

Corrections

EVOLUTION, ANTHROPOLOGY. For the article “Genera of the human lineage,” by Camilo J. Cela-Conde and Francisco J. Ayala, which appeared in issue 13, June 24, 2003, of *Proc. Natl. Acad. Sci. USA* (100, 7684–7689; First Published June 6, 2003; 10.1073/

pnas.0832372100), the authors note that, due to a printer’s error, the references in the heading of Table 1 on page 7688 should be 16 and 17 rather than 32 and 33. The reference in the footnote should be 17 rather than 32. The corrected table appears below.

Table 1. Modification of previous taxonomies (16, 17), including formal taxonomic designations and reference to geological and geographical ranges

Family Hominidae Gray, 1825. Miocene to the present, worldwide.

- Genus †*Sahelanthropus* Brunet et al., 2002, *incertae sedis*. Miocene, Central Africa.
- Species †*Sahelanthropus tchadensis* Brunet et al., 2002. Miocene, Central Africa.

Subfamily Preanthropinae Cela-Conde and Altaba, 2002. Miocene–Pliocene, Africa.

- Genus †*Praeanthropus* Senyürek 1955 (includes *Orrorin* Senut et al., 2001). Miocene–Pliocene, Africa.
- Species †*Praeanthropus tugenensis** Senut et al., 2001. Miocene, East Africa.
- Species †*Praeanthropus africanus* Weinert, 1950 (= *Australopithecus afarensis* Johanson et al. 1978). Pliocene, East Africa.
- Species †*Praeanthropus bahrelghazali* Brunet et al., 1996. Pliocene, Subsahara.
- Species †*Praeanthropus anamensis* M. G. Leakey et al., 1995. Pliocene, East Africa.
- Species †*Praeanthropus garhi* Asfaw et al., 1999. Pliocene, East Africa.

Genus †*Ardipithecus* White et al., 1995. Miocene–Pliocene, East Africa.

- Species †*Ardipithecus ramidus* White et al., 1994. Miocene–Pliocene, East Africa.

Subfamily Australopithecinae Gregory and Hellman, 1939. Pliocene, Africa.

- Genus †*Australopithecus* Dart 1925 (includes *Plesianthropus* Broom, 1938; *Paranthropus* Broom, 1938; *Zinjanthropus* L. S. B. Leakey, 1959; and *Paraustralopithecus* Arambourg and Coppens, 1967). Pliocene, Africa.
- Species †*Australopithecus africanus** Dart, 1925. Pliocene, Africa.
- Species †*Australopithecus aethiopicus* Arambourg and Coppens, 1968. Pliocene, East Africa.
- Species †*Australopithecus boisei* L. S. B. Leakey, 1959. Pliocene–Pleistocene, East Africa.
- Species †*Australopithecus robustus* Broom, 1938. Pleistocene, southern Africa.

Subfamily Homininae Gray, 1825. Pliocene to the present, worldwide.

- Genus *Homo* Linnaeus, 1758 (includes *Pithecanthropus* Dubois, 1894; *Protanthropus* Haeckel, 1895; *Sinanthropus* Black, 1927; *Cyphanthropus* Pycraft, 1928; *Africanthropus* Dreyer, 1935; *Telanthropus* Broom and Robinson, 1949; *Atlanthropus* Arambourg, 1954; *Tchadanthropus* Coppens, 1965; and *Kenyanthropus* M. G. Leakey et al., 2001). Pliocene to the present, worldwide.
- Species †*Homo platyops** M. G. Leakey et al., 2001. Pliocene, East Africa.
- Species †*Homo rudolfensis* Alexeev, 1986. Pliocene, Africa.
- Species †*Homo habilis* L. S. B. Leakey et al., 1964. Pliocene, Africa.
- Species †*Homo ergaster* Groves and Mazák, 1975. Plio-Pleistocene, Africa and ? Eurasia.
- Species †*Homo erectus* Dubois, 1892. Pleistocene, Africa and Eurasia.
- Species †*Homo antecessor* Bermúdez de Castro et al., 1997. Plio-Pleistocene, Europe and ? Africa.
- Species †*Homo heidelbergensis* Schoetensack, 1908. Pleistocene, Africa and Eurasia.
- Species †*Homo neanderthalensis* King, 1864. Pleistocene, western Eurasia.
- Species *Homo sapiens* Linnaeus, 1758. Pleistocene to the present, worldwide.

†, Taxon is extinct; *, taxon considered *species geminalis* (17), i.e., a species originating a genus; ?, uncertainty about the taxon’s presence in that region.

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NEUROSCIENCE. For the article “Mifepristone (RU486) protects Purkinje cells from cell death in organotypic slice cultures of postnatal rat and mouse cerebellum,” by A. M. Ghoumari, I. Dusart, M. El-Etr, F. Tronche, C. Sotelo, M. Schumacher, and E.-E. Baulieu, which appeared in issue 13, June 24, 2003, of *Proc. Natl. Acad. Sci. USA* (**100**, 7953–7958; First Published June 16, 2003; 10.1073/pnas.1332667100), the authors note that “(suppress cultures)” should be removed from the Fig. 2 legend, and that “and mouse” should be removed from the first sentence of the Fig. 5 legend. The sentence should have read, “Purkinje cell death in organotypic slice cultures of postnatal rat cerebella does not result from oxidative stress.” The figures and their corrected legends appear below.

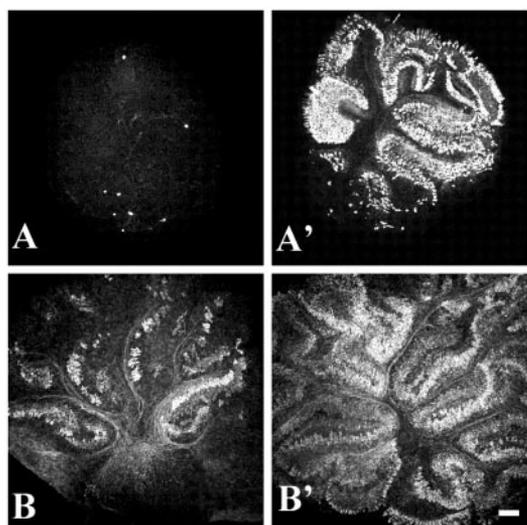


Fig. 2. Effects of RU486 on Purkinje cell survival in P5 and P7 rat cerebella. Organotypic slices of P5 and P7 rat cerebella (*A* and *B*, respectively) were cultured for 5 DIV in the absence (*A* and *B*) or presence (*A'* and *B'*) of 20 μ M RU486. At all ages, RU486 protects Purkinje neurons from cell death. (Scale bar = 250 μ m.)

