerning climatic changes, the marine sediment sequences demonstrate that climate variability and aridity increase near 2.8 Myr (deMenocal, 2004). Faunal assemblages portray more varied and open habitats at 2.9-2.3 Myr. The 2.9-2.5 Myr interval corresponds to an increase in the proportion of arid-adapted fauna and a change to open grassland as the dominant type of environment (Reed, 1997; Bobe *et al.*, 2002; Alemseged, 2003). Soil carbonate stable isotopic analysis (Cerling *et al.*, 1994; Wynn, 2004) and marine paleoclimatic records (deMenocal, 1995) indicate another intensification of aridity that is associated particularly with more open habitats near 1.8-1.6 Myr.

If we consider that the beginning of humankind is one point that defines the Quaternary, then the boundary of the Quaternary must be extended back to at least 2.45 Myr. It is in accordance with a boundary of the Quaternary at 2.6 Myr, which has been proposed previously by Pillans & Naish (2004), corresponding to major sedimentological and climate changes, with a strong influence by bi-polar glaciation.

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