



# Emergence of the genus Homo: From concept to taxonomy

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Emergence of the genus *Homo*: from concept to taxonomy  
Emergence du genre *Homo* : du concept à la taxonomie

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Abstract

The main goal of this paper is to present an overview of hypotheses concerning early *Homo* specimens and to discuss the definition of the genus *Homo* in the light of recent discoveries. For some authors, all the specimens attributed to early *Homo* belong to one unique species. For others, this group (*Homo habilis* sensu lato) is heterogeneous and could be splitted into two groups: *Homo habilis* and *Homo rudolfensis*. Some researchers have also proposed to put the species *habilis* and *rudolfensis* into the genera *Australopithecus* or *Kenyanthropus*. Therefore, two scenarios concerning first humans seem to emerge. An emergence of the genus *Homo*, as early as 2.8 Ma, with *Homo* sp. specimens and the species *Homo habilis* and *Homo rudolfensis*, another at 1.9 Ma with *Homo ergaster*. According to the recent archaeological and palaeoanthropological discoveries, these criteria often considered to be crucial for the definition of the genus *Homo*, as the cranial capacity, the human-like manipulative abilities, the habitual erect posture and bipedal gait, the language ability and the capacity to make tools are now obsolete.

Résumé

Le but de cet article est de présenter une vue d'ensemble des hypothèses concernant les premiers représentants du genre *Homo* et de discuter de la définition notre genre à la lumière des découvertes récentes. Pour certains auteurs, tous les spécimens attribués aux premiers représentants du genre *Homo* appartiennent à une unique espèce. Pour d'autres auteurs, ce groupe (*Homo habilis* sensu lato) est hétérogène et pourrait être séparé en deux groupes : *Homo habilis* et *Homo rudolfensis*. Certains chercheurs ont également proposé de placer les espèces *habilis* et *rudolfensis* dans les genres *Australopithecus* ou *Kenyanthropus*. Par conséquent, deux scénarios pour l'émergence du genre *Homo* semblent se dessiner. Une émergence du genre *Homo*, dès 2,8 Ma, avec les spécimens *Homo* sp. et les espèces *Homo habilis* et *Homo rudolfensis*, ou à 1,9 Ma avec *Homo ergaster*. D'après les récentes découvertes archéologiques et paléoanthropologiques, les critères souvent considérés comme cruciaux pour la définition du genre *Homo*, comme la capacité crânienne, les capacités de manipulation de type humain, la posture érigée et la démarche bipède, la capacité de langage et la capacité de fabriquer des outils sont désormais caduques.

Mots clefs : *Homo habilis*, *Homo rudolfensis*, taxonomie, définition  
Keywords : *Homo habilis*, *Homo rudolfensis*, taxonomy, definition

## 1. Introduction

For nearly 70 years, *Homo erectus* (formerly *Pithecanthropus erectus*), whose first remains were discovered at Java (Indonesia) in 1890 by Eugène Dubois, were considered to be the oldest specimens of the genus *Homo*. In 1964, Louis Leakey, Phillip Tobias and John Napier, by discovering and naming the species *Homo habilis*, from individuals dating back to 1.75 million years (Ma), changed the picture of our family tree (Leakey *et al.*, 1964). Our oldest ancestors are now considered as african and are dated nowadays to 2.8 Ma with the discovery of the hemi-mandible from Ledi Geraru site (Villmoare *et al.*, 2015).

The debate that ensued, and which is still ongoing, concerns the number of species within the early taxa of the genus *Homo* and therefore the definition of our genus. The purpose of this paper is to present an overview of problematics concerning the early *Homo* specimens and to discuss about the definition of the genus *Homo* in the light of recent discoveries. Three species currently seem to be subject of consensus: *habilis*, *rudolfensis* and *ergaster*. However, two major debates concern these fossil groups. One relates to early *Homo*, the other to the definition of *Homo erectus* and on the possible inclusion of african and caucasian individuals in this species, which is not the focus of this paper. These two debates refer to a recurrent discussion in palaeoanthropology concerning the existence of one or several species within fossil hominin groups. Two schools of thought diverge on this point. The first, called "splitting" leads to multiply the number of taxa discovered. The second, called "lumpers", reduces the number of fossil species to a minimum. It has to be noticed that the definition of a fossil species is highly subjective since, due to the nature of the object studied: the fossil, it cannot follow the notion of species defined by Mayr (1940, 1987) as 'species are groups of interfertile natural populations that are reproductively isolated from other similar groups' (Mayr, 1987: 306).

## 2. Some historical milestones

As early as 1871, Darwin already mentioned in "the Descent of Man" (Darwin, 1871) that human origin must have been in Africa. It was with the prospect to discover the oldest human remains in Africa that Louis and Mary Leakey have undertaken research in the Olduvai Gorge in Tanzania. These fossils were allocated to the genus *Homo* and named *Homo habilis* in 1964 (Leakey *et al.*, 1964) after a lot of reconstructions and comparisons. It was the subject of much criticism. These concerned in particular the nature of the anatomical characters used and the characteristics of the metric variability that made it possible to distinguish the species *Homo habilis* from both *Australopithecus* and *Homo erectus*, leading some authors (e.g. Holloway, 1965; Robinson, 1965; Brace *et al.*, 1973) to consider *Homo habilis* as an artificial cluster of *Australopithecus* and *Homo erectus* specimens. Despite these discussions, the concept of the existence of the species *Homo habilis* was definitively validated by the scientific community in 1968 following the discovery of the OH 24 skull in Olduvai.

