SHORT REPORT

"What's in a Name?" *The Taxonomy & Phylogeny of Early* Homo

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Hominin systematics, encompassing both taxonomy and phylogeny (Strait, 2013), has significant implications for how the evolution of species and traits are understood and communicated. Following a recent influx of fossils (e.g., Brown *et al.,* 2004; Lordkipanidze *et al.,* 2013; Villmoare *et al.,* 2015a; Berger *et al.* 2015) the amount of diversity in fossil morphology has increased correspondingly. As researchers do not yet approach diversity in a uniform manner, the literature has been flooded with conflicting theories and methodologies (Strait, 2013). Particularly volatile has been the study of the origin of the genus *Homo* and the extent of variation therein: much controversy arises from conflicting views of the number of valid species subsumed within 'early *Homo*' given unspecified definitions of species and genera. Additionally, there is still a lack of understanding of the extent of and mechanism behind variation, especially within Hominina. The first section of the following paper addresses 'how can species be identified?' and 'how should species be classified into higher taxa?' The second section reviews the prevalent arguments used to systematise fossils frequently classified as 'early *Homo*.' It considers: the validity of *Homo rudolfensis*; the morphological, spatial & temporal overlap of earlier *Homo* with *Homo ergaster*; the systematic significance of the recently discovered LD 350-1; and finally, the appropriateness of 'early *Homo*' as an adaptive grade.

1: Principles in Hominin Systematics

1.1 How can species be identified?

Species are important as the primary units of organisation in classifying taxa (Groves, 2004). Linnaean taxonomy provides a universal hierarchy in which every organism can be placed. Hence, taxonomy should be uniform in its applicability to taxa. Additionally, the process of identifying species should be objective. While the merits and requirements of classification are well recognised, actual species concepts that guide the identification of species are still debated.

The most widely used definition is the Biological Species Concept (BSC) (**Table 1**). Despite its pervasiveness in biological literature, it is fundamentally flawed. Firstly, it cannot be objectively applied to allopatric species (Groves, 2004). In sympatric species two populations that do not interbreed may logically be assumed to belong to different species. However, allopatric species are already isolated through geography and so it becomes necessary to make assumptions about whether they *would* interbreed (Groves, 2004). Additionally, the BSC does not indicate the extent of difference necessary to

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demarcate two species. Consequently, species could be identical except that they do not interbreed (Groves, 2004). Finally, and fundamentally, the BSC is entirely inapplicable to extinct species (Strait, 2013).

Most other species concepts are also problematic. The Recognition Species Concept (**Table 1**), for example, improves on the BSC in that it refers to what *can* be observed in the interaction between species, but cannot be applied to non-sexually reproducing taxa, to taxa primarily observed in captivity, or to extinct taxa (Groves, 2004).

The Phylogenetic Species Concept (PSC) (**Table 1**), however, is promising (Groves, 2004). This concept is predicated on the ability to distinguish species based upon their unique collection of heritable traits. Importantly, the PSC does not stipulate what form the differences must take (e.g. genetic distance or reproductive strategy) and so it is applicable across taxa. Additionally, it is

falsifiable and observational, unlike many other concepts that require a significant amount of speculation about the evolutionary mechanisms underlying an observation (Groves, 2004).

According to Strait (2013), the PSC may be the preferred species concept employed by palaeoanthropologists, though the Evolutionary Species Concept (ESC) (**Table 1**) is also employed. While superficially similar, the ESC and the PSC are separated by an important practical difference: the ESC describes the mechanism underlying a pattern of evolutionary relationships, while the PSC refers only to the pattern itself (Groves, 2004). The definition of a species under the ESC is very clear but offers no practical application, which has led to the introduction of other related species concepts (3–5 in **Table 1**), but the applicability of these related concepts to fossil taxa is equally problematic (Groves, 2004).

