Species of Hominids

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Despite some claims to the contrary (e.g., Stanley 1981), paleoanthropological scenarios have tended to incorporate both anagenesis and cladogenesis, though in a "transformational" framework. After the initial focus on stasis and cladogenesis in the fossil record by Eldredge and Gould (1972), the seminal attempt to place hominid evolution in such a novel framework (Eldredge and Tattersall 1975) unfortunately appeared as an afterthought to a discussion of theoretical systematics.

In the last few years, however, there have been several major attempts by paleontologists to present hominid evolution in a punctuated equilibria framework (Gould and Eldredge 1977; Stanley 1979, 1981; Eldredge and Tattersall 1982). Punctuated equilibria is a theory about the tempo of morphological change; more specifically, it is a statement about the duration of a morphology relative to the origin of the morphology (Gould 1982a, b). A key assumption is that the emergence of a morphology is equivalent to the emergence of a species, and consequently that species (i.e., morphospecies) are formed very rapidly in relation to their longevity.
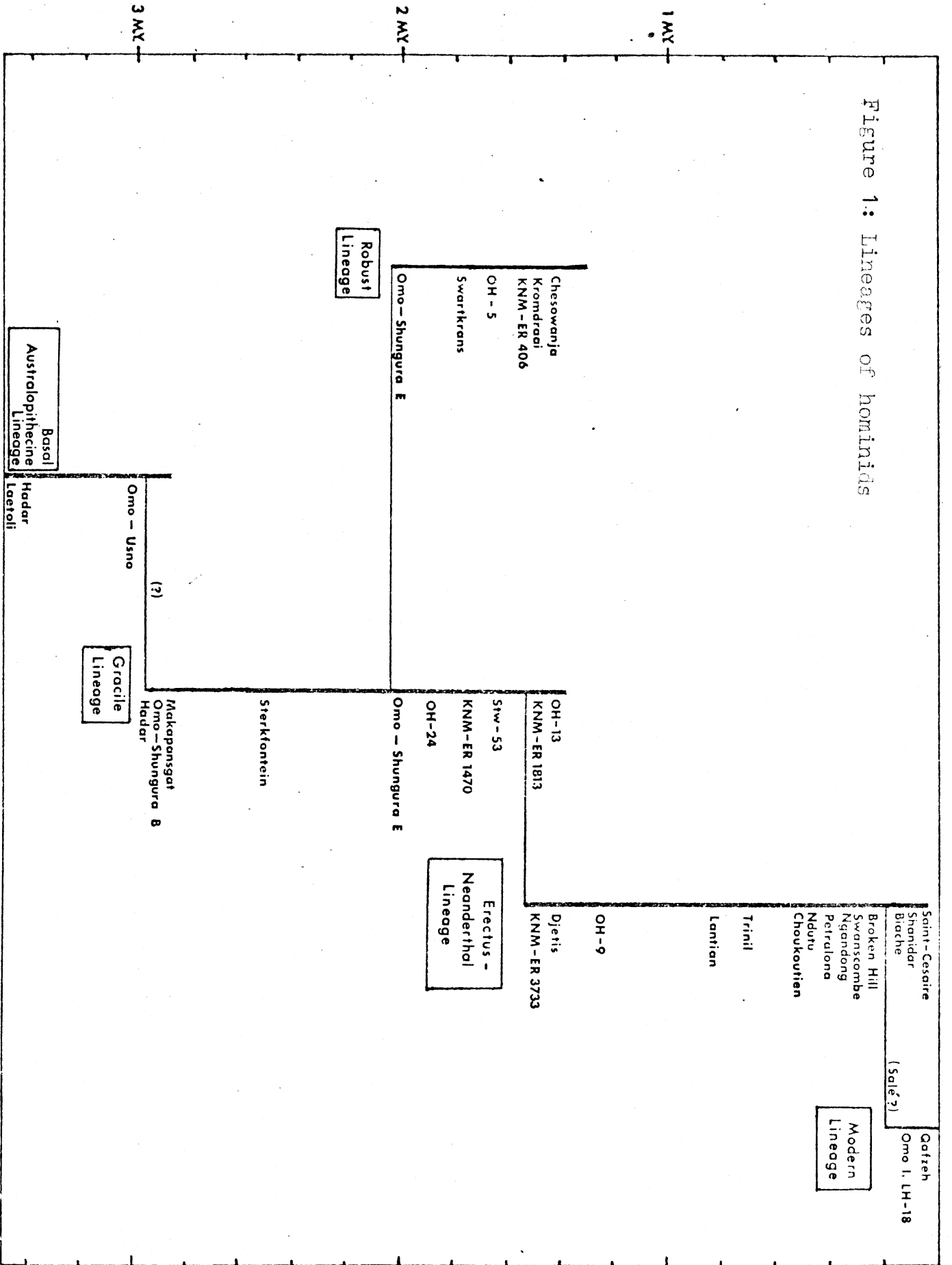
If species are the units of macroevolution, and if punctuated equilibria is put forward to describe the macroevolutionary tempo of a group of species, it is, therefore, of paramount importance that the species be clearly delineated and unambiguously defined. For if the species themselves are ambiguous, how can we make sensible statements about "speciation and its deployment in geological time" (Gould 1982a:84)? Obviously, we cannot, and the failure to recognize the severe limitations of hominid taxa has undermined the attempts to impose a punctuational framework upon paleoanthropology.

