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C. Owen Lovejoy

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The Origin of Man

C. Owen Lovejoy

During the last quarter-century, the study of human origins has proved remarkably successful. Crucial fossils and primate behavioral data are now available from which to reconstruct man's evolution during the last 15 million years. Equally important is the recognition of a close genetic relationship between man and the other extant hominoids (especially *Pan* and *Gorilla*) (1).

Material Culture

The most commonly cited distinction between man and apes is the former's reliance on material culture. The belief that tools were pivotal to the divergence of hominids was initiated by Darwin (3) and has remained the most popular view (4-6). Darwin was impressed by the absence of large canines in man and attrib-

Summary. Five characters separate man from other hominoids—a large neocortex, bipedality, reduced anterior dentition with molar dominance, material culture, and unique sexual and reproductive behavior. Evidence provided by the fossil record, primate behavior, and demographic analysis shows that the traditional view that early human evolution was a direct consequence of brain expansion and material culture is incorrect, and that the unique sexual and reproductive behavior of man may be the *sine qua non* of human origin.

Experiments on DNA hybridization indicate at least 98 percent identity in non-repeated DNA in man and chimpanzee, sufficient similarity to suggest the possibility of a viable hybrid. These data confirm studies by comparative anatomists who have emphasized the striking anatomical similarities of apes and man (2). As a consequence of this physical similarity, models of human origin must directly address the few primary differences separating humans from apes. Clearly, the rate of acquisition of these differences, the fossil evidence bearing on their first appearance, and their underlying selection are crucial to an understanding of human evolution.

uted their reduction to tool use. As Holloway (7) and Jolly (8) have cogently argued, however, tool use is not an explanation of canine reduction since there is no behavioral contradiction in having both functional canines and tools. There is little doubt that material culture has played a role in the evolution of *Homo sapiens* and *H. erectus*, but this does not require it to have been a significant factor in the origin of hominids. In fact, the earliest recognizable tools are only about 2 million years old (9), but there is considerable evidence placing the phyletic origin of hominids in the middle to late Miocene (12 to 6 million years ago) (10-12). Although the earliest tools will have

left no record because of the use of perishable materials, there is still the necessary presumption of a 6- to 10-million-year period dominated by reliance on material culture—a view with numerous shortcomings.

The use of primitive tools by extant pongids (13) supports the contention of comparable abilities in early hominids, but it also demonstrates that tool use is a general capacity of pongids, none of which exhibit the unique characters of hominids (14). If tools were the primary determinant of early hominization, why should their first appearance be so late in the hominid record? More importantly, what activity requiring tools was critical to early hominid survival and phyletic origin (15)? It is now clear that hunting does not qualify as such an activity (16). From the first recognizable tools to the industrial revolution required only 2 million years, whereas if tools played a part in the origin of hominids, they must have remained primitive and unchanged for at least 5 million years. It is likely that either the earliest hominids made no use of tools at all, or that such use was comparable to that in other extant hominoids and was not critical to their survival or pivotal to their origin.

Expansion of the Neocortex

It is now clear that the marked expansion of the hominid cerebral cortex took place during the last 2 to 3 million years (17, 18). Detailed study of the Hadar crania from Ethiopia, recently attributed to *Australopithecus afarensis* (19), has revealed that they were strikingly primitive (20). Preliminary estimates of cranial capacity indicate a brain size well within the range of extant pongids (21). The pelvis of the skeleton known as "Lucy" from Afar Locality (A.L.) 288 has been fully reconstructed (22). One of its most salient features is a birth canal whose shape and dimensions show little or no effects of selection for passage of enlarged fetal crania, adaptations that so clearly dominate the form of the modern human pelvis (23, 24).

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Bipedality

Bipedality is an unusual mode of mammalian locomotion. Contrary to the so-called efficiency argument, energy expenditure for bipedal walking is probably not significantly different from that during quadrupedal locomotion (23, 25). Yet the adoption of nonsaltatory bipedal progression is disadvantageous because both speed and agility are markedly reduced (23, 24, 26). All present evidence, especially that made available by the postcranium of *A. afarensis*, confirms an essentially complete adaptation to bipedal locomotion by at least 4 million years ago (22, 27). This conclusion is provided unequivocal support by the hominid footprints discovered at Laetoli in Tanzania (28).

Dentition

Additional distinctions between hominids and pongids are found in their respective jaws and teeth. In fact, these differences have allowed the identification of possible hominids in the Miocene—there are no distinctive postcranial or cranial remains of undoubted hominid affinities before about 4 million years ago. As a result of recent field work in Mio-Pliocene deposits (29, 30), it is now possible to suggest a broad schedule of phases in the evolution of the hominoid dentition that can serve as an outline of hominoid phyletic events during the last 23 million years.