The original description of *Homo habilis* emphasized the similarity of its features to *Homo sapiens* and the increase in brain volume compared to australopithecines. By integrating the species *habilis* into the genus *Homo*, it became necessary to revise the diagnosis of this genus established by Le Gros Clark (1955) as a genus of the family Hominidae, distinguished by a high cranial capacity with an average value of over 1100 cm<sup>3</sup> but with a range of variation from about 900 to 2000 cm<sup>3</sup>. The discoverers of the species *Homo habilis* therefore proposed this new definition: "... the cranial capacity is very variable but is, on the average, larger than the range of capacities of members of the genus *Australopithecus*, although the lower part of the range of capacities in the genus *Homo* overlaps with the upper part of the range in *Australopithecus*; the capacity is (on the average) large relative to body-size and ranges from about 600 c.c. in earlier forms to more than 1600 c.c...." (Leakey *et al.*, 1964, p. 7).

In 1972, Richard and Meave Leakey found nearly three hundred cranial fragments of a single individual on the surface, which, when completely reconstructed, became the skull KNM-ER 1470. Its chronological dating was established at 2.42 Ma at the time of discovery (Fitch *et al.*, 1976) and later re-evaluated at 1.85 Ma (Feibel *et al.*, 1989) and now to 2.05 +/- 0.034 Ma (Joordens *et al.*, 2013). Its specific attribution was (and still is) subject of debate. Richard Leakey initially placed this specimen in the taxon *Homo* sp. (Leakey, 1976a), but later considered that it belongs to *Homo habilis* (Leakey, 1976b). After a re-examination of this

specimen, Alexeev proposed in 1978 a new species: *Homo rudolfensis*. The diagnosis and description of this species was published in Russian (Alexeev, 1978) and later in English (Alexeev, 1986), based on the Kenyan specimen KNM-ER 1470. In this paper, the author mentions neither the type locality, nor the distribution, nor the hypodigm of this taxon, and puts forward only few distinctive anatomical characters. This species was not recognized by the scientific community until the early 1990s, partly due to the Bernard Wood's work (Wood, 1992). The systematic validity of this species, with respect to the rules of international nomenclature, was and remains the subject of controversy (Kennedy, 1999; Wood, 1999).

Since the first discoveries in the 1960s, more than 200 remains, mainly cranial and dental elements, have been attributed to early *Homo* (*habilis*, *rudolfensis* and *Homo* sp. older than 2 Ma). These remains are mostly located at Hadar and Omo Valley in Ethiopia, West and East Turkana and Chemeron in Kenya, Olduvai in Tanzania, Uraha in Malawi and Drimolen, Sterkfontein and Swartkrans in South Africa (Figure 1). From a chronological point of view, the early *Homo* individuals range from 2.8 Ma to 1.65 Ma.

## INSERT FIGURE 1 : Map

### 3. Current issues. One or more species? *Homo* or *Australopithecus*?

Since the mid-1980s, the development of statistical methods (particularly multivariate) and cladistics has contributed to questioning the certainties concerning the unity of *Homo habilis* sensu lato and its generic allocation. The debate has indeed refocused on the problem of intra-specific variability within this taxon. Are we dealing with one or two palaeontological species? Two schools of thought illustrating the different interpretations were put forward. For some, the variability is consistent with intra-specific variability, i.e. all these specimens belong to the same group (1 species). Conversely, for others, two groups can be determined from these specimens that are both metrically and morphologically distinct (2 species).

#### 3.1. One or two species?

##### 3.1.1. One species: *Homo habilis* sensu lato

For some authors (e.g. Howell, 1978; Blumenschine *et al.*, 2003; Tobias, 1978, 1987, 1991, 2003), all the specimens attributed to early *Homo* belong to one unique species. The metric and morphological variability between these specimens would be compatible with an intra-specific variability. *Homo habilis* is thus considered as a polymorphic species. The specimens grouped in a single species *Homo habilis* sensu lato show a reduction of the masticatory apparatus, with an insertion of the masticatory muscles less important compared to australopithecines. The facial and alveolar regions are less prognathic, the anterior pillar of the face as well as the frontal trigone (observed in *Paranthropus*) and the maxillary sulcus are absent. The mandible is parabolic in shape, the mandibular body is less high and robust, and the chin prominence is slightly developed in some individuals. The temporo-mandibular articulation is close to the third molar, which is related to the low projection of the face. The nuchal region is relatively smaller than in australopithecines. The foramen magnum is located more anteriorly. Concerning the dentition, the upper anterior teeth (incisors, canines) are not aligned and large, unlike those of specimens attributed to *Paranthropus*. The upper molars are small. The upper third molar is the smallest while the lower third molar is sometimes larger than the second. The lower molars are characterized by an elongation in length (mesio-distal diameter) and a narrowing in width (vestibulo-lingual diameter). Other distinctions are essentially related to brain growth and concern the development of the cranial vault (especially the development of the parietal and upper temporal regions). *Homo habilis* is characterized by a cranial capacity between 509 and 824 cm<sup>3</sup> (Holloway, 2004; Spoor *et al.*, 2015), which is on average greater than that of australopithecines.

