

A Systematic Assessment of Early African Hominids

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Paleoanthropological research in eastern and southern Africa has provided an extensive fossil record documenting human evolution over the last 2.5 million years. The accumulated fossil remains from sites such as Koobi Fora, Olduvai Gorge, Omo, Sterkfontein, and Swartkrans (Fig. 1) have been studied, described, and afforded diverse phylogenetic and taxonomic interpretations (1-6).

The sites of Laetolil in Tanzania and Hadar in Ethiopia (Fig. 1) have yielded abundant remains of human ancestors that have been dated firmly between 3 and 4 million years ago. These new hominid fossils, recovered since 1973, constitute the earliest definitive evidence of the family Hominidae (7). The morphology and attributes of these remains are demonstrably more primitive than those of hominid specimens from other sites. Because of their great age, abundance, state of preservation, and distinctive morphology, the Laetolil and Hadar fossils provide a new perspective on human phylogeny during Pliocene and Pleistocene times.

It is not our aim in this article to review the extensive literature that deals with hominid origins, phylogeny, and taxonomy. Our first intention is to describe some of the most salient morphological features of the newly recovered Pliocene hominids from Laetolil and Hadar. We will then assess the phylogenetic position of the new specimens within the Hominidae in light of their distinctive skeletal anatomy. Finally, we will express the implications of these findings in a taxonomic evaluation.

Background

The major hominid collections from Laetolil were made by Mary D. Leakey's expedition. Laetolil lies about 50 kilometers (30 miles) south of Olduvai Gorge in northern Tanzania (Fig. 1). The ongoing fieldwork was initiated at Laetolil in 1974, and the geology, paleontology, and history of the site have been de-

Summary. A large sample of Pliocene fossil hominid remains has been recovered from the African sites of Hadar in Ethiopia and Laetolil in Tanzania. These collections, dating approximately between 2.9 and 3.8 million years ago, constitute the earliest substantial record of the family Hominidae. This article assesses the phylogenetic relationships of the newly discovered fossil hominids and provides a taxonomy consistent with that assessment. A new taxon, *Australopithecus afarensis*, has been created to accommodate these Pliocene hominid fossils.

scribed by Leakey *et al.* (8). The fossil hominids consist primarily of dental and gnathic remains derived from the Laetolil Beds and are radiometrically placed between 3.6 and 3.8 million years ago (8). Laetolil hominids (L.H.) 1 through 14 have been described (9) and nine additional specimens have been recovered.

Hadar is located in the Afar triangle of Ethiopia (Fig. 1). Intensive paleoanthropological fieldwork was conducted at the site between 1972 and 1977 by the International Afar Research Expedition (10-13). Abundant, diverse, well-preserved fossils were recovered from the Hadar Formation. On the basis of geochronologic and biostratigraphic evidence, this formation has been dated between 2.6 and 3.3 million years ago (11). A remarkable collection of hominid specimens

representing a minimum of 35 and a maximum of more than 65 individuals was recovered. Preservation is outstanding and some Hadar specimens are exceptionally complete. In several cases there are associated skeletal parts of the same individual (Fig. 5; 12, 14, 15). Nearly all anatomical regions of the body are represented in the collections from Hadar. This situation is unprecedented for the earlier portion of the fossil hominid record. For example, we have nearly 40 percent of a skeleton known as "Lucy" from Afar Locality (A.L.) 288 and more than 200 specimens representing an absolute minimum of 13 individuals from A.L. 333 and 333w. Some of the material has been presented (12-21), but a large portion of the sample is currently under investigation and will be fully described in the near future.

A comparative study of the Hadar and Laetolil hominids has clarified the relationship between the two collections. The strong morphological and chronological continuity seen between the Hadar and Laetolil fossil hominid samples

strongly suggests that these collections are most conveniently and effectively considered together in the following systematic assessment.

Anatomical Evidence

The Laetolil and Hadar fossil hominid remains have a distinctive suite of primitive cranial and postcranial characteristics. Some of these have been men-

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Table 1. Combined metric data for the Laetolil and Hadar hominid dentitions. Only measurements on intact teeth are provided. The measurement technique is described elsewhere (9). Mesiodistal diameters for postcanine teeth are corrected for interproximal attrition except in cases where that was impossible. For anterior teeth, (w) indicates worn teeth representing range values. Other abbreviations: MD, mesiodistal; BL, buccolingual; N, number; R, range; \bar{X} , mean; and S.D., standard deviation.

Dentition	Lower		Upper	
	MD	BL	MD	BL
<i>Permanent</i>				
First incisor (I1)				
N	1	3	4	5
R		7.3-7.7	9.0w-11.8	7.1-8.6
\bar{X}	5.6w	7.50	10.36	8.16
S.D.		0.20	1.17	0.60
Second incisor (I2)				
N	4	3	6	8
R	5.7w-7.1w	6.7-7.8	6.7w-8.2	6.2-8.1
\bar{X}	6.28	7.37	7.65	7.18
S.D.	0.59	0.59	0.59	0.65
Canine (C)				
N	5	9	10	10
R	7.9-11.7	8.8-12.0	8.9-11.6	9.3-12.5
\bar{X}	9.16	10.17	9.92	10.94
S.D.	1.54	1.15	0.74	1.11
Third premolar (P3)				
N	14	14	8	7
R	8.2-12.6	9.5-12.6	7.2-9.3	9.8-13.4
\bar{X}	9.51	10.60	8.50	12.03
S.D.	1.09	0.98	0.74	1.19
Fourth premolar (P4)				
N	13	12	8	5
R	7.7-10.9	9.8-12.8	7.6-9.7	11.1-12.6
\bar{X}	9.58	10.93	8.95	12.00
S.D.	0.95	0.92	0.68	0.60
First molar (M1)				
N	18	16	9	9
R	10.1-14.6	11.0-13.9	10.8-13.7	11.2-15.0
\bar{X}	12.85	12.62	12.22	13.23
S.D.	1.05	0.90	0.92	1.24
Second molar (M2)				
N	17	17	3	3
R	12.1-15.4	12.1-15.2	12.1-13.5	13.4-15.0
\bar{X}	14.02	13.44	12.83	14.40
S.D.	1.08	1.06	0.70	0.87
Third molar (M3)				
N	11	12	5	5
R	13.3-16.3	11.7-14.9	11.4-14.3	13.1-15.5
\bar{X}	14.55	13.23	12.54	14.22
S.D.	0.8	1.02	1.32	1.05
<i>Deciduous</i>				
First deciduous incisor (di1)				
N	1	1		
R				
\bar{X}	4.2	3.6		
S.D.				
Second deciduous incisor (di2)				
N	2	3	1	1
R	4.8-5.7	4.2-5.0		
\bar{X}	5.25	4.63	5.7	4.5
S.D.		0.40		
Deciduous canine (dc)				
N	3	2	3	4
R	6.2-6.6	5.8	6.8-7.7	5.3-6.5
\bar{X}	6.43	5.8	7.37	5.95
S.D.	0.21		0.49	0.49
First deciduous molar (dm1)				
N	4	4	4	3
R	8.5-9.6	7.6-8.4	8.1-9.4	8.9-9.3
\bar{X}	9.15	7.93	8.68	9.17
S.D.	0.48	0.36	0.54	0.23
Second deciduous molar (dm2)				
N	2	2	4	4
R	11.6-12.6	9.7-10.6	9.9-10.8	10.5-12.6
\bar{X}	12.1	10.15	10.23	11.20
S.D.			0.40	0.95

tioned in earlier publications but this is the first report on the combined sample as of September 1978. It is not possible in an article of this length to describe them in detail; instead, some of the major anatomical features of the material are outlined below.