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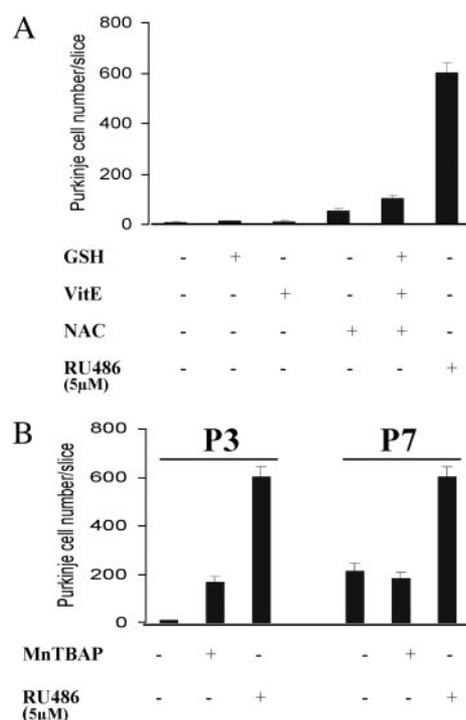


Fig. 5. Purkinje cell death in organotypic slice cultures of postnatal rat cerebella does not result from oxidative stress. P3 cerebellar slices were treated with different antioxidant agents. (*A*) VitE (50 μ M), NAC (5 mM), and GSH were used alone or in combination. (*B*) MnTBAP (200 μ M), a cell-permeable superoxide dismutase (SOD) mimetic and peroxynitrite scavenger, was also used.

MEDICAL SCIENCES. For the article “Blockade of vascular endothelial growth factor receptor-3 signaling inhibits fibroblast growth factor-2-induced lymphangiogenesis in mouse cornea,” by Hajime Kubo, Renhai Cao, Ebba Bräkenhielm, Taija Mäkinen, Yihai Cao, and Kari Alitalo, which appeared in issue 13, June 25, 2002, of *Proc. Natl. Acad. Sci. USA* (**99**, 8868–8873; First Published June 17, 2002; 10.1073/pnas.062040199), the authors note that the indication of black and white bars was inverted in the legend of Fig. 3. The legend should have read, “Black bars, angiogenic score; white bars, lymphangiogenic score.” The figure and its corrected legend appear below.

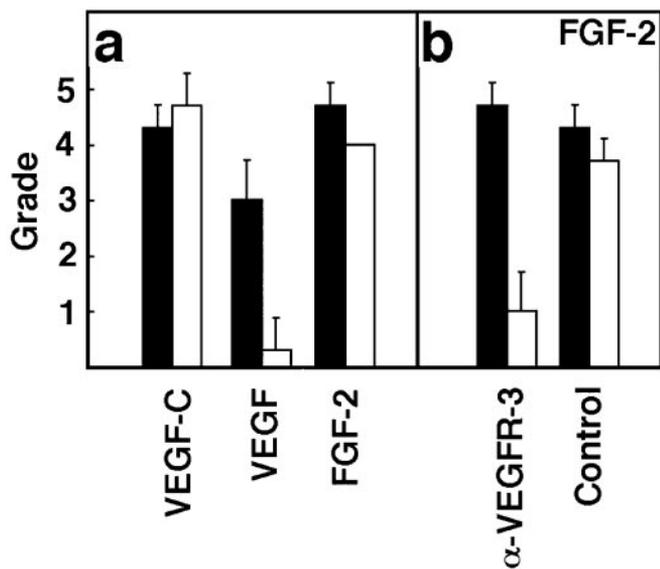


Fig. 3. Quantification of the corneal angiogenesis and lymphangiogenesis. (a) Quantification of the angiogenesis and lymphangiogenesis induced by VEGF, VEGF-C, and FGF-2 ($n = 3$ each) analyzed by immunostaining as described in *Materials and Methods*. (b) Quantification of the angiogenesis and lymphangiogenesis in FGF-2-implanted corneas treated with anti-VEGFR3 (α -VEGFR-3) in comparison with the corneas of animals treated with nonblocking anti-VEGFR-2 control antibodies (Control). Black bars, angiogenic score; white bars, lymphangiogenic score. The graphs represent mean values \pm SEM.

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Genera of the human lineage

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Human fossils dated between 3.5 and nearly 7 million years old discovered during the last 8 years have been assigned to as many as four new genera of the family Hominidae: *Ardipithecus*, *Orrorin*, *Kenyanthropus*, and *Sahelanthropus*. These specimens are described as having morphological traits that justify placing them in the family Hominidae while creating a new genus for the classification of each. The discovery of these fossils pushed backward by >2 million years the date of the oldest hominids known. Only two or three hominid genera, *Australopithecus*, *Paranthropus*, and *Homo*, had been previously accepted, with *Paranthropus* considered a subgenus of *Australopithecus* by some authors. Two questions arise from the classification of the newly discovered fossils: (i) Should each one of these specimens be placed in the family Hominidae? (ii) Are these specimens sufficiently distinct to justify the creation of four new genera? The answers depend, in turn, on the concepts of what is a hominid and how the genus category is defined. These specimens seem to possess a sufficient number of morphological traits to be placed in the Hominidae. However, the nature of the morphological evidence and the adaptation-rooted concept of what a genus is do not justify the establishment of four new genera. We propose a classification that includes four well defined genera: *Praeanthropus*, *Ardipithecus*, *Australopithecus*, and *Homo*, plus one tentative *incertae sedis* genus: *Sahelanthropus*.

