RESEARCH ARTICLE

Why ‘Lucy’ (*Australopithecus afarensis*) Needs to be Included in *Homo* as a Subgenus: a Look at Including *Species Germinalis* in Human Lineage

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Current understandings of our Hominid family tree urge us to redefine the term *Homo* to include our earliest known human ancestors. A taxonomic term put in place by Darwin of *species germinalis* may offer a solution to including species accepted as very close to the human species but still separated by different genera [Lewis, 1987]. The issue of monophyly was used to define the specific member species of a lineage from a single common ancestor. However, in the genus *Homo* the lineage can not be traced to one origin but several branches of species and subspecies belonging to several different genera [Cela-Conde & Ayala, 2003]. Hence, the *Homo* genus may be seen as paraphyletic and as such a revision of the characteristics of what defines the Homo genus needs to be suggested. Species that demonstrate strikingly similar features and traits of a species should be accepted to join its genus. The human lineage consists of various species that science has described as deserving of *Homo* genus inclusion [Campbell et al., 2002], due to their holding of the criteria of having human sized brains, tool use and walking up-right (bipedalism). These criteria are problematic and suggest that Australopithecus and Homo be a joint genera under one genus: Homo [Cela-Conde & Altaba, 2002].

Key words: taxonomy, species, genera, genus, Hominid, Australopithecus, Homo

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INTRODUCTION

The existing species included in the *Homo* genus do not seem to share the exact criteria for "what defines human" as a means to identify its species of lineage, in that some members of *Homo* are more closely comparable to Australopithecus than to the *Homo Sapiens* in physical anatomical proportions and features [Cela-Conde & Ayala, 2003]. Furthermore, the criteria of walking in an upright position may seem lacking in *Homo habilis* reflected in arm and hand features and in respect to brain size and teeth *H. habilis* is comparable more to *Australopithecus* from modern humans [Cela-Cond & Altaba, 2002].

It is argued that *Homo Habilis* thus should not be included in the *Homo* genus and designated as *Australopithecus* although it would contribute to further variation in this already complicated genus and disregard the close affiliation it evidently has with humans (i.e. brain traits and cultural attributes) It may not be easy to identify who has more commonalities with *Homo sapiens* to be regarded as *homo*, and *Homo Habilis* exemplifies this with his early hominid traits reminiscent of Australopithecus and other features a kin to humans [Cela-Conde & Ayala, 2003]. By deciding on members of a genus researchers conclude who is the first transitional species that entered the realm of this genus from a different or close group [Cela-Conde & Altaba, 2002].

Because so many traits of a species may be of early ancestors and modern form drawing a line between differing genuses in a family of hominids is challenging. A solution to this problem is to accept ancestral species retaining common traits as a *species germinalis* of that genus. This placement is appropriate when characteristics are apparent with links to primitive close relatives than to modern humans [Cela-Conde & Altaba, 2002]. In this fashion *Australopithecus africanus* may be accepted as an early species of *Homo Habilis* or of being its *species germinalis* of *Homo* [Cela-Conde & Ayala, 2003]. Keeping in mind that *Australopithecus* was mostly a vegetarian savannah bush dweller and other *Homo* species manufactured stone tools yet their traits are intertwined in a labyrinth of differences and commonalities [Cela-Cond & Altaba, 2002].

With hominid remains found as far back as seven million years it is an understandable difficulty to try to define who is of human lineage and who is close to it and to what degree do they remain simply in a genus of the hominid family or included in *homo* genera [Edgar, 1995].

Variations of features in *Australopithecus africanus* and *homo* species afforded the latter a genus of his own simply due to differing brain size that is more ‘early’ hominid in form as the chimpanzees [Chamberlain, 1991]. It is thought that chimpanzees separated from man between 4 or 5 million years ago and thus they are included in the hominid family [Cela-Conde & Ayala, 2003]. Yet human ancestry was described as *homo* by genus within hominidea on account of bipedalism, teeth and brain size. These features in Australopithecines tend to vary from one side of primitive chimp-like traits to the *homo* type [Cela-Conde & Altaba, 2002].

In the case of the hominid genus of *Orrorin tugenesis*, whose upper canine teeth resemble those of chimps whilst having the *homo* trait of little thickened molar teeth. These features may find the human chimp lineage connection [Campbell et al., 2002]. So, the question is raised why declare a new genus for species who already may fit the criteria of a known genus as the earliest member of its species or its origin transitional member as the *species germinalis*? A genus accepts new found members to its group if it demonstrates shared lineage traits of its early appearance in evolutionary transition from close kin from another genus [Cela-Conde & Altaba, 2002].