Dentition. As with other paleontological materials from these sites, the dental elements comprise the largest portion of the Pliocene hominid sample from Hadar and Laetolil.

Incisors. The upper centrals are characterized by their great mesiodistal dimension, which contrasts with the diminutive mesiodistal diameter of the lateral incisors (A.L. 200-1a; L.H.-3).

Canines. The large, asymmetric, pointed lowers project slightly above the tooth row and usually have a pronounced lingual ridge (A.L. 400-1a, 128-23; L.H.-3). The uppers also are large and project slightly. When worn, they often bear an exposed strip of dentine along the distal occlusal edge (A.L. 200-1a; L.H.-5). Apical wear is often present as well. Both upper and lower canine roots are massive and long.

Premolars. The lower third premolars (P_3) are characterized by a dominant, mesiodistally elongate buccal cusp. The extensive buccal face often shows vertical wear striae produced by occlusion with the overlapping upper canine. A smaller lingual cusp is usually present, but some specimens (A.L. 288-1, 128-23) display only an inflated lingual ridge. The P_3 often possesses two distinct roots with the anterior one angulated mesio-buccally (A.L. 333w-60; L.H.-4). In occlusal view, P_3 crown shape is normally an elongate oval, the long axis of which is oriented mesiobuccal to distolingual at 45° to 60° to the mediobuccal axis of the tooth row. The upper third premolar (P^3) is sometimes three-rooted, with a pointed buccal cusp and an extensive, asymmetric buccal face (A.L. 200-1a; L.H.-6). The buccal cervicoenamel line projects toward the mesiobuccal root, and in occlusal view the mesial placement of the lingual cusp gives the crown an asymmetric appearance. The P^3 tends to be slightly larger than the upper fourth premolar (P^4), and the latter does not show mesiodistal elongation of the buccal crown portion.

Molars. The lower molars, particularly the first and second, tend to be square in outline. The cusps are usually arranged in a simple Y-5 pattern, surrounding wide occlusal foveae. The third molars are generally larger and their distal outlines are rounded. The molar size sequence is normally $M_3 > M_2 > M_1$. The

upper molars usually follow the same size sequence, their occlusal foveae are wide, and their hypocones are fully developed.

Deciduous dentition. The deciduous canines are morphologically similar to their adult counterparts in relative size, morphology, and occlusal projection (A.L. 333-99, 104; L.H.-2). The deciduous first molars conform to the molarized human pattern and show deep buccal grooves (A.L. 333-43, -86; L.H.-2).

Overall, the adult and deciduous dentitions are variably intermediate between Hominidae and Pongidae in most of the features enumerated by Le Gros Clark (22). Neither metric data (Table 1) (23) nor morphological considerations (24) suggest to us that more than one evolving hominid lineage is represented in the dental samples from Hadar and Laetolil.

Cranium. Portions of several adult and juvenile faces are available from Hadar and Laetolil. The adults show strong alveolar prognathism associated with somewhat procumbent incisors, the curved roots of which promote a convex clivus. The lower margin of the pyriform aperture is marked laterally by a raised border (A.L. 200-1a, 333-1). The large canine roots are reflected in strong canine jugae, which contribute to the formation of pillars lateral to the pyriform aperture. These pillars act to set this region apart from the zygomatic processes of the maxillae. The anterior margins of these large processes are located above the junction of P⁴ and M¹ and are oriented nearly perpendicular to the tooth rows. The inferior margins of the zygomatic arches are flared anteriorly and laterally. The palates are shallow anteriorly and their lateral margins tend to converge posteriorly (Fig. 2). The dental arcades are long, narrow, and straight-sided instead of parabolic. The tooth row is sometimes interrupted by diastemata between the lateral incisors and canines (A.L. 200-1a).

Preserved portions of the adult crania A.L. 333-45 (Fig. 3) and A.L. 288-1 show a host of primitive features. There are strong muscle markings including a compound temporal-nuchal crest on both sides of A.L. 333-45. The temporal lines converge anteriorly and closely approximate the midline. An anteriorly placed sagittal crest is possible, but the relevant portions are not preserved. The smaller specimen, A.L. 288-1, is less robust but is morphologically similar in its preserved portions (25). Specimen A.L. 333-45 is heavily pneumatized in lateral portions of the cranial base. The nuchal plane is concave and is longer than the



Fig. 1. Geographic location of the major fossil hominid sites discussed in the text: 1, Hadar; 2, Omo; 3, Koobi Fora; 4, Olduvai Gorge; 5, Laetolil; 6, Makapansgat; 7, Sterkfontein, Swartkrans, and Kromdraai, and 8, Taung.

occipital plane. The mastoid region is flattened posteriorly and the mastoid tips point anteroinferiorly. The external auditory meatus takes on a tubular appearance when viewed basally, strongly resembling the pongid condition. The mandibular fossae are broad, have little relief, and are placed only partially beneath the braincase. There is a strong entoglenoid process. A very weak articular eminence results in a mandibular fossa that is open anteriorly. The preserved occipital condyle is located below the external auditory meatus in lateral view and bears a strong angulation across its articular surface. It has not yet been possible to make satisfactory estimates of cranial capacity on the basis of preserved portions of crania, although pre-

liminary observations suggest that it is small, probably within the known range of other *Australopithecus* species (*sensu stricto*). Studies of the cranial remains from Hadar and Laetolil have shown the distinctiveness of this anatomical region and promise to provide additional information concerning the ontogeny and functional anatomy of these early hominids (26).

Mandible. A combined sample of at least 25 adult and juvenile individuals represented by mandibular remains is available from Hadar and Laetolil. The mandibles from the two sites are strikingly similar (Fig. 4). Some major parts of the complex of features distinguishing this collection from other fossil hominid mandibles are described here.

Although ascending rami are poorly represented, available adult mandible specimens (A.L. 333-108) indicate large but not necessarily high mandibular rami. The condyles (A.L. 333w-1e, -16) are large and concordant with the broad articular surfaces of the preserved crania. The A.L. 288-1 mandibular ramus slopes somewhat posteriorly. The ramus usually joins the corpus at a high position, defining a narrow, restricted extramolar sulcus (A.L. 266-1; L.H.-4).

