tive locations on the two CRT screens, their relative phases were adjusted until an observer with good stereopsis reported that the fused pattern appeared in the plane of the CRT face.

8. Observers adapted to the light of the observing chamber for at least 5 minutes before each session. Observers were instructed to keep both eyes open and to fixate the center of the screen throughout all trials. They initiated their own trials by depressing a pushbutton and indicated whether a grating pattern appeared during the first or second 1-second interval by throwing a lever switch left or right, respectively. Correct responses produced a feedback tone to the observer. Before each block of trials, observers were allowed to trigger a number (10 to 12) of trials with the grating pattern set at high (10 percent) contrast to familiarize themselves with the stimulus to be detected. Rest periods could be taken at any time and were followed by a readaptation period.
9. D. Green, *Signal Detection and Recognition by Human Observers*, J. A. Swets, Ed. (Wiley, New York, 1964).
10. The same apparatus and procedure were used for this experiment. The grating pattern was displayed on only one of the two CRT's. For the certainty conditions, the same eye was stimulated throughout a block of 100 trials; for the uncertainty condition, the eye stimulated was randomly varied from trial to trial. For each observer the same spatial frequency was used throughout the experiment. Again, observers triggered a number of familiarization trials at high contrast before each block of trials. After the uncertainty condition, the certainty condition was repeated. Performance always returned to the earlier certainty levels.
11. All observers were tested for stereopsis with a modified Howard-Dolman device, the modified Ortho-Rater, and random-element stereograms (*3*). The three stereoblind observers have other visual characteristics: R.S. displays a convergent strabismus of approximately 10°, with corrected acuities of 20/22 [oculus dexter (O.D.)] and 20/40 [oculus sinister (O.S.)]; S.L. displays a 6.33° esophoria, has no history of manifest strabismus, and has corrected acuities of 20/18 (O.D.) and 20/17 (O.S.); A.G. is a former esotrope who was surgically corrected at the age of 4, with follow-up surgery at the age of 11, is currently orthophoric but mildly ambliopic with acuities of 20/20 (O.D.) and 20/30 (O.S.). Observers with refractive corrections wore them during testing.
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14. D. Westendorf, A. Langston, D. Chambers, and C. Allegretti [*Percept. Psychophys.* **24**, 209 (1978)] reported stereoblind binocular detection performance to be near that expected from probability summation, as if the eyes were independent detectors. These results complement those of the present study.
15. Supported by NIH grant EY01596 and NSF grant BNS 7817948. R.B. holds NIH career development award EY00106.

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On the Status of *Australopithecus afarensis*

In this comment it is our purpose to establish the relationship between *Meganthropus africanus* Weinert 1950 and Johanson's replacement name for this taxon, as well as to discuss the errors that we believe to have been incorporated by Johanson and White (*1*) into their taxonomic speculations.

The first publication making the name *Australopithecus afarensis* available was apparently a report of a meeting sponsored by the Swedish Academy of Sciences (*2*). Since this is an unusual and potentially hazardous means of announcing a new zoological name, it must be asked if the name proposed in this publication satisfies the International Code of Zoological Nomenclature (*3*) in terms of availability. Reference to the Code indicates that it does. Ideally the description of a new taxon should be accompanied by a differential diagnosis; however, this is not required by the Code. The statement in (*2*) that "This taxon is characterised by definite bipedalism, marked sexual dimorphism (larger males, smaller females) but no brain expansion" satisfies the criterion of the purported differentiation of a taxon. The correct author citation of the new name is: *Australopithecus afarensis* Johanson, 1978 since the authorship of a new taxon goes to its proposer and not to the person reporting its announcement (Article 50a).

Johanson indicated in the original description, as reported by Hinrichsen (*2*), that the type-series used as the basis of his new name consisted of the Pliocene hominids from Hadar and Laetoli; however, no type-specimen was designated. Although the fact that the original publication did not include the designation of a type-specimen affects neither the availability nor the potential validity of the new name, the issue of the type-specimen of *A. afarensis* does present other problems that must be clarified. In cases such as this where a type-specimen was not designated in the original publication, Article 74a (i) provides that a subsequent worker may designate a lectotype from the type-series. The first reviewers of this taxon to designate a type-specimen were the proposer of the name and two other workers (*4*). Although the date of publication of this review is incompletely specified [Article 21b (ii)], it is certain that it was published substantially later than the original publication, since one of us (M.D.L.) withdrew her name from the review as late as August 1978. In the review (*4*), the Laetoli hominid (L.H. 4) mandibular specimen was, therefore, erroneously designated as the holotype rather than the lectotype, since a holotype can only be designated in the original publication of a new taxon.