In new descriptions of Australopithecines in relation to *Homo* genus it is argued if *Homo habilis* need to be redefined as Australopithecus, as *H. habilis* is physically, anatomically, functionally and evolutionarily as close to humans as they are to Australopithecines [Campbell et al., 2002],. If one origin of human lineage is to wished for then *h. habilis* needs to be redefined or else it will diversify the genus of *homo* as if *A. africanus* was included in *homo* genus too [Cela-Conde & Ayala, 2003]. A species in question of identity should be included in an existing genera if it has early and modern traits together connecting it to the lineage of *homo* [Cela-Conde & Altaba, 2002].

MATERIALS

Data Collection

Australopithecines are regarded to be the earliest bipedal hominids and share a parallel genera with the genus *homo*, who made tools of stone, ate meat, yet kept common features with Australopithecines [Edgar, 1995]. *A. afarensis* shares commonalities with chimps by having a sharp trochlear humerous crest [Cela-Conde & Ayala, 2003].

The three and a half million year old *Kenyanthropus platyops* hominid from Kenya exhibits a small skull alike Australopithecines yet whose face was flat as *H. rudolfensis*, and unlike that of *A. afarensis* with outward projecting facial features [Cela-Conde & Altaba, 2002; Rak, 1983]. Along with this, *K. platyops* has similar dental traits alike *h. habilis* in the small enamel and thinness of its teeth [Cela-Conde & Ayala, 2003].

The lack of more developed *homo* traits does not dilute the fact that it has been requested that *K. pltyops* be accepted in the *homo* genus as a germinal species or early form of it. It was also pointed out that *K. platyops, h. habilis* and *h. rudolfensis* be included in Australopithecus genus due to their important commonalities in trait. In solving this problem of identity, it is agreed to group them in the homo genus. This conclusion if accepted will put the homo genus as far back as three and a half million years [Cela-Conde & Altaba, 2002].

As seen with *Orrorin* as maybe being the common ancestor of chimps and man, and *K. platyops* having features similar to *h. habilis* but not to later homo species (*h. erectus*) [Walker & Leaky, 1993] explains that primitive hominid lineages were diverse [Cela-Conde & Ayala, 2003]. As the divide between robust (Australopithecus) and nonrobust (homo) ancestry’s occurred 3.5 million years ago the gracile hominids need to be all included in homo [Cela-Conde & Altaba, 2002].

It is plausible to see all Australopithecine included under the same accord as *H. habilis* and *h. rudolfensis*. By accepting *K. playtops* as a first form species of homo, and the agreement to see no need in dividing a genera in terms of robustism or gracilism just because the robust line was a vegetarian and the others were meat eaters and had bigger brains and made rock tools, a revision of homo genus in terms of Aust. is possible [Cela-Conde & Ayala, 2003].

An important evolution took place from 1.8 to 2.5 million years ago in homo development [Campbell et al., 2002], from bigger statures, to smaller teeth, larger brains and a transforming of limbs and level of retaining of arboreal tendencies and bipedal specialization [Johanson & White, 1979]. Yet *homo habilis* kept multiple physical and postcranial features present in Australopithecines. As emphasis is being given more to finding the *Species germinalis* of homo, changes and similarities between the two are looked into [Cela-Conde & Ayala, 2003].

It is known homo developed out of Australopithecines. However the line separating between the two genus is blurred as different species have different primitive or derived characteristics that make a linear presentation of evolutionary change difficult [Johanson & White, 1979]. Sister species are decided upon by their similarities that outweigh those of the other members of the genus [Smith & Spencer, 1984]. For the reasons described above, debate still persists about defining the first homo member. If one decides to define homo through rock tools than the paleontology goes back 2.5 million years in the past [Campbell et al., 2002].

The development of an upright walk in Australopithecus, another criterion for homo members, resulted in the expansion or enlargement of joints mainly hip [Walker & Leaky, 1993], knee spine and pelvis [Lewin, 1983b]. Australopithecus Afarensis, “Lucy”, had intermediate characteristics of these that are between homo sapiens and pan troglodytes [Johanson & White, 1979].