The mandibular corpora are variable in size, and larger specimens are relatively deep in their anterior portions. The lateral contours in the region of the mental foramen are usually hollowed (A.L. 333w-60; L.H.-4). The mental foramina tend to occupy positions low on the corpus and open anterosuperiorly (A.L. 277-1, 288-1; L.H.-4). The mandibular canal passes immediately below

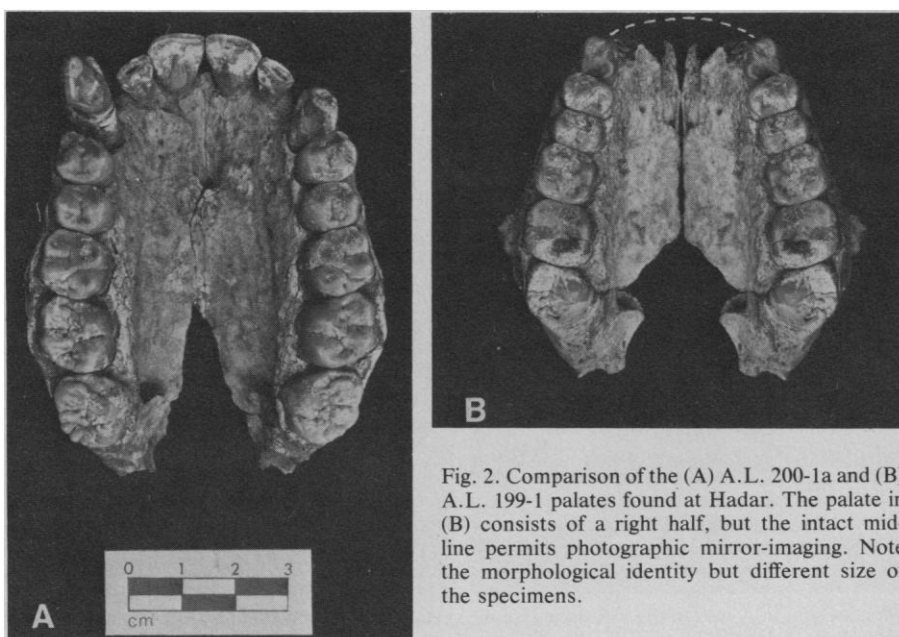


Fig. 2. Comparison of the (A) A.L. 200-1a and (B) A.L. 199-1 palates found at Hadar. The palate in (B) consists of a right half, but the intact midline permits photographic mirror-imaging. Note the morphological identity but different size of the specimens.

the distal root of the third lower molar (M_3). The base of the corpus is everted, and the anterior portion of the corpus is rounded and bulbous. The symphyseal section usually shows a moderate superior transverse torus. The inferior transverse torus is low and rounded rather than shelf-like. There is strong posterior

angulation of the symphyseal axis (A.L. 400-1a; L.H.-4). In occlusal aspect, the molars and premolars form straight rows and the anterior portion of the dental arcade tends to be narrow, especially in the smaller specimens. Some specimens show slight postcanine diastemata (A.L. 266-1; L.H.-4). The dramatic size dif-

ferences seen between such morphologically similar mandibular specimens as A.L. 333w-60 and A.L. 333w-12 suggest a high level of sexual dimorphism within a single hominid lineage (27).

Postcranium. Comparison of the Hadar and Laetolil postcranial material with other Plio-Pleistocene remains is hampered at this time by difficulties in associating cranial and postcranial material found at other sites. In addition, a number of skeletal elements found at Hadar (particularly some of the hand and foot bones) are either absent or poorly represented at other sites, which makes meaningful comparisons impossible. However, some anatomical features of the postcranium are already obvious and deserve mention.

The postcranial skeleton is well represented, and all analyses so far indicate that the hominids were adapted to bipedal locomotion. This is especially evident from the analysis of the knee joint anatomy (28).

The most complete adult skeleton is that of A.L. 288-1 ("Lucy," Fig. 5). The small body size of this evidently female individual (about 3.5 to 4.0 feet in height) is matched by some other postcranial remains (A.L. 128, 129) and these smaller specimens can be contrasted with other larger but morphologically identical individuals from Hadar (A.L. 333 and 333w, Fig. 6). We consider that much of this body size difference reflects sexual dimorphism (29). All of the postcranial elements indicate high levels of skeletal robustness with regard to muscular and tendinous insertions.

The humerofemoral index (ratio of the length of the humerus to the length of the femur) of the A.L. 288-1 specimen is approximately 83.9 (12). This value is high relative to modern humans. The hand bones from Hadar also differ from those of modern humans—for instance, in the "waisted" appearance of the capitate (A.L. 288-1, 333-40), the lack of a styloid process on the third metacarpal (A.L. 333-16, -65), and the longitudinal curvature of the phalanges (A.L. 333-19, -63). A cervical vertebra with a long spinous process (A.L. 333-106) is quite distinct. Two pedal navicular bones (A.L. 333-47, -36) exhibit extensive cuboideonavicular facets and the pedal phalanges are highly curved. One of the potentially most significant bones, the A.L. 288-1 innominate, is currently being reconstructed. Its morphology is commensurate with a bipedal mode of locomotion. The specimen displays a straight anterior margin between the anterior superior and inferior spines, lending a heightened appear-

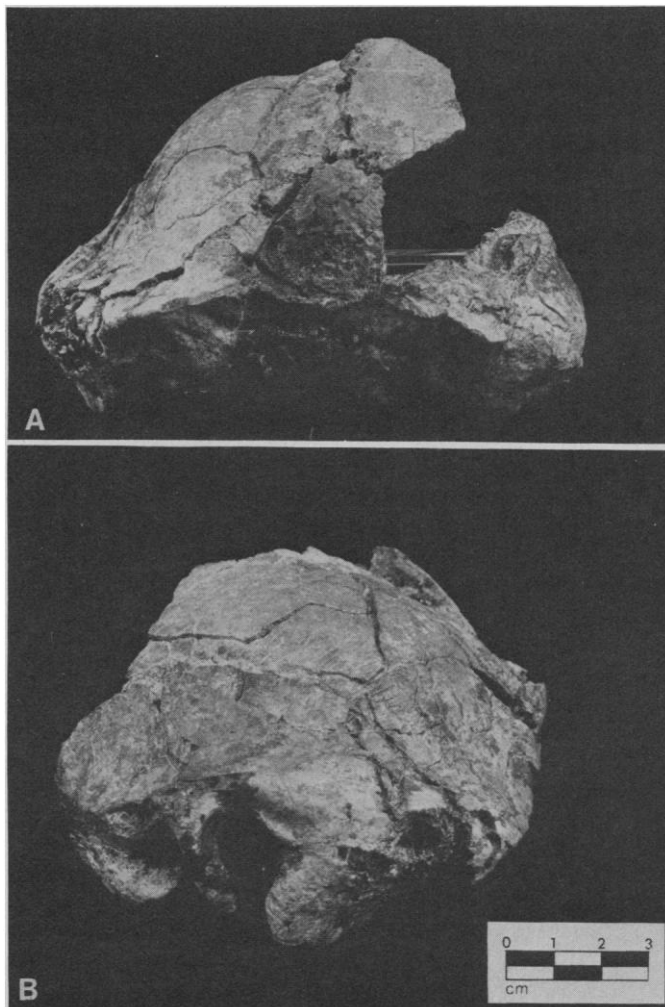


Fig. 3. (A) Occipital and (B) left lateral views of the A.L. 333-45 partial cranium from Hadar. The specimen suffered postmortem distortion, but many important anatomical details are discernible.