Phase I. This phase has a generalized dryopithecine dentition including a distinct Y-5 lower molar cusp pattern with bunodont crowns, thin enamel, and cheek teeth small relative to body size; incisors are broad with canine-premolar

shear. This phase is associated with forest faunas and floras (31) and is shared by all hominoids before 15 million years ago (range, 23 to 15 million years) (30–32).

Phase II. This phase shows a shift toward greater molar dominance. About 14 million years ago, hominoids fall into two groups. The first retained phase I characters and may constitute ancestral populations of extant apes (*Proconsul*, “*Rangwapithecus*,” and *Limnopithecus*, *Dryopithecus*) (30). A second group exhibits enamel thickening, increased molar wear gradient, and moderate anterior dental reduction or increased relative molar size, or both. Mandibles are more robust and prognathism is reduced. The shift toward greater molar dominance has partially been attributed to greater reliance on terrestrial food sources. This group includes genera (*Ramapithecus* and *Sivapithecus*) probably related to hominids, an extinct ape (*Gigantopithecus*), and possibly the modern orang-utan (range, 14 to 8 million years) (12, 30–34).

Phase III. This phase represents a conservative period. The dentition of *A. afarensis* appears only moderately changed in morphology and proportions from phase II; the features include comparatively large incisors, frequently a unicuspid lower first premolar, canines of moderate size, molars of moderate size (relative to body size and later hominids), and loss of canine-premolar shear (range, 7 to 2½ million years) (12, 17).

Phase IV. This phase represents Plio-Pleistocene specialization. The sample in this time range is divisible into two clades or phyletic lines (17). The first was possibly restricted to savannah and grassland. It displays extreme anterior tooth reduction and excessive molar

dominance and became extinct by mid-Pleistocene (*A. africanus* → *A. robustus* → “*A. boisei*”). A second clade, ancestral to *H. erectus*, retained a more generalized dentition in the early Pleistocene but underwent dentognathic reduction in the middle and upper Pleistocene as a consequence of reliance on material culture [for example, reduced dental manipulation and greater preoral food preparation (35)]. My view is that this clade occupied more varied habitats. Both groups are probably directly descendant from *A. afarensis* (17).

Models of Human Origin

A model of hominid origin proposed by Jolly (8) uses analogy to anatomical and behavioral characters shared by *Theropithecus gelada* and some early hominids. He suggests that early hominid populations relied on small-object feeding, that this dietary specialization led to a suite of adaptations to the grassland savannah, and that bipedality developed in response to feeding posture. Yet geladas, which do rely on small-object feeding, are not bipedal and show no significant adaptations to bipedality. Bipedal locomotion is clearly not required for extensive small-object feeding especially on grasslands where speed and agility are of great value in animals who also lack wide visual fields and sensitive olfaction (36). Furthermore, the dental morphology of *A. afarensis* is considerably more generalized than that of later hominids. The dietary specialization seen in *A. robustus* is possibly accountable by Jolly’s model, but the more generalized dentition of *A. afarensis* is not (37). It is more likely that hominids venturing into open habitats were already bipedal and that their regular occupation of savannahs was not possible until intensified social behavior was well developed.

Other theorists have viewed hominization as the direct result of savannah occupation by prehomnids. Proponents of this view believe that the selective pressures of life on grassland savannahs directly produced the human character complex. Bipedal locomotion is posited as sentinel behavior and as an adaptation allowing weapons to be used against predators. Intelligence is said to be favored because highly integrated troop behavior is necessary for predator repulsion. Differences in some behaviors of chimpanzee populations now living in woodland savannahs versus those inhabiting more forested areas are cited as evidence (38).

There are many problems with this

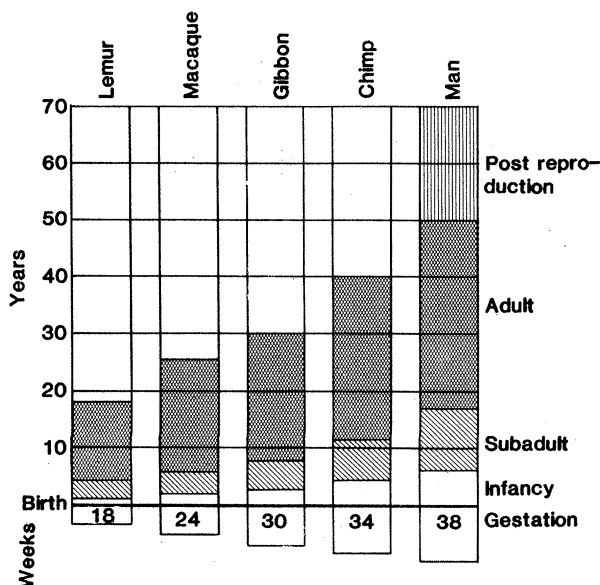


Fig. 1. Progressive prolongation of life phases and gestation in primates. Note the proportionality of the four indicated phases. The post-reproductive phase is restricted to man and is probably a recent development (101, after 102).

view. Bipedality is useless for avoidance or escape from predators. Occasional bipedality, as seen in many primates, is sufficient for the use of weapons. Most importantly, brain expansion and cultural development remotely postdate hominid divergence.