With Lucy's up right walking, came stress on these joints and their expansion occurred [Johanson, 1981]. Her relatively smaller lumbo-sacral joints and leg joints suggested these stresses were lessened and thus the joint surface areas were reduced in size due to her tree climbing tendencies as can be conferred from her curved feet and hand bones. Her locomotion and motor features appeared in *H. habilis* and other early homo genus species, perhaps up to *H. erectus* [Lewin, 1988]. As such, origin homo members kept the Australopithecine hip joint formation and gradually as the strain increased they developed longer femur leg bones and bigger joints [McHenry & Coffing, 2000].

In comparing skeletal remains of 3 million year old "Lucy" (*A. afarensis*) [Johanson, 1981] and the 1.8 million years old, 1987 new OH 62 Olduvai fossil of *H. habilis*, a striking similarity arises between the two, namely in their size which was around 3 feet in height, thus *h. habilis* can be shown as the link between h. erectus and Australopithecines as their brain size and body increases greatly from the early *A. afarensis* to *H. erectus. H. erectus* [Walker & Leakey, 1993] has been dated as far back as 1.6 million years ago with average brain size of 1000 cc compared with the 438 cc of *A. afarensis* and *h. habilis* 612 cc. OH 62, *H. habilis*, [McHenry & Coffing, 2000] continues to blur the line between Australopithecines and homo as it posses early features thought not present in homo in regards to its small size [Johanson & White, 1979].

Along side this gender dimorphism of larger males than females up to to times it size was characteristic of *A. afarensis* and *h. habilis* also, though this changed in *H. erectus* to smaller sex differences [Walker & Leaky, 1993].

Lucy's primitive features including long arms in comparison to her legs [Lewin, 1983], and arboreal linked tendency of curved foot and hand bones have been shown to persist through *h. habilis* and earliest h. erectus (up to 2 million years in appearance) [McHenry & Coffing, 2000]. Hence, *H. habilis*, possessing such Australopithecine features could also be a tree climber too even though he has features of later homo genus as well.

The elongated arms of *H. habilis* OH 62 are as long as *A. Afarensis* in the humerus' comparison to the size of the leg or thigh femur, reaching a 95% match of the humerus thus the primitive traits consist here also [Campbell et al., 2002]. Such a ratio is leaning towards *pan troglodytes* who have similarly high ratio rather than *homo sapiens* who has a lower one of 70%. There is also a held opinion that *A. afarensis* and *h. habilis* do not change in the mobility function of their feet either. 1.6 to 1.8 millions years ago major derived differences appeared from the development of *H. habilis* to *H. erectus* [Walker & Leaky, 1993].

The traits of later homo genus members is seen in *h.erectus* with the enlargement of joints and their surface area depended on for bipedalism, enlargement of brain size or cranial capacity [McHenry & Coffing, 2000]. As drastic as these shifts in derived features may seem they can be noted as a part of a continuous development started in Australopithecine through *h. habilis* and compiled in *h. erectus* [Walker & Leaky, 1993].

Data Analysis

In the genus homo walking upright is a trait consistant with its members yet the changes appear in form and body structure (Table 1) [McHenry & Coffing, 2000]. The estimated cranial capacity or brain size of *A. afarensis* is between 342 and 540 cc (close to *pan troglodytes* 434 cc). The cranial capacity doesn't change much across the

Australopithecines, though *H. habilis*' average of 582 cc is closer to A. afarensis than to the 1000cc of *H. erectus* [Lewis, 1987].

When calculating body weight in relation to size of brain or endocranial capacity of *A. afarensis* with *h. habilis* who are of siilar stature size, they lean toward the primitive features of Australopithecine, and *H. rudolfensis* who is closely related to *h. habils* leans toward the more advanced homo members but this is due to his bigger stature [McHenry & Coffing, 2000].

Furthermore, *H. habilis* has a short build, but also a bigger cranial or brain capacity compared to other Australopithecines. This explains that within the transferal of Australopithecus into homo various traits persisted unchanged for 2 million years almost whilst having fast transformations within close member species of the genus or sister species from an earlier existence in a previous genus [McHenry & Coffing, 2000].

It is hard to identify specific changes between Australopithecus and *H. habilis* due to very increased variations of skull, cranial and dental or chewing systems within these species.