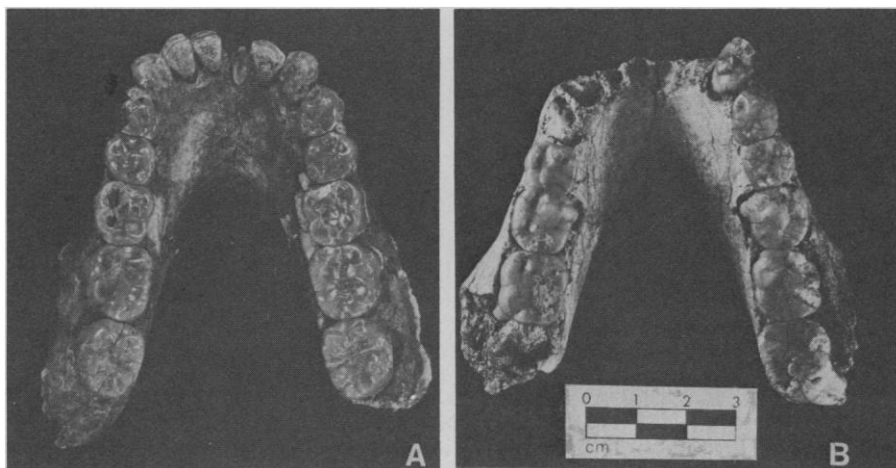


Fig. 4. Occlusal views of the mandibles from (A) Hadar (A.L. 400-1a) and (B) Laetolil (L.H.-4). Note the similarities in dentition, dental arcade shape, and mandibular morphology.

ance to the ilium. These and additional postcranial features will be elucidated by biomechanical and anatomical studies (30).

In summary, the Hadar and Laetolil remains seem to represent a distinctive early hominid form characterized by substantial sexual dimorphism and a host of primitive dental and cranial characteristics. We interpret this material as representing a single hominid lineage (31). An alternative interpretation would be that some smaller individuals, particularly the partial "Lucy" skeleton, represent a distinct lineage contemporary with the majority of the Hadar and Laetolil fossil hominids (32, 33). For the reasons discussed above, we consider that the available evidence cannot be used to convincingly argue for the presence of two distinct hominid species at either site. The Hadar and Laetolil hominids are most parsimoniously interpreted as representing one sexually dimorphic hominid taxon.

Phylogenetic Considerations

The overview of the Laetolil and Hadar remains presented above indicates that these forms represent the most primitive group of demonstrable hominids yet recovered from the fossil record. Although clearly hominid in their dentition, mandibles, cranium, and postcranium, these forms retain hints of a still poorly known Miocene ancestor.

The Laetolil and Hadar fossil hominids are important primarily because of their bearing on questions of early hominid phylogeny. They allow a perception of human evolution that was hitherto impossible. However, before we deal specifically with hominid phylogeny, it is necessary to view hominoid evolution in broader perspective.

Miocene relations. The ancestry of the Laetolil and Hadar hominids is not well understood. It must lie within the Miocene hominoid radiation of Africa and Eurasia, and *Ramapithecus* is the candidate most often considered to fulfill this role (34). Pilbeam *et al.* (35) suggested that characters typical of extant Pongidae are not necessarily useful in understanding or classifying Miocene hominoid radiation. They proposed instead that the more advanced members of this radiation be divided into two families, the Dryopithecidae and the Ramapithecidae. We concur with the observation that *Ramapithecus* shares numerous adaptive similarities in its dental and gnathic composition with other Miocene

forms such as *Sivapithecus* and *Gigantopithecus*. Many of these features were once thought to be distinctive of the family Hominidae (36).

Some interpretations of the postcranial anatomy (37, 38) and biochemical affinities (39, 40) of modern humans and extant African apes suggest that the pongid-hominid divergence was late in time. Some paleontologists, anatomists, and biochemists, however, place the divergence earlier—in the middle Miocene or even the Oligocene (34, 41, 42). Of course, genetic divergence (lineage separation) does not necessarily coincide with morphological divergence. The lack of a consistent definition of *Ramapi-*

thecus and its detailed similarity to other Miocene hominoid genera combine with the primitive appearance of the Laetolil and Hadar material to suggest that a late divergence must remain a possibility. Ultimate resolution of the question will come only with the collection and analysis of further hominoid remains dating between 5 and 15 million years ago. Critical to this resolution will be the recovery of specimens representing lineages of the extant pongids.

Plio-Pleistocene relations. Bipedalism appears to have been the dominant form of terrestrial locomotion employed by the Hadar and the Laetolil hominids. Morphological features associated with this locomotor mode are clearly manifested in these hominids, and for this reason the Laetolil and Hadar hominoid remains are unequivocally assigned to the family Hominidae. Representing, as they do, the earliest well-known hominids, what are their relationships with previously discovered Plio-Pleistocene hominids dating later in time? Our interpretations of hominid phylogeny during this period are given in Fig. 7, which indicates some of the more important sites and specimens along with their chronological placement.

The interpretation of hominid phylogeny presented in Fig. 7 relies heavily on the remains recovered since 1960 in eastern Africa. To fully appreciate this new resolution of early hominid phylogeny, it is necessary to consider the historical framework of fossil hominid discoveries. This is particularly true because the recent discoveries from eastern Africa have usually been interpreted in terms of a framework formulated on the basis of the South African discoveries.