The differences are important between cranial specimens allocated to early *Homo* and *Paranthropus*. However, they are less marked with the *A. africanus* and *A. afarensis* individuals. Some remains have been attributed either to *Homo habilis* or to *Australopithecus africanus* or another hominin taxa, depending on

the authors. This is notably the case for the South African specimen Stw 53 (e.g. Kuman and Clarke, 2000; Curnoe and Tobias, 2006; Curnoe, 2010; Zanolli *et al.*, 2022).

### 3.1.2. Two species: *Homo habilis sensu stricto* and *Homo rudolfensis*

For other authors, this group (*Homo habilis sensu lato*) is heterogeneous and could be separated into two groups: *Homo habilis* and *Homo rudolfensis* (e.g. Alexeev, 1978, 1986 ; Chamberlain and Wood, 1987, Donnelly, 1996, Ferguson, 1995 ; Lieberman and Pilbeam, 1988; Lieberman *et al.*, 1996; Prat, 1997, 2000, 2004; Rightmire, 1993 ; Stringer, 1986 ; Walker & Leakey, 1978 ; Wood, 1991, 1992). Different parameters were used: morphological characters, variation in endocranial volume, degree and pattern of variation in craniofacial measurements and cranial angles. This view is followed by the majority of researchers, although there is no consensus, concerning the specimens allocated to each taxon.

The table presented here (Table 1) is based on a literature review of the work of different researchers (Chamberlain, 1987; Lieberman *et al.*, 1996; Prat 1997, Prat 2000; Rightmire, 1993; Skelton *et al.*, 1986; Skelton and McHenry 1992; Strait *et al.* 1997; Tobias, 1991; Wood, 1991). This table therefore offer a synthetic view, reflecting the greatest consensus on anatomical distinctions. It should be noted, however, that there is some divergence with respect to the individuals that constitute each taxon. Some trait assignments are related to the developmental age of the individual or are highly dimorphic in extant great apes (see for discussion and data Prat (2000)).

#### **INSERER Table 1**

Thirty-two morphological traits allow to distinguish these two species *habilis* and *rudolfensis* (Table 1). The maxillofacial complex plays a major role in this differentiation (e.g. Prat, 1997, 2004; Rightmire, 1993). They are discriminated by the different proportions of the upper and middle face (identical width in *Homo habilis*), the alveolar prognathism (smaller in *Homo rudolfensis*) and the size of the zygomatic bone (smaller in *Homo habilis*). Among the latter, a zygomatico-maxillary fossa can be observed in some specimens. The orientation of the zygomatic process of the maxillary bone is vertical, when the skull is positioned in the Frankfurt reference plane. Distinctions can also be seen in the orbital region and superior nasal bones. The shape of the orbits is more square in *Homo rudolfensis* specimens (notably KNM-ER 1470) and the superior orbital margin is ovoid. The horizontal distance between the tempo-mandibular joint and the upper M2/M3 is small in *Homo habilis*, which is related to the low projection of the face for these individuals. Anatomical differences can also be observed between the mandibular remains attributed to early *Homo*, but it should be noticed that only two main mandibles KNM-ER 1802 and UR 501 are related to the species *Homo rudolfensis*. The two species differ mainly in the shape of the chin region, which is sub-rectangular in *Homo rudolfensis* specimens. In the latter, the alveolar planum is large. Concerning the upper dentition, the anterior teeth (incisors, canines) are smaller in *Homo habilis*. The occlusal surface of the first molar is small. The premolars generally have two roots, unlike *Homo rudolfensis*, where three roots are observed. In the lower dentition, the anterior dentition is also smaller in *Homo habilis* specimens. The premolar of these individuals generally has only one root, unlike *Homo rudolfensis*, where the first premolar can either have two roots or a bifid root and the second premolar has two roots. The third molar has a larger occlusal surface than the second molar in *Homo rudolfensis* fossils. The occlusal surface of the first molar is larger than in *Homo habilis*.

### 3.2. Do the species *habilis* and *rudolfensis* belong to the genus *Homo*?

For several years, the criteria used by Leakey and co-authors in 1964 to redefine the genus *Homo* have been considered insufficient and/or inappropriate by many researchers. Traditionally, there are two ways of grouping several species within a single genus:

- 1) a genus groups together species sharing a common ancestor that occupy different ecological areas which are different from those of species belonging to other genera. A group of species can be either monophyletic (i.e. it includes the common ancestor and all its descendants) or paraphyletic (i.e. it includes a common ancestor and some of its descendants);
- 2) a genus is a monophyletic group according to cladistic classification methods.