H. Habilis is the closest kin to other members of homo genus by means of derived traits, and since he is as close to robust Australopithecines and *Paranthropus* members as to *H. rudolfensis* they should be placed in the same genus of homo on a monophyletic basis. Thus the rest of the homo genus is also closely related to the gracile Australopithecine (*A. afarensis*) under the same pretences [McHenry & Coffing, 2000]. Together a gradual decrease in cheek teeth size and an increase in endocranial capacity can be seen from early to later species of homo.

In regards to cheek teeth size or chewing apparatuses a gradual increase can be seen from Australopithecines to later homo species; *A. afarensis* “Lucy” = 460 mm^2, *H. habilis* = 478 mm^2, *H. ergater/H. erectus* = 377 mm^2 and *H. sapiens* = 334 mm^2 (Table 1).

Moreover, the average size of the teeth of the dental system is connected to thickness and robustness of the shape and form of the head and skull and its facial characteristics. *H. rudolfensis*, with teeth measurements of 572 mm^2, and a close brother species of *h. habilis* shares its robust facial traits and dentals with Australopithecines, however in relation to body weight his teeth have decreased in size [Rak, 1983]. It should be noted also that *H. habilis* exhibits a maxillary seen in earlier hominid species found at Olduvai [McHenry & Coffing, 2000].

In regards to the foot of *A. afarensis,* it shows traits of earlier hominids in the structure and form of it, for instance, the back side of metatarsals area doesn’t expand from left to right as in members of the later members homo genus and the toes are rather bent and elongated as well although these qualities were seen in *h. habilis* also. In *H. ergaster H. erectus* [Walker & Leaky, 1993] the toe phalanges weren’t as bent or as long as *Australopithecus afarensis* [McHenry & Coffing, 2000].

Other changes include lowering of gender dimorphism which is thought to be the result of group or communal efforts of males in h. erectus, rather than a competition based social organization of earlier hominids [Lewin, 1987]. The average weight of male or female individuals of a species can be seen to decrease as the homo genus progresses: with *A. afarensis* possessing a body mass in kilograms of males = 45, females = 29; *H. habilis* males = 37, females = 32; and *H. egraster* males = 66, females = 56 (kg) (Table

1). From *A. afarensis* to *H. habilis* a drop in dimorphism is apparent [McHenry & Coffing, 2000].

Regarding the upright walking evolution of early homo members, the leg bones of *H. habilis* and Australopithecines have especially flat talar facets and their fibula and tibia are more derived than primitive in their features. Along side this *H. habilis* and *A. afarensis* had another trait in common – both exhibited a femur length which was lesser than the humerus [McHenry & Coffing, 2000]. From the femur shafts of *H. habils* OH 62 a striking similarity arises with *A. afarensis* and this may reveal clues about hip structure which is possibly also as comparable to *A. afarensis* [Lewin, 1988].

Regarding development of the pelvis and hip structure a substantial change occurred between the Australopithecines and homo genus [Lewin, 1988] with the sacrum turning anteriorly, the pelvis blades decreasing in size and pelvic girdles [Lewin, 1983a] thus exhibiting a better progressing evolution in walking upright on two legs [McHenry & Coffing, 2000].

Furthermore, hip joints developed in size and widened surface area to address the stresses from bipedalism on the hind limbs and lower vertebrae [Lewin, 1988]. *A. afarensis* had relatively little hips compared with later members of the homo genus, yet these changes were gradual and occurred within early and late species of homo too.

A development also took place in the birth canal in females, from Australopithecines to homo, as the species became better equipped and comfortable with walking upright this change decreased the size of the pelvic canal anterior to posterior and the pelvic blades. This suggests the presence of variations and gradual transitions within homo members from the ones possessing primitive traits to modern ones [McHenry & Coffing, 2000].

Even though the hip and pelvis of *A. afarensis* is reduced in size compared to later homo genus members it is shaped and structured like the ones exhibited by them [Campbell et al., 2002].

The thorax of *A. afarensis* is cone shaped correlating with that of early hominids like pan troglodytes, such a structure can suggest the shoulder and upper back muscles involved in arboreal activities [Campbell et al., 2002]. This differs from later members of homo in their roll shape thorax [Walker & Leaky, 1993]. However the shoulder and thorax structure is shared both in *A. afarensis* and *H. habilis* compiling the arboreal traits for these two species but not for other members of homo.

