

# Multiplying genera versus moving species: a new taxonomic proposal for the family Hominidae

Camilo J. Cela-Conde\*<sup>†</sup> and Cristian R. Altaba\*

RECENT FINDINGS AND ANALYSES HAVE enriched knowledge of the human lineage, forcing us to question once more the taxonomy of hominids. On the one hand, new genera are proposed so as to accommodate recently discovered specimens. On the other hand, the generic position of early hominids has been changing with the purpose of avoiding paraphyletic groups. We argue that multiplying genera may not be the best solution to improve the taxonomy of the Hominidae. Accepting that any genus must be an adaptive, particular unit, we propose the application of a suggestion by Darwin for a new taxonomic convention, *species germinalis*, for classifying doubtful specimens of the human lineage without needing either to designate new genera or to switch taxa from one genus to another. The family Hominidae can, by this means, be classified in terms of four genera and three subfamilies.

Three new genera belonging to the human ancestry — *Ardipithecus*,<sup>1</sup> *Orrorin*<sup>2</sup> and *Kenyanthropus*<sup>3</sup> — have been proposed to classify some recently found, early specimens that, in the opinion of the authors proposing the new taxa, cannot be placed in any previously defined genus.<sup>4,5</sup> To support such proposals, White quotes the Introduction to the *International Code of Zoological Nomenclature*, which stresses 'the freedom of scientists to classify animals according to taxonomic judgments', and makes clear that the code 'refrains from infringing upon taxonomic judgement, which must not be made subject to regulation or restraint' (T.D. White, pers. comm.). Erecting new genera should, in our opinion, rely on solid arguments, however, unless taxonomic proposals are to be considered aside from evolutionary events.

In searching for an adequate taxonomy of *Homo*, Wood and Collard<sup>4,5</sup> work on the basis that any genus must be monophyletic (that is, have a single origin and include all its descendants), and must express a novel adaptive solution. In *Homo*, monophyly is under suspicion. They examined six studies that have

adequately tested the monophyly of *Homo*: three suggest that the genus is monophyletic, but the other three suggest that it is paraphyletic.

Difficulties in obtaining accurate cladograms are not exclusive to *Homo*. To build phylogenetic hypotheses, several distinct steps are necessary — the assignment of characters to hypodigms so as to define the traits of a given species; the choice of the species to be assigned to each genus; and the assignment of individual specimens to that species. This procedure often leads to insoluble problems. In the conclusions of the International Colloquium on Human Systematics held in Palma de Mallorca in February 2000, for example, point 9 asserts that: 'No consensual means of identifying biological species in the fossil record exists at the present time'.<sup>6,7</sup> If species cannot unambiguously be identified in the fossil record without extended discussions about taxa, then hypodigms are difficult to establish and, as a result, many nominal species are kept under suspicion. Fortunately, genera seem to be less controversial. Or perhaps not?

The second condition proposed by Wood and Collard<sup>4,5</sup> for the existence of a genus is that of adaptive coherence. This is a basic issue, because any taxonomic proposal ought to reflect changes in adaptive strategy, assuming that systematics is indeed within the evolutionary paradigm. If several species remain close enough to deserve inclusion in the same genus, then it is likely that their adaptive solutions may not differ significantly. Wood and Collard contend that, in the case of *Homo*, none of the examined traits complies with this requirement:

1. Body size and shape in some of the different species grouped within the genus are occasionally closer to those of australopiths than to *Homo sapiens*.
2. Regarding totally developed bipedalism, arguably the fundamental apomorphy (derived trait) of the genus, Wood and Collard cite traits in the hand structure of OH 7, as well as in the arm size of OH 62 and KNM-ER 3735, as evidence of incomplete

bipedalism in *Homo habilis*.