Wood and Collard have proposed in 1999 (Wood and Collard, 1999a, Wood and Collard, 1999b) to modify the definition of the genus by taking into account both conditions: species will be grouped in a genus if and only if they are part of the same monophyletic group and share the same adaptive strategies. The application of this definition to hominin fossils therefore leads them to suggest that a fossil species can be included in the genus *Homo* if it can be shown that:

- 1- it is closer, based on cladistic analysis, to *Homo sapiens* than to *Australopithecus*;
- 2- it shares more adaptive strategies with *Homo sapiens* than with australopithecines;
- body mass and body proportions closer to *Homo sapiens* than to australopithecines;
- post-cranial skeleton exhibiting a morphology consistent with terrestrial bipedalism and a weak climbing capacity;
- dentition and masticatory system closer in relative size to *Homo sapiens* than to australopithecines;
- period of growth and development close to that of *Homo sapiens*.

In order to test the monophyly of the *Homo* genus, these authors had taken into account the six main cladistic studies carried out on hominins in the previous fifteen years. They have showed that the species *habilis* and *rudolfensis* do not form a monophyletic group with the later species allocated to the genus *Homo* (from *ergaster* to *sapiens*). Then, they have assessed the adaptive coherence of species within the genus *Homo* by examining the criteria described above. For all these criteria, the species *Homo habilis* and *Homo rudolfensis* are closer to australopithecines than to *Homo sapiens*.

In 2001, Meave Leakey and his team (Leakey *et al.*, 2001) created a new genus *Kenyanthropus* and a new species *Kenyanthropus platyops*. The holotype skull KNM-WT 40000 (found in the western part of Lake Turkana and dated at 3.5 Ma) shows some morphological similarities with the Koobi Fora specimen KNM-ER 1470, notably in the shape and orientation of the naso-alveolar clivus, and the size and orientation of the zygomatic region. Based on these similarities, these authors have proposed that "the transfer to this species to *Australopithecus* has been recommended, but *Kenyanthropus* may be a more appropriate genus" (Leakey *et al.*, 2001 p.439).

However, other studies based on the same cladistic approach have shown that the genus *Homo* is monophyletic even if the specimens of the species *habilis* and *rudolfensis* are included into this genus and therefore these species did not belong to the genus *Australopithecus* and *Kenyanthropus*, using either as terminal taxa, the specimen (Prat, 2004) or the species (e.g., Dembo *et al.*, 2015, 2016; Strait and Grine, 2004).

Moreover, the study undertaken by Caparros and Prat (Caparros and Prat, 2021) using phylogenetic approach combining Maximum Parsimony and Phylogenetic Networks methods (Caparros and Prat, 2022) show that these two species belong to *Homo* sensu lato, that the side-edge *H. habilis*, *H. floresiensis* represents probable phylogenetic divergence that might be construed as evolutionary dead-ends, and *H. rudolfensis* is part of a clear reticulate radiative structure called by the authors as *Homo* hybridization subnetwork.

Therefore, two scenarios of the first humans seem to emerge (Figure 2). An emergence of the genus *Homo*, as early as 2.8 Ma, with *Homo* sp. specimens and the species *Homo habilis* and *Homo rudolfensis*, or at 1.9 Ma with *Homo ergaster*.

**INSERER FIGURE 2. scenarios**

#### 4. Can we define the genus *Homo*?

The inclusion of the new species *Homo habilis* into the genus *Homo* had required a revision of the diagnosis of the genus *Homo*. Three criteria appeared to be highly important in the definition of Leakey and his collaborators (Leakey et al., 1964) : endocranial volume, power and precision grip, habitual erect posture and bipedal gait.

The issue about a minimum cranial capacity associated with the genus *Homo* was raised by Keith as early as 1948 (Keith, 1948). This limit was, according to him, 750 cm<sup>3</sup>. Leakey and co-authors later have lowered this threshold to 600 cm<sup>3</sup>. This notion of "cerebral rubicon" remains problematic today because there is an overlap between the cranial capacities of *Australopithecus* and *Homo* : *A. africanus* (428-515 cm<sup>3</sup>), *Homo habilis* (509-824 cm<sup>3</sup>), *Homo floresiensis* [426 cm<sup>3</sup> (Kubo et al., 2013) dated to 100-60 ka (Sutikna et al., 2016)], or *Homo naledi* [465-560 cm<sup>3</sup> (Garvin et al., 2017) dated to 335-236 Ka; (Dirks et al., 2017)]. This has no real meaning in terms of cognitive capacities as it has been shown that there is no direct and causal influence between total brain volume and overall cognitive performance (e.g. Schoenemann et al., 2000, Louail et al., 2019). Furthermore, it is problematic because the meaning of cranial capacity when related to body mass is questionable (Martin, 1981). Moreover, the human-like cortical reorganization does not appear to be specific to the genus *Homo* (see Beaudet et al., 2019 for a review of hominin brain reorganization). It is already present 3-4 Ma ago in *Australopithecus africanus* specimens (occipital (visual cortex) and prefrontal (inferior frontal gyrus) reorganizations, e.g. Holloway et al. (2004) and Beaudet et al. (2018)), *Paranthropus robustus* (occipital reorganization, prefrontal reorganization(?) (Holloway, 1972)) and debated in *Australopithecus afarensis* (occipital organization (e.g. Gunz et al., 2020; Holloway and Kimbel, 1986)). Furthermore, it is also observed in more recent *Australopithecus* species as *Australopithecus sediba* (1.9 Ma) with the reorganization of the prefrontal cortex (Carlson et al., 2011). Moreover, according to Ponce de León and collaborators, the brain of the early specimens from Africa and Georgia retained a great ape-like organization of the frontal lobe, and by contrast, specimens younger than 1.5 Ma in Africa and Asia exhibited a human-like brain organization (Ponce de León et al., 2021).