1	**Biological Species Concept (BSC)**	"A group of actually or potentially interbreeding natural populations which is reproductively isolated from other such groups"	Mayr (1942)
2	**The Evolutionary Species Concept**	"A lineage evolving separately from others and with its own unitary evolutionary role and tendencies"	Simpson (1961)
3	**Ecological Species Concept**	"A lineage (or set of lineages) which occupies an adaptive zone"	Van Valen (1976)
4	**Species-as-Individuals Concept**	"The most extensive units in the natural economy such that reproductive cohesion occurs among their parts"	Ghiselin (1974)
5	**Cohesion Species Concept**	"The most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms, genetic or demographic"	Templeton (1989)
6	**The Recognition Species Concept**	"The most inclusive population of biparental organisms which share a common fertilization system"	Paterson (1985)
7	**Phylogenetic Species Concept (PSC)**	"The smallest cluster of individual organisms within which there is a parental pattern of ancestry and descent and that is diagnosably distinct from other such clusters by a unique combination of fixed character states."	Cracraft (1983)

Table 1: derived from species concepts outlined in Groves (2004: 1107–1110).

While clear species concepts help define and identify natural species, species as defined in palaeoanthropology act more as communicative tools, and are subject to personal preferences (Schrenk, 2013). Hence, a description of two chronospecies (e.g. *Australopithecus anamensis* and *Australopithecus afarensis*) may be theoretically and practically useful, distinguishing two similar, phylogenetically related, morphs that followed one another chronologically, with the latter possibly evolving via anagensis (Kimbel *et al.* 2006). Similarly, the typological distinctions of morphospecies (e.g., *H. ergaster* and *Homo georgicus*) may be pragmatically employed for distinctions between biogeographic morphs, though despite the morphological overlap represented by these taxa possibly warranting sub-species designation biogeographic designation ("subspecies are populations, geographic segments of a species, not morphs co-occurring with other variants, and […] they differ from each other on average, not absolutely" [Groves, 2004: 1112]), sub-species are comparatively uncommon among hominins. A degree of flexibility in defining species renders palaeoanthropology (and broader palaeontology) vulnerable to political and/or unscientific allocations of species status to undeserving fossils (Schrenk, 2013; e.g. the currently sparse fossil evidence for *Kenyanthropus platyops*). Furthermore, the generally fragmentary/distorted nature of many fossils (e.g. OH 7 and KNM-WT 40000) may obscure differences and/or similarities between fossils that can be more easily identified in extant specimens, resulting in different taxonomic biases.

1.2 How should species be classified into higher taxa?

Supraspecific taxonomy classifies species into increasingly nested hierarchical groups (Strait, 2013). While most higher taxa are defined by clades (Groves, 2004), this is not always true for genera. A clade is a monophyletic group, therefore representing species that mutually descend from a *single* and *exclusive* ancestor. The alternative to clades are grades in which species descend from a *recent* common ancestor and express a number of adaptations that are "functionally, behaviourally, and/or ecologically similar" (Strait, 2013: 39). Hence, clades exclusively communicate phylogeny, whereas grades provide significant information about adaptation and only broad information about phylogeny (Strait, 2013). However, others (e.g., Wood and Lonergan, 2008) would debate that grades provide *any* phylogenetic information. While there are merits to both systems, palaeoanthropologists have not uniformly defined hominin taxa using one system. For example, the genus *Paranthropus* was introduced to subsume the specimens and species that collectively exhibit extreme megadontia and the osteological scaffolding required to accommodate its highly-developed masticatory musculature (Wood and Lonergan, 2008). However, megadontia is exhibited by all australopithecines and the extreme megadontic adaptations in the 'robust' specimens are possibly due to convergence (Foley, 2002). If this is the case, *Paranthropus* would therefore not be a valid, monophyletic clade and these species could be subsumed under *Australopithecus*. Yet, under this scenario, some (e.g. Foley, 2002) would still argue to retain *Paranthropus* as a valid genus (grade), indicating that the 'adaptive radiation' the group of species represents is still meaningful, if not monophyletic. Frequently this is implied via the distinction between the 'gracile' and the 'robust' australopithecines (e.g. Villmoore and Kimbel, 2011). The current classification of the hominin lineage is a confusing mosaic of the clade- and grade-based systems (Strait, 2013). The logistical implications of redefining the hominin lineage to be exclusively clade-based may be a primary deterrent against attempts to implement the change.