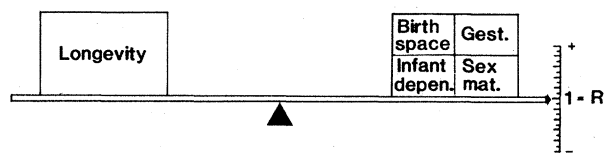
Furthermore, Miocene ecology is inconsistent with the savannah selection theory. While cooling, aridity, and increased seasonality had pronounced effects on Old World floras, the predominant effect of these climatic trends, in areas where hominids are known to have been present, appears to have been the development of diversified mosaics, rather than broad-scale forest reduction (39-41). It would be more correct to say that hominids of the middle and late Miocene were presented with a greater variety of possible habitats than to view them as having suffered an imposed "terrestrialization." It is also clear that some Miocene sites at which possible hominids have been recovered had canopy forest conditions (12, 42). While increased seasonality would have imposed a need for larger feeding ranges, occasional use of woodlands and edaphic grasslands would not necessarily impose elevated carnivore pressure. Nor, as was pointed out above, would early hominids be required to abandon quadrupedality in order to use more orthograde positional behavior during feeding. Quite the contrary, it would appear that late Miocene habitat mosaics would allow adoption of bipedality (in forests and transition mosaics) rather than directly select for it. All present evidence therefore indicates that hominid clade evolved in forest or mosaic conditions, or both (43), rather than only on grassland or savannahs. and that bipedal locomotion was not a response to feeding posture, material culture, or predator avoidance.

In summary, four major character complexes are usually cited as distinguishing hominids from pongids. Hominids have remarkable brain expansion, a complex material culture, anterior dental reduction and molar dominance, and bipedal locomotion. Only bipedal locomotion and partial dental modifications can be shown to have an antiquity even approximating the earliest appearance of unquestioned, developed hominids (*A. afarensis*).

Demographic Strategy and the Evolution of Hominids

The order Primates has long been recognized to display a *scala naturae* consisting of "intercalary types"—extant forms that represent earlier stages in the

Fig. 2. Mechanical model of demographic variables in hominoids. The R is the intrinsic rate of population increase ($1 =$ static population size). An increase in the lengths of the four periods



on the bar to the right (birth space, gestation, infant dependency, and sexual maturity) is accompanied by a comparable shift of longevity to the left, but without realization of that longevity, prolonged maturation reduces R and leads to extinction or replacement by populations in which life phases are chronologically shorter. Of the four variables on the right, only birth space can be significantly shortened (shifted to the left) without alteration of primate aging physiology.

development of major adaptive trends. Figure 1 is a well-known diagram of the chronology of life phases in living primates. There is an obvious trend toward prolonged life-span, which has both physiological and demographic correlates bearing directly on the phyletic origin of hominids.

The physiological correlates (Fig. 1) include a longer period of infant dependency, prolonged gestation, single births, and successively greater periods between pregnancies. Cutler (44) has demonstrated that such developmental parameters are "qualitatively and sequentially similar in different mammalian species" but proceed "at different characteristic rates defined by the reciprocal of their MLP" (maximum life potential). The progressive slowing of life phases can in turn be accounted for by an increasingly K-type demographic strategy (45). With each step in the *scala naturae*, populations devote a greater proportion of their reproductive energy to subadult care, with increased investment in the survival of fewer offspring. Among chimpanzee populations, this trend appears to have resulted in marginal demographic conditions. Field studies at Gombe in Tanzania show the average period between successful births to be 5.6 years (46). This can be attributed in part to a greatly prolonged period of subadult dependency. Van Lawick-Goodall's (47) description of the chimpanzee life phases is instructive:

The infant does not start to walk until he is six months old, and he seldom ventures more than a few yards from his mother until he is over nine months old. He may ingest a few scraps of solid food when he is six months, but solids do not become a significant part of his diet until he is about two years of age and he continues to nurse until he is between four-and-a-half and six years old. Moreover, while he may travel short distances . . . when he is about four years old, he continues to make long journeys riding on his mother's back until he is five or six. . . .