The second criterion advanced concerns the human-like manipulative abilities which involves the last phalanges of the thumb and index finger. In a broader sense, these manual abilities are forceful precision grips and precision handling sensu Marzke (Marzke, 1997) or pad-to-pad precision grasping sensu Napier (1956) and Almécija and Alba (2014), which are linked to the evolution of increasingly complex tool technologies within the hominin clade (Marzke, 1997). However, this anatomical ability to use and even make lithic tools is not exclusive to the genus *Homo*. Indeed, these anatomical and potential behavioral abilities seem also present in two hominin genera different from *Homo*. As a matter of fact, morphological evidence (even if they are limited) suggests the potential for human-like precision grip in *Australopithecus* (*afarensis*, *africanus*, *sediba*) and *Paranthropus* (*robustus* and *boisei*).

Indeed, *A. afarensis* is mainly characterized by human-like hand functions illustrated for example by substantial mobility of carpometacarpal joints, the overall morphology of the distal pollical phalanx (Ward et al., 2012) and modern human-like manual proportions with a relatively long thumb and short medial digits (e.g. Alba et al., 2013; Almécija and Alba, 2014, Drapeau et al., 2005; Ward et al., 2012). According to Marzke (Marzke, 1983, 1997, 2013), *A. afarensis* individuals were able to use pad-to-side as well as three-jaw chuck precision grips and precision handling, all three manipulative abilities which are involved in stone tools behaviors and considered unique to the human hand compared to extant hominids. However, Rolian and Gordon (Rolian and Gordon, 2013) have proposed that the manual proportions of *A. afarensis* are intermediate between gorillas and humans, and have suggested that *A. afarensis* did not possess the efficient precision grip typical of modern humans. Concerning *Australopithecus africanus*, based on the specimens classically put into Member 4 deposit from Sterkfontein site (recently dated to 3.4 Ma; Granger et al., 2022), it has been shown that the individuals of this species was able to use a human-like pad-to-pad precision grasp (Green and Gordon, 2008), pad-to-side and handling grips (Marzke, 1997, Ricklan, 1987), but with not the full range of human-like manipulative behaviors seen in later hominins (Green and Gordon,

2008). More recently, based on the internal structure of metacarpals, Skinner and co-authors (Skinner *et al.*, 2015) confirm that *A. africanus* would have had, during precision and power grips, the capacity of forceful human-like opposition of the thumb and fingers. Furthermore, according to Kivell and co-authors (Kivell *et al.*, 2011), individuals belonging to a more recent *Australopithecus* species: *A. sebiba* (Malapa site, South Africa, 1.977 Ma) possessed forceful precision gripping and hand proportions that show enhanced dexterity, confirmed by other recent studies using trabecular bone analyses and musculoskeletal modeling (Bardo *et al.*, 2018; Dunmore *et al.*, 2020).

Concerning *Paranthropus* genus, the anatomy of the hand of specimens belonging to *P. boisei* (e.g. specimens from East Turkana, Kenya), highlights that this species exhibit manual dexterity required to use or make stone tools, but did not possess the robust thumb observed in *Homo erectus*, which are linked to the intensification of forceful precision grips and tool use (Richmond *et al.*, 2020). In southern Africa, the remains (phalanges and metacarpals) discovered mainly from Member 1 and allocated to *P. robustus* (Susman, 1988, 1994, 1998), made it possible to highlight that these hominins possessed, in particular, the opposing muscle of the thumb and the fifth finger. These muscles allow respectively a human-like precision grasping by stabilizing the opposing the thumb and the fifth finger to the other fingers which are considered as adaptations for tool-using and tool-making (Susman, 1994, 1998). However, according to Moyà-Solà and co-authors (which consider that OH 7 hand bones belong to *Paranthropus boisei*), *Paranthropus* individuals exhibit more robust hand bone than *Homo* and lack the disproportionately hypertrophied first metacarpal characteristic of the genus *Homo* (Moyà-Solà *et al.*, 2008). For these authors, the *Paranthropus* pattern probably reflects an adaptation to manual activities other than toolmaking more related to manipulative feeding behaviours like specialized food gathering and processing, such as it can be observed in extant hominids (Gérard *et al.*, 2022; Marzke *et al.*, 2015; Neufuss *et al.*, 2018).