South African discoveries. The description and naming of the Taung skull from South Africa as the holotype of *Australopithecus africanus* by Dart in 1925 (43) represented a milestone in human evolutionary studies. Until the discovery of the Olduvai Hominid 5 (O.H. 5) cranium in 1959 (44), Plio-Pleistocene hominids from the South African cave breccias at Taung, Sterkfontein, Makapansgat, Kromdraai, and Swartkrans dominated thinking on the earlier phases of human evolution. The distinctive character of the Kromdraai find led Broom, in 1938 (45), to propose a different type of hominid, which he called *Paranthropus robustus*. Additional discoveries at Swartkrans reinforced Broom's recognition of a distinct, robust hominid lineage. However, hints of a second hominid type in the deposit at Swartkrans prompted Broom and Robin-

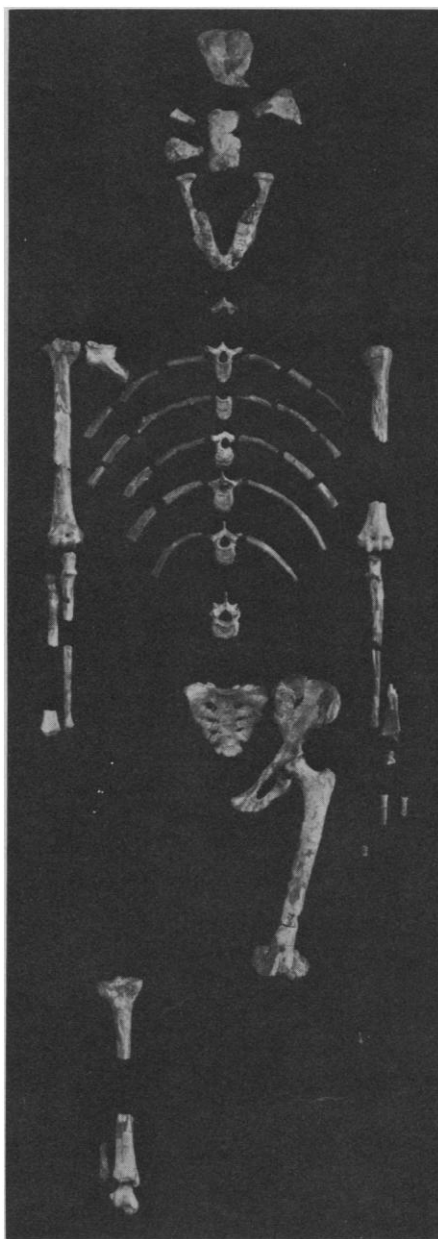


Fig. 5. Partial skeleton of "Lucy" (A.L. 288-1). This specimen is the most complete Pliocene hominid thus far discovered. The total length of the femur is 28 cm.



Fig. 6. Comparison of large (A.L. 333-4) and small (A.L. 129-1a) distal femora from Hadar. Note the size difference but morphological identity.

son in 1949 (46) to name the species *Telanthropus capensis*, which they considered to be ancestral to later forms of humans. Differences between fossil hominids from Taung, the Sterkfontein Type Site, and Makapansgat (collectively known as gracile australopithecines) and those from Kromdraai and Swartkrans (collectively known as robust australopithecines, with the exception of *Telanthropus*) were detailed by Broom (47) and Robinson (6, 48). Doubts concerning the dating of these hominids have obscured their phylogenetic relationships, and some authors have suggested that the gracile and robust hominids represent nothing more than large and small forms of the same hominid species (49).

East African discoveries. The 1959 discovery of a very large and robust cranium at Olduvai Gorge demonstrated the presence of the robust hominid form in East Africa and focused attention on this part of the world. Soon thereafter, a smaller-toothed and apparently larger-brained hominid (O.H. 7) was recovered from equivalent levels and named *Homo habilis* (50). Debate concerning the differences between *H. habilis* and the gracile australopithecines from South Africa ensued (51). The debate illustrates the difficulties encountered when interpreting the East African collections in a framework devised for the South African fossil hominids. While taxonomic considerations received paramount attention, phylogenetic aspects tended to be obscured. More recently, Brace (52) and Wolpoff (53) have claimed that only one lineage of Plio-Pleistocene hominid could be demonstrated in southern or eastern Africa at any point in the past.

In 1975, fieldwork at Koobi Fora in northern Kenya resulted in the demonstration of contemporaneity between

KNM-ER 3733, an unequivocal *Homo erectus* cranium, and KNM-ER 406, an obvious robust australopithecine (54). This was dramatic confirmation of earlier interpretations that had suggested the existence of two distinct hominid lineages in the African early Pleistocene. One lineage, commonly referred to as robust australopithecine, is represented by specimens exhibiting craniofacial and dental features that apparently reflect an adaptation involving a very heavily masticated diet (55). Members of this lineage have been recovered from both eastern and southern African deposits. Important derived characteristics that differentiate more evolved members of

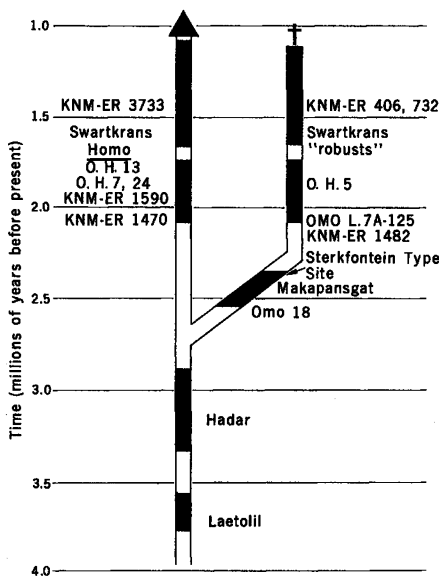


Fig. 7. Hominid phylogeny in the Pliocene and early Pleistocene based on the available fossil record. Some of the more important fossil samples and specimens are shown in their approximate chronological positions. The dark portions indicate periods from which hominid fossils are well known.

this lineage have been recognized by numerous authors (6, 46-48, 56, 57). These include extremely molarized deciduous and adult premolars, a relatively expanded postcanine dentition, and development of mandibular and cranial features related to a large masticatory apparatus. The latter are seen especially well in such specimens as O.H. 5 and KNM-ER 406, which have large, anteriorly placed zygomatics, large temporal fossae, and anteriorly placed sagittal crests. The mandibles have broad, deep rami and heavy buttressing of the corpus. Most if not all of these anatomical specializations are related to a craniofacial adaptation that maximizes vertical occlusal force and spreads this force across an enlarged postcanine dentition (58). This lineage displays no substantial tendency to expand cranial capacity.

Members of the second lineage are characterized by a contrasting suite of dental and cranial features and have been referred to the genus *Homo*. This lineage lacks the specializations related to a heavily masticated diet, but exhibits a definite tendency toward expansion of the brain. Among hominid populations comprising this second lineage there were undoubtedly substantial ranges of variation in cranial capacity, and to sort single specimens into either lineage solely on the basis of this criterion could be misleading. Mandibles, dentitions, and other cranial characteristics, aside from overall cranial capacity, serve to distinguish this from the other, more specialized lineage. Ultimately, the tendencies for brain expansion and gracilization of the masticatory apparatus characteristic of the earliest portions of this lineage culminated in the species *Homo sapiens* (59-61). Some investigators (1, 32, 33, 62) have alluded to the existence of a third lineage in eastern Africa between 1 and 2 million years ago. The evidence for this third species, usually regarded as northern gracile *Australopithecus*, consists of three or four fragmentary crania. The morphology and dimensions of these specimens suggest to us that they are better considered as representatives of a variable, sexually dimorphic *Homo* lineage sampled through time.