The review by Johanson *et al.* (*4*) also introduces a number of other far more serious problems into the already unnecessarily confused realm of hominid taxonomy. In addition to designating a lectotype under the term holotype, they give a list of the specimens of the type-series under the inappropriate heading of paratypes (this should be paralectotypes according to Recommendation 74E of the Code) in which they include the Garusi maxillary fragment collected by Kohl-Larsen in 1939 (*5*). This important specimen from the Laetoli locality in Tanzania is the holotype of *Meganthropus africanus* Weinert, 1950 (*6*). Their inclusion of the Garusi 1 specimen in the type-series of *A. afarensis* and their listing of *M. africanus* as a synonym of this name has the effect of making *A. afarensis* a replacement name (junior subjective synonym) for Weinert's *M. africanus*. Johanson was correct in giving a new name to Weinert's species because his inclusion of this species in the genus *Australopithecus* Dart, 1925 (*7*) meant that the nominal species *Australopithecus africanus* (Weinert, 1950) had to be rejected since it was now a junior secondary homonym of *Australopithecus africanus* Dart, 1925 (Article 53). This article of the Code is essential because it precludes the absurdity of two species within the same genus bearing the same specific name.

As used by Johanson *et al.* (*4*), the name *A. afarensis* clearly does not identify a new species. Rather, it only enlarges the hypodigm of Weinert's species *M. africanus* and provides a necessary replacement name to apply to this species when it is included within the genus *Australopithecus*. The name *afarensis* is valid as a substitute for Weinert's prior name only (i) when Weinert's holotype and the L.H. 4 lectotype are included in the same species and (ii) when this species is classified in a genus in which Weinert's name is a junior homonym. If ever this species is considered to be generically distinct from the taxon represented by Dart's holotype of *A. africanus*, then the valid specific name must revert to *africanus* Weinert if it is the senior available name within the recognized species-group (Article 59c). In this latter case, Johanson's name becomes an invalid junior synonym. This procedure complies with the rules set out in the Code (Articles 59b and 60b) requiring that all junior homonyms be rejected and replaced and that a junior secondary homonym be restored as the valid name of a taxon whenever a zoologist believes that the two species-group taxa in question are not congeneric (Article 59b).

In Johanson and White's article on the

specimens from Laetoli and Hadar (*1*), the issue is further confused. Of their nine suggested taxonomic schemes for Plio-Pleistocene hominid evolution, no fewer than four (b, e, f, and h) are invalid and do not comply with the rules of nomenclature. In schemes e and f, they have failed to appreciate that Weinert's specific name is valid within the genus *Homo* when Dart's holotype from Taung is excluded from this genus. In both of these schemes, the taxon labeled *Homo afarensis* should have been identified as *H. africanus*. With reference to schemes b and h, the name *Australopithecus africanus* (Dart, 1925) has priority over *Paranthropus robustus* (Broom, 1938) (*8*); thus when these two species are united in the same genus, the valid name of this taxon cannot be *Paranthropus* (Article 23). Finally, in scheme h, where the species identified as *afarensis* is not included in the same genus with *A. africanus* Dart, its specific name must revert to *africanus* Weinert. Furthermore, it is impossible to recognize, under present circumstances, a genus *Australopithecus* that does not include the Taung holotype (*9*). The basal taxon in scheme h would thus have been correctly indicated as either *Praeanthropus africanus* or *Meganthropus africanus*.

Johanson *et al.* (*4*) also claim that the generic name *Praeanthropus* as proposed by Hennig (*10*) is invalid. Since Hennig's publication did not include the fixation of a type-species, the name *Praeanthropus* is not available as of Hennig's work and it is therefore a *nomen nudum*. The distinction between availability and validity that has been confused here is one of the most elementary distinctions that exists within the Code. While it is correct that the generic name *Praeanthropus* is not available from Hennig, it does become available from Senyürek (11) as a new generic name for Weinert's taxon *Meganthropus africanus*. *Praeanthropus* Senyürek, 1955 is thus an available name for a nominal genus whose type-species is *M. africanus* Weinert, 1950.

In view of the problems created in the usage of *A. afarensis*, it seems particularly confusing that the lectotype designated for this geographically descriptive name should have been selected from the Tanzanian Laetoli specimens. The wisdom of this decision is made even more questionable since the Afar material, which constitutes the majority of the specimens in the type-series, includes some Pliocene specimens of unequaled morphological completeness such as A.L. 288-1.