In his *Systema Naturae*, Carolus Linnaeus (1) placed the human species into the genus *Homo*, though such placement conveyed a taxonomic meaning different from that of present usage. Linnaeus distinguished between *Homo diurnus*, with different forms corresponding to European, American, Asian, and African humans, and *Homo nocturnus*, corresponding to the orangutan. With the passage of time, the genus *Homo* acquired the connotation presently associated with this taxon, which includes only one living species, *Homo sapiens*, and some of its near hominid relatives. Some fossil forms now included in *Homo* initially received different taxonomic identifications at the genus level, such as *Pithecanthropus* (2), *Sinanthropus* (3), *Africanthropus* (4), *Telanthropus* (5), and *Atlantropus* (6), among others. All of these genera designated relatively recent relatives in the human family, no older than what is currently considered the middle Pleistocene. These genera referred to either ancestors or parallel lineages that shared distinctive features with modern humans, including, notably, large brains, tool-making ability, and, speculatively, at least incipient language skills.

The appearance of Pliocene specimens from the South African site of Taung made researchers aware of the existence of another type of hominid, different in relevant respects from modern humans. The large morphological differences between the Taung fossil and *Homo* motivated Dart (7) to create a new genus, *Australopithecus*. After some initial reluctance (e.g., refs. 8–11), *Australopithecus* became generally accepted as a separate genus that comprised hominids with a chimpanzee-sized brain who did not make stone tools. During the ensuing decades, *Australopithecus* and *Homo* seemed adequate to encompass the taxonomic range necessary to house the human lineage; thus, all other genera were abandoned [with the exception of *Paranthropus* (12), accepted by a significant number of authors as a genus corresponding to robust australopithecines]. Proposals for new

genera, such as *Zinjanthropus* (13) and *Paraaustralopithecus* (14) were also eventually discarded.[§]

The scenario of hominids being represented by only a few genera has critically changed in recent years with the discovery of very early hominid specimens with ages between 3.5 and 7 million years (Myr). These newly discovered specimens are sufficiently informative, according to their describers, to support the proposal of four new genera: *Ardipithecus*,[¶] *Orrorin* (20), *Kenyanthropus* (21), and *Sahelanthropus* (22). The subsequent increase from three to seven hominid genera in the few years from 1995 to the present constitutes an exceptional event in hominid systematics. The questions that need to be asked are whether these recently discovered specimens are in fact hominids, and whether their different characteristics justify the creation of four new genera.

What Is a Hominid?

Three of the new genera are represented by specimens much older than previously known hominid fossils and raise questions about the timing of the split between the lineages leading to humans (*Homo*) and chimpanzees (*Pan*). The so-called “late-divergence hypothesis” (23), which is based on molecular studies, suggests that the separation may have taken place no more than 4 or 5 Myr ago. Recent analyses of genes (and other DNA sequences) support a date 5–6 Myr ago (24–27), although some authors place the divergence between *Pan* and *Homo* as early as 10.5 Myr ago (28). The genera *Orrorin* and *Sahelanthropus* support dates close to 7 Myr or older, provided that these specimens pertain to the human lineage (after the divergence). The authors who have proposed these two new genera have no doubt of their place in the human lineage (20, 22).

A commonly accepted, two-pronged criterion for including a certain specimen in the hominid family was proposed by Pilbeam (29): habitual upright bipedalism as the chief method of locomotion and teeth that are essentially human in form.

Sahelanthropus, *Orrorin*, and *Ardipithecus* have been described or inferred as having been bipedal, at least to a certain extent. The holotype of *Sahelanthropus*, TM 266-01-060-1, is an almost complete cranium. Although it is damaged in the occipital area, the foramen magnum is longer than it is wide and not at all rounded as is typical of *Pan* (22). The basioccipital is described as “correlatively short and shaped like a truncated triangle as in *Ardipithecus*” (22), but not as triangular as in other early hominids. The available information seems insufficient to infer reliably whether *Sahelanthropus* was a habitual biped, but, the authors claim, “such an inference would not be unreasonable

Abbreviation: Myr, million years.

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[§]A minority of authors prefer to use *Praeanthropus* as the name for the Rift and Tchat specimens grouped in *Australopithecus* (15–17), in accordance with the preference rules of taxonomy, but this does not change the current prevailing consideration of only three genera.

[¶]White and colleagues first classified their Aramis fossils as *Australopithecus ramidus* (18), but later (19) proposed a new generic classification as *Ardipithecus*, on the grounds that *ramidus* is likely to be the sister taxon of the hominid clade rather than a direct ancestor of *Homo*.

given the skull's other basic cranial and facial similarities to later fossil hominids that were clearly bipedal" (22).¹

The two left femora described for *Orrorin tugenensis* (BAR 1002-00 and BAR 1003-00) have been interpreted as indicating that it "was already adapted to habitual or perhaps even obligate bipedalism when on the ground" (20). The shortened basioccipital component of the cranial bone for *Ardipithecus* from Aramis is similar to that of other hominids and unlike that of chimpanzees (18). This interpretation is corroborated by a proximal foot phalange, AME-VP-1/71, later found in Middle Awash (Ethiopia), described as "derived relative to all known apes and . . . consistent with an early form of terrestrial bipedality" (32).

The second hominid feature identified by Pilbeam (29) is a distinctive dentition. The small canines of *Sahelanthropus*, such as TM 266-01-060-1 (holotype) and TM 266-02-154-2, are derived features bringing the specimen close to later hominids; the thickness of the postcanine enamel of *Sahelanthropus* is intermediate, thicker than that of chimpanzees but thinner than that of later australopithecines (22).

The molars of *Orrorin tugenensis* "are smaller than those of australopithecines and are closer in size to those of *Ardipithecus*" (20). The molar enamel of *Orrorin* in the upper central incisor and in the lower cheek teeth is "thick," as in other hominids, but other features of the incisors and canines, and the lower premolar P₄, are less hominid-like and more ape-like.

The dentition of *Ardipithecus* is ambiguous and has revived the argument of whether enamel thickness is a defining feature of hominid lineages. The Aramis specimens have thin molar enamel (18), whereas the other hominids show thick tooth enamel. Chimpanzees and gorillas have thin enamel, whereas orangutans show an intermediate thickness (33). Moreover, the *Ardipithecus* fossils from Middle Awash, which are 0.8–1.4 Myr older than those found at Aramis, have challenged the enamel characteristics attributed to the genus. The enamel characteristics of *Ardipithecus ramidus kadabba* are incomplete, but it has been proposed that the available broken and little-worn teeth suggest a molar enamel thickness similar to or slightly greater than those of the younger Aramis samples of *Ar. ramidus* (32). In any case, the significance of tooth enamel is not definitive, but should be considered together with tooth shape and consideration of diet.