Recently, Cartmill (2012) has suggested that all supraspecific taxonomy may be found entirely superfluous. Cartmill suggests that parallelisms are inevitable in closely related taxa due to the similarities

in their morphology and the selective pressures that are exerted upon them. The difference between clades at *any* taxonomic level occurs at the species-level through cladogenesis, and the difference between the two clades, regardless of how adaptively distinct they may seem, is literally only the difference between those species closest to the cladogenetic event (**Figure 1**). Any future adaptive distinctions between clades are due entirely to subsequent anagenetic and cladogenetic evolution within the clade and due to extinctions (**Figure 2**). Hence, supraspecific taxa, which are often heralded for containing the suite of traits that define the adaptive shift(s) represented in the clade, are actually entirely illusory (Cartmill 2012). It is that, historically, we have only been able to observe a subsection of all diversity; that which is contained in the world's extant taxa. The discovery of otherwise unseen diversity in all areas of life via novel, transitionary fossil evidence is arguably reducing the length of the great adaptive leaps that are represented by today's supraspecific taxonomy. The practical implication of Cartmill's theoretical argument is that defining hominin taxa based upon seemingly important adaptive distinctions,

such as the specialised dietary adaptations of the paranthropines, will become increasingly biologically meaningless as a greater proportion of the fossil record is uncovered. Instead, it will become necessary to either accept that the monophyletic clades used to define taxa are the result of small distinctions between similar taxa, or that higher taxa can include low levels of polyphyly.

2: Naming and Reconstructing the Phylogeny of 'Early *Homo*'

Researchers disagree on multiple aspects relating to the origin of the genus *Homo*. This is partially as a result of how *Homo* is defined (Aiello and Wells, 2002). *Homo* has been suggested to describe species that exhibit anatomical traits associated with 'human' behavioural adaptations (Strait, 2013), such as an increase in relative brain size, a reduction in the general robusticity of the molar and premolar dentition, and a complete reliance on bipedal locomotion (Wood, 1992). However, it is now known that these traits do not appear simultaneously, and not all members of *Homo* exhibit all of these adaptations to the same degree (Strait, 2013). In fact, some of the earliest members of *Homo*
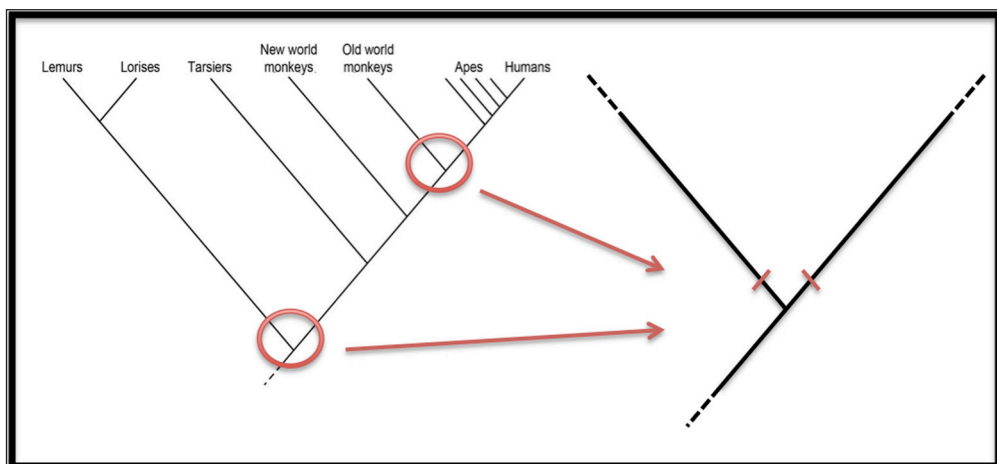