3. Cranial capacity — another trait that, with its large increase over time, identifies the taxon *Homo* — raises similar doubts. The results of calculating relative brain size indicate that *H. habilis*, as well as *H. rudolfensis*, *H. ergaster* and *H. heidelbergensis*, are closer to australopiths than they are to living humans, whereas *H. erectus* is equidistant.
4. Finally, the chewing apparatus points to a closer relationship of *Homo habilis* to the australopiths and paranthropes than to *Homo sapiens*.

Wood and Collard concluded that, when *H. habilis* and *H. rudolfensis* are included in *Homo*, the genus thus defined does not reflect an adaptive unit. They proposed, therefore, to limit the taxa included in the genus *Homo* to those that are closer to living humans than to the australopithecines, that is, to drop both *H. habilis* and *H. rudolfensis* and transfer them to *Australopithecus*.<sup>8</sup> As pointed out by several participants in the Palma de Mallorca meeting, such transferring would increase the already considerable diversity and the paraphyly of the recipient genus. Wood and Collard do indeed refer to this problem, but they prefer it to the alternative of having to define a new genus within the hominid family. Some of Wood and Collard's reasons for disregarding *H. habilis* and *H. rudolfensis* as members of the genus *Homo* seem arguable, however. The presence in some specimens often classified as *H. habilis* of a protrusion in the Broca and Wernicke brain areas, for instance, together with the cultural evidence coming from sites where either *H. habilis* or *H. rudolfensis* have been found, make it difficult to disregard the affinities of these taxa with our own species.

Putting to one side the issue of what is the best taxonomy in this particular case, however, the general question that arises is the following: when faced with an early specimen difficult to place in one or other genus, are we forced to choose between unwanted paraphyly and the unreasonable multiplication of hominid genera? This dilemma appears quite often in strict cladogram-based taxonomies. Given that cladistics is a highly useful tool in systematics, however, a choice seems inevitable. Tobias once had 'the temerity to suggest the taxonomic device of a bi-generic nomen for the very case of *Australopithecus/Homo habilis*' (P.V. Tobias, pers. comm.). This device might solve the problem, as it both avoids the proposal of a new genus and explicitly states that the species in question is transitional among genera. We would like to offer a different solution,

\*Laboratory of Human Systematics, University of the Balearic Islands, Carretera de Valldemossa, km 7.5 07071, Palma de Mallorca, Spain.

<sup>†</sup>Author for correspondence. E-mail: cela-conde@uib.es

however, that is closer to current taxonomic practice.

### A novel taxonomic solution

In response to the dilemma outlined above, we propose a novel approach that relies on scholarship but without increasing taxa beyond reasonable limits.

To solve the problem of having either to propose paraphyletic genera or to multiply the Pliocene hominid genera when trying to accommodate new specimens, it is worth recalling Darwin's wise admonishment on the subject: 'Whether primeval man, when he possessed but few arts, and those of the rudest kind, and when his power of language was extremely imperfect, would have deserved to be called man, must depend on the definition which we employ. In a series of forms graduating insensibly from some ape-like creature to man as he now exists, it would be impossible to fix on any definite point when the term "man" ought to be used. But this is a matter of very little importance.'<sup>9</sup>

Darwin was expressing what we now call anagenesis, that is, evolutionary change within a lineage through time. A chronospecies, which is a diagnosable section of a lineage evolving in this way, may or may not have precisely definable limits<sup>10,11</sup> The fossil record suggests that changes occurred gradually (albeit at variable speed) along the various branches of the hominid tree.<sup>12,13</sup> Thus, within the early episodes of an evolving lineage there is but little place — as Darwin says — for the nominalist designations that strict cladistic taxonomy demands. The use of cladograms, however, requires that the taxonomy based on them yield monophyletic groups.