The features related to bipedalism and those of the dentition follow a mosaic evolutionary trend, showing different mixtures of primitive and derived morphological features in all early hominids from *Orrorin* and *Sahelanthropus* to the Rift Valley (*Praeanthropus africanus*) and the South African (*Australopithecus africanus*) australopithecines. This mixture is hardly unexpected, because evolution is a gradual process (albeit rate-variable) and these Miocene specimens are close to the proposed time of divergence of chimpanzees and humans. But a mixture of primitive and derived characters poses a problem. The phylogenetic definition of a certain taxon will depend on whether we emphasize the primitive features or the derived features. Thus, the authors who documented the new Miocene findings claim "hominidness" for their specimens and at the same time cast doubt on the hominid status of specimens discovered by others. Haile-Selassie (32), who asserts the hominidness of *Ardipithecus*, writes about *Orrorin*: "There is nothing to preclude *Orrorin* from representing the last common ancestor, and thereby antedating the cladogenesis of hominids. It is equally plausible that it represents a previously unknown African hominoid with no living descendants, or an exclusive precursor of chimpanzees,

gorillas or humans." Brunet *et al.* (22), who promote *Sahelanthropus* as a hominid, note the similarity between the upper canine of *Orrorin* "and that of a female chimpanzee." But the discoverers of *Orrorin* argue that "small, thick enameled molars are an archaic feature for the hominid lineage, which is retained in *Homo*," whereas *Ardipithecus* "has thin enameled cheek teeth, which may be a derived feature for the Gorillidae" (20).

The important issue at hand is not primarily whether we may want to classify a particular taxon as being a hominid or not, but rather whether the specimens included in that taxon are more recently related to present humans than to chimpanzees. For the nominalist taxonomist, it is quite arbitrary to include or exclude apes from the family Hominidae, as first defined by Gray in 1825. But the historically substantive issues, and the ones cladists or other modern taxonomists want to answer, are as follows: Is *Ardipithecus* part of the chimpanzee lineage? Is *Orrorin* a common ancestor of both humans and chimpanzees? Is *Sahelanthropus* an early hominid that lived outside the Rift Valley, or is it an ape, as proposed by Wolpoff *et al.* (30)?

There are additional meaningful taxonomic questions, such as whether it is appropriate to create a new genus for specimens that are not particularly different from those included in an already established genus. The issues relevant to such questions, namely how to reconstruct (and test) a phylogeny and what should constitute a new genus, are related but distinct.

What Is a Genus? The Cladistic Criterion

Even before the recent discovery of hominid specimens and the proposal of four new genera for them (*Ardipithecus*, *Orrorin*, *Kenyanthropus*, and *Sahelanthropus*), the simple, classic three-genus scheme (*Australopithecus*, *Paranthropus*, *Homo*) encountered difficulties with regard to adequately including all known specimens assigned to the Hominidae. As far as possible, a genus is supposed to be monophyletic; that is to say, it must contain only species that form a clade (a complete lineage sharing a common ancestor within the family's evolutionary tree). This is an unrealistic taxonomic expectation, given the fact that phylogeny is a continuum, with the exception of terminal twigs or extant taxa (34). Furthermore, there is evidence already available that indicates, at least to some authors, that all three genera are paraphyletic (containing species that belong to different lineages): *Australopithecus* (15), *Paranthropus* (34), and *Homo* (16).

Cladistic analyses seeking to determine the branching relationships of given taxa follow a series of ordered steps. For example, in their reappraisal of early hominid phylogeny, Strait *et al.* (15) proceeded in this way: (i) nine species (from *Australopithecus afarensis* to *H. sapiens*) were selected; (ii) in each taxon, all specimens that formed the hypodigm (i.e., the entire fossil record considered for a given taxon) were included; (iii) the characters of each hypodigm were analyzed; and (iv) the best cladogram was selected on the basis of computer algorithms that use a parsimony criterion that chooses the one with the fewest steps and that minimizes the number of convergent traits that evolve independently in each clade. This procedure, of course, assumes that all of the taxa examined are the results of lineage splitting and do not represent stages in a lineage (35).

Claims of objectivity notwithstanding, the matter of which cladogram is "best" depends largely on the decisions made at each step. But no step is free from difficulties. For example, does the fragmentary cranial vault and face KNM-ER 2602 of Koobi Fora (Kenya) pertain to the hypodigm of *A. afarensis* or to that of *Australopithecus boisei*? Do *Homo habilis* and *Homo rudolfensis* represent one or two species? Does *H. habilis* exist at Sterkfontein (South Africa) or must the Stw 53 and Sts 19 specimens be regarded as *A. africanus*?

The way in which the species are chosen and the hypodigms are constructed leads to very different cladograms. In their revision of the genus *Homo*, Wood and Collard (16) evaluated six

¹Wolpoff *et al.* (30), based on a consideration of the morphology of the masticatory apparatus, face, and skull, differ on the alleged bipedalism of *Sahelanthropus*. They opine that *Sahelanthropus* "was an ape living in an environment that was later inhabited by australopithecines." For a response defending the phylogenetic position of *Sahelanthropus* as a hominid, see ref. 31.

different cladistic studies to elucidate the monophyly of *Homo*. Three studies concluded that *Homo* is monophyletic (i.e., holophyletic), whereas the remaining three suggested that it is paraphyletic. The authors (16) concluded on the basis of their own morphological, functional, and developmental analyses that *H. habilis* and *H. rudolfensis* cannot reliably be assumed to be more closely related to *H. sapiens* than to the australopithecids, and thus proposed that *H. habilis* and *H. rudolfensis* should be removed from *Homo* if monophyly is to be preserved. This proposal, however, leads to another problem. If *H. habilis* and *H. rudolfensis* cannot be classified in the genus *Homo*, the only alternatives are to include them in *Australopithecus* or to create a new genus for them. The first option would increase the paraphyly in *Australopithecus* even more than already occurs, whereas the second alternative would excessively increase the number of hominid genera.