Figure 1: Diagram to illustrate Cartmill's (2012) suggestion that the differentiation between two clades at any taxonomic level is due to the initial differentiation of two species. Immediately following cladogenesis, the two species are theoretically practically identical as they possess most of the same adaptations and probably inhabit similar environments and therefore are subject to similar selective pressures.
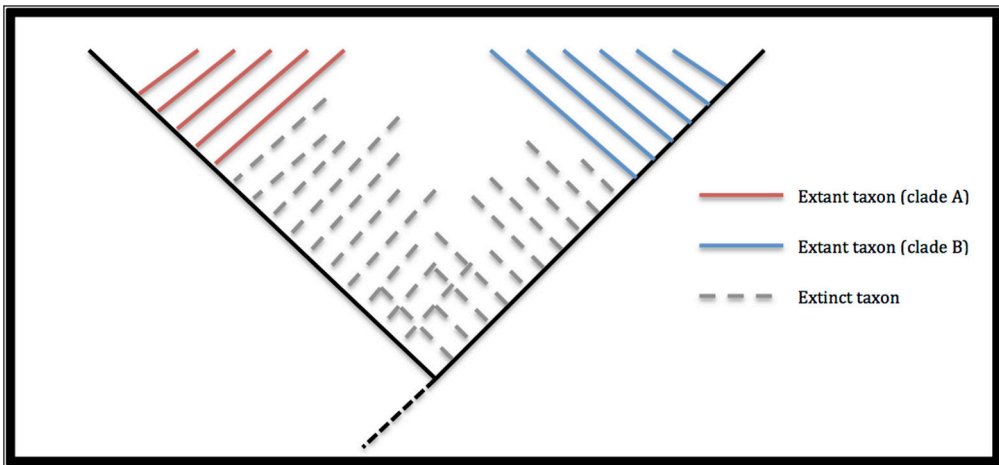
Figure 2: Diagram to illustrate Cartmill's (2012) suggestion that the observable difference between extant clades are due to anagenesis and the extinction of species. In the above schematic cladogram, the grey dotted lines represent extinct lineages that create the illusion of distinctiveness between the extant clades, which are represented by solid lines in red and blue.

may lack some of these adaptations entirely (Strait, 2013). Many consider 'early *Homo*' to include fossils attributed to *Homo habilis s.l.* as well as *H. ergaster* (e.g., McHenry and Coffing, 2000). Wood and Collard (1999), however, have suggested that *H. ergaster* is the first species within *Homo,* as its anatomy is demonstrably more similar to *Homo sapiens* than earlier putative species of *Homo*. Inherent to this confusing array of taxonomic designations is the non-disclosure of the species concept being employed and, where applicable, how much variation may be reasonably subsumed with a taxon. For example, one view of *Homo* is that it represents a single evolving lineage and, therefore, one/two long, very variable species (Wolpoff, 1999). This implies minimal cladogenesis, with possibly only one speciation event at the base of *Homo*. Subsequent variation observed in the fossil record would otherwise be due to spatio-temporal variation via anagenesis. Under this scenario, the variable morphology of specimens such as KNM-ER 1470 and KNM-ER 1813 would be subsumed under *Homo habilis* (*sensu lato*) and specimens as diverse as LB1 and Trinil 2 would

be equally valid members of *Homo erectus* (*sensu lato*) (**Table 2**, "Lumping Taxonomy"). Alternatively, these populations, or possibly sub-species, under a different species concept could be classified as distinct species (**Table 2**, "Splitting Taxonomy"). This perspective is based upon the observation that for some extant species, such as among lemurs (Tattersall and Schwartz, 1991), only subtle morphological and behavioural differences are necessary to designate them as sister species, and these are not detectable via hard-tissue anatomy (Tattersall, 1992). Hence, any small difference observable between fossils is thought to likely indicate different species (Tattersall, 1986). Crucially, researchers also disagree about the number of separately evolving lineages within early *Homo* (Wood and Lonergan, 2008), which under the PSC has a major impact on the number of species within early *Homo*.

2.1 Evidence for the validity of Homo rudolfensis

The taxon *H. habilis* was first described following the discovery of the distorted holotype OH 7 at Olduvai Gorge (Leakey, 1964).

Splitting Taxonomy	Lumping Taxonomy
Homo habilis sensu stricto (e.g. OH 4, 7*, KNM-ER 1813)	*Homo habilis sensu lato*
Homo rudolfensis (e.g. KNM-ER 819, 1470*)	
Homo gautengensis (e.g. Stw-53*, SE 255, 1508)	
Homo ergaster (e.g. KNM-ER 730, 992*, WT15000)	*Homo erectus sensu lato*
Homo erectus sensu stricto (e.g. Kedung Brubus 1, Trinil 2*)	
Homo georgicus (e.g. D2700, D4500, D2735, D2600*)	
Homo floresiensis (e.g. LB1*, LB2)	

Table 2: The difference in the number of species in 'early *Homo*' based upon a more conservative ('lumper') or more speciose ('splitter') perspective of hominin diversity (adapted from Wood and Lonergan, 2008).
* Holotype