Gracile australopithecine affinities. With the demonstration of two evolving lineages in the early Pleistocene (1.5 million years ago) of eastern Africa, it is necessary to reassess the phylogenetic affinities of the South African fossil hominids. Many students of early hominid evolution consider the gracile australopithecines to most closely approximate the ancestral hominid stock (56). Both

robust australopithecines and the earliest representatives of the genus *Homo* are thought to have arisen either from the gracile species represented at Taung, the Sterkfontein Type Site, and Makapansgat or from a closely related form. Before the recovery and analysis of the Pliocene fossils from Hadar and Laetolil, such an evolutionary model best fit the available evidence. We presently enjoy a unique perspective afforded by the Hadar and Laetolil material. Study of these new fossils has prompted us to reexamine earlier hypotheses concerning affinities of the South African gracile australopithecines.

Of primary consideration in the phylogenetic interpretation of the South African gracile australopithecines is their chronological placement. The South African cave breccias have not been radiometrically dated. Consideration of the fauna from these sites relative to dated fauna in eastern Africa leads to the placement indicated in Fig. 7 (63, 64). It should be noted that faunal data place the Sterkfontein Type Site and Makapansgat deposits earlier than Bed I Olduvai, and postdating the Hadar and Laetolil remains. The third site yielding a gracile australopithecine, in fact the holotype of *A. africanus* (43), is Taung. Despite the recent claims of Partridge (65) and Butzer (66), Taung must be considered undated (67).

It is significant that some of the gracile australopithecine specimens from Makapansgat have been considered robust by various workers (68, 69). Even 48 years after its description, the Taung specimen was hypothesized to represent a late surviving *A. robustus* (70). Many workers have pointed out the similarities between gracile and robust australopithecines from South Africa in dietary adaptation (53, 56, 69) as well as locomotion (60, 61). Others have consistently maintained a generic distinction between the forms (6, 48, 71). Our own examination of the relevant fossils suggests an alternative to these opposing interpretations.

Detailed morphological analysis of the gracile australopithecine sample from South Africa indicates an evolutionary status consistent with its relative chronological placement. The sample differs from the Hadar and Laetolil material in the direction of robust australopithecines. The South African gracile australopithecine group lacks elements in the suite of primitive characteristics described above for the Hadar and Laetolil hominids. It seems to share several distinctive, derived characters with later robust australopithecines. These in-

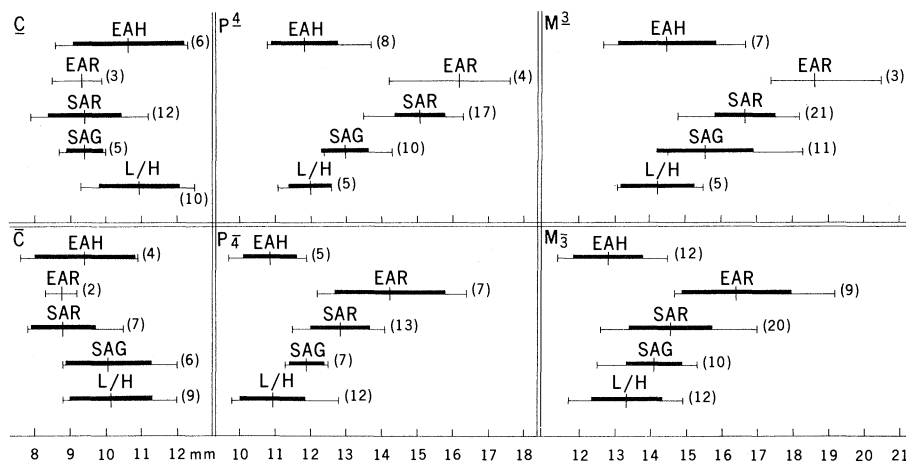
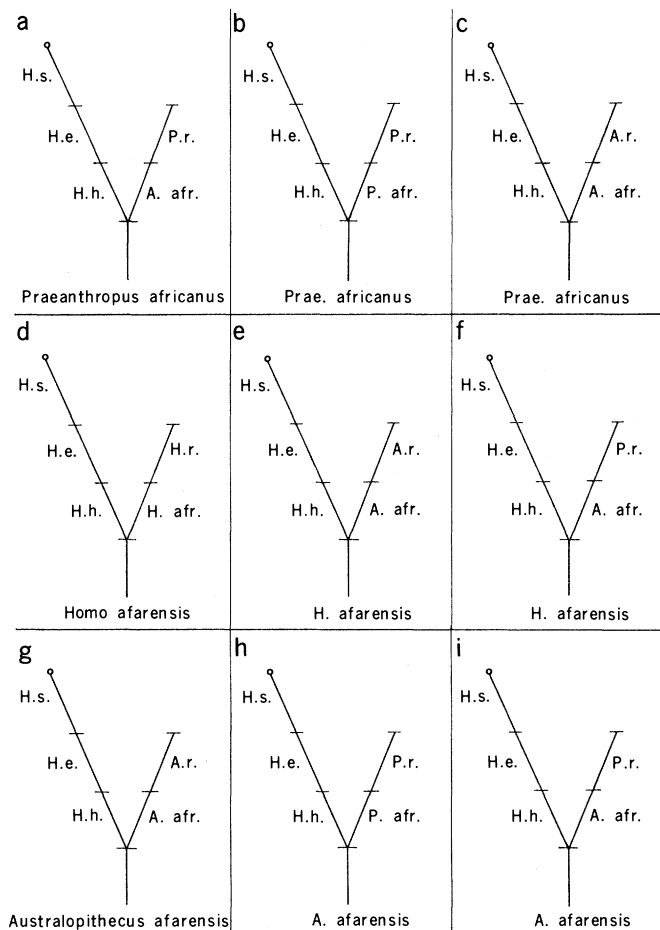


Fig. 8. Buccolingual tooth crown dimensions for the fossil hominids discussed in the text. The observed sample ranges are indicated by light horizontal lines, the arithmetic means by light vertical lines, and 1 standard deviation from the mean by darker horizontal bars. The number of specimens is shown in parentheses. Mesiodistal crown lengths and crown areas show the same tendencies, but buccolingual dimensions are used in this graphic treatment because they are not affected by interproximal attrition during the life of an individual. Only tooth crowns that are complete or that can be estimated within 0.2 mm are included. All specimens were measured and assigned to a sample set by one of the authors. Abbreviations: L/H, Laetolil and Hadar; SAG, South African gracile (Taung, Makapansgat, Sterkfontein Type Site); SAR, South African robust (Kromdraai, Swartkrans non-*Homo*); EAH, East African robust (Olduvai Beds I and II, East Turkana Lower and Upper Members, Natron, Chesowanja); and EAH, East African *Homo* (Olduvai Beds I and II, East Turkana Lower and Upper Members). Note the relative placement of the gracile australopithecine sample between the earlier Laetolil and Hadar sample and the later robust australopithecines of South Africa. Only C, P4, and M3 are displayed graphically, but the mesiodistal and buccolingual means of the SAG sample are intermediate between the means for the L/H and SAR samples for every postcanine tooth, upper and lower (except the P3 buccolingual dimension, which is larger in SAG than in SAR). These diagrams lend graphic support to morphological considerations described in the text. They are presented merely as supplementary evidence for the arguments presented there.