Other cladistic analyses often lead to a similar dilemma in human phylogeny. However, one way out of the dilemma might be to rely on the assumption that the first species of any new genus conserves some primitive features close to those of the previous ancestral genus. We will adopt this convention in this article to avoid (or, at least, minimize) the two horns of the dilemma: too many genera and paraphyly. Our proposal is to identify the early species of a new genus as the *species geminalis* of the genus, even though these species do not meet all of the defining characteristics of the genus, thus eliminating the need to include them in the previous genus or to create a new one. *Species geminalis*, because of their intermediate features, must not be included in computational cladistic analyses (17).

Genus as Single Adaptive Zone

Beyond cladistic issues, the matter of a genus being a taxon that occupies a “single adaptive zone,” as defined by Mayr (36), has been applied to hominid taxa (e.g., ref. 16). This evolutionary and ecological concept of the genus leads to identification of three hominid genera, corresponding to three distinctive adaptive zones: (i) *Australopithecus*, encompassing the first hominids that gradually developed bipedalism; (ii) *Paranthropus*, the evolutionary branch (incorporating the robust australopithecines) that colonized the open spaces of the savanna with specialized feeding on hard vegetables (12); and (iii) *Homo*, the branch that evolved large brains and retained from *Australopithecus* gracile features, used stone tools, and developed a more carnivorous diet. Presently, we encounter four newly proposed genera for recently discovered fossils: *Ardipithecus*, *Orrorin*, *Kenyanthropus*, and *Sahelanthropus*. Do these taxa represent new ancestors of modern humans that occupied distinctive adaptive zones?

The Aramis specimens of *Ardipithecus* have been described as exhibiting incipient bipedalism while retaining a tree-climbing ability, so that they were still largely “ecological apes” (37). Other specimens of *Ardipithecus* also fit this description. The humerus of *Ar. ramidus kadabba* has “a relatively sharp lateral trochlear crest” similar to that of modern apes and some *A. afarensis*, whereas the proximal foot phalanx from Amba, dated at 5.2 Myr, is clearly derived relative to all known apes and suggests an early form of terrestrial bipedality (32). The lack of *Sahelanthropus* postcranial remains prevents establishment of the degree of its bipedalism, though the cranium clearly shows a mosaic of derived and primitive ape-like features. The most informative anatomical features of the *Sahelanthropus tchadensis* cranium are in the face, which shows a mosaic of primitive and derived features. “The face is tall with a massive brow ridge, yet the mid-face is short (in the superoinferior dimension) and less prognathic than in *Pan* or *Australopithecus*. This unusual combination of features is in turn associated with a relatively long braincase, comparable in size to those of extant apes” (22).

The authors describing the Miocene exemplars of *Ardipithecus* and *Sahelanthropus* claim that the mosaic combination of their

specimens’ features is unique, thus justifying the proposal of a new genus in each case. The issue here is to determine to what extent these differences justify the naming not only of a new species, but also of a new genus. In fact, none of the new Miocene specimens clearly reflects an exclusive and peculiar single adaptive zone. The most significant difference between them and the later, smaller *Australopithecus* is size. Indeed, the specimens ARA-VP-7/2 (*Ar. ramidus ramidus*) and ASK-VP-3/78 (*Ar. ramidus kadabba*) are larger than the nonrobust australopithecines, such as *A. afarensis* AL 288-1m and AL 322-1 (32). Consideration, in particular, of *Ar. ramidus kadabba* specimens supports, in our view, the inclusion of *Ardipithecus* in the family Hominidae, although its evolutionary relationships with *Praeanthropus* and *Australopithecus* remain obscure. We tentatively propose placing *Sahelanthropus* in a new genus (*incertae sedis*), but without including it in the same subfamily (or genus) as the more definitively bipedal *Ardipithecus*, *Orrorin*, and *Australopithecus*.

The humerus and femur of *Orrorin* are 1.5 times larger than those of *A. afarensis* AL 288-1 (Lucy), which confirms that early human ancestors were larger than previously believed (20). *Orrorin*’s femora indicate that it was a biped when on the ground, while its humerus and manual phalanx show that it retained some arboreal adaptations (20). We propose that the specimens described as *Orrorin* may be classified within the genus *Praeanthropus*, which also includes *A. afarensis* of Johanson *et al.* (38) and other late, nonrobust australopithecines, as belonging to the same adaptive zone.

Kenyanthropus platyops (21) of Lomekwi (West Turkana, Kenya), aged at 3.5 Myr, represents a different case. The holotype KNM-WT 40000 combines a cranium with a capacity in the range of the australopithecines, a flat transverse facial contour at a level just below the nasal bones, and a tall malar region with a zygomaticoalveolar crest low and curved. The result is an orthognathic (flat) face, very different from the prognathic (protruding) face of the nonrobust australopithecines, and similar to that of *Paranthropus* and *H. rudolfensis*. But in the case of robust hominids (*Paranthropus*), the flattened face is associated with molar megadonty, whereas *Kenyanthropus* has small cheek teeth. More generally, *Kenyanthropus* lacks almost all of the derived features of *Paranthropus*, showing a unique pattern of facial and dental morphology that suggests a distinct dietary adaptive zone (21). Consequently, *Kenyanthropus* is best placed in a genus different from *Paranthropus*. It has been suggested that the particular morphology of the KNM-WT 40000 specimen could be the result of a distortion caused by “artifacts of postmortem fossilization processes” (39). However, there seem to be other reasons to distinguish KNM-WT 40000 from the australopithecines. The thinner enamel and smaller teeth of *Kenyanthropus* bring it closer to the *Homo* exemplars of the Plio-Pleistocene (*H. habilis* and, mainly, *H. rudolfensis*), although it lacks the more advanced features of *Homo* that appear with *Homo erectus* and *Homo ergaster*. Not surprisingly, Lieberman (40) asserts that this new taxon “will act as a sort of party spoiler, highlighting the confusion that confronts research into evolutionary relationships.” We propose, conservatively, to include *K. platyops* in the genus *Homo*, but as *species geminalis* (see below), on account of its lacking some of the distinctive features of later *Homo*.