While OH 7 was dated to be synchronous with paranthropine species, the cranial capacity of OH 7 was estimated to be notably larger (Schrenk, 2013). Hence, *H. habilis* was suggested to be the first species on the trajectory towards *H. sapiens* (Schrenk, 2013). While many early *Homo*-like fossils were attributed to *H. habilis*, the discovery of two fossils at Koobi Fora, KNM-ER 1470 and KNM-ER 1813 questioned the uniformity of the *H. habilis* hypodigm. KNM-ER 1470 has a comparatively flat face, a large cranial capacity, and generally larger dentition, while KNM-ER 1813 has overall smaller dentition, cranial capacity and face compared to KNM-ER 1470 (Lieberman *et al.,* 1996). The differences between these two specimens have led to the assertion by multiple researchers (Wood 1992; Schrenk *et al.* 1993) that early *Homo* was represented by at least two morphs. The first morph represented by KNM-ER 1813 is *H. habilis s.s.*, while the fossil KNM-ER 1470 represents the other morph, suggested by some to represent a new species, *Homo rudolfensis* (Schrenk, 2013). In cases where *H. rudolfensis* is subsumed under *H. habilis*, *H. habilis* is considered to be extremely variable (Schrenk, 2013). In order to test the validity of the suggestion that these two morphs should represent distinct species, Wood (1991) performed a character analysis on the early *Homo* fossils from Koobi Fora. Wood concluded that the high degree of variation in the represented fossils could not be explained by sexual dimorphism alone as the amount of variation exceeded that observed in extant primate taxa. A subsequent study by Lieberman *et al.* (1996) also corroborated separate specimen groupings representing *Homo habilis s.s.* (including KNM-ER 1813, 1805, 1501, 1502, OH 7, 13, 16, 24, 62) and *Homo rudolfensis* (including KNM-ER 1470, 1590, 3732, 1801, 1802). Furthermore, the authors found that many of the morphological similarities between the specimens tentatively assigned to *Homo rudolfensis* and australopiths, such as their anteriorly projecting zygomatics, are probably homoplastic, which has implications for this taxon's generic placement and/or the validity of the derived features generally associated with *Australopithecus* (Lieberman *et al.,* 1996).

In light of the increasing tendency for researchers to recognise the two morphs

as distinct species within *Homo* (Schrenk, 2013), the discovery of a fossil hominin maxilla at Olduvai, OH 65, seriously questioned the validity of *Homo rudolfensis* as a biologically meaningful taxon (Blumenschine *et al.*, 2003). Blumenschine *et al.* (2003) outlined that this new specimen was similar to KNM-ER 1470 in its sub-nasal morphology and the position of the anterior portion of its zygomatics. Furthermore, the authors considered that these similarities in specimens, and the fact that OH 65 was discovered in Olduvai, indicated that KNM-ER 1470 and OH 7 were conspecific, rendering KNM-ER 1470 not a member of *Homo rudolfensis*, but rather of *Homo habilis* (Blumenschine *et al.*, 2003). The authors still noted the morphological distinctiveness between these specimens and those more similar to KNM-ER 1813, indicating that there was still likely multiple species of early *Homo* during the Pliocene, though 'Homo rudolfensis' would be defunct (Blumenschine *et al.*, 2003). Crucially, however, this reassessment relied upon the supposed similarities between KNM-ER 1470 and the distorted, sub-adult OH 7 mandible and parietals. Recently, Spoor *et al.* (2015) performed a reanalysis of the OH 7 fossil to correct for post-depositional distortion, and discovered that the dental arcade of OH 7 was more similar to the parallel, primitive condition seen in most australopith specimens, rather than the parabolic dental arcade of later *Homo*. Additionally, the authors estimated that the cranial capacity of OH 7 was greater than had been previously stated in earlier estimates. This corrected model also allowed Spoor *et al.* (2015) to re-examine the supposed similarities between OH 7 and specimens of *Homo rudolfensis*, particularly KNM-ER 1470. The authors concluded that in fact OH 7 and specimens assigned to *Homo rudolfensis* were morphologically distinct and that the diversity and mosaicism in gnathic morphology and cranial capacity across early *Homo* specimens warrants the inclusion of at least two Pliocene *Homo* species (Spoor *et al.*, 2015). While the phylogenetic relationships of *H. habilis* and

H. rudolfensis have yet to be resolved (Wood 1991, 1992; Strait and Grine, 2004), Strait (2013) suggests that these species likely differentiated early in the evolution of *Homo*, though the noted potential polyphyly of these early *Homo* species (Stringer, 2015) will likely call for substantial phylogenetic and taxonomic revisions in future years.