In terms of upper arm or humerus proportions *A. afarensis* and *h. habilis* share traits of robust structure compared to other members of homo exhibiting lighter features of the upper and lower arm [Campbell et al., 2002]. *A. afarensis* also presents lower arms that are more elongated than the upper one. *H. habilis* also possessed arms which were longer than his legs [Lewin, 1983b]. In *H. rudolfensis* the estimated length of humerus and femur was more alike the later homo members. This suggests the existence of different variations in features derived and primitive along the early homo members and later ones [McHenry & Coffing, 2000; Smith & Spencer, 1984].

Finally, in terms of cultural development and tool making from stone the skeletal remains of members of early homo members and sister species can correlate tool making from stone for carving meat from bones and breaking bones, digging tools (and later weapons) to the evolution of the hand dexterity and motor abilities [Campbell et al., 2002].

From 2.5 million years in the past such stone tools lasted the test of time and survived for current research. Australopithecine remnants were found in context with such tools from this time (from Middle Awash River) and imply that *A. garhi* could also have made them and may put pressure on accepting Australopithecines in homo genus even though the stone tool remnants of this time period are less sophisticated [McHenry & Coffing, 2000]. *A. africanus* had traits of homo species in the hand structure in that they can connect between thumb and fingers for grasping and accuracy motor skills needed for tool making from stones, yet traits of earlier hominids were present in the metacarpals of the hands equally so [Campbell et al., 2002].

Interestingly enough, and compiling the claim of *A. afarensis* in homo genus are the derived later homo characteristic traits of hand bones possessing the ability to grasp and hold items in an accuracy enabling function for making such tools that was considered unique to members of homo genus yet it differs in thumb movement of later homo members and early traits implying of climbing abilities [Campbell et al., 2002]. These climbing traits include bent proximal finger bone phalanges which exhibit roughened lines or crests that connect to flexor sheath and long pisiform carpals and widened proximal and distal edges of metacarpals [McHenry & Coffing, 2000; Smith & Spencer, 1984].

Similarly so, H. habilis also exhibited similar homo strong grasping and accuracy handling traits found also in Australopithecines in the manual bones along side early hominid traits of Australopithecines with rather bent and robust phalanges of the hand, though the area of his finding was scattered with rock tool remnants correlated to him and H. habilis' traits were gradually more developed in derived features than *A. afarensis* [McHenry & Coffing, 2000]. *H. habilis* even had similar hand mobility problems that in gradually resolved the motor skills issues as homo progressed and more sophisticated stone tools evolved with it [Campbell et al., 2002].

Discussion

In regards to deciding what features determine homo traits or credentials one must place importance on all aspects such as brain size, skull structure, pelvis form, bipedalism [McHenry & Coffing, 2000], derived and primitive features equally as variation within the homo genus is as great between homo and Australopithecus as within them [Campbell et al., 2002; Walker & Leaky 1993]. Hence, *A. Aafarensis*' relation to *H. habilis* or the latter to other Australopithecine or homo species should be more accepted as variation within the homo genus and be seen as variations derived [Walker & Leaky, 1993] from gradual change whose developing traits can not be specifically and linearly identified but need to be seen in the broader framework of homo as they lead to with their features to the modern human and how homo sapiens gained its present form [Cela-Conde & Ayala, 2003].

Though the gradual differences from development from Australopithecine to homo genus is more profound in the transformation from *H. habilis* to *h. erectus*. It does not deny the facts of *h. habilis* and other early homo member's traits that correlate and lean toward Australopithecus much more than to other Homo genus [Edgar, 1995; Campbell et al., 2002]. *H. habilis* is thus the connector between Australopithecus and homo, due to striking parallels in stature and structure and in the post cranial traits. In order to better represent the gradual and non-linear changes of early homo development *A. afarensis* should be given similar homo status under the pretenses of having similar primitive and derived traits as *h. habilis* [Walker & Leaky, 1993].

1.8 million years ago *H. erectus* and *H. ergaster* started to exhibit traits of later homo species and strikingly resembling *h. sapiens*. Before then, *h. habilis* and other early homo members were possessing derived and primitive traits unequally yet gradual in its presence along the continuation of time between 2.6 to 2 million years ago. Australopithecines and early homo members clearly should these changes of traits in time and as cranial capacity grew [Walker & Leaky, 1993] and limbs became more human proportioned, body statures grew and became similar amongst the sexes, bipedal adaptation became more efficient and a framework of development was brought to light [McHenry & Coffing, 2000].