As noted by Tobias (41), there has recently been an inclination toward creating new hominid species and genera based on samples from just one or two sites. Indeed, recent finds bridge the gap between taxa that were, until now, considered as different. KGA10-525 (42) supposedly links *Paranthropus aethiopicus*, *Paranthropus robustus*, and *Paranthropus boisei*. The “Daka” calvaria (43) purportedly brings *H. ergaster* closer to *H. erectus*. OH 65, the latest Olduvai discovery of *H. habilis*, is claimed to cast “doubts on *Homo rudolfensis* as a biologically

valid taxon” (44). In any case, for the purpose of determining the number and definition of hominid genera, there is no need to decide whether one or more species should be distinguished in each of these cases.

H. ergaster and *H. erectus* raise no cladistic problems about including them in the same genus, but morphological (and cultural) considerations may favor considering them as separate species. The “robust” *Australopithecus/Paranthropus* lineage raises some difficulties about including all of the taxa in a single, monophyletic group (34), though Grine and Martin (45) have offered morphological reasons for their inclusion in a single lineage.

H. rudolfensis could be reduced to “a taxonomic junior synonym of *Homo habilis*” (41), but one must, then, take into account the strong similarities of KNM-ER 1470 (*H. rudolfensis*) with KNM-WT 40000 (*K. platyops*). One possibility would be placing all three taxa (*H. habilis*, *H. rudolfensis*, and *K. platyops*) into the genus *Australopithecus*, as has been proposed for *H. habilis* and *H. rudolfensis* (16, 46). However, this solution would greatly increase the paraphyly of *Australopithecus*. A second alternative would be to include the three taxa within a separate genus, *Kenyanthropus*. But the current state of knowledge makes it difficult to assign KNM-ER 1470 (*H. rudolfensis*) to this genus unless *H. habilis* is also moved to *Kenyanthropus* (21, 47).

We agree with the view that *K. platyops*, *H. habilis*, and *H. rudolfensis* should be classified together, but we propose to include them within the genus *Homo*. *H. habilis* and *H. rudolfensis* share the morphological traits that, in 1964, led Leakey, Tobias, and Napier to define *Homo* as a new taxon. Although *K. platyops* (KNM-WT 40000) “does not show the derived features associated with *Homo* (excluding *H. rudolfensis* and *H. habilis*)” (21), it may be considered as the earliest member (i.e., *species geminalis*) of the genus, which would also include *H. habilis* and *H. rudolfensis* as early forms of the lineage that adapted to the savanna by means of a nonspecialized diet, eventually developing lithic tools for scavenging and hunting purposes. This proposal places the appearance of the genus *Homo* as early as 3.5 Myr ago.

Phylogeny of the Hominidae

The reconstruction of human phylogeny is fraught with seemingly insurmountable obstacles, especially if one seeks to employ only a reasonable number of hominid genera while abiding by the cladistic objective of a classification to encompass only monophyletic lineages. The obstacles come, first and foremost, from the great gaps in the fossil record. Our lack of knowledge of the ancestors in the chimpanzee lineage, for example, handicaps the task of establishing the accurate place for taxa close to the divergence of humans and chimpanzees, such as *Orrorin*, *Sahelanthropus*, and *Ardipithecus*. But other obstacles exist that cannot be overcome simply by the discovery of new exemplars. Our present methods do not permit an unambiguous determination of the ancestor–descendant relationship between any two given taxa. We can only identify, within certain limits, sister groups, i.e., taxa immediately proceeding from a common ancestor (which, again, cannot be identified). An additional difficulty lies in identifying similarity among taxa that are close to any point of divergence. It seems impossible at present to determine beyond any doubt where to fit the new Miocene specimens. The best we can do is to assign them tentative places in the phylogeny, subject to eventual revision with the discovery of new specimens.

The new fossil findings warrant two conclusions: first, the diversity of lineages among very early hominids is greater than previously believed; moreover, their geographical range has been expanded with the discovery of *Sahelanthropus* from Chad, west-central Africa. Nevertheless, and until new evidence makes it possible to decide on the degree of bipedalism of *Orrorin*, *Sahelanthropus*, and *Ardipithecus*, a parsimonious option would

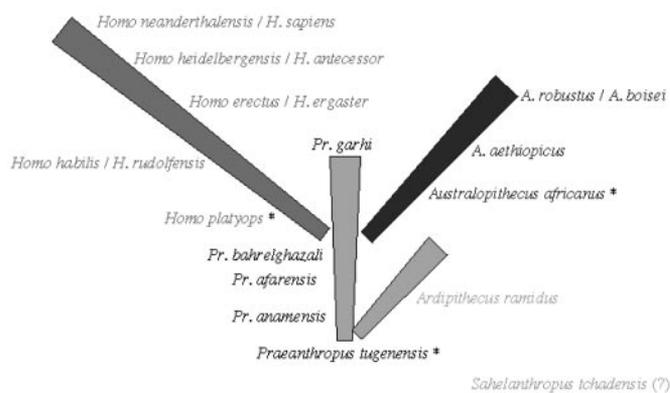


Fig. 1. Phylogeny of the genera belonging to the Hominid family. Four different genera are proposed, corresponding to four kinds of adaptation. The genus *Praeanthropus* (formerly named *Australopithecus*) evolved incipient bipedalism on the ground of tropical forests. The genus *Ardipithecus* evolved a dietary adaptation that developed thin molar enamel, similar to that of the African great apes. The genus *Australopithecus* (formerly also named *Paranthropus*) exploited hard vegetal resources of the savanna by developing a robust masticatory apparatus. The genus *Homo* retained gracile maxillae and dentition and later initiated the development of larger crania and cultural adaptation to the savanna by means of lithic industries. The proposed names follow the rules of taxonomy, favoring the names given initially, when the first taxon of the genus was established. The phylogenetic location and taxonomic classification of *Sahelanthropus* are uncertain. Pairs of *Homo* taxa separated by a slash represent closely related (or, according to some authors, the same) species. An asterisk marks each *species geminalis*, i.e., originating a genus.

be to retain only four genera in Hominidae: *Praeanthropus*, *Ardipithecus*, *Australopithecus*, and *Homo* (plus one genus *incertae sedis*, whose definitive status can only later be determined) (Fig. 1). A tentative outline of hominid evolution involving four major (genus-determining) episodes is shown in Table 1.