2.2 Morphological, spatial & temporal overlap of earlier Homo with Homo ergaster

Increasingly, the amount of variation that is subsumed under *H. ergaster* is extending given recent discoveries of fossils of small brain and body size (Lordkipanidze et al. 2007; Spoor et al. 2007). *H. georgicus* (Gabunia *et al.* 2002, in Antón, 2013) was initially introduced due to the primitive facial morphology and the cranial capacity of the Dmanisi *H. ergaster* specimens, such as in D2600 (Antón, 2013). However, Antón (2013) suggests that the range of variation already exhibited in *H. ergaster*, as well as the apparent similarities between the Dmanisi (D2280 and D2282) and *H. ergaster* fossils (e.g. KNM-ER 3733, 3833, and WT15000), such as in the moderate size of their supraporbital tori, the presence of a thick vault, and the absence of a compound temporal-nuchal crest (Gabunia *et al.*, 2000), suggest that they are conspecific. Given the diversity of morphologies in *H. ergaster* from the diminutive Dmanisi fossil D2700 (Rightmire *et al.*, 2006), to the later, more derived morphs, such as Sangiran 17, with its distinctively thick tympanic plate and convex subnasal clivus (Rightmire, 1990), it is becoming increasingly difficult to distinguish between species of early *Homo*. This is further confounded by an overlap in time of early *H. ergaster* and other species of early *Homo*, for almost half a million years (Spoor *et al.*, 2007). As *H. ergaster* fossils are increasingly more variable, neither body size nor cranial capacity can be used as a proxy for differentiating between *H. ergaster* and other early *Homo* fossils (Antón, 2013).

The discovery of the late-surviving but primitive-looking hominin fossils on the island of Flores, Indonesia, have led to a number of possible explanations regarding its phylogenetic placement. Increasingly, similarities between the fossils of *Homo floresiensis* (especially the holotype LB1) and early *Homo* (e.g. the absence of laterally projecting "trigones" which are a distinctive feature of *Homo erectus*) are causing researchers to suggest a possible early dispersal out of Africa, potentially prior to the emergence of *H. ergaster* (Jungers, 2013). For example, the megadontia in *H. floresiensis* has been suggested to be most similar to that seen in *H. habilis* (Brown *et al.*, 2004). While some of the similarities of *H. floresiensis* to early hominins could be due to reversals, their affinity to early *Homo* is more parsimonious (Jungers, 2013). Furthermore, in a study by Argue *et al.* (2006) LB1 was found to be morphologically most similar to specimens of *H. habilis* and *H. ergaster*, especially D27000. While it has not yet been established where *H. floresiensis* fits phylogenetically, it has been suggested by Argue *et al.* (2009) that it diverged early in the *Homo* lineage.

Recently, a new species, *Homo naledi*, has been defined based upon a large assemblage of hominin fossils discovered in the Rising Star cave system, in South Africa (Berger *et al.*, 2015). Following an extensive analysis of the 1500 fossils uncovered, Berger *et al.* (2015) designated the specimens a novel species of *Homo* based upon the unique combination of cranial and post-cranial features represented. Crucially, the features that it shares with other *Homo* specimens are postulated to relate to functional adaptations such as striding-bipedal locomotion (presence of a linea aspera, derived ankle and foot morphology, and a long lower-limb; see also Harcourt-Smith *et al.*, 2015), increased manual dexterity and precision (more derived carpal morphology and the relative proportions of the elements of the hand are similar to that seen in species of later *Homo*; see also Kivell *et al.*, 2015),

and a relaxation on the dietary selective pressures evident in *Australopithecus* and *Paranthropus* (absolutely and relatively small dentition, more gracile mandibular corpus, and laterally-oriented temporal muscle attachment) (Berger *et al.*, 2015). However, several elements of the appendicular skeleton were described as more similar to the australopith-condition, particularly in the morphology of the shoulder and the pelvis (Berger *et al.*, 2015). Despite the overall similarities of the cranial morphology to *Homo* specimens, the cranial capacity of all specimens represented has been reconstructed to be well within the range of variation observed for australopiths and considerably smaller than the majority of *Homo* specimens (Berger *et al.*, 2015). Given that the assemblage has yet to be dated, the full implication of this new assemblage is largely obscured. However, early musings have indicated that a date of >2myr would likely place the *Homo naledi* specimens close to the base of the *Homo* group (Stringer, 2015). A more recent date might have equally far-reaching implications, as it would indicate that a late-surviving species of *Homo* with an australopith-like cranial capacity may have lived synchronously with Middle and Late Pleistocene hominins (Stringer, 2015). Furthermore, as the spatial range of *Homo naledi* is also not yet known, it may be that other small-bodied hominins, particularly those attributed to *Homo erectus/ergaster* are re-evaluated in light of these new finds (Dembo *et al.*, 2015; Stringer, 2015).