For example, a chart of the duration of hominid species by Stanley (1979:81) presents Homo habilis Leakey et al. 1964 as a lineage existing independently of Australopithecus africanus Dart 1925 ; and A. boisei (Leakey 1959) as a lineage existing independently of A. robustus (Broom 1938). But this seems less to demonstrate stasis within species than it does an uncritical acceptance of taxa in the literature of anthropological systematics.

If we wish to discuss tempo and mode in hominid evolution, a fundamental prerequisite is the delimitation of the fossil species on purely morphological grounds, in the absence of the social, political, academic, and economic biases which frequently affect paleoanthropology (Holden 1981). This aspect of the tempo-and-mode controversy has been overlooked by both the "gradualists" (Cronin et al. 1981) and "punctuationists". The purpose of this paper is to demonstrate that, given a temporal framework, the distribution of hominid morphologies through time reveals four persistent lineages over the last three million years, each presumably equivalent to Simpson's (1961) evolutionary species (Figure 1). Between lineages there are small but apparent discontinuities; however, within each lineage considerable microevolution and anagenesis,

Figure 1: Lineages of hominids

Robust Lineage

Chesowanja
Kromdraai
KNM-ER 406
OH-5
Swartkrans
Omo-Shungura E

Basal Australopithecine Lineage
Hadar
Laetoli

Omo-Usno

Gracile Lineage

(?)

Makapansgat
Omo-Shungura B
Hadar

Sterkfontein

Omo-Shungura E
OH-24
KNM-ER 1470
Stw-53
KNM-ER 1813
OH-13

Erectus - Neanderthal Lineage

Djetis
KNM-ER 3733
OH-9
Lantian
Trinil
Choukoutien
Nduru
Petralona
Ngandong
Swanscombe
Broken Hill
Biache
Shanidar
Saint-Cesaire

(Sale?)

Modern Lineage

Qafzeh
Omo I, LH-18

rather than stasis, are evident. Thus, punctuated equilibria is a necessary, but not sufficient, explanation for hominid evolutionary patterns: the general usage of the theory should be extended.

It is not my intention to give a thorough review of the hominid fossil record here; for that, the reader is referred to any good physical anthropology textbook. Further, I am exploring the pattern of evolution as revealed in the hominid fossil record; and patterns are frequently difficult to discern unless one stands back a bit from the data. Consequently, I shall make use of second-order phenomena in this paper (for example, using disagreements about the taxonomic status of specific fossils as data). The fact that given two fossils of equal completeness, taxonomic disagreements might exist over one fossil and not over the other, is a datum in itself.

Hominid Taxa

1. Basal Australopithecines

After the eight-million-year-old ramapithecids from the Siwalik Hills, Pakistan, the picture of the australopithecine transition becomes exceedingly blurry. Outside of a mandibular fragment from Lothagam, an arm fragment from Kanapoi (Patterson et al. 1970), a tooth from Lukeino (Pickford et al. 1975), and perhaps a facial bone from Chemeron (Bishop and Chapman 1970), the fossil record is silent until later than 4 MYA.

