

Paleobiology

..... *Current Happenings*

SHORT SURMISINGS OF RECENT WORK

Mailing Date: October 14, 1981

Paleobiology, 7(3), 1981, pp. 298-305

CURRENT ITEM 2.

Paleoanthropology: Pliocene and Pleistocene human evolution

By Eric Delson, *Anthropology, Lehman College (C.U.N.Y.), Bronx, N.Y., 10486 and Vertebrate Paleontology, American Museum of Natural History, New York, NY 10024*

Modern paleoanthropology is broadly interdisciplinary, integrating the results of studies in hominid (or more generally primate) paleontology, morphology and systematics with archeology, stratigraphy, chronometry, general paleontology, taphonomy and ecology, among other fields. (I here employ the term "hominid" to include all advanced hominoids of Miocene to Pleistocene age, following Delson and Andrews, 1975; similarly "hominine" (or "human") refers to members of the subfamily Homininae of this usage, especially *Australopithecus* and *Homo*.

Many other authors restrict hominine/human to *Homo* alone, employing hominid where I use hominine.) This integrative approach has been both spectacular and successful in eastern Africa (see Laporte 1980), due to the influence of F. C. Howell, the Leakeys and their colleagues, but it has also been responsible for recent advances in other temporal and spatial intervals in human evolution. In this review, I will concentrate on the morpho-evolutionary aspects of recent paleo-anthropological studies, indicating major sources and new developments. Most fossils not other-

wise referenced are discussed, albeit often with a different interpretation, in Wolpoff's (1980a) text.

The most spectacular finds of the past few years have been the new fossils of Pliocene early humans, *Australopithecus*, and their implications for later human evolution. Until the mid-1970's, the widely accepted view of this group was that later Pliocene *Australopithecus* evolved into the Pleistocene *Homo*. Two species of *Australopithecus* were generally recognized, the larger and more derived (away from *Homo*) *A. robustus* and the smaller, "gracile" *A. africanus* (see Delson 1978 and other papers in Jolly 1978 from a 1974 conference). Some authors recognized only one species (or lineage) in the Pliocene, others accepted the genus (or subgenus) *Paranthropus* for the robust group of one or more species, but almost all accepted the "graciles" as ancestral in the broad sense to later humans of the genus *Homo*, first known in deposits of possibly later Pliocene age but common only in the Pleistocene.

A major review of *Australopithecus* (and all other African fossil humans) is presented in Howell (1978). This work of monographic scope and length recognized three distinct species of robust australopithecids, in addition to *A. africanus* and *A. afarensis* (see below). Howell presented detailed diagnoses and descriptions of each of these taxa (and of later *Homo* species), as well as full lists of included specimens and excellent line-drawn cranial reconstructions of most. He argued that the Kromdraai type sample of *Australopithecus robustus* was as distinct from the Swartkrans population (usually considered identical) as each was from the larger East African *A. boisei*, while recognizing the essential unity of the robust group. This unity had been effectively denied by Campbell (e.g., 1978) who included the South African specimens as a subspecies of *A. africanus*, purely on temporal and distributional (not morphological) grounds; I still prefer a single robust species.

The Laetoli region yielded scattered fossils, including one battered hominine maxilla, in the 1930's and was long considered to be of "earlier Pleistocene" age, but intensive collecting by Mary Leakey was rewarded with a vast assemblage of fossil mammals, among them numerous human jaws and teeth, as well as a sequence of

now-famous animal trails, including hominine footprints all dated to about 3.7 Myr. About the same time, Don Johanson, Maurice Taieb, Yves Coppens and collaborators recovered fossils from the newly discovered (by Taieb) Hadar Formation in the Afar triangle (for an entertaining and informative, if somewhat engagingly muckracking, account of these finds and a history of Pliocene paleoanthropology, see Johanson and Edey 1981). Johanson and colleagues recovered a diverse faunal assemblage including many hominines, of which the prizes were the "Lucy" partial skeleton, consisting of a mandible and skull fragments, most of both forelimbs (but neither hand) one hindlimb (without foot) and part of the spine and ribcage, and an association of some 13 partial individuals known as the "First Family" (parts of several crania, numerous jaws and postcrania including hand and foot elements). The 150 m Hadar sequence at first was thought to be about 3 Myr old, but revised dates suggest a span from 4.2- \leq 3 Myr, with human remains from 4-3.2. The Hadar hominine remains seemed at first to represent two taxa, a larger *Homo* (as was originally thought to occur at Laetoli) and a smaller *Australopithecus* (including "Lucy"), with the possibility of a few robust specimens also.