When Leakey, Tobias and Napier defined the taxon *Homo habilis*, they were certain that the Olduvai fossils included as holotype and paratype belonged to the genus *Homo* because these specimens were already on the track that would ultimately lead to *H. sapiens*, through increasing brain and manual abilities.<sup>14</sup> Both *H. habilis* and *H. rudolfensis* retain many primitive characters that indeed link them to *Australopithecus*, but they also share significant synapomorphies with later taxa.<sup>15</sup> Recognizing this fact is not a criticism of Wood and Collard's approach, because what these authors intended was to establish morphological criteria for a taxonomy not derived from functional traits, which are always difficult to assess. The very meaning of the genus can render such purpose virtually impossible, however. When we group different fossil

species in a genus, we do it because we agree that an important evolutionary step has taken place in the last common ancestor of the species included in that genus, giving rise to a novel adaptive solution in it and in its descendants. Our species — that of extant modern humans — is the mirror upon which we look at ourselves in order to define the apomorphies of the genus *Homo*. But which are the earliest fossil specimens that actually demonstrate them?

Darwin's point is pertinent here: it is highly likely that the earliest individuals of the new genus were difficult to distinguish from their equivalents in their sister group. Not enough time would have elapsed since the divergence of lineages and, as a consequence, the weight of primitive characters would have been very large. It may therefore be inappropriate to set *Homo sapiens* apart from the australopithecines when comparing doubtful specimens, since this is a purely phenetic approach. Inevitably, the early specimens of the new genus would not yet have developed the clade's apomorphies fully, and thus must show a greater overall similarity to the coeval individuals belonging to the sister group. A parallel difficulty appears with the specimens classified as *Orrorin tugenensis* and *Kenyanthropus platyops*. The type specimen of the latter, KNM-WT 4000, has in fact been described as 'a dizzying mosaic of features'.<sup>16</sup>

This problem is pervasive, not only among hominoids, nor only at the genus level. Plesiadapiformes (a suborder from the Palaeogene, probably extending back into the Cretaceous, and becoming extinct in the late Eocene) were classified as Primates by Simons and Tattersall<sup>17</sup> because of their molar morphology, and have been so considered by a number of scholars.<sup>18–21</sup> These Plesiadapiformes, in particular the ptilocercine tree-shrews,<sup>19</sup> retain many plesiomorphies relating them to various archontans, such as claws on all digits, divergent but non-opposable hallux, and lack of orbital rings. They have been classified either as an outgroup 'pre-Primates'<sup>22</sup> or in-group 'archaic Primates',<sup>21,23</sup> which acknowledges an early phylogenetic link that nevertheless still needs to be determined more precisely. At a higher level, the paraphyletic synapsids have variously been considered either as mammal-like reptiles<sup>21</sup> or as already (reptile-like) mammals.<sup>24,25</sup> *Branisella boliviana*, from the Oligocene of South America, appears to be close to the base of the New World monkey radiation. Given that it cannot be assigned to either of the

two extant major clades, it has been accommodated within the Platyrrhines, but as a group *incertae sedis*.<sup>26</sup> Such labelling seems adequate for *Ardipithecus ramidus*, because it is not yet clear whether or not it belongs to the human lineage.<sup>2</sup> It is inappropriate, however, when the problem is not the impossibility of allocating an incomplete specimen, but instead the treatment of an early representative of a later adaptive radiation classified into definable clades.

The issue raised by these instances is not restricted to the fossil record. The same methodological problems are posed by living groups that have traditionally been considered as belonging to well-recognized higher taxa. For example, the 'lower heterobranchs' and 'cephalaspideans' are diverse, undoubtedly paraphyletic groups of gastropods with mosaic sets of prosobranch and opisthobranch characters, that have been placed either close to the Euthyneura or clearly within them.<sup>25,27,28</sup>

To define a lineage it is necessary to quantify morphological traits, establish a hypodigm, and identify significant characters. We will always, therefore, find a serious problem when we are confronted with a mosaic of numerous plesiomorphies existing together with novel traits that suggest the appearance of a new genus. This problem is widely recognized, and leads to lengthy discussions about the need correctly to polarize character states and minimize redundant characters, a task that, incidentally, requires the use of functional criteria.