Fig. 9. Alternative taxonomic schemes available for representing Plio-Pleistocene human evolution. Abbreviations: H., *Homo*; A., *Australopithecus*; Prae., *Praeanthropus*; P., *Paranthropus*; s., *sapiens*; e., *erectus*; h., *habilis*; r., *robustus*; and afr., *africanus*. *Australopithecus boisei* is considered conspecific with *A. robustus*.



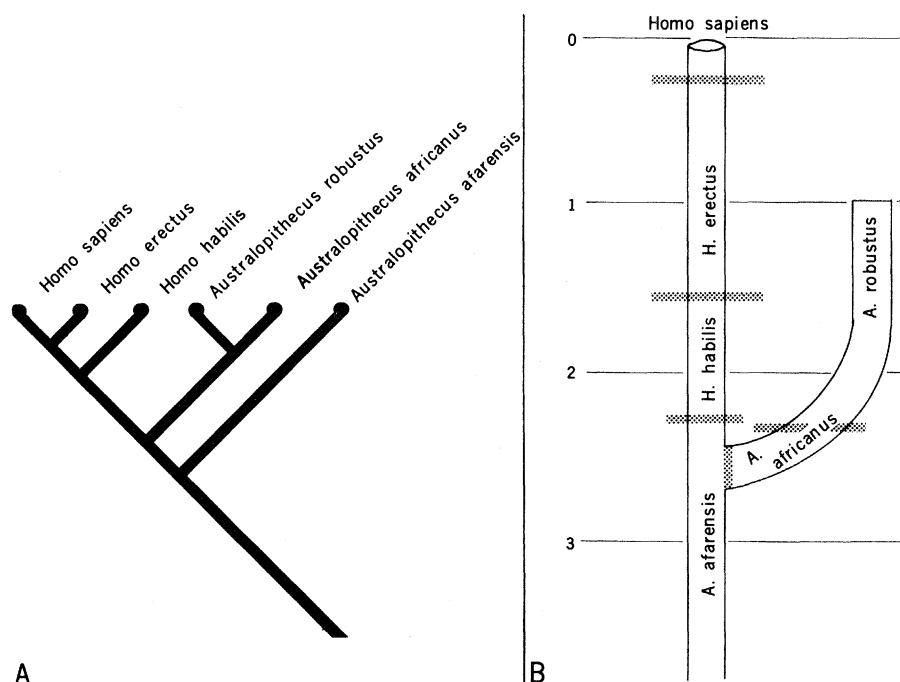


Fig. 10. (A) Cladogram of the family Hominidae. (B) Phylogenetic tree of the family Hominidae. See text for a discussion of the views represented by these diagrams.

clude stronger molarization of the premolars, increased relative size of the postcanine dentition, increased buttressing of the mandibular corpus in the symphyseal region, and increased robustness of the corpus itself. Dental metrics reinforce the hypothesis that the Sterkfontein Type Site and Makapansgat gracile australopithecines represent a link between the basal, undifferentiated hominids at Hadar and Laetolil and the later robust australopithecines (Fig. 8).

Of course, morphological and metrical comparisons should not be expected to unerringly place every single individual along an evolving lineage. Our interpretation of the South African gracile australopithecines is based on a consideration of the available sample characteristics for the fossil hominids. We are fully aware that individual traits and even single specimens can be matched in samples that we consider to represent different evolutionary entities and ultimately taxa. For example, the matching of individual specimens and demonstration of overlap between the samples from Sterkfontein and Swartkrans serve to point out the general similarities of these groups, but at the same time conceal real and biologically meaningful differences which we consider to have phylogenetic significance.

Likewise, it is possible to emphasize the similarities between the Laetolil and Hadar fossils and the gracile australopithecines from South Africa. To include the more archaic material from eastern Africa in an already established

gracile australopithecine phylogenetic or taxonomic category would obscure the evolutionary relationships and significance of the new material. We propose below a taxonomy consistent with these observations.

Taxonomic Considerations

The ultimate goal of human evolutionary studies is to understand phylogenetic relationships and adaptive patterns among the hominids. Such understanding has sometimes been hampered by an emphasis on naming the hominid specimens. We recognize the usefulness of classifying fossil materials, and we agree with Simpson (72) that "classification is not intended to be an adequate expression of phylogeny but only to be consistent with conclusions as to evolutionary affinities." The evolutionary affinities of the Hadar and Laetolil material are discussed above. Our interpretation of hominid phylogeny during the Pliocene and Pleistocene is presented in Fig. 7.

Taxonomic debate often stems from the inability of Linnean nomenclature to cope with an evolutionary progression of paleontological remains. This becomes particularly evident when the members of an evolving lineage are represented by a fairly complete fossil record. To us, this appears to be the case for Plio-Pleistocene hominids, and this situation is not unique among vertebrates (63, 73).

Several alternative taxonomic

schemes may be generated on the basis of our phylogenetic reconstruction (Fig. 7). A number of examples are shown in Fig. 9. Alternatives a to c would adopt generic distinction for the new material based on Şenyürek's study (74) of the original Garusi maxillary fragment recovered from Laetolil in 1939. He used the genus *Praeanthropus* of Henning (75) and the species name *africanus* suggested by Weinert (76), producing the binomen *Praeanthropus africanus*. Among other problems, adoption of such a distinction would imply that the Hadar and Laetolil fossil hominids were significantly different in their adaptation from later hominids. Our examination of the material suggests that such distinction is inconsistent with its observed phylogenetic and adaptive affinities.

A scheme that places the Laetolil and Hadar remains in the genus *Homo* (Fig. 9, d to f) will undoubtedly be favored by some. Such a scheme, as shown in Fig. 9d, follows Mayr's suggestion (49) that all hominid fossils be placed in species of the genus *Homo*. He later withdrew this suggestion (77), stating that "The extraordinary brain evolution between *Australopithecus* and *Homo* justifies the generic separation of the two taxa, no matter how similar they might be in many other morphological characters." We concur with this contention that the unique adaptive and evolutionary trends seen in the lineage leading to *H. sapiens* merit generic distinction. This trend is not yet evident in the Laetolil and Hadar hominids. For this reason, we favor the schemes shown in Fig. 9, g to i.

The alternatives shown in Fig. 9, h and i, would tend to obscure phylogenetic continuity by unnecessary generic splitting. The taxonomic scheme we consider most useful in expressing our phylogenetic findings is shown in Fig. 9g. We follow Mayr (49) in his perception of the genus *Homo* as being characterized by progressive brain enlargement associated with increasing cultural elaboration. The first species for which these trends can be discerned is *Homo habilis* (50).