Based on the detailed study of the combined Hadar and Laetoli samples, Johanson and Tim White (who had primary responsibility for description of the Laetoli hominines) came to a series of novel conclusions: 1) despite their apparent difference in age (now probably resolved) and the great range of metrical and morphological variability in the combined sample, the Hadar and Laetoli hominines represented only a single taxon; 2) this taxon was new, distinct from all known species of *Australopithecus* and *Homo*, but referable to the former genus as *A. afarensis*; 3) compared to both *A. afarensis* and modern apes, *A. africanus* presented derived traits shared with *A. robustus* but not with *Homo* species—thus *A. afarensis* might be in or near the ancestry of both *Homo* and later *Australopithecus*, but *A. africanus* was the sister-taxon of *A. robustus* and far from the *Homo* lineage (Johanson and White 1979). Needless to say, these conclusions were quickly attacked (or supported) individually and jointly by numerous

colleagues. The detailed publication of the Hadar fossils and their analytical comparison with other fossil hominines and modern hominoids is now in press, as are several rebuttals, but my own review is based on some study of these and other original remains and discussions with participants of all views.

It is now agreed that there was indeed much greater sexual dimorphism in early humans than in modern or Pleistocene fossil forms, but the Hadar range of size variation, if interpreted as dimorphism, is far greater—yet that is not unexpected if gorilla to chimpanzee-like dimorphism is accepted as the ancestral condition.

There is no clear pattern at Hadar of morphological differences linked to size: instead, large and small jaws and postcrania seem morphologically identical (except for allometric factors of shaft thickness and the like), while dental variation is independent of size. Nor is there a pattern of small front teeth in the same jaw as massive cheek teeth, which is the hallmark of *A. robustus*. Another argument of Johanson's is that the bipedalism documented by the Hadar postcrania (and the Laetoli footprints) preceded the increase in brain size characteristic of later humans. While it is true that the massive brain is a feature only of (mostly Pleistocene) *Homo*, there is a real question whether the brain of *afarensis* would have been comparable to or larger than that of a modern ape of similar mass ("Lucy" may have been only slightly over 1 m tall, with a mass of under 30 kg, the larger males perhaps up to 1.5 × as tall and over twice as heavy). I think that some relative brain expansion had already taken place, but thorough study of the partial endocrania must be awaited to know if the "encephalization level" of later *Australopithecus* had been reached.

Two strongly divergent alternatives to Johanson and White's conclusions have now been proposed. Phillip Tobias (1981) has published a major review of *A. afarensis* (without benefit of the new dates), in which he argues that the Hadar and Laetoli samples represent two distinct subspecies of *A. africanus* (the Sterkfontein plus Makapan sample is also recognized as distinct from the Tannu holotype). Tobias concluded that the diagnosis of *afarensis* does not clearly distinguish it from other *Australopithecus*, and after a detailed consideration of cranial

and dental morphology he found few significant differences from the South African sample of *africanus*, but roughly equal distinction among the three populations; unfortunately, he proposed a new subspecific name for the Hadar sample on the condition that it is distinct, which contravenes Article 15 of the International Code of Zoological Nomenclature, thus rendering his nomen *A. a. aethiopicus* unavailable. Phylogenetically, Tobias supported the widely held view that *A. africanus* may have been the common ancestor of robustus and *Homo*, rather than sharing derived conditions only with the former.

On the other hand, Olson (1981) presents a detailed analysis of the basicranial morphology of Pliocene to modern hominoids, finding that the large Hadar occiput shares derived characters with *Australopithecus robustus*, which he places in the genus *Paranthropus* (as opposed to *Homo*, which includes *A. africanus*). Olson's interpretation of manibibles and dentition from Hadar supports this view, leading to his proposal that two taxa are present: a large, robust *Paranthropus africanus* (holotype, the 1939 Gaurist (=Laetoli) maxilla of "Mganthropus africanus") and a smaller *Homo* species ("Lucy" and other small *A. africanus*-like specimens). These two clades are thought by Olson to have diverged earlier than 4 Myr.