We must, therefore, take into account three facts. First, by definition, the earliest specimens of any new genus will be very similar to those of the coeval specimens from its sister group. Second, it nevertheless makes sense to consider such early specimens as initial members of a novel adaptive formula. Third, using morphological criteria alone makes it difficult to classify such specimens, while considering functional criteria may be risky.

One way to avoid the contradictions arising from these three facts is to include such early and problematic specimens as belonging to a 'germinal species' of the new genus — *species germinalis* (*spec. germ.*). A *species germinalis* is a fully developed species, so the term has a very different meaning from the previously used 'species in statu nascendi'. Applied in the way we propose, *spec. germ.* should be used to designate a species that represents the early stages of a new supraspecific taxon. Incidentally, the discovery of highly relevant specimens has often led to

major taxonomic reinterpretations, both within Hominidae and beyond.<sup>29</sup>

Specimens should be placed in *species germinalis* of a new genus when: 1) we have sound reasons to suspect that they are the early members of a new cluster, even though the derived traits typical of the new clade are difficult to identify in those early specimens; and 2) those specimens still retain many primitive traits linking them to the ancestral or sister group. In this manner both parphyly and the multiplying of new genera can be avoided.

When the definition of a genus as postulated by Wood and Collard<sup>4,5</sup> is combined with our proposal of *species germinalis*, no genus should be erected unless its adaptive distinctiveness can explicitly be clarified. Every species showing a mosaic of traits, including apomorphies of a genus that are not fully developed, should be considered as a *spec. germ.* of that genus. If we apply this taxonomic proposal to the genera recently defined in Hominidae, a parsimonious solution may be to reject *Orrorin* until its adaptive novelties are made explicit. In the absence of such analysis, *O. tugenensis* should be considered as *spec. germ.* of *Australopithecus*. In the case of KNM-WT 40000, it seems more appropriate to accept *Kenyanthropus* as a distinct adaptive cluster constituting the 'gracile' lineage of the classical alternative. If *H. rudolfensis* is eventually placed within it,<sup>2,30</sup> however, then the more primitive nasal and neurocranial morphology of *K. platyops* justifies defining the latter as *spec. germ.* of *Kenyanthropus*. This classification does not conflict with it being the type species of *Kenyanthropus*. In respect of the 'robust' lineage, all species can be allocated to *Australopithecus*, rendering *Paranthropus* a junior subjective synonym of it. The oldest taxon, *A. africanus* (also the type species of the genus), does not exhibit the highly apomorphic traits of the most derived paranthropes, and should therefore be considered as *spec. germ.* of the genus. *H. habilis*, in turn, being difficult to distinguish from *K. rudolfensis*, should be classified as *spec. germ.* of *Homo*.

When we apply the above method, the taxonomy of the family Hominidae<sup>31</sup> includes three subfamilies (the new Praeanthropinae, the redefined Australopithecinae and a restricted Homininae) (Table 1). This taxonomy reflects the fact that several fossil species have a *spec. germ.* condition, as beginners of the genera constituting each of the proposed subfamilies. Preanthropines were early hominids that gradually developed bipedalism. Australopithecines were

**Table 1.** Modification of Wood & Collard's<sup>4</sup> taxonomy, including formal taxonomic designations and approximate geographical ranges. The symbol † indicates that the taxon is extinct.