The third argument relating to bipedal gaits is also questioned. From an evolutionary perspective, bipedalism is now perceived as a complex evolutionary process and not as a one-off event in human evolution (e.g. Crompton 2008 ; Niemitz, 2010; Preuschoft 2004). Recent analyses in functional anatomy and biomechanics and the locomotor record of extant primates and fossil hominins illustrate several forms of bipedalism (i.e. arboreal locomotion with some adaptation to bipedal walking, effective bipedal walking with some arboreal grasping adaptations, long distance walking and running (e.g. Holowka and Lieberman, 2018)) which can occur in genera other than *Homo* genus. As for example occasional bipedal walking can represent a part of the positional repertoire of nonhuman primates (in Catarrhines e.g. Berillon *et al.*, 2010; Carvalho *et al.*, 2012; Druelle and Berillon, 2014). Furthermore, during the course of hominin evolution, first bipedal gait are considered to be present in the oldest hominins taxa, with evidence of an upright terrestrial bipedalism with substantial non-stereotypical arboreal behaviors. We can mention *Salehanthropus tchadensis* (Daver *et al.*, 2022 and Zollikofer *et al.*, 2005), *Orrorin tugenensis* (Senut *et al.*, 2001), *Ardipithecus ramidus* (Lovejoy *et al.*, 2010), *Ardipithecus kaddaba* (Haile-Selassie *et al.*, 2009), and in *Australopithecus* species for example *A. anamensis* (e.g. Ward *et al.*, 1999; Ward *et al.*, 2020), *A. afarensis* (e.g. Ward *et al.*, 2012; with a debate if the initial hypodigm is based on a single species developing upright bipedalism associated or not with arboreal behaviors (see review in Ward (2002) and Chevalier (2006)) and in *Paranthropus* species (Domínguez-Rodrigo *et al.*, 2013), with different bipedal patterns. Nowadays, only long-distance walking and running are considered to be specific to humans (e.g. Bramble and Lieberman, 2004; Harcourt-Smith, 2013; Holowka and Lieberman, 2018).

The aptitude for language, the manufacture of lithic tools and the notion of social behaviour (hunting, etc.), although they are not included in the diagnosis of the genus *Homo*, are often considered to be characteristic of our genus and would constitute key stages in the hominization process. Nowadays, there is no consensus on the definition of language. Nevertheless, the notion of articulation or more precisely of double articulation of language has been put forward as a characteristic of human language, but it does not refer to physiological and/or anatomical characteristics relating to a phonatory capacity. Indeed, a language is said to be doubly articulated, i.e. constructed of minimal units at two levels. The second articulation is that of sound units which can be assembled to form units of first articulation. The first articulation which



corresponds to the units of meaning which allow an infinite number of statements to be composed. Furthermore, this linguistic notion seems to be obsolete, as there are non-oral natural languages (for example, sign language). The language ability of a fossil species is therefore difficult to demonstrate on the basis of fossil remains. Indeed, as pointed out by some researchers this ability is difficult to deduce from endocranial casts (e.g. Gannon *et al.*, 1998; Holloway, 1983) because very often the areas considered to be involved in the function of language, such as Broca's and Wernicke's areas, are not easily observable on endocranial casts or their functional implications and direct relationship with the origin of language seem unclear, i.e. size, shape and asymmetries of the third frontal convolution (e.g. Tobias (1987) and Balzeau *et al.*, (2014); see also review in Beaudet *et al.*, 2017; Bruner, 2017)). Furthermore, the human-like structural brain asymmetries are observed in several nonlinguistic primates such as chimpanzees or baboons which can be related to the lateralization of gestural communicative system (see review in Becker et Meguerditchian, 2022). Moreover, the presence of these neuroanatomical landmarks clearly states that they are not human-or language specific (Becker et Meguerditchian, 2022). Therefore, endocranial morphology does not imply *de facto* linguistic ability. Considering the fossil record, according to Holloway in 2017 (Holloway, 2017), Australopithecines lack a human-like Broca's cap region and Australopithecines and early *Homo* individuals could have used vocal signals as a way of communication (Aboitiz, 2018)