My own view is that *A. afarensis* is probably a taxon distinct from but very similar to *A. africanus*. It is more conservative than any later hominines, and although it has been termed apc-like, it is in fact morphologically more similar to the Late Miocene "apes" than to modern forms. The most intriguing of Johanson and White's hypotheses, in my opinion, is that *A. afarensis* stands at or near the split between the *Homo* and later *Australopithecus* lineages. Olson has indicated cranial features which link *afarensis* to the robust group, while Tobias has shown that its overall morphology is quite *afarensis*-like; I consider that it is cranially distinct from both of these in several features, some of which seem to be conservative features shared also with *Homo* (see White, Johanson, and Kimbel 1981).

A problem often noted with Johanson and White's model of human phylogeny is the gap left in eastern Africa between *A. afarensis* older

than 3.2 Myr and the earliest *Homo* somewhat older than 2 Myr (see below). Some of this time may be filled, according to Howell (1978), by specimens tentatively referred to *A. africanus* from the Omo deposits (and perhaps even younger at Olduvai), but they have not yet been compared in detail to either *A. africanus* or *A. afarensis*. If a taxon like *A. africanus* is temporally and morphologically intermediate between *A. afarensis* and *Homo* in both eastern and southern Africa, it is likely to have been intermediate phylogenetically as well: cranial material of the eastern African form is urgently needed. At present, it seems that the relationships among *A. afarensis*,

A. africanus and *A. robustus* are by no means clear and may be more complex than proposed in any published scenario. The lack of clear associations (see below) of stone tools with any *Australopithecus* fossils leads me, among others, to suggest that these species were not habitual stone tool makers (although probably ad hoc users of stone and organic implements) nor active hunters, but perhaps collectors of vegetable foods and scavengers of small game. Some of these dietary questions may be resolved through detailed studies of food-wear scratches on fossil teeth now being conducted (with the aid of SEM technology) by Alan Walker (1981); preliminary results suggest that *Australopithecus* species concentrated on eating fruits of both tough and perhaps softer varieties.

Most recently, Owen Lovejoy has proposed (1981) that the early appearance of bipedal locomotion in humans was due to the selective advantage it gave to males who could thus procure food at a distance and carry it back to a home base occupied by females and young. Pair-bonding and increased male investment in both male and offspring would serve to increase survivorship despite the increase in all life periods which characterized hominoid evolution. Development of the strongly-knit human nuclear family, as well as of the distinctive human sexuality and secondary sexual morphology, are all tied together in this model, which has just been incisively (and critically) reviewed by Isaac (1981) and Hrdy (1981), from the viewpoints of archeology and primatology, respectively.

The earliest *Homo* is now usually assigned to *H. habilis*, based on material from Olduvai

Gorge complemented by fossils from East Turkana, Omo, and southern Africa (Howell 1978). This taxon is characterized by its enlarged brain, body size comparable to large *Australopithecus* and generally conservative dentition. Tobias (1980) has presented evidence that *Homo* displays a helioid pattern of dental wear, as compared to uniformly sloped wear in *Australopithecus*, but Ward (1981) has argued for a much wider distribution of helioid wear as a result of dental function and morphogenesis. This wear pattern, in part, has been used to document the presence of *Homo cf. habilis* in South Africa, including a newly recovered partial cranium from the upper level at Sterkfontein (see Tobias 1980) and several partial skulls and teeth from Swartkrans, contemporarily with *A. robustus*. The face of the Sterkfontein skull is rather *A. africanus*-like, but an associated occiput indicates a quite voluminous brain, comparable to some of the smaller specimens from East Turkana (Tobias and Hughes, personal communications 1981). However, some workers (especially Walker and Leakey 1978) consider many of these fossils to be late *Australopithecus* and question the validity of *Homo habilis*. All of the best specimens of

Homo habilis derive from 2.0–1.5 Myr old deposits, with only uncertainly referred scraps the same layers, in both eastern and southern sites; the oldest now seem to be from Hadar, in levels devoid of any hominids but dating around 2.5 Myr. These Oldowan tools are characteristically small sharp flakes (slicers?) and polyhedral core implements (choppers, pounders?) suggestive of both vegetable food preparation and hunting of small game, while rare butchery finds of larger mammals indicate scavenging activity.