Tobias (1973) had predicted a basal australopithecine lineage (Australopithecus africanus) to have lived about 4 MYA, and this was subsequently fulfilled with the discovery of fossils from Ethiopia and Tanzania collectively referred to Australopithecus afarensis (Johanson et al. 1979). Although considerable taxonomic controversy has surrounded these fossils (Anonymous 1979; Johan-

son and White 1979b; Day et al. 1980b; Leakey and Walker 1980; Johanson and White 1980), the fossils themselves tell us of a bipedal, small-brained creature with large canines, a primitive tooth-row, and diastemata (Johanson and White 1979a). The mode of locomotion was apparently of a somewhat different nature than modern bipedalism (Jungers 1982; Stern and Susman 1983), but presumably the capacity for bipedalism is synapomorphous in A. afarensis and H. sapiens. The overall affinities of A. afarensis have been suggested as being closest to Ramapithecus (R. Leakey 1976); A. africanus (Tobias 1981); and A. robustus (Olson 1981).

Although the basal australopithecine deposits from Hadar, Ethiopia were originally dated to 3.0 MYA (Aronson et al. 1977), they are now considered to be 2.9-3.6 MYA (Walter and Aronson 1982). This makes the Hadar assemblage somewhat younger than the Laetoli fossils (3.49-3.76 MYA), and may throw into question the homogeneity of the A. afarensis sample (Day 1982; Brown 1982; Boaz et al. 1982). The primitive Laetoli fossils (M. Leakey et al. 1976; White 1977; 1980) certainly resemble some of the Hadar remains, yet there seems little reason to regard the Hadar fossils as a homogeneous assemblage (e.g., Behrensmeyer 1983).

That the Laetoli and part of the Hadar finds represent a species ancestral to later australopithecines can hardly be disputed (White et al. 1981). Tobias (1981), however, argues that the range of variation for A. africanus will encompass the A. afarensis collection, a point denied by Johanson and White (1979b). If we accept the inhomogeneity of the Hadar sample (Olson 1981) and take it to represent (with Laetoli and Omo-Usno; Howell 1978) A. afarensis and (with Makapansgat [Boaz et al. 1982]) A. africanus, much of the systematic ambiguity would probably vanish.

2. Gracile Australopithecines

Dating from about 3.0-1.4 MYA, there appears a collection of fossils still debated taxonomically, but broadly continuous in morphology, and probably representing a single evolutionary species.

Gracile australopithecines are dated from Tuff B of the Shungura formation in the Omo at 3.0 MYA (Curtis 1981). The South African australopithecines are slightly younger, but notorious in their inability to be securely dated. Most recent estimates, however, have the fossils from Makapansgat at nearly 3.0 MYA, and those from Sterkfontein about 2.5-3.0 MYA (Tobias 1981).

Slightly later, fossils attributed to Homo habilis appear in East Africa (L. Leakey et al. 1964). Olduvai hominid 24 is from Bed I, about 1.9 MYA, and East Turkana's KNM-ER 1470 is about 1.87 MYA (Gleadow 1980). The latter skull is variously identified as A. africanus or H. habilis, depending upon the author (e.g., Walker and Leakey 1978). Fragments of "early Homo" are also known from later deposits at Sterkfontein (Hughes and Tobias 1977). Two points are worth noting about this taxon, however: 1) nearly all specimens placed in H. habilis are either crushed, highly fragmentary, or immature; and 2) the signal difference between this and A. africanus is the larger cranial capacity in H. habilis, a holdover from the "cerebral Rubicon" days of paleoanthropology.

I do not wish to affirm or deny the validity of the taxon Homo habilis here, but merely to emphasize the strong morphological continuity of this with A. africanus. Thus, specimen ER-1813 from Lake Turkana is a relatively complete skull showing H. habilis-like dental-maxillary features, yet the small cranial capacity generally used to distin-guish the two genera. Consequently, identification of the skull tends to be confusing: Walker and Leakey (1978) call the skull australopithecine, Szalay and Delson (1979:511) call attention to both the Homo and Australopithecus affinities of the skull, and Wolpoff (1980:164) identifies the skull as a female H. habilis.