If the central issues raised in the study of man's past are to continue to be more clearly understood, we believe that the internationally agreed rules of nomenclatural procedure must be strictly observed.

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Johanson and White followed the announcement of a new species of *Australopithecus* with a phylogenetic hypothesis of early human evolution (*1*). The hypothesis places *A. afarensis* as the ancestral species from which modern humans arose by evolutionary progression (*2*) through successive species of *Homo*.

We considered this scheme and thought it less likely than another (*3*) for several reasons, only two of which are given here. First, we think it much more likely that humans arose by a speciation event or events rather than by progression (anagenesis). This fits both the widely accepted model of geographic speciation (*4*) and the evidence of the later hominid fossil record. Johanson and White invoke a speciation event for the origin of *A. africanus*, but not one for the origin of *Homo*, in which greater morphological change was involved.

Second, there is evidence from East Africa for late-surviving small *Australopithecus* individuals that were contemporaneous first with *H. habilis*, then with *H. erectus*. The more complete specimens include KNM-ER 1805 and 1813 from East Turkana and OH 13 and 24 from Olduvai. Unlike the Laetoli and Hadar sample, these are calvariae associated with facial skeletons and upper teeth; two even have associated mandibles and lower teeth. They are thus less likely to mislead us than more fragmentary remains. To include these later gracile specimens as females of an evolving *Homo* species presents the following difficulties: (i) The known range of cranial variation in *H. erectus* would have to be broadened greatly, but only for the African and not the Oriental sample, as such gracile crania are not known outside Africa. (ii) It is true, as Johanson and White hinted, that certain features of the jaws and teeth of the later gracile sample resemble those found in some Hadar specimens. The apparent lack of change in these features in early *Homo* would be surprising since the archeological record indicates marked changes in diet and technology that might be expected to alter the selection pressures on those body parts. (iii) These gracile individuals, presumed by Johanson and White to be females of early *Homo*, are morphologically distinct from KNM-ER 1808, an associated *H. erectus* skeleton (*5*) that is judged female on the basis of pelvic morphology. This skeleton shows close cranial and dental resemblances to KNM-ER 3733, an undoubted *H. erectus*, but is unlike small *Australopithecus* in both size and morphology.

We suggest that the ambiguities that appear when the scheme of Johanson and White is faced with the later hominid record may also be present in their scheme for the earlier record, since the question of when the other lineages arose is still open.

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31 May 1979

Johanson and White's (*1*) human evolutionary scheme is supported by the results of our investigation of mandibular molar morphology based on crown component measurements of extant and fossil hominoids (*2*). Figure 1 shows the relative position of the fossil hominid second mandibular molar (*3*) with the Penrose shape distance from modern *Homo* *sapiens* plotted horizontally (*4*) and geological time graphed vertically (*1*). The sequence of distances follows the phenetic pattern we would expect for support of the Johanson-White phyletic model: the distance from modern *H. sapiens* increases steadily from *H. erectus* to *H. habilis* to *Australopithecus afarensis* to *A. africanus* to *A. robustus* to *A. boisei*. When plotted against time, these phenetic relationships are most parsimonious with the two lineage model with *A. afarensis* at the base, one lineage hominizing toward *H. sapiens* and the other (starting with *A. africanus*) specializing in a unique direction. This pattern is also shown by more intricate analysis based on canonical variates analysis of shape variables [*Q*-mode standardized after removal of allometric residuals by regression (*5*)]. The morphological distances show that less change is necessary to connect *A. afarensis* to *H. habilis* than to relate *A. africanus* to *H. habilis*. In these analyses *A. africanus* is virtually indistinguishable from *A. robustus*.

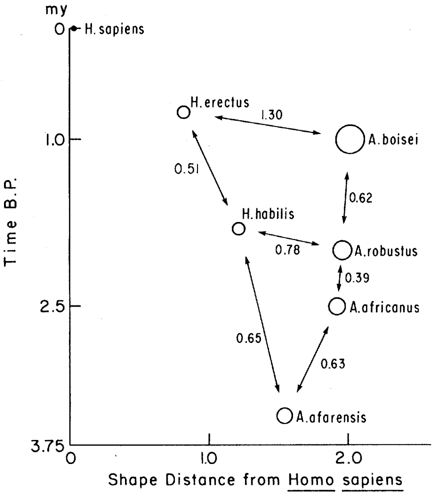

Fig. 1. Distribution of hominid fossils according to their Penrose shape distances (*4*) from modern *Homo sapiens* (horizontal axis) and their geological age (vertical axis) based on the second mandibular molar. The size of the circles is proportionate to the Penrose size difference from *H. sapiens*.