The divergence of the chimpanzee and human lineages occurred close to 7 Myr ago. The early hominid species occupy a single adaptive zone, which involves gradual colonization of the ground by bipedalism, while preserving notable tree-climbing abilities. These species are included in a single genus, which according to the preference rules of taxonomy, would be *Praeanthropus* (48). East and central African australopithecines (*A. afarensis*, ref. 38; *A. anamensis*, ref. 49; *A. bahreighazali*, ref. 50; *A. garhi*, ref. 51) are included in this genus, as is *Orrorin*, which, despite some doubts about its bipedalism (32), possesses enough derived features to be included in *Praeanthropus*. With regard to other Miocene specimens, the alternatives are to keep them in *Praeanthropus* if their bipedalism is confirmed, or to place them in a genus *incertae sedis* if they are understood to be too close to the divergence process. The absence of *Sahelanthropus* postcranial remains (together with its geographic location) necessitates recognition of this taxon as *incertae sedis*. Regarding *Ardipithecus*, bipedalism inferred from the postcranial remains of *Ar. ramidus kadabba* favors placing it in Hominidae, but the presence of thin tooth enamel in the later *Ar. ramidus* sets this taxon apart from the australopithecines.

A divergence episode close to 3.5 Myr ago separates robust and gracile lineages, which are also characterized by different dietary adaptive zones. The robust lineage entails the appearance of *Australopithecus*, whereas the genus *Homo* corresponds to the gracile lineage. The most parsimonious solution consists of placing all gracile specimens in the same genus, which according to the taxonomic rules, must be *Homo*. *H. habilis* and *H. rudolfensis* (formerly considered also as *Kenyanthropus rudolfensis*; ref. 21) would represent an anagenetic evolutionary

Table 1. Modification of previous taxonomies (32, 33), including formal taxonomic designations and reference to geological and geographical ranges

Family Hominidae Gray, 1825. Miocene to the present, worldwide.
Genus † <i>Sahelanthropus</i> Brunet <i>et al.</i> , 2002, <i>incertae sedis</i> . Miocene, Central Africa.
Species † <i>Sahelanthropus tchadensis</i> Brunet <i>et al.</i> , 2002. Miocene, Central Africa.
Subfamily Preanthropinae Cela-Conde and Altaba, 2002. Miocene–Pliocene, Africa.
Genus † <i>Praeanthropus</i> Senyürek 1955 (includes <i>Orrorin</i> Senut <i>et al.</i> , 2001). Miocene–Pliocene, Africa.
Species † <i>Praeanthropus tugenensis</i> * Senut <i>et al.</i> , 2001. Miocene, East Africa.
Species † <i>Praeanthropus africanus</i> Weinert, 1950 (= <i>Australopithecus afarensis</i> Johanson <i>et al.</i> 1978). Pliocene, East Africa.
Species † <i>Praeanthropus bahrelghazali</i> Brunet <i>et al.</i> , 1996. Pliocene, Subsahara.
Species † <i>Praeanthropus anamensis</i> M. G. Leakey <i>et al.</i> , 1995. Pliocene, East Africa.
Species † <i>Praeanthropus garhi</i> Asfaw <i>et al.</i> , 1999. Pliocene, East Africa.
Genus † <i>Ardipithecus</i> White <i>et al.</i> , 1995. Miocene–Pliocene, East Africa.
Species † <i>Ardipithecus ramidus</i> White <i>et al.</i> , 1994. Miocene–Pliocene, East Africa.
Subfamily Australopithecinae Gregory and 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.
Species † <i>Australopithecus africanus</i> * Dart, 1925. Pliocene, Africa.
Species † <i>Australopithecus aethiopicus</i> Arambourg and Coppens, 1968. Pliocene, East Africa.
Species † <i>Australopithecus boisei</i> L. S. B. Leakey, 1959. Pliocene–Pleistocene, East Africa.
Species † <i>Australopithecus robustus</i> Broom, 1938. Pleistocene, southern Africa.
Subfamily Homininae Gray, 1825. Pliocene to the present, worldwide.
Genus <i>Homo</i> Linnaeus, 1758 (includes <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>Atlanthropus</i> Arambourg, 1954; <i>Tchadanthropus</i> Coppens, 1965; and <i>Kenyanthropus</i> M. G. Leakey <i>et al.</i> , 2001). Pliocene to the present, worldwide.
Species † <i>Homo platyops</i> * M. G. Leakey <i>et al.</i> , 2001. Pliocene, East Africa.
Species † <i>Homo rudolfensis</i> Alexeev, 1986. Pliocene, Africa.
Species † <i>Homo habilis</i> L. S. B. Leakey <i>et al.</i> , 1964. Pliocene, Africa.
Species † <i>Homo ergaster</i> Groves and Mazák, 1975. Plio-Pleistocene, Africa and ? Eurasia.
Species † <i>Homo erectus</i> Dubois, 1892. Pleistocene, Africa and Eurasia.
Species † <i>Homo antecessor</i> Bermúdez de Castro <i>et al.</i> , 1997. Plio-Pleistocene, Europe and ? Africa.
Species † <i>Homo heidelbergensis</i> Schoetensack, 1908. Pleistocene, Africa and Eurasia.
Species † <i>Homo neanderthalensis</i> King, 1864. Pleistocene, western Eurasia.
Species <i>Homo sapiens</i> Linnaeus, 1758. Pleistocene to the present, worldwide.

†, Taxon is extinct; *, taxon considered *species germinalis* (32), i.e., a species originating a genus; ?, uncertainty about the taxon's presence in that region.

advance relative to the species *Kenyanthropus platyops*, which would also be included in *Homo*, as the stem species (*species germinalis*) of the genus.