Finally, the fragmentary OH-13 from lower Bed II, Olduvai Gorge is a paratype for Homo habilis (L. Leakey et al. 1964). Nevertheless, it has been seen as similar to the very earliest dental fragments ("Telanthropus") from Swartkrans (Tobias and Von Koenigswald 1964). Similarly, the Homo habilis dentition has been likened to the Asian "Meganthropus" (Tobias and Von Koenigswald 1964), which others have called a robust australopithecine (Robinson 1955). This ambiguity, however, is most likely illusory, for the total morphological pattern of these hominids sets them readily into distinct lineages. The apparent ambiguity arises from the fact "that teeth and mandibles alone cannot be used to distinguish australopithecines and Homo erectus without associated cranial material, except at the extremes of the ranges" (Wolpoff 1980:189).

There is thus a continuity of form within the gracile lineage, and a small discontinuity of form between the gracile lineage and its antecedent and descendant taxa (cf. below). This has led Pilbeam (1975) to recognize "a period of relative stasis...from 3 to 1.5 million years" in this group.

3. Robust Lineage

The robust and gracile lineages are readily separable in terms of their total morphological patterns, with minor exceptions. The relatively late (1.6 MYA) demicranium KNM-ER 732 has been called a female robust

australopithecine by Walker and Leakey (1978) and Wolpoff (1980); although Day (1977) has seen it as a gracile. The problem is that the specimen possesses a large supra-mastoid crest, though little of it is present; yet it has no sagittal crest and only a single fragmentary tooth crown -- but these are the features generally used to identify robust australopithecines. Also perhaps insecure in its identification is the Taung child, because of its immaturity.

The earliest robust australopithecines seem to be present at about 2 MYA at the Omo (Curtis 1981). Again, the South African fossils are difficult to date, but faunal correlations suggest that the material from Kromdraai and Swartkrans are contemporaneous with the anatomically more extreme East African counterpart. Although the East and South African are usually classified as distinct at the species level, it is unlikely that such distinction corresponds to any significant biological reality -- the variation is quantitative and slight and can scarcely be considered more than ecotypic. One possible way of resolving this taxonomic problem is to view the lineage as a superspecies composed of semispecies (Tobias 1973; Delson et al. 1977; Delson 1978). But if we apply Simpson's (1961) definition of an evolutionary species ("a lineage evolving separately from others and with its own unitary evolutionary role and tendencies"), it seems unlikely that more than one role and tendency is represented here. It is therefore unlikely that specific discrimination within the robust australopithecines is warranted. A contrary view, however, is expressed by Grine (1981), who sees three species of robust australopithecines based solely upon enamel prism patterns of teeth. However, the mere discovery of between-group variation is not sufficient to establish the groups as good species -- especially when the variation is in a single character!

Thus, Stanley (1981:143), recognizing the incorrectness of seeing more than one distinct species of robust australopithecines (cf. Stanley 1979:81), incorporates them as a single lineage in his second punctuational scheme for the hominids.

Robust australopithecines are known from Chesowanja, about 1.4 MYA (Gowlett et al. 1981), and slightly later at East Turkana. Throughout their duration, they do not appear to demonstrate any anagenetic trends. On the other hand, consistent microevolutionary variation between the South and East African forms is apparent.

Erectus-Neanderthal Lineage

The onset of the Pleistocene coincides with the debut of Homo erectus (Dubois 1892) as pointed out by Delson (1981). These hominids, quite distinct from the australopithecines in skull morphology, nevertheless are broadly similar in many ways to the later Neanderthals. They are both characterized by a thick skull vault, pronounced post-orbital constriction and massive supra-orbital tori, skeletal robusticity, and a characteristic long, low skull with prominent occiput.

These derived characters (i.e. not found in australopithecines) are diagnostic of both Homo erectus and the Neanderthals and their collateral relatives might, with little danger of exaggeration, be considered as a "Homo erectus with an inflated brain" (Eldredge and Tattersall 1975). The minor shape changes which differentiate H. erectus from Neanderthals by criteria other than size may be accountable as 1) allometric effects resulting from the size changes, 2) anagenetic responses to natural selection, and 3) microevolutionary

divergence of populations. These features include maximum skull breadth and greater facial height in the Neanderthals. Such differences, however, are dwarfed by the constellation of cranial features shared by the two groups.