Current estimates of the start of the Pleistocene center on 1.6 Myr ago, and this also seems to mark a major change in human evolution, with the first appearances of *Homo erectus* and the Acheulean culture complex. After the major activity of the 1930's and 1940's in China and Java, interest in this species waned somewhat, despite slow but steady recovery of fossils in Asia and Africa—it was simply eclipsed by fascination with *Australopithecus*. Now new fossils are combining with theoretical models to

produce a resurgence of study and interpretation of *H. erectus*. Several crania, including one described from Indonesia, a fine new skull (as yet unpublished) was recovered in Anhwei province (China) and several excellent skulls and other specimens from East Turkana and Olduvai are being analyzed (Howell 1978; Leakey et al. in prep.). Santa Luca (1980) has just published a complete restudy of the Solo (Ngandong) series of faceless crania which places them definitely as *Homo erectus*, rather than as archaic forms of *Homo sapiens* as some authors had argued. Howells (1980) has suggested that known *Homo erectus* specimens document an evolutionary pattern closer to punctuated equilibrium than to the gradualism long associated with human evolution. Rightmire (1981) has attempted to substantiate this view quantitatively, with some degree of success. On the other hand, Thorne and Wolpoff (1981) suggested that more local continuity and gradual evolution may have taken place in *Homo erectus*. It seems that the real question is whether the observed morphological variation in *erectus* fossils is under temporal control, so that all populations "advance" in relative synchrony (implying major gene flow), or if regions are isolated but show independent (parallel?) gradualism, or if factors of sexual and individual variability overshadow any time-related changes within this taxon; new approaches to this problem should prosper in the coming years. Culturally, *Homo erectus* worldwide is accompanied by variants of the Acheulean or "hand-axe" technocomplex, with flake tools and scrapers, hand-axes, cleavers and other bifaces varying in relative frequency. It appears that (as for the Oldovan), raw material composition is at least as important as local style in determining the composition of Acheulean toolkits. Although it was long thought that handaxes did not occur east of India, some Chinese sites yielded rare but typical bifaces and Okladnikov (1978) reported fine Acheulean hand-axes in association with flint-like raw materials. The overall interpretation of *Homo erectus*-like remains that of gathering combined with increased, group-cooperative (male?) hunting of large game in tropical and temperate climatic zones across Africa and southern Asia. No clearly *erectus* remains have been re-

covered in Europe (or in India, which must have been at least traversed), and archaeological occurrences are rare older than about 0.5 Myr. These suggest that *Homo erectus* or similar humans may have inhabited southern Europe sparsely and nomadically in the Early and early Middle Pleistocene. The oldest human remains from Europe are not well dated faunally, much less by chromometric methods but seem to be younger than 0.5 Myr, comparable in age to the earliest major continental glaciations. The most important specimens are the Mauer (Heidelberg) mandible, an occipital from Vertessollos (Hungary), a face and several mandibles from Arago (France) and, especially, a nearly complete skull from Petralona (Greece, see Stringer et al. 1979). Based on my own assessment of published faunal evidence and correlations with deep-sea cores and terrestrial terminology as utilized by European prehistorians, these finds probably date between 0.45 and 0.35 Myr (later "Mindelian"). As discussed by Stringer et al. (1979; see also Wolpoff 1980b), they appear to represent a population only slightly different from *Homo erectus*, but the distinctions (e.g., occipital form, relative vault and Penderocranial expansion, facial pneumatization) are all synapomorphic with later *Homo sapiens*, to which species they are referred. Based on the most recent Chinese studies (Woo Rutkang, pers. comm., 1980), the Choukoutien sample of *Homo erectus* is roughly contemporary with these finds, while African material of this age is poorly dated and/or studied. The origin of *Homo sapiens* from *Homo erectus* is still a matter of question; in fact, some paleoanthropologists question the validity of the latter as a "real" species, as distinct from *H. sapiens*. I suggest that the first appearance of relevant fossils in a previously little inhabited region indicates the possibility that marginal allopatric speciation may be important here—if some *erectus* population(s) were isolated in Europe as a result of glacial conditions and the survivors adapted to the new environment (or conceivably just were affected by genetic drift), perhaps the result is what we can call early *Homo sapiens* (*H. s. heidelbergensis*). At present, this is a nearly untestable scenario, but one which appeals to me more than does orthogenesis, polyphyly or ignorance of the problem.