CONCLUSION

Instead of stuggling to place *H. Habilis* in Australopithecus genera why not include *Australopithecus Africanus* into the Homo genus as a subgenera and thus not have to redefine human lineage or disrupt the course as been agreed upon by evolution [Johanson, 1981]. The traits of both of these species are comparable enough to encompass being in the sub group of Homo.

Instead of diversifying the hominid genus by adding more genera an inclusion of origin linked species sharing common features [Smith & Spencer, 1984] with humans into an existing genus is preferable and rightfully designate their place in the human family tree of hominids.

However, I would suggest instead of destabilizing the homo genus by removing *h. habilis* to Australopithecines, include *Austalopithecus afarensis* “Lucy” in homo for the same reasons *H. habilis* is it this genus of homo, and their closeness can be tranfered also in the same manner to other Australopithecineand early homo members in terms of defining the origin species of the human lineage. Thus, giving *A. afarensis* the definition of *species germinalis* alongside *h. habilis*.

One may see in these derived traits apparent in *H. habilis* and *A. afarensis* and other Australopithecine in varying levels as reason enough to include all robust and gracile Australopithecines in a sub genus of homo and their intermediate relation between homo and pan should consider accepting pan as species germinalis of Australopithecine on account of brain size parallels, anatomy, limb proportions, arboreal tendency and teeth size etc which are all a gradual but being a labyrinth of features that are seen amongst early members of homo and Autalopithecines. By adding Australopithecines in the genus of homo as origin species and Pan could be placed in a homo subgenus that places *A. afarensis* as an intermediate between the genus *homo* and *pan*.

Lastly, *H. habilis* and his closest resemblance to *A. afarensis* in stature, limb proportions with arms longer than legs [Lewin, 1983a], and structure of body and upper leg bone anatomy [Walker & Leaky, 1993] imply that *A. afarensis* should at least be seen as the first homo species as her framework was retained in his but with the exception of a bigger brain but smaller than following homo members.

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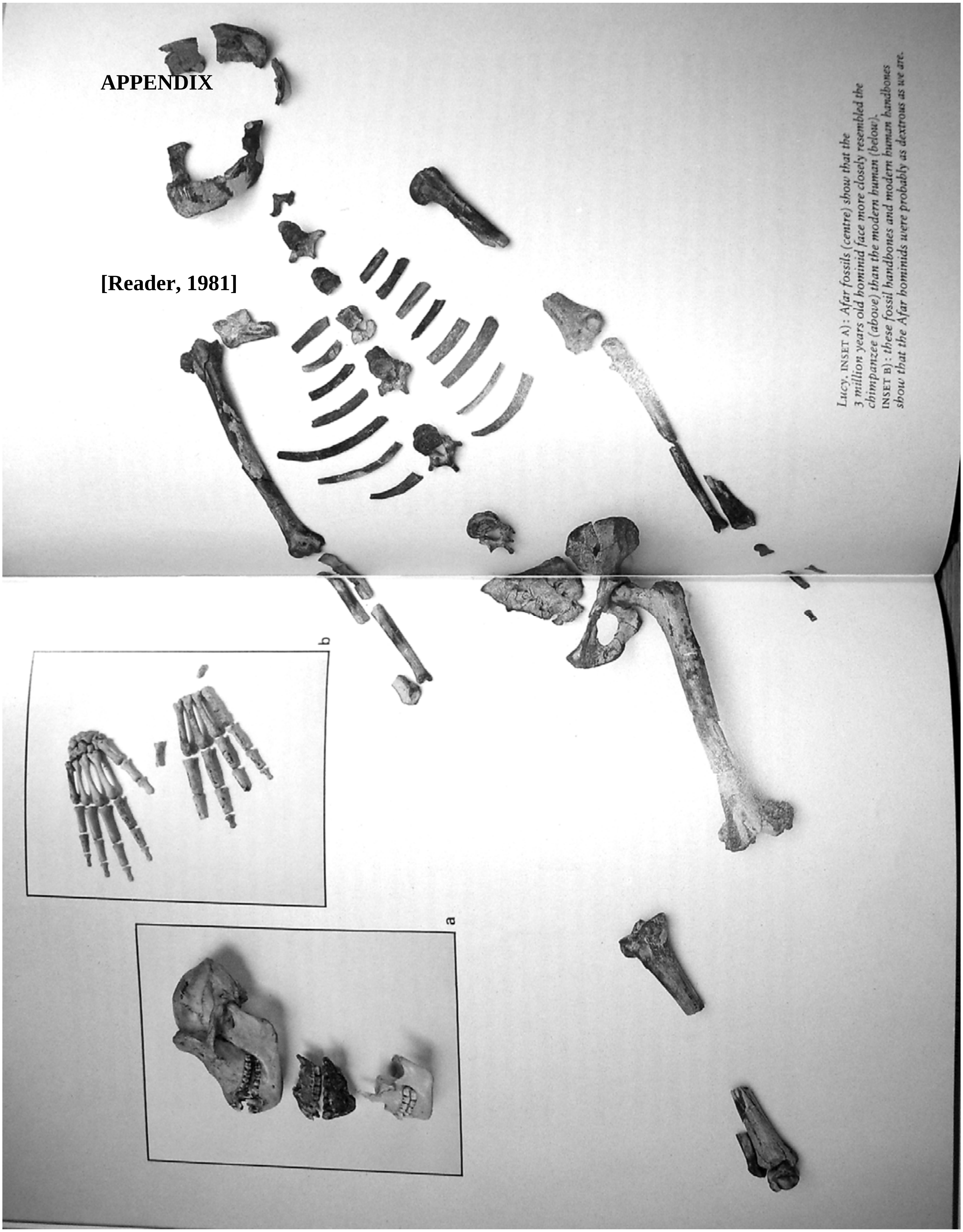
APPENDIX