Family Hominidae Gray, 1825. Miocene to the present, worldwide.	
Genus † <i>Ardipithecus</i> White <i>et al.</i> , 1995, <i>incertae sedis</i> . Pliocene, East Africa.	
† <i>Ardipithecus ramidus</i> (White <i>et al.</i> , 1994). Pliocene, East Africa.	
Subfamily Praeanthropinae subfam. nov.	
Genus † <i>Praeanthropus</i> Senyürek 1955 [includes <i>Orrorin</i> Senut <i>et al.</i> , 2001]. Miocene–Pliocene, Africa.	
† <i>Praeanthropus</i> ( <i>spec. germ.</i> ) <i>tugenensis</i> (Senut <i>et al.</i> , 2001). Pliocene, East Africa.	
† <i>Praeanthropus africanus</i> (Weinert, 1950) (= <i>A. afarensis</i> Johanson <i>et al.</i> , 1978). Pliocene, East Africa.	
† <i>Praeanthropus bahrelghazali</i> (Brunet <i>et al.</i> , 1996). Pliocene, Subsahara.	
† <i>Praeanthropus anamensis</i> (M.G. Leakey <i>et al.</i> , 1995). Pliocene, East Africa.	
† <i>Praeanthropus garhi</i> (Asfaw <i>et al.</i> , 1999). Pliocene, East Africa.	
Subfamily Australopithecinae Gregory & Hellman, 1939. Pliocene, Africa.	
Genus † <i>Australopithecus</i> Dart 1925 [includes <i>Plesianthropus</i> Broom, 1938; <i>Paranthropus</i> Broom, 1938; <i>Zinjanthropus</i> L.S.B. Leakey, 1959; and <i>Paraustralopithecus</i> Arambourg and Coppens, 1967]. Pliocene, Africa	
† <i>Australopithecus</i> ( <i>spec. germ.</i> ) <i>africanus</i> Dart, 1925. Pliocene, Africa.	
† <i>Australopithecus aethiopicus</i> (Arambourg and Coppens, 1968). Pliocene, East Africa.	
† <i>Australopithecus boisei</i> (L.S.B. Leakey, 1959). Pliocene–Pleistocene, East Africa.	
† <i>Australopithecus robustus</i> (Broom, 1938). Pleistocene, southern Africa.	
Subfamily Homininae Gray, 1825. Pliocene to the present, worldwide	
Genus † <i>Kenyanthropus</i> M.G. Leakey <i>et al.</i> , 2001. Pliocene, East Africa.	
† <i>Kenyanthropus</i> ( <i>spec. germ.</i> ) <i>platyops</i> M.G. Leakey <i>et al.</i> , 2001. Pliocene, East Africa.	
† <i>Kenyanthropus rudolfensis</i> (Alexeev, 1986). Pliocene, East Africa.	
Genus <i>Homo</i> Linnaeus, 1758 [includes, for example, <i>Pithecanthropus</i> Dubois, 1894; <i>Protanthropus</i> Haeckel, 1895; <i>Sinanthropus</i> Black, 1927; <i>Cyphanthropus</i> Pycraft, 1928; <i>Africanthropus</i> Dreyer, 1935; <i>Telanthropus</i> Broom and Robinson, 1949; <i>Atlantthropus</i> Arambourg, 1954; and <i>Tchadanthropus</i> Coppens, 1965]. Pliocene to the present, worldwide.	
† <i>Homo</i> ( <i>spec. germ.</i> ) <i>habilis</i> L.S.B. Leakey <i>et al.</i> , 1964. Pliocene, Africa.	
† <i>Homo ergaster</i> Groves and Mazák, 1975. Plio-Pleistocene, Africa and ?Eurasia.	
† <i>Homo erectus</i> (Dubois, 1892). Pleistocene, Africa and Eurasia.	
† <i>Homo antecessor</i> Bermúdez de Castro <i>et al.</i> , 1997. Plio-Pleistocene. Europe and ?Africa.	
† <i>Homo heidelbergensis</i> Schoetensack, 1908. Pleistocene, Africa and Eurasia.	
† <i>Homo neanderthalensis</i> King, 1864. Pleistocene, western Eurasia.	
<i>Homo sapiens</i> Linnaeus, 1758. Pleistocene to the present, worldwide.	