The systematic problems in dealing with this taxon may be related to the fact that the concept of lumping many groups of fossils into a single taxon of H. erectus, although informally proposed by Weidenreich (1940), suddenly gained popular and uncritical acceptance when proposed by Mayr (1951) -- a neontological ornithologist.

The earliest (and most complete) Homo erectus specimen is ER-3733 (1.5 MYA) from Lake Turkana, but the earliest fossils from Java are probably nearly as old (Howells 1980). Olduvai hominid 9 is from Upper Bed II, dating to about 1.2 MYA. An early H. erectus fossil from Lantien has been dated to 0.8-1.2 MYA (Jia Lanpo 1980). Later fossils from the Trinil Beds in Java, Choukoutien, and Lake Ndutu (Clark 1976; Howells 1980) all seem to fall about 0.4-0.6 MYA.

These fossils show between-group variation geographically (Coon 1962). However, the evolutionary patterns are a source of contention. Rightmire (1981) has claimed that there is statistically no anagenetic trend evident in skull size in Homo erectus. His treatment, however, is flawed in several respects. First, Rightmire regressed skull size on time — yet rather than enter each of the 24 points as data, he instead regressed merely the mean values for each time interval, reducing his analysis to 6 points. Thus, the Sale skull, as the only one at 0.2 MYA, is given weight equal to the 7 skulls at 0.6 MYA. Yet Wolpoff (1980:225) focusses on the rounded contour of the occiput as evidence that the skull is an early archaic H. sapiens.

Jaeger (1981) also points out the ambiguous nature of this specimen; yet it is late and very small and strongly biases Rightmire's statistical treatment. Another questionable inclusion is that of Holloway's (1973) low estimate of 727 cc for the late and very fragmentary OH-12. Indeed, this is the seventh Rightmire groups with the six from Choukoutien at 0.6 MYA, which range form 915-1225 cc. Yet even Holloway (1973) is unabashedly skeptical of the estimate of 727 cc for this specimen; and given that estimates for substantially more complete specimens may very by 10% (see Day 1977:63 for estimates of Steinheim), it is probably unwise to have let the conclusions of his statistical treatment be unduly biased by such fragmentary material. If the analysis is corrected for theses problems, an anagenetic trend in cranial capacity becomes highly evident, in fundamental agreement with a previous study by Bilsborough (1976).

At about 0.4 MYA, we begin to encounter several fossils which seem to fall on the border between H. erectus and the Neanderthals. Thus, the lineage continues in the large, heavy, thick-vaulted specimens from Ngandong. Although identified by some workers (e.g., Von Koeningswald 1962) as Neanderthal, they are also widely accepted as H. erectus (e.g., Santa Luca 1980). Similarly, the Petralona skull has affinities with both groups (e.g., Trinkaus and Howells 1979), as do Arago (de Lumley and de Lumley 1974); Bodo (Conroy et al. 1978); and other skulls such as Broken Hill and Saldanha (Coon 1963; Howells 1973). The major character linking these to H. sapiens is cranial capacity, yet anatomically, these are all continuous with one another and with the H. erectus sample (cf. Krantz 1980; Merrill 1982).

It would seem, therefore, that the most parsimonious explanation for the

evolutionary patterns observed here involve a single, widely distributed lineage, changing anagenetically through time and exhibiting extensive microevolutionary variation.

Although Delson (1977 and pers. comm.) has argued that the traits shared by H. erectus and the Neanderthals are merely symplesiomorphous, this is a tautology. The Neanderthals succeed H. erectus temporally with little, if any, ambiguity. Yet if two populations are phylogenetically ancestor and descendant, it necessarily follows that any inherited trait they hold in common must be a conservative retention in the descendants. However, those diagnostic traits which Neanderthals share with H. erectus are clearly derived in the ancestral population, H. erectus; therefore, these traits can be used to establish the two (or more) populations as closely related phena. The view I am advocating involves simply the recognition of the unity of these thick-skulled, platycephalic hominids as a single continuous lineage. Two factors, I believe, favor this over alternative explanations: 1) the relative ease with which the earliest H. erectus may be diagnosed from contemporaneous populations of australopithecines, and 2) the existence of biostratigraphic and morphological intermediates linking H. erectus and Neanderthals.