[Reader, 1981]



LUCY. INSET A): *Afar fossils (centre) show that the 3 million years old hominid face more closely resembled the chimpanzee (above) than the modern human (below).*
INSET B): *these fossil handbones and modern human handbones show that the Afar hominids were probably as dextrous as we are.*

APPENDIX II

[McHenry & Coffing, 2000]

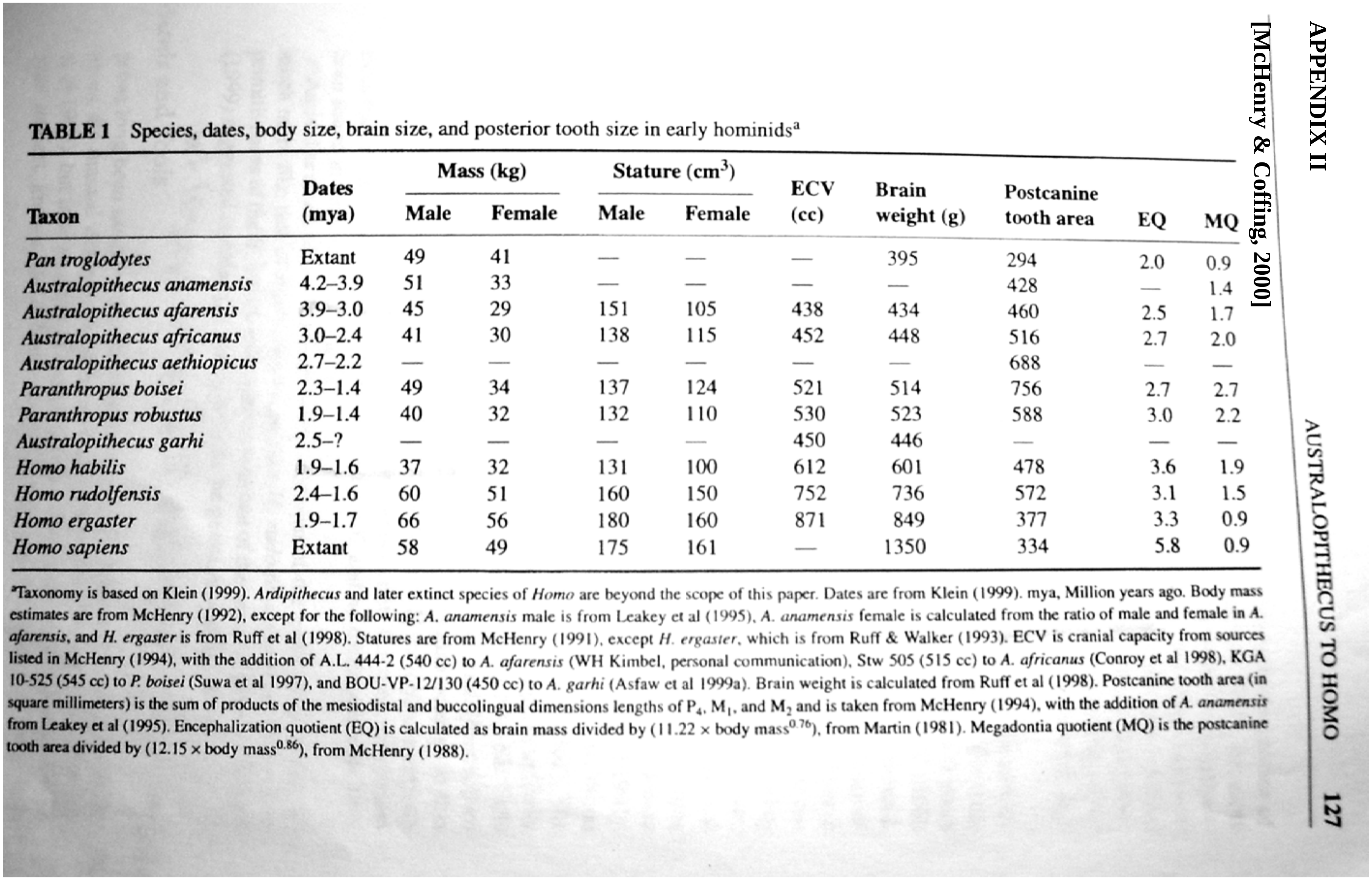


TABLE 1 Species, dates, body size, brain size, and posterior tooth size in early hominids[a]

Taxon	Dates (mya)	Mass (kg)		Stature (cm^3)		ECV (cc)	Brain weight (g)	Postcanine tooth area	EQ	MQ
		Male	Female	Male	Female					
Pan troglodytes	Extant	49	41	—	—	—	395	294	2.0	0.9
Australopithecus anamensis	4.2–3.9	51	33	—	—	—	—	428	—	1.4
Australopithecus afarensis	3.9–3.0	45	29	151	105	438	434	460	2.5	1.7
Australopithecus africanus	3.0–2.4	41	30	138	115	452	448	516	2.7	2.0
Australopithecus aethiopicus	2.7–2.2	—	—	—	—	—	—	688	—	—
Paranthropus boisei	2.3–1.4	49	34	137	124	521	514	756	2.7	2.7
Paranthropus robustus	1.9–1.4	40	32	132	110	530	523	588	3.0	2.2
Australopithecus garhi	2.5–?	—	—	—	—	450	446	—	—	—
Homo habilis	1.9–1.6	37	32	131	100	612	601	478	3.6	1.9
Homo rudolfensis	2.4–1.6	60	51	160	150	752	736	572	3.1	1.5
Homo ergaster	1.9–1.7	66	56	180	160	871	849	377	3.3	0.9
Homo sapiens	Extant	58	49	175	161	—	1350	334	5.8	0.9