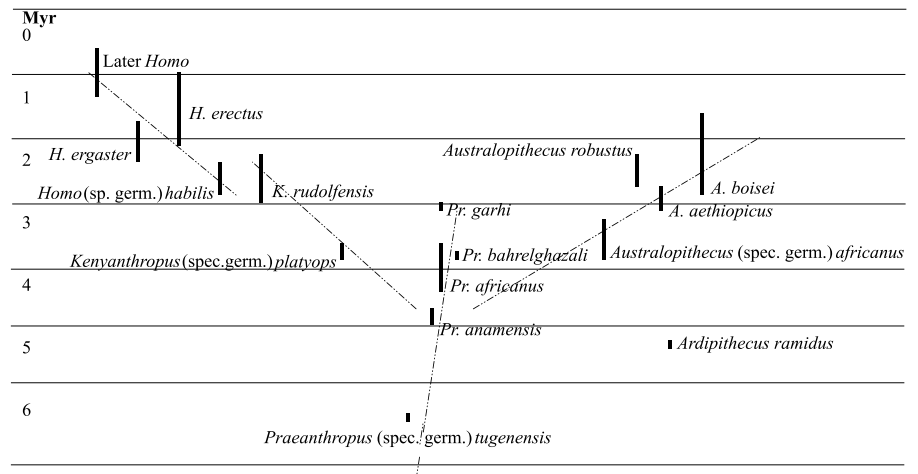
hominids that gradually specialized into feeding on hard plants of the open savanna. Hominines were hominids that gradually developed big brains, fabricating increasingly sophisticated tools. Each higher taxon had a *species germinalis* that exhibited a mosaic of apomorphies and plesiomorphies, making it difficult to distinguish that species from coeval specimens of the sister group. The assumed phylogenetic links are displayed in Fig. 1.

Such proposals might be considered too radical. They are, nevertheless, firmly

grounded on available evidence, correctly formulated in terms of taxonomic conventions, and adequately aimed at solving some of the most persistent problems in palaeoanthropology.

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**Fig. 1.** Time span of hominid species, considering *Homo habilis*, *Kenyanthropus platyops*, *Australopithecus africanus* and *Praeanthropus tugenensis* as *species germinalis* of their respective genera.

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**Sense and Nonsense.** By Kevin Laland and Gillian Brown. Oxford University Press. £16.95. A thorough assessment of the responses to the sociobiological questions raised by E.O. Wilson in his famous book on the subject.

**The New Nuclear Danger.** By Helen Caldicott. New Press. \$16.95. The author argues that the big increase in military spending ordered in particular by the United States, after the terrorist attacks of 11 September, could trigger another nuclear arms race.

**Sakharov: A Biography.** By Richard Lourie. Brandeis University Press. \$30. The story of the eminent Russian physicist who turned against his Soviet masters.

**Instability Rules: The Ten Most Amazing Ideas of Modern Science.** By Charles Flowers. John Wiley. \$18.50.

### Biological Sciences

**Erwin Stresemann (1889–1972): Life and Work of a Pioneer of Scientific Ornithology.** By Jürgen Haffer, Erich Rutschke and Klaus Wunderlich. Pp. 465. Deutsche Akademie der Naturforscher Leopoldina. DM68.

**The Ribosome.** CSH Symposia on Quantitative Biology, vol. LXVI. Pp. 620. Cold Spring Harbor Laboratory Press. \$258 (hbk); \$110 (pbk).

**Bacterial Disease Mechanisms: An Introduction to Cellular Microbiology.** Pp. 560. Cambridge University Press. £75 (hbk); £29.50 (pbk).

**Conservation Biology.** By Andrew S. Pullin. Pp. 360. Cambridge University Press. £75 (hbk); £27.95 (pbk).

**DNA Microarrays: A Molecular Cloning Manual.** Edited by David Bortwell and Joseph Sambrook. Pp. 500. Cold Spring Harbor Laboratory Press. \$195 (hbk); \$125 (pbk).

**The Human Immunodeficiency Virus: Biology, Immunology and Therapy.** Edited by Emilio A. Emimi. Princeton University Press. \$75.

**Science Fictions: A Scientific Mystery, a Massive Cover-up, and the Dark Legacy of Robert Gallo.** By John Crewdson. Pp. 672. Little, Brown. \$27.95. Further elaborations on the discovery of HIV and the response of science to its implications.