2.3 The significance of LD 350-1 for early Homo systematics

Villmoore *et al.* (2015a) recently reported a new well-preserved fossil mandible, LD 350-1, at Ledi-Geraru, Ethiopia, that has been assigned to *Homo*. Securely dated to 2.8-2.75mya, it is currently the earliest *Homo* fossil and has a mosaic of primitive and derived traits (Gibbons, 2015; Hublin, 2015). While LD 350-1 may be a late surviving member of *Au. afarensis,* given a number of morphological similarities, such as in the overall

dimensions of the dentition and mandibular corpus and the orientation of the mandibular symphysis, there are also a number of important differences that the authors interpret as distinct enough to suggest that they are not conspecific (Villmoore *et al.*, 2015a). In particular, the absence of the distinctive wear patterns between the maxillary canine and the mandibular P_3 (Hublin, 2015) and the uniform depth of the mandibular corpus between the P_3 and the M_2 (Villmoore *et al.*, 2015a). Importantly, many of the features that distinguish it from *Australopithecus* are also features that it shares with early *Homo* (Villmoore *et al.*, 2015a). Given the similarities between LD 350-1 and the fossils associated with early *Homo*, the authors suggest that it is a species that is close to the origin of *Homo* (Villmoore *et al.*, 2015a). Importantly, the fossil pushes the origin of the genus to at least 400,000 years earlier than originally thought. Additionally, given that LD 350-1 was found at 2.8-2.75mya as a likely ancestor to *Homo* suggests that hypotheses that include *Australopithecus sediba* as the ancestor to early *Homo* at a much later date of 1.98mya (Berger *et al.*, 2010) are increasingly unlikely (Villmoore *et al.*, 2015a). Furthermore, the fossil demonstrates that some of the dental and mandibular changes between *Homo* and *Australopithecus* occurred early (Villmoore *et al.*, 2015a) and may indicate an important divergence in dietary adaptations (Hublin, 2015).

LD 350-1 has a more primitive morphology of the anterior portion of the mandibular corpus than to specimens attributed to either *Homo habilis* or *Homo rudolfensis* though it does display some similarity to *Homo habilis*, such as in the curvature of the row of the anterior dentition (Villmoore *et al.*, 2015a), which suggests that they may belong to the same lineage, but separated by ~1myr (Gibbons, 2015). Nevertheless, LD 350-1 has been conservatively assigned to *Homo* species indeterminate pending the discovery of additional fossils (Villmoore *et al.*, 2015a; see also Hawks *et al.*, 2015 and Villmoore *et al.*, 2015b).

2.4 Definition of early **Homo** *as an adaptive grade*

The phyletic divergence of *Homo* has frequently been attributed to adaptive shifts due to dramatic environmental change and the innovation of lithic technology (Antón, 2013). Many authors suggest that it is the increasing aridification (deMenocal, 2004) or some other environmental correlate (e.g. Vrba's (1993) turn over hypothesis) that explains the synchronous emergence of *Homo* and *Paranthropus*. However, Grove (2011) suggests that it may have been selection for phenotypic plasticity that lead to behavioural flexibility in *Homo*. The period that Grove (2011) associates with a peak in selection for phenotypic plasticity is 2.7-2mya. According to Schrenk (2013), much of the systematics of early *Homo* are drawn from biogeographic perspectives with respect to the environmental and faunal context in which it speciated. For example, the synchronic appearance of *Homo* and *Paranthropus* has been suggested to be due to environmental changes between 2.8-2.5mya in which open habitats extended with more tough food resources (Schrenk, 2013). The expansion of arid environments during this period has been suggested to have influenced the selective pressures differentially in these two lineages (Hublin, 2015). In one, leading to the paranthropines, they became more specialised for processing tough and fibrous vegetation, which selected for the pronounced megadontia and the highly developed masticatory musculature in the associated specimens (Hublin, 2015). In the other lineage, which includes the putative early members of *Homo*, the hominins developed increasingly omnivorous diets with greater reliance on meat, possibly facilitated by increased encephalisation and the development of - or improvement upon - lithic technologies (Hublin, 2015). Hence, it is suggested that these environmental stressors caused the emergence of *Homo* and *Paranthropus* during the Plio-Pleistocene transition (Schrenk, 2013).