Finally, there was an increase of the robust and gracile tendencies ≈2.5 Myr ago. The robust lineage evolved megadonty adapted to eating hard vegetable materials, while the gracile lineage incorporated a more carnivorous diet with the development of stone-tool manufacture and large crania. Both tenden-

cies can be considered evolutionary events that do not, at present, call for an assessment of either a cladistic or an anagenetic differentiation of genera. The classification we favor is conservative, and new discoveries may make it advisable to recognize the existence of additional genera, particularly with regard to our very ample, anagenetically stretched genus *Homo*.

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- Linnaeus, C. (1735; 10th and definitive edition, 1758) *Systema Naturae per Naturae Regna Tria, Secundum Classes, Ordines, Genera, Species cum Characteribus, Synonymis, Locis* (Laurentii Sylvi, Stockholm).
- Dubois, E. (1894) *Pithecanthropus erectus: Eine menschanähnliche Übergangsform aus Java* (Landsdruckerei, Batavia).
- Black, D. (1927) *Paleontol. Sin. Ser. D* 7, 1–29.
- Dreyer, T. F. (1935) *Kon. Ned. Akad. Wet.* 38, 118–128.
- Broom, R. & Robinson, J. T. (1949) *Nature* 164, 322–323.
- Arambourg, C. (1955) *Am. J. Phys. Anthropol.* 13, 191–202.
- Dart, R. (1925) *Nature* 115, 195–199.
- Elliot Smith, G. (1925) *Nature* 115, 235.
- Keith, A. (1925) *Nature* 115, 234–235.
- Woodward, A. (1925) *Nature* 115, 235–236.
- Duckworth, W. J. H. (1925) *Nature* 115, 236.
- Broom, R. (1938) *Nature* 142, 377–379.
- Leakey, L. (1959) *Nature* 184, 491–493.
- Arambourg, C. & Coppens, Y. (1968) *S. Afr. J. Sci.* 64, 58–59.
- Strait, D. S., Grine, F. E. & Moniz, M. A. (1997) *J. Hum. Evol.* 32, 17–82.
- Wood, B. & Collard, M. (1999) *Science* 284, 65–71.
- Cela-Conde, C. J. & Altaba, C. R. (2002) *S. Afr. J. Sci.* 98, 229–232.
- White, T. D., Suwa, G. & Asfaw, B. (1994) *Nature* 371, 306–312.
- White, T. D., Suwa, G. & Asfaw, B. (1995) *Nature* 375, 88.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y. (2001) *C. R. Acad. Sci. Ser. Ila* 332, 137–144.
- Leakey, M. G., Spoor, F., Brown, F. H., Gathogo, P. N., Kiarie, C., Leakey, L. N. & McDougall, I. (2001) *Nature* 410, 433–440.
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H. T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J. R., *et al.* (2002) *Nature* 418, 145–151.
- Sarich, V. & Wilson, A. C. (1967) *Science* 158, 1200–1203.
- Horai, S., Hayasaka, K., Kondo, R., Tsugane, K. & Takahata, N. (1995) *Proc. Natl. Acad. Sci. USA* 92, 532–536.
- Chen, F. C. & Li, W. H. (2001) *Am. J. Hum. Genet.* 68, 444–456.
- Stauffer, R. L., Walker, A., Ryder, O. A., Lyons-Weiler, M. & Hedges, S. B. (2001) *J. Hered.* 92, 469–474.
- Nei, N. & Glakko, G. V. (2002) *J. Hered.* 93, 157–164.
- Arnason, U., Gullberg, A., Burguete, A. S. & Janke, A. (2000) *Hereditas* 133, 217–228.
- Pilbeam, D. R. (1968) *Nature* 219, 1335–1338.
- Wolpoff, M. H., Senut, B., Pickford, M. & Hawks, J. (2002) *Nature* 419, 581–582.
- Brunet, M. (2002) *Nature* 419, 582 (lett.).
- Haile-Selassie, Y. (2001) *Nature* 412, 178–181.
- Martin, L. B. (1985) *Nature* 314, 260–263.

34. Wood, B. A. (1988) in *Evolutionary History of the "Robust" Australopithecines*, ed. Grine, F. E. (de Gruyter, New York), pp. 269–284.
35. Szalay, F. S. (2001) *Ludus Vitalis* **15**, 143–169.
36. Mayr, E. (1950) *Cold Spring Harbor Symp. Quant. Biol.* **15**, 109–118.
37. Andrews, P. (1995) *Nature* **376**, 555–556.
38. Johanson, D., White, T. & Coppens, Y. (1978) *Kirtlandia* **28**, 1–14.
39. White, T. (2003) *Science* **299**, 1994–1997.
40. Lieberman, D. E. (2001) *Nature* **410**, 419–420.
41. Tobias, P. V. (2003) *Science* **299**, 1193–1194.
42. Suwa, G., Asfaw, B., Beyene, Y., White, T. D., Katoh, S., Nagaoka, S., Nakaya, H., Uzawa, K., Renne, P. & WoldeGabriel, G. (1997) *Nature* **389**, 489–492.
43. Asfaw, B., Glibert, W. H., Beyene, Y., Hart, W. K., Renne, P. R., WoldeGabriel, G., Vrba, E. S. & White, T. D. (2002) *Nature* **416**, 317–320.
44. Blumenschine, R. J., Peters, C. R., Masao, F. T., Clarke, R. J., Deino, A. L., Hay, R. L., Swisher, C. C., Stanistreet, I. G., Ashley, G. M., McHenry, L. J., et al. (2003) *Science* **299**, 1217–1221.
45. Grine, F. E. & Martin, L. B. (1988) in *Evolutionary History of the "Robust" Australopithecines*, ed. Grine, F. E. (de Gruyter, New York), pp. 3–42.
46. Wood, B. & Collard, M. (1999) *Evol. Anthropol.* **8**, 195–207.
47. Aiello, L. & Collard, M. (2001) *Nature* **410**, 526–527.
48. Senyürek, M. (1955) *Belleten* **19**, 1–57.
49. Leakey, M. G., Feibel, C. S., McDougall, I. & Walker, A. (1995) *Nature* **376**, 565–572.
50. Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A. H. E. & Pilbeam, D. (1996) *C. R. Acad. Sci. Ser. Ila* **322**, 907–913.
51. Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. & Suwa, G. (1999) *Science* **284**, 629–635.