In part due to the lack of well-preserved fossils elsewhere, paleoanthropologists have often concentrated on Europe in the study of *Homo sapiens* evolution as if it represented the source area for all moderns. The so-called Neanderthal problem, questioning the source and possible descendants of this mainly early Late Pleistocene Mediterranean group, is the archetypal example, so that numerous supposedly contemporary fossils have been termed local variants of Neanderthals and the possibility of their contributing to the ancestry of early Europeans has become a question of ancestry for all moderns (see Howells 1974 for review). New studies, especially those considering shared derived characters in forming hypotheses of relationship among populations of a broadly defined *Homo sapiens*, as well as some new fossils, have tipped the scales convincingly in this debate. The late Middle Pleistocene in Europe has yielded cranial remains such as those of Holsheim or early Rissian age (0.35–0.25 Myr old) from Bilingsteden and Steinheim in Germany and Swanscombe in England. Although the last of these was once thought to relate to moderns rather than to Neanderthals, all three are now seen to show Neanderthal derived characters and to form a continuum with Late Pleistocene intermediates as Biache and La Chaise (age circa 0.15 Myr) [Note that on such an infra-subspecific scale, "intermediary" may have a real meaning even in an otherwise punctuational framework.] The clearest presentations of this view are by Santa Luca (1978), Hublin (1981) and Stringer (1981); Wolpoff (1980b) provides a general review of most of these specimens with a consideration of sexual dimorphism but less clear phyletic reasoning. As Hublin suggests, it is necessary to reject the "Eurocentrism" of past work and consider as on the Neanderthal lineage any fossils demonstrating derived Neanderthal morphology (as do all those of post-Mindelian age in Europe).

The later Neanderthals have been most recently reviewed popularly by Trinkaus and Howells (1979; and see Wolpoff's 1980a text), who wondered about the origin of this group's adaptations. The more typical Neanderthals (as opposed to earlier "anteneanderthals") occur across Europe and the Near East from the Eemian to the mid-Wurmian (0.13–0.04 Myr), with the late western European specimens (the "classics") being the most derived in facial morphology. It has been suggested that the basic adaptation was to cold climate, but Trinkaus and Howells query this, arguing that if that were the case, why should the adaptations arise in the temperate Wurmian Near East. The answer may again lie with their ancestry: the Neanderthal morphology became fixed during the cold Rissian, with Biache and La Chaise specimens showing it in essentially Wurmian form, and it persisted in later temperate regions and times, while becoming more derived under the harsher West European glacial conditions. Less is known about the later Middle and early Late Pleistocene human fossils of Africa and Asia. In China, several fragmentary specimens have been recovered recently, but the nearly complete Dali cranium (Wu 1981) is the most important, as it seems to show some conservative links to Chinese *Homo erectus*, along with derived features reminiscent of modern eastern Asians. It is the best evidence I know for the now usually discounted concept of locally continuous evolution from *H. erectus* to modern peoples (see also Thorne and Wolpoff 1981). In Africa, the Rhodesian or Kabwe skull (Zambia) and that from Saldanha (South Africa; see Howell 1978) are now complemented in the east by the crania from Bodo (Ethiopia; see Conroy 1980) and perhaps Ndutu (Tanzania). These specimens have been considered by Stringer et al. (1979) as comparable in grade to the Petralona skull, but they could also be seen as a parallel, cohesive unit on a separate lineage. Although some were considered archaic and young, recent evidence suggests an age range between 0.4 and 0.2 Myr, and I note an apparent development of a rounder vault than in the relatively elongate Neanderthal skulls, suggesting possible links to the earliest modern humans. Africa has not been the usual postulated source area for early moderns, but in fact the three oldest potential candidates are from this region. The uppermost or Kibish Formation of the Omo Group (Ethiopia) has yielded two partial and incompletely studied skulls, one more like the Rhodesian group, the second more modern; a skull from the Ngoloba Beds, stratigraph-

ically above Laetoli, is comparable to these (Day et al. 1980). All these specimens may be 0.125–0.1 Myr old. Even more intriguing is the Border Cave sample from South Africa. Rightmire's (1979) analysis of the most complete cranium indicated clearly: modern African ("Bushman-Hottentot") affinities, while Beaumont et al. (1979) reported that the skull is associated with a Late Paleolithic toolkit and may be at least 90,000 yr old. The implication of these findings is that by about 0.1 Myr ago, the modern African stock(s) may have separated from those of Eurasia, already linked to the type of tools found almost exclusively in association with humans of modern morphology. While the antenanderthals (and Rhodesians) are generally found in association with developed Acheulean tools, often presenting an advanced prepared-core form of technique, the Neanderthals and most contemporaries manufactured Middle Paleolithic flake-based hunting tools. The Late Paleolithic, occurring in Europe only after 35,000 yr ago, is characterized by apparently more efficient means of flake detachment and more "specialized" tool forms. Although some early Near Eastern "moderns" have been found with Middle Paleolithic tools, until recently only moderns were recovered with the Late Paleolithic, which lends greater weight to the Border Cave find. Most recently, however, a well-preserved partial skull was found at Saint-Césaire (France) in an earliest Late Paleolithic layer (Laveque and Vandermeersch 1981); there is little doubt that it represents a "classic" Neanderthal! How much the Neanderthals contributed to the gene pool of early modern Europeans is still very much a moot point.