Homo habilis has been repeatedly associated with the innovation of lithic technology

(Napier, 1962). However, the discovery of OH 62 as reported by Johanson *et al.* (1987), suggested that some aspects of the morphology of *H. habilis* were more similar to *Australopithecus africanus* than other known *Homo* specimens (Schrenk, 2013). Additionally, in a recent study by Skinner *et al.* (2015), the structure of the trabecular bone of the carpals of *Au. africanus,* in addition to other taxa of Pleistocene hominins, indicates that they may have used lithics. While the majority of fossil evidence has thus far indicated an emergence of lithic technologies to coincide with *H. habilis* (Semaw *et al.,* 2003), recent indirect evidence of tool use was dated to 3.4mya, and possibly associated with *Au. afarensis* (McPherron *et al.,* 2010). Additionally, the recent discovery at Lomekwi 3, West Turkana, of stone tools dated to 3.3mya and associated with non-*Homo* fossils further indicates that lithic technologies pre-date the emergence of *Homo* by at least 0.5myr (Harmand *et al.,* 2015). Hence, if lithics did originate with *Australopithecus* then this innovation clearly did not require the full suite of *Homo*-like hand morphology and/or cranial capacity (Skinner *et al.,* 2015). Furthermore, behavioural studies of chimpanzee (*Pan troglodytes*) tool use, particularly in percussive nut-cracking (Sakura and Matsuzawa, 1991), question whether the innovation of stone tool technologies may have originated in the hominin clade at all. For example, it has been suggested that the knapping techniques that may have been employed to produce the 'Lomekwian' tools are similar to those used by chimpanzees during nut-cracking (Harmand *et al.,* 2015). Hence, it may be that the Lomekwian tools represent a transitional technological stage between a method of accidental flake production similar to that observed in contemporary chimpanzee behaviour, and the freehand knapping techniques exhibited in the later Oldowan technology (Harmand *et al.,* 2015; Bril *et al.,* 2015). Consequently, the production and use of various forms of lithic technologies may have been incorporated gradually within various pre-*Homo*

lineages, with perhaps a pre-adaptation originating in their hominoid ancestry.

Summary & Conclusions

New fossil evidence is having profound influence on our understanding of hominin diversity and systematics. Increasingly, it appears that the early evolution of the genus *Homo* included multiple different lineages that diverged early. Additionally, the origin of *Homo* is being pushed back, with fossil evidence now securely dated to 2.8-2.75mya. The morphology of the earliest morphs of *Homo* also appears to be increasingly similar to australopiths, disproving suggestions of a dramatic adaptive shift leading to its cladogenesis. Furthermore, increasing diversity recognised in other taxa, most notably *Homo ergaster*, renders it increasingly difficult to differentiate between species of early *Homo*. Unfortunately, palaeoanthropology continues to be plagued by contrasting paradigms in systematics with some researchers favouring fewer lineages while others put forward a more speciose hominin tree. These disagreements in the literature are further compounded by two classification systems, clades and grades, which are used interchangeably in the naming of genera. While supraspecific taxa may prove to be obsolete in future years (Cartmill, 2012), both clades and grades are immensely useful in describing evolutionary and adaptive histories. Hence, the present author calls for more rigorous definitions to be used in hominin systematics, possibly with two parallel classification systems, clades and grades, that remain distinct in their objectives, clades to describe the route of evolution and grades to describe the product (Wood and Lonergan, 2008), but that each can be separately used to communicate our understanding of hominin evolution and adaptation. The implementation of this suggestion, however, would require many specimens to be renamed and for two classification systems to be learned. The clade system may be subject to more frequent revision as phylogenetic relationships between taxa are increasingly understood and as such

the grade system might be more frequently used in the non-academic sphere.

Competing interests
The author declares that they have no competing interests.

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