[a] Taxonomy is based on Klein (1999). *Ardipithecus* and later extinct species of *Homo* are beyond the scope of this paper. Dates are from Klein (1999). mya, Million years ago. Body mass estimates are from McHenry (1992), except for the following: *A. anamensis* male is from Leakey et al (1995), *A. anamensis* female is calculated from the ratio of male and female in *A. afarensis*, and *H. ergaster* is from Ruff et al (1998). Statures are from McHenry (1991), except *H. ergaster*, which is from Ruff & Walker (1993). ECV is cranial capacity from sources listed in McHenry (1994), with the addition of A.L. 444-2 (540 cc) to *A. afarensis* (WH Kimbel, personal communication), Stw 505 (515 cc) to *A. africanus* (Conroy et al 1998), KGA 10-525 (545 cc) to *P. boisei* (Suwa et al 1997), and BOU-VP-12/130 (450 cc) to *A. garhi* (Asfaw et al 1999a). Brain weight is calculated from Ruff et al (1998). Postcanine tooth area (in square millimeters) is the sum of products of the mesiodistal and buccolingual dimensions lengths of P_4, M_1, and M_2 and is taken from McHenry (1994), with the addition of *A. anamensis* from Leakey et al (1995). Encephalization quotient (EQ) is calculated as brain mass divided by ($11.22 \times$ body mass$^{0.76}$), from Martin (1981). Megadontia quotient (MQ) is the postcanine tooth area divided by ($12.15 \times$ body mass$^{0.86}$), from McHenry (1988).