The metrically defined morphological pattern of *A. afarensis* is as follows: M_2 is short as in hominines, but broad as in all hominids; mandible is quite thick, but not as shallow vertically as in later australopithecines at M_2; occlusal length (central trigonid fovea to distal marginal ridge) is intermediate, as it lengthens in the *Homo* lineage while shortening in australopithecines; metaconid is moderate in size; entoconid is small as in later australopithecines, but becomes progressively larger in *Homo*, where it absorbs more of the talonid enlargement; hypoconulid is smaller than in later australopithecines but the same as in *Homo*; hypoconid is primitively small and enlarges in both later lineages but especially in australopithecines; protoconid is primitively and uniquely large for a hominid (it is reduced somewhat in later australopithecines and much more in *Homo*); cervical length of molars is small in relation to breadth; maximum trigonid and talonid breadths are subequal and only moderately expanded over cervix; diagonal length is small but larger than in both *Homo* (squaring trend through hypoconulid reduction) and later australopithecines (squaring through hypoconulid centralization); crown height is more than in pongids but less than in later *Homo* or *A. boisei*. In terms of the analysis of the entire mandible, *A. afarensis* shows a primitive large M_3; an M_2 that is broad but still long relative to jaw size, as in modern apes; only moderate hypsodonty; M_1 talonid expansion that is incomplete relative to later hominids; low P_4 talonid and entoconid and hypoconid less developed than in later lineages; corpus inferior to P_4 that is broad but still primitively deep; P_3 that is quite short but not yet buccolingually expanded; and canine that is small but not as much so as in other hominids relative to overall tooth and mandible size.

We emphasize that these observations are not based on subjective impressions of morphology, but are metrically defined as traits. The phenetic distance sequence is also parsimonious with the Johanson-White interpretation from a pongid (ancestral) perspective, as the earliest hominids show the smallest distance to *Pan* while representatives of the later lineages (*H. habilis* and *A. africanus*) are progressively more distant. Furthermore, the 5.5 million year old Lothagam mandible (*6*) is consistently and significantly nearer *P. troglodytes*, *P. paniscus*, *Gorilla*, and *Pongo* than is *A. afarensis* in the M_1 analysis, although Lothagam is most similar to *A. afarensis* among the hominids. The Lukeino molar (*7*), on the other hand, is metrically indistinguishable from *P. troglodytes* in the M_2 analysis, showing no hint of development of hominid apomorphies.

Our analyses show that *Ramapithecus* is a less likely ancestor from which to derive living pongids and hominids than is a form resembling extant *Pan* (*8*). In fact, the lower molars of *A. afarensis* are more similar to modern *Pan* than they are to *Ramapithecus*, particularly the relative expansion of the talonid. The incisors of *Ramapithecus* are relatively smaller than those of early australopithecines, so an evolutionary path connecting *Ramapithecus* and *H. sapiens* would have incisors unparsimoniously decreasing in relative size, then increasing, and finally decreasing again. *Pan* and *Ramapithecus* clearly represent very different, virtually irreconcilable models for the common ancestor of pongids and hominids.

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We appreciate this opportunity to respond to the commentary generated by our recent appraisal of early hominid evolution (*1*). It was the stated intent of our article to provide data and ideas that would be useful in the evaluation of human evolution. McHenry and Corruccini's comment is constructive in this regard as it provides another approach for investigating hominid phylogeny. The comments by Day *et al.* and by Leakey and Walker fail to provide new information or constructive criticisms.

Day *et al.*'s remarks concern only nomenclatural details, even though these authors either discovered or studied the original specimens assigned to *Australopithecus afarensis* (*2*). Our method of announcing *A. afarensis* was not unusual and reflected our eagerness to communicate with colleagues at an important scientific symposium. It was only hazardous when Hinrichsen (*3*) ignored recommendation 50A of the International Code of Zoological Nomenclature (*4*) urging reporters not to include new names of taxa in their published reports. (In fact, the presumed diagnosis offered in Hinrichsen applies equally to birds, dinosaurs, and kangaroos as well as to most varieties of fossil hominid.) Hence, this publication (*3*) violated Article 13a(i) of the Code, which states that the published name must be "accompanied by a statement that purports to give characters *differentiating* the taxon." Therefore, the name *A. afarensis* was unavailable until properly proposed by Johanson, White, and Coppens (*2*).