The juvenile status of the Taung holotype specimen of *A. africanus* precludes its precise phylogenetic placement. We agree with the traditional and widely accepted approach in which the specimen is considered to be indistinguishable from the Sterkfontein Type Site fossils (4, 6, 22, 48, 49, 56, 57, 69, 78, 79). Since the latter sample is significantly less primitive than the Hadar and Laetolil material, a new species of the genus *Australopithecus* has been created (80). This most primitive *Australopithecus* species is *A. afarensis* and is based on the holo-

type specimen L.H.-4 as well as a series of paratypes from both Laetolil and Hadar. It obtains its name from the Afar region of Ethiopia, which has produced the most abundant evidence.

Discussion

We have presented the phylogenetic hypothesis that most parsimoniously accommodates the new fossil hominids from Laetolil and Hadar (Fig. 10). The recovery of the well-dated Hadar and Laetolil hominids extends our understanding of human origins well into the Pliocene. The implications of the new material for understanding the mode and tempo of hominid evolution are great. The apparent lack of morphological differences between fossils separated by at least 0.5 million years at Laetolil and Hadar suggests relative stasis in the earliest documented portions of hominid evolution. The dramatic morphological changes initiated between 2 and 3 million years ago suggest that this relative stasis was upset. Although the precise reasons for the phyletic divergence that led to *A. robustus* through the earlier, intermediate *A. africanus* are not well understood, a South African origin for this stock is plausible. Whatever the case, the clear niche divergence between *H. erectus* and *A. robustus* about 1.5 million years ago indicated by the eastern African fossil record indicates that an increased evolutionary rate for the period between 2 and 3 million years ago may ultimately be shown by larger fossil samples.

Another implication of the new fossil hominid material concerns sexual dimorphism. The extent of size and morphological variation in the Pliocene hominids from Hadar and Laetolil comes as no surprise, since later portions of the hominid fossil record also show greater sexual dimorphism than exists among modern humans (52, 81, 82). However, although the Laetolil and Hadar fossil hominids show marked body size dimorphism, the metric and morphological dimorphism of the canine teeth is not as pronounced as in most other extant, ground-dwelling primates. This implies a functional pattern different from that seen in other primates and may have significant behavioral implications.

In this article we have avoided placing emphasis on taxonomic problems inherent in paleontological material. Instead, we have tried to provide a phylogenetic framework for the early Hominidae that will allow anatomical, biomechanical, and behavioral studies of fossil humans to proceed constructively.

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24. The lack of a distinct P_3 metaconid in some Hadar specimens may be interpreted by some as taxonomically diagnostic. However, our own investigation of the variability in this feature in both extant and extinct hominoids suggests that the presence or absence of a P_3 metaconid has minimal phyletic valence.
25. Not enough of the A.L. 288-1 cranium is preserved to provide meaningful metric comparisons between it and the A.L. 333-45 specimen. However, differences in vault thickness, temporal line expression, and nuchal crest development are indicative of a degree of sexual dimorphism similar to that found in the common chimpanzee.
26. W. H. Kimbel of the Cleveland Museum of Natural History, together with the authors, is currently undertaking an in-depth study of the cranial remains from Hadar.
27. The variation in Hadar and Laetolil adult mandible height and breadth measurements at the junction of M_1 and M_2 is large [$N = 12$, coefficient of variation (CV) for height = 11.40; CV for breadth = 11.19], but not excessive when compared to the variation observed in samples of modern *Homo sapiens* ($N = 20$; CV for height = 8.85; CV for breadth = 11.59). *Pan troglodytes* ($N = 21$; CV for height = 10.79; CV for breadth = 9.42), and *Gorilla gorilla* ($N = 22$; CV for height = 11.07; CV for breadth = 7.54). The high degree of variation in mandibular breadth among hominids reflects the relatively forward position of the corpus-ramus junction.
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Fission Power: An Evolutionary Strategy

Harold A. Feiveson, Frank von Hippel, Robert H. Williams

The spread of civilian nuclear power technology is being accompanied by the spread of the knowledge and material required for the production of nuclear weapons. Concern has focused especially on the plutonium fuel cycle—in the

power systems that might be more nuclear weapons "proliferation resistant" (1). Our purpose here is to explore the potential role of such alternative systems in the development of nuclear power in the United States and abroad.

Summary. Motivated by concerns about the difficulty of safeguarding the large flows of plutonium in a breeder reactor fuel cycle, we explore the resource and economic implications of a strategy in which there is no nuclear weapons-usable material in fresh reactor fuel. The strategy involves the deployment of already developed types of advanced converter reactors which, unlike the breeder, can be operated effectively on proliferation-resistant once-through fuel cycles. Advanced converter reactors could be much more uranium-efficient on once-through fuel cycles than current systems and therefore could compete economically with breeders up to very high uranium prices. If necessary, the uranium requirements of an advanced converter reactor system could be reduced much further with the recycling of isotopically denatured uranium, but any commitment to a closed fuel cycle would be unnecessary for many decades.

short term on efforts to commercialize nuclear fuel reprocessing for the recovery of plutonium and in the long term on the related efforts to commercialize the plutonium breeder reactor.

In response to these concerns the Carter Administration in 1977 called for a deferral of U.S. programs aimed at the commercialization of the plutonium fuel cycle, and initiated national and international studies of alternative nuclear

We do not pretend that the problem of nuclear proliferation can be solved simply by developing an alternative to the plutonium breeder. A large number of nations could develop a nuclear weapons capability outside their nuclear power programs (2). One cannot, therefore, expect a nonproliferation strategy to succeed if it does not grapple with the political and security incentives and disincentives for countries to acquire nucle-

ar weapons. More fundamentally, it is unlikely that in the long term, proliferation of nuclear weapons can be stopped while the nuclear weapons states continue to act as if nuclear weapons are politically useful things to have.

Nevertheless, we believe that proliferation resistance should be an important criterion guiding the choice of future nuclear power technologies, because some of these technologies, by providing nations access to weapons-usable material, can directly contribute to a process of "latent proliferation," whereby nations move inexorably closer to a weapons capability without having to declare or decide in advance their actual intentions (3). Reprocessing for recycling of plutonium is one of these technologies, since it involves the recovery of a nuclear weapons-usable material from "spent" reactor fuel and its subsequent processing and redistribution in chemically separable form in fresh fuel (see Fig. 1).

We have discussed the relative proliferation resistance of different fuel cycles elsewhere (4-6). Here we present an analysis of the technical and economic viability of some of the systems that we have proposed as alternatives to the plutonium breeder. In particular, we explore the question of whether the proposed alternatives to the plutonium-fueled breeder reactor would allow the development of fission power on a large scale.

Our current nuclear power system does not assure the long-term future of nuclear energy. It is extremely wasteful of our limited resources of uranium in high-grade ore because it exploits only about one-half of 1 percent of the fission

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