Finally, tools and the ability to make tools take a special place in the literature in the definition of the genus *Homo*. The possible relationship between the Oldowan lithic industry and the Olduvai *H. habilis* specimens is however not mentioned in the diagnosis of Leakey *et al.* (1964) but in the following paragraph entitled "Cultural Association", as follows: "When the skull of *Australopithecus (Zinjanthropus) boisei* was found on a living floor at F.L.K. 1, no remains of any other type of hominid were known from the early part of the Olduvai sequence. It seemed reasonable, therefore, to assume that this skull represented the makers of the Oldowan culture. The subsequent discovery of remains of *Homo habilis* in association with the Oldowan culture at three other sites has considerably altered the position. While it is possible that *Zinjanthropus* and *Homo habilis* both made stone tools, it is probable that the latter was the more advanced tool maker and that the *Zinjanthropus* skull represents an intruder (or a victim) on a *Homo habilis* living site" (Leakey *et al.*, 1964, p.9). The attribution of the lithic remains in the Olduvai site to *Homo habilis* rather than *Zinjanthropus boisei* (*Paranthropus boisei*) thus appears to be more an ideological choice than a scientific interpretation. The oldest known oldowan tools found *in situ*, which are dated at 2.6 Ma in Ethiopia (Semaw *et al.*, 1997; Braun *et al.*, 2019) and 2.34 Ma in Kenya (Kibunjia *et al.*, 1992; Kibunjia, 1994; Roche *et al.* 1999), are contemporaneous in eastern Africa with both early *Homo*, *Paranthropus* (*P. aethiopicus*) and *Australopithecus* (*A. garhi*, Semaw *et al.*, 2003). Furthermore, some stone and bone artefacts have been discovered in association with individuals allocated to *P. robustus* which supports the hypothesis that *P. robustus* probably used and/or made bone tool [e.g. Swartkrans (Brain, 1993, Backwell et D'Errico 2001, Backwell et D'Errico, 2003); Drimolen (Backwell et D'Errico, 2008); Coopers'D (Hanon *et al.*, 2021)]. The attribution of artefacts to *Homo habilis* rather than *Paranthropus* appears to be once again to be more ideological than scientific.

In addition, the recent discovery in Kenya of stone-tools dated to 3.3 Ma (LOM3 site) (Harmand *et al.*, 2015), i.e. 700 000 years older than earliest Oldowan technology and 500,000 years before the oldest fossils attributed to the genus *Homo* (*Homo* sp. remains at Ledi Geraru (Villmoare *et al.*, 2015)). They have been found in the same chronological and geographical frameworks than specimens allocated to *Kenyanthropus platyops* and are also contemporaneous with individuals attributed to *Australopithecus afarensis* and *Australopithecus deyiremeda*. These findings have reopened the debate on the association between lithic industry and the genus *Homo* (Harmand *et al.*, 2015; Lewis and Harmand, 2016). The stone artefacts from Lomekwi 3 are larger in width, length and thickness than those coming from Oldowan sites. Two modes of knapping have been recognized (passive hammer and bipolar). The knappers have combined battering activities and core reduction, and may have used the lithic artefacts variously: as anvils, core in order to produce flakes and/or as pounding tools. These findings put into the light that species that occurred far long before the emergence of the genus *Homo* present important manipulative and cognitive ability.

Moreover, the unique and specific attribution to the genus *Homo* of a capacity to make lithic tools is therefore no longer valid for those periods.

## 5. Conclusion

In fine, the increase in the fossil record has shown the extent of both the morphological and cultural complexity of hominins and evolutionary scenarios that led to the appearance of the genus *Homo*. According to the recent archaeological and palaeoanthropological discoveries, the criteria often considered to be crucial for the definition of the genus *Homo*, as the cranial capacity, the human-like manipulative abilities, the habitual erect posture and bipedal gait, the language ability and the capacity to make tools are not anymore valid. Trying to characterize the genus *Homo* factually through for example the notion of hominization leads to a certain arbitrariness inherent in any definition and conceptually questionable: is humans are capable of defining themselves, and it is possible to be both the object of study and the one who studies him? In any case, as demonstrated in previous paper (Caparros et Prat, 2021), hominin biological evolution reveals a reticulate nature. The incompleteness of the fossil record, the complexity of genomic transfers within this evolution and the persistence of this taxon in time and of their behavioural cultural evolutions question the definitive conceptual limit of the species in Palaeoanthropology, where species can be seen more as conceptual objects that can fuel debates on evolutionary scenarios.

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Legend list

Figure 1. Location of the main sites where early *Homo* remains have been discovered

Figure 1. Localisation des principaux sites où des restes attribués aux premiers représentants du genre *Homo* ont été mis au jour

Figure 2. Scenarios for the emergence of the genus *Homo*.

Figure 2. Scenarios relatifs à l'émergence du genre *Homo*

Table 1. Morphological comparisons between *Homo habilis sensu stricto* and *Homo rudolfensis*. \* : trait assignment related to the developmental age of the individual, # high polymorphism in extant great apes).