The culmination of the microevolutionary trend would obviously be in the classic Neanderthals of Europe and Western Asia (0.1-.035 MYA). The recent discovery of Neanderthals associated with cultural implements of Chatelperronian type at Saint-Cesaire (Leveque and Vandermeersch 1981) gives a last glimpse of this lineage about 34,000 years ago.

Modern Lineage

Roughly contemporary with the Saint-Cesaire finds (indeed, slightly antedating them) are remains of anatomically modern man with typically Neanderthal (Mousterian) tools; for example, at Qafzeh. This biological lineage can be traced back to "archaic" modern forms from the Kibish formation of the Omo (Howell 1978), the Ngaloba formation at Laetoli (Day et al. 1980a), and Border Cave, each of which are somewhat older than 100,000 years. Interestingly, there are no specimens thrust back and forth between Neanderthal and Modern Man in the same way that specimens are ambiguously identified as Neanderthal or H. erectus.

Further, there are two independent suggestions of a rapid and abrupt formation of a new species slightly before the dates attributed to the three early modern fossils. The first is through a critical examination of Middle Pleistocene hominid morphology by Rightmire (1981), who concluded that the morphological suite characteristic of our species was formed "during a short pulse of evolution, late in the Middle Pleistocene." The second is through the examination of mitochondrial DNA in living populations, under the assumption of a molecular clock (Brown 1980). That study concludes that a population crash occurred within the hominid lineage between 0.36 and 0.18 MYA, which may roughly date the appearance of the lineage of modern people.

The relationship of modern man with the Neanderthals and other Upper Pleistocene hominids has traditionally been the subject of extreme disagreement among anthropologists (e.g., Brose and Wolpoff 1971; Howells 1974). I suggest that a major cause of this is the failure to recognize that Homo sapiens, as currently defined with two subspecies, is a grade, determined largely by cranial capacity. It is also instructive to recall that

historically the uncritical acceptance of Homo sapiens sapiens and Homo sapiens neanderthalensis as comprising a single species is due to Dobzhansky (1944). Dobzhansky, like Mayr for Homo erectus, was a professional student of neither fossils nor primates. Neither Doazhansky's nor Mayr's species were framed diachronically, in terms of the linkage of ancestral and descendant populations, as Simpson's species were, with an eye towards linking populations temporally separated. Homo erectus and Homo sapiens neanderthalensis are more closely linked by virtue of sharing the same Bauplan, or total morphological pattern, than are Homo sapiens neanderthalensis and Homo sapiens sapiens.

Both H. s. neanderthalensis and H. s. sapiens are descendants of a Middle-Upper Pleistocene stock of "Neanderthaloids" or "Collaterals" — represented by such specimens as Steinheim, Broken Hill, Saldanha, etc.. Subsequently, a new lineage of round-headed, small-browed, thinner-vaulted, vertical-faced hominids arose near the beginning of the Upper Pleistocene, while the ancestral form continued. The divergence between the two lineages became more marked through time, such that Stringer (1974) could argue forcefully that there is no close cranial relationship between the late Neanderthals and modern populations.

It is important to recognize that what is generally considered to be "rapid" speciation in paleontology is a divergence on the order of 50,000 years. The divergence, indeed the duration, of the modern lineage is of the same order of magnitude as a "rapid" speciation event in paleontology. As a consequence, it is likely that the hominid record would reveal data on the process of divergence of the species and replacement of one by the other. Smith (1982) traces the latter process for Eastern Europe, and Jelinek (1982) traces cultural

replacement through Tabun Cave, Israel. Perhaps in the systematic framework I propose here, many of the problems which have existed heretofore in the recent evolutionary patterns of the Hominidae will be shown to be spurious.