This sampler of current paleoanthropology reveals the same pattern of new phrasing of old questions and new applications of alternative approaches which characterizes other aspects of paleontology. In that the subject is our own history, paleoanthropology may have a greater fascination than study of forams or turtles, but it is equally able to incorporate or produce new methods and philosophies. The gradualist vs. punctationalist controversy, for example, is now receiving due attention in most discussions of human evolution. Especially in this day of a Creationist resurgence, paleoanthropology needs to refresh its links to paleontology and evolutionary theory as a two-way street.

(NOTE ADDED IN PROOF.) As if to reinforce the view that human evolution is an active discipline, a number of important new publications have appeared in the few months since manuscript submission. Reference to some has been inserted where possible, but three deserve more comment. The results of two broad symposia, parts of which are cited before were published as "The Emergence of Man" (Phil. Trans., Roy. Soc. London, ser. B, vol. 292, 1981) and *Aspects of Human Evolution* (see Olsson reference). Of special interest is a review article "Tempo and mode in human evolution", by J. E. Cronin, N. T. Boaz, C. B. Stringer and Y. Rak (Nature, 292: 113–122). Cronin et al. recognize essentially the same taxa as I do here and argue that the presence of specimens "intermediate" in morphology between pairs of successive taxa (excluding robust *Australopithecus*), combined with apparently "continuous" trend to increase of brain size and body weight in these taxa suggest that human evolution was characterized by "gradual change with periods of varying rates of evolution". This was contrasted to a model of relative stasis interrupted by rapid evolution and speciation (punctuated equilibrium), which I prefer, at least for the pre-*Homo sapiens* phase of human evolution. Many of the points made by Cronin et al., including some of their age assessments (which affect estimates of evolutionary rate and species overlap) are open to question, and this article should be the focus of some debate this year.

Acknowledgments

Preparation of this report was aided by research grants from the National Science Foundation (BNS 79-15091) and the C. U. N. Y. PSC-BHE Program (12188 and 13453). Drs. Ian M. Tattersall, Noel Boaz, Chris Stringer, and Erik Trinkaus offered helpful suggestions on the manuscript.

Literature Cited

BEAUMONT, P. B., H. DE VILLIERS, AND J. C. VOGLT. 1978. Modern man in sub-Saharan Africa prior to 49,000 years B.P.: a review and evaluation, with particular reference to Border Cave. South African J. Sci. 74:409–419.

CAMPBELL, B. G. 1978. Some problems in hominid classification and nomenclature. Pp. 567–581. In Jolly, C. J., ed. Early Hominids of Africa. Duckworth, London.

COSGROVE, G. C. 1980. New evidence of Middle Pleistocene hom-

inds from the Aar desert—Ethiopia. Anthropos (Athens) 7:96–107.

DAY, M. H., M. D. LEAKEY, AND C. MCGOBB. 1980. A new hominid fossil skull (L. H. 181 from the Ndolola Beds, Laetoli, northern Tanzania. Nature, 284:55–57.

DETRON, E. 1978. Models of early hominid phylogeny. Pp. 517–541. In Jolly, C. J., ed. Early Hominids of Africa. Duckworth, London.

HOWELL, F. C. 1978. Hominidae. Pp. 184–248. In Maglio, V. J. and H. B. S. Cooke, eds. Evolution of African Mammals. Harvard Univ. Press, Cambridge, Mass.

HOWELL, W. W. 1974. Neanderthal names, hypotheses and stratigraphic method. Am. Anthropologist 76:24–38.

HOWELL, W. W. 1980. Homo erectus: who, when and where. Yearbook Phys. Anthropol. 23:1–23.