Since *A. afarensis* has a different type specimen (L.H. 4) than Weinert's *Meganthropus africanus* (*5*) (the Garusi maxilla), it cannot be considered a replacement name for the latter taxon. We do not accept a generic status for the Garusi maxilla separate from *Australopithecus* as suggested by Şenyürek (*6*), and therefore the original Garusi specimen was considered as one of the paratypes for *A. afarensis* (*2*).

The statement by Day *et al*. that our alternative taxonomic schemes b, e, f, and h are invalid is incorrect. Schemes b and h follow Tobias's suggestion (*7, 8*) that the holotype *A. africanus* specimen be placed in *A. robustus*; Tobias is a world-recognized authority on early hominid taxonomy and has seriously proposed this alternative, although the placement of the nominal species *A. africanus* Dart in *Paranthropus* creates an invalid binomen. In reference to schemes e and f, Day *et al*. question the use of the trivial name *afarensis* instead of Weinert's trivial name *africanus* within the genus *Homo*. If *H. africanus* were clearly available, the criticism would be correct. However, as Mayr (*9*) asserts and Robinson (*10*) discusses, the trivial name *africanus* may be preoccupied within the genus *Homo* (*11*).

Concerning our selection of a holotype specimen, we refer Day *et al*. to Simpson (*12*): "A nomenclatural type is simply something to which a name is attached by purely legalistic convention. It should have nothing to do with the nomenclatural processes of defining the species and should have no special role in identifying other specimens. . . . It is nominalistic absurdity to confuse a set of objects with the name or symbol for that set."

Leakey and Walker claim to have considered and dismissed our hypothesis of early human evolution in their *Scientific American* article (*13*). That article does not even mention the Laetoli or Hadar discoveries, let alone the phylogenetic placement of these fossils.

In the second paragraph of their comment, Leakey and Walker advocate a cladogenetic mode of evolution within the genus *Homo*. In the following paragraph they predict that anagenetic gradualism should characterize evolution within the genus *Homo*. Furthermore, in their earlier article (*13*) they stated that "the *habilis* populations are directly antecedent to *Homo erectus*." We find this approach to evolutionary biology confusing.

Leakey and Walker claim that evidence from East Africa shows late-surviving, small *Australopithecus* individuals (presumably *A. africanus*) "contemporaneous first with *H. habilis*, then with *H. erectus*" (*14*). The scientist responsible for the description and interpretation of much of this evidence, B. A. Wood, recently expressed his reservations, stating, "If there is taxonomic variation within East African 'gracile' hominids, it is by no means certain that it is due to the presence of *Australopithecus africanus*" (*15*).

In fact, the term "contemporaneous" has a peculiar meaning for the East Rudolf hominids. This is particularly evident in the first major scientific monograph published by the Koobi Fora Research Project, where it is stated that "Certain hominid morphotypes occur throughout the same stratigraphic interval, and this is the meaning of 'contemporaneous' for the Koobi Fora faunal record" (*16*). For example, the most important cranium of this supposed small *Australopithecus* species, KNM-ER 1813, was first reported as being probably from the Lower Member (*17*), then shifted provisionally to the Upper Member, where it is suggested to be "no less than 1.2 million and may be more than 1.6 million years old" (*13*).

Leakey and Walker's comments hinge on a recognition of three Lower Pleistocene hominid lineages. We recognized two in our assessment (*1*). We do not deny the possibility of a third lineage but merely question whether it has been satisfactorily demonstrated, defined, or described. The most comprehensive definition offered to this date is that of R. E. Leakey (*14*), who gives as typical characteristics "gracile mandibles with small cheek teeth, cranial capacity values at 600cc or less and sagittal crests rare or nonexistent." Modern chimpanzees, by this definition, would be classified as *A. africanus*.

The Leakey and Walker claims for morphological homogeneity within *H. erectus* suggest that they may have been seriously misled even in their treatment of relatively complete crania. A large amount of variation in crania (Trinil 1, Olduvai Hominid 9, "*Pithecanthropus*" VIII) and mandibles (Ternifine 3, "*Pithecanthropus*" B, Choukoutein) is universally accepted as falling within *H. erectus*. Variation in the Asian *H. erectus* sample is substantial, and we wonder why Leakey and Walker do not recognize similar levels of variation in East African *H. habilis* and *H. erectus* populations, particularly since they are not hesitant to recognize enormous variation in the *A. robustus* (*A. boisei*) sample from a single site (Koobi Fora) (*13, 18*).

Since Leakey and Walker suggest that our scheme is characterized by ambiguities, we find it disappointing that they have failed to provide an adequate, consistent, or understandable alternative for the fossil evidence presently available. We realize that all phylogenetic hypotheses require modification with new evidence.

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