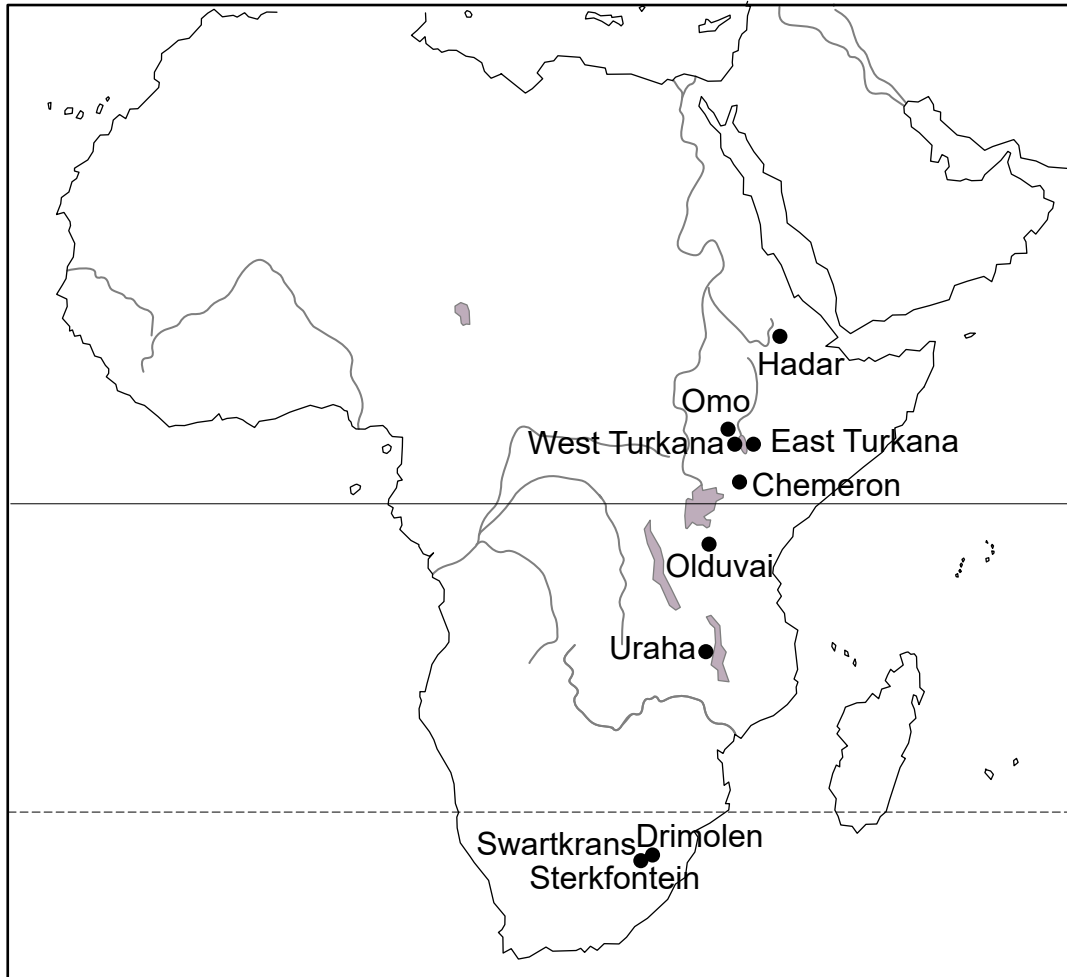
Tableau 1 : Comparaisons morphologiques entre *Homo habilis sensu stricto* et *Homo rudolfensis* : \* : état de caractère lié à l'âge developmental de l'individu, # fortement dimorphique chez les grands singes actuels.

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	<i>Homo habilis sensu stricto</i>	<i>Homo rudolfensis</i>
Frontal bone		
Supratrigonal depression	presence	absence
Lateral postorbital depression	presence	absence
Supratoral sulcus	presence	absence
Temporal bone		
Shape of the temporal squama	triangular and low	round and high
Orientation of the anterior part of the temporal squama	vertical	anterior
Supramastoid crest at porion	medium	weak
Confluence between the mastoid and supramastoid crests*	absence	presence
Shape of the root of the zygomatic process of the temporal bone	elliptic; plane	plane
Articular eminence shape *	two joint areas	plane
Position of the pregenoid process relative to the lateral part of the tympanic	same level	medial
Parietal bone		
Position of the temporal lines *	high	median
Occipital bone		
Nuchal plane inclination *, #	high	weak
Occipital torus #	medial development	no
Maxillo-facial complex		
Midfacial/upper facial width	same	wide

Alveolar prognathism	reduced	low
Size of the zygomatic bone	small	strong
Naso-alveolar clivus	flat	convexe
Individualization of the incisor region relative to the nasal aperture	yes	no
Zygomatico-maxillary fossa	yes	no
Orientation of the zygomatic process relative to the Francfort plane*	vertical	posterior
Position of the frontomaxillary point	M1-M2	P4-M1
Horizontal distance between the Temporo-mandibular articulation and M2/M3	high	short
Orbital shape *	rectangular	square
Shape of the superior orbital margin	round	ovoid
Position of the superior orbital margin relative to the inferior one	anterior	same plan
Palatal breath	narrow	large
Occlusal surface of upper M1	moderate	small
Number of upper premolar roots	three	two
Chin region shape	subrectangular	rounded
Planum alveolar	large	small
Number of lower premolar roots	two or one bifid for lower P3, two for lower P4	generally only one
Occlusal surface of the lower M3 compared to M2	M3>M2	M3<M2





## 4 Hypotheses

- (a) • 1 species ? *Homo habilis*  
• 2 species ? Which genus?
- (b) • *Homo* *H. habilis* *H. rudolfensis*
- (c) • *Australopithecus* *A. habilis* *A. rudolfensis*
- (d) • *Kenyanthropus* *K. rudolfensis*

**Implications for the emergence of the genus *Homo***