HUGHES, J. J. 1981. Que retenir des présumés eurogènes? Table ronde sur l'anthropogénèse et l'orthogénèse, Paris.

HUXY, S. B. AND W. BENNETT. 1981. Lucy's husband: what did he stand for? Harvard Mag. 1981 July-August:7–9, 46.

ISAAC, G. I. J. 1981. The early development of protohuman social-cultural behavior. Quart. Rev. Archaeology, 2:1–4.

JOHANSSON, D. C. AND M. ELEY. 1981. Lucy: The Beginnings of Mankind. Simon and Schuster, New York.

JOHANSSON, D. C. AND T. D. WHITE. 1979. A systematic assessment of early African hominids. Science 203:321–330.

LAVOURE, L. F. 1980. Human origins and the East African evidence. Paleobiology, 6:139–140.

LEAKEY, R. E. E., M. D. ROSE, AND A. C. WALKER. In prep. New *Homo erectus* specimens from East Turkana, Kenya.

LEVY, E. F. AND B. VANDERMEERSCH. 1981. Le néanderthalien de Saint-Césaire. La Recherche 12:242–244.

LOVJOY, C. O. 1981. The origin of man. Science 217:341–350.

OLSON, A. P. 1978. The Paleolithics of Mongolia. Pp. 317–325. In Haeve-Smith, E., ed. Early Paleolith in South and East Asia. Mouton, The Hague.

OLSON, T. R. 1981. Basistral morphology of the extant hominids and Pliocene hominids: the new material from the Hadar Formation, Ethiopia, and its significance in early human evolution and taxonomy. Pp. 99–128. In Stringer, C. B., ed. Aspects of human evolution. London: Taylor and Francis.

RIGHTMIRE, G. P. 1979. Implications of Border Cave skeletal remains for later Pleistocene human evolution. Curr. Anthropol. 20:23–36.

RIGHTMIRE, G. P. 1981. Patterns in the evolution of *Homo erectus*. Paleobiology, 7:241–246.

SANTIA LUCIA, A. P. 1978. A re-examination of presumed Neanderthal-like fossils. J. Human Evol. 7:619–636.

SANTIA LUCIA, A. P. 1980. The Neander. Fossil Hominids. Yale Univ. Press in Anthropology, 28:1–175. Yale Univ. Press, New Haven, Conn.

STRINGER, C. B. 1981. The dating of European middle Pleistocene hominids and the existence of *Homo erectus* in Europe. Anthropologie (Brno) 19:1–14.

STRINGER, C. B., F. C. HOWELL, AND J. K. MERTENS. 1979. The significance of the fossil hominid skull from Petralona, Greece. J. Archaeol. Sci. 6:235–253.

TROSKER, A. G., AND M. H. WOLPOFF. 1981. Regional continuity in Australasian Pleistocene hominid evolution. Amer. J. Physical Anthropology, 55:347–349.

TOBIAS, P. V. 1980. The natural history of the petrolonid occlusal plane and its evolution in early *Homo*. Am. J. Phys. Anthropol. 53:173–188.

TOBIAS, P. V. 1981. "Australopithecus africanus" and *A. africanus*: critique and an alternative hypothesis. Paleontologica africana 24:1–17 (6or 1980).

TRINKAUS, E. AND W. W. HOWELL. 1979. The Neanderthals. Sci. Am. 241:118–124.

WALKER, A. C. 1981. Dietary hypotheses and human evolution. Phil. Trans. Roy. Soc. London, Ser. B, 302:57–64.

WALKER, A. C. AND R. E. LEAKEY. 1978. The hominids of East Turkana. Sci. Am. 238:54–66.

WARR, S. C. 1981. The role of axial nodular angulation in mediating bifacial wear in Miocene apes, Pliocene hominids and *Homo*. Am. J. Phys. Anthropol. 54:288 (abstract, also paper presented April 1981).

WHITE, T. D., D. C. JOHANSSON, AND W. KIMMEL. 1981. *Australopithecus africanus*: its phyletic position reconsidered. South African J. Sci. In press.

WOLPOFF, M. H. 1980a. Paleoanthropology. Random House, New York.

WOLPOFF, M. H. 1980b. Cranial remains of Middle Pleistocene European hominids. J. Human Evol. 6:349–358.

WU, X.-Z. 1981. A well-preserved cranium of an archaic type of early *Homo sapiens* from Dali, China. Scientia Sinica, 24:530–539.