Discussion

A population crash leading to severe genetic "founder effects" in outlying areas of a species' range is the most likely cause of an apparently punctuational event (Mayr 1942:234ff., 1954; Carson 1970; Eldredge and Gould 1972). In the absence of such demographic processes, a widely-distributed species should tend to change gradually through time, in accordance with selective pressures, without significant morphological discontinuities. The hominids seem to display both of these evolutionary patterns. On the one hand, there are lineages within which morphologies change gradually: these are marked throughout by "transitional fossils," which have proven difficult for anthropologists to identify unambiguously. On the other hand, these lineages tend to originate suddenly, such that the earliest member of a new lineage can be readily distinguished from the later members of the ancestral lineage.

However, among the hominids, it is quite difficult to state that these punctuation events represent speciation, in any biologically meaningful sense of the term. What is punctuational is the appearance of a new morphology, not necessarily the emergence of reproductive isolation (cf. Delson 1981). Consequently, although the Neanderthals are distinctive from Moderns in their morphology, it is unlikely that such morphological distinction merits the status of a biological species (Trinkaus and Howells 1979): the emergence of modern man is generally

regarded as a product of microevolution, not macroevolution.

This is a problem not of anthropology, nor of the hominid fossil record -- it is a problem stemming from the fundamental disharmony between the concepts of the "biological" species and the "evolutionary" species. The former is a reproductive community, defined by fertility at a single time; the latter is an ecological community, defined by anatomical continuity through time. Although the Neanderthals and contemporaneous Moderns might have been inter-fertile, it is clear that a distinct ecological gap separated the two populations. This should merit a recognition of the two populations as separate evolutionary species. On the other hand, no such ecological gap is evident between any two contemporaneous populations of Middle Pleistocene hominids.

Further, it is difficult to argue for stasis being the rule within each persistent lineage of hominids. Although the establishment of a morphological pattern seems to occur rapidly in this family, within each lineage there may be considerable anagenetic change evident. Thus, we have strong morphological continuity (but not stasis) within the A. africanus-H. habilis lineage and within the H. erectus-Neanderthal lineage -- despite a relative lack of continuity marking the origin of each lineage.

Conclusions

It has obviously not been my intention to provide an exhaustive treatment of the hominid fossil record in this paper. Rather, I have pointed out morphological gradations and discontinuities in the hominid record, which I have tried to place in an operative systematic framework. Consequently, regardless of the taxonomic level at which "Homo habilis" is recognized, it is difficult to argue that the specimens attributed to it are not at least morphologically strongly continuous with A. africanus (Cronin et al. 1981) and part of the same evolving lineage.

The necessity of seeing rapid speciation in the fossil record (i.e., punctuation) as biological speciation is also called into question. Although certain events (e.g., origin of the robust lineage) could well have involved the establishment of a reproductive barrier between the ancestral and descendant lineages, other events (e.g., origin of the modern lineage) are unlikely to have been speciation in the strict sense, or biological speciation.

I therefore suggest that with systematic framework proposed here, the tempo and mode of hominid evolution may be explored with considerably less ambiguity. My acknowledgment of rapid and abrupt change between lineages is in disagreement with the extreme gradualist analysis of Cronin et al. (1981); however, I believe there is clearly considerable microevolutionary divergence and anagenesis visible within lineages, in contrast with the views of "punctuationists" (e.g., Stanley 1979; 1981; Godfrey and Jacobs 1981; Rightmire 1981).

If the lineages I have recognized here are considered to be species (as I believe them to be), the proper nomenclature is as presented in Figure 2.

Family Hominidae (Blyth 1875)

    Genus *Australopithecus* (Dart 1925)
        Australopithecus afarensis (Johanson, White & Coppens 1975)
        Australopithecus africanus (Dart 1925)
            A. a. africanus (Dart 1925)
            A. a. habilis (Leakey et al. 1964)
        Australopithecus robustus (Broom 1938)
            A. r. robustus (Broom 1938)
            A. r. boisei (Leakey 1959)

    Genus *Homo* (Linnaeus 1758)
        Homo sapiens (Linnaeus 1758)
        Homo neanderthalensis (King 1864)
            H. n. neanderthalensis (King 1864)
            H. n. erectus (Dubois 1892)

Figure 2. Proposed nomenclature for family Hominidae.

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