This extreme degree of parental investment has profound demographic consequences. A chimpanzee female does not reach sexual maturity until she is about 10 years old (46). If she is to reproduce herself and her mate, that is, main-

tain a stable population, she must survive to an age of 21 years (48). Whereas in rhesus macaques, the age is only about 9 years (49, 50).

Figure 2 shows a balance depicting the reciprocal relation between longevity and the primary demographic elements of parental investment. The two sides of this hypothetical balance are physiologically interdependent; as longevity is increased, each of the developmental stages is proportionately prolonged. The relationships between these variables, in fact, are not exactly linear, but they do have remarkably high correlations in most mammals (44). As the scale indicates, greater longevity is accompanied by a proportionate delay in reproductive rate and therefore requires a female to survive to an older age in order to maintain the same reproductive value (measured at birth) (51). Put another way, the total reproductive rate of a primate species can remain constant with progressive increases in longevity only if the crude mortality rate is correspondingly reduced. Actual mortality rate is dependent on both maximum life potential, a genetic factor, and environmental interaction. Deaths caused by predation, accident, parasitism, infection, failure of food supply, and so forth, are at least partially stochastic events beyond the complete control of the organism. Only if mechanisms are developed to increase an organism's resistance to such factors, can the effects of increased longevity be reproductively accommodated. Strong social bonds, high levels of intelligence, intense parenting, and long periods of learning are among factors used by higher primates to depress environmentally induced mortality. It is of some interest that such factors also require greater longevity (for brain development, learning, acquisition of social and parenting skills) and that they constitute reciprocal links leading to greater longevity. This positive feedback system, however, has an absolute limit; environmentally induced mortality can never be completely under organism control, no matter how effective the mechanisms developed to resist it.

Suppose that late Miocene hominoids

were approaching the effective limit of this feedback system or at least were sufficiently near the limit not to thrive in novel environments (52). Two demographic variables could be altered to improve reproductive success—survivorship (the probability of surviving) and the time period between successive births (the birth space). All other factors are direct linear functions of mammalian developmental physiology and could not be altered. The argument is subject to the following simple quantification

$$RV = l(s) \int_s^{MLP} l(x)b(x)dx \quad (1)$$

where RV is reproductive value of a cohort measured at birth, that is, the expected number of offspring produced by a unit radix; $b(x)$ is fertility at age x ; $l(x)$ is survivorship at age x ; s is age at sexual maturation; and MLP = maximum life potential. Assuming that a female gives birth at age s years and subsequently every β (birth space) years until reaching MLP, her total offspring would be given by

$$\frac{MLP - s}{\beta} \quad (2)$$

Fertility is then seen to be dependent on birth space β according to

$$\int_s^{MLP} b(x)dx = \frac{MLP - s}{\beta} \quad (3)$$

A simple solution (but one which is fully acceptable because of the proportionate relation between MLP and s) is $b(x) = 1/\beta$. The expression for RV then becomes

$$RV = \frac{1}{\beta} [l(s) \int_s^{MLP} l(x)dx] \quad (4)$$

Because the term in brackets is independent of β , RV is inversely proportional to β , and RV is increased by a shorter birth space, by greater values of $l(x)$ for any age, or by both. Table 1 provides reproductive values for chimpanzees, Old World monkeys, and man from estimated values of β , s , and MLP under the simplifying assumption of $l(x) = l^x$. It can be seen from this table that both chimpanzees and humans have considerably lower reproductive values than Old World monkeys for low values of $l(x)$. As the values used for calculation are conservative, the existence of successful hominid clades in Pliocene mosaics suggests that both birth space reduction and elevation of survivorship had probably been accomplished. This is without explanation unless a major

change in reproductive strategy accompanied occupation of novel environments by these hominids. Yet neither brain expansion nor significant material culture appear at this time level and were therefore not responsible for this shift.

A Behavioral Model for Early Hominid Evolution

Any behavioral change that increases reproductive rate, survivorship, or both, is under selection of maximum intensity. Higher primates rely on social behavioral mechanisms to promote survivorship during all phases of the life cycle, and one could cite numerous methods by which it theoretically could be increased. Avoidance of dietary toxins, use of more reliable food sources, and increased competence in arboreal locomotion are obvious examples. Yet these are among many that have remained under strong selection throughout much of the course of primate evolution, and it is therefore unlikely that early hominid adaptation was a product of intensified selection for adaptations almost universal to anthropoid primates. For early hominids we must look beyond such common variables to novel forms of behavioral change. The tendency has been to concentrate on singular, extraordinary traits of later human evolution such as intense technology, organized hunting, and the massive human brain. Yet these adaptations were not likely to have arisen de novo from elemental behaviors seen in extant nonhuman primates, such as the primitive tool using of the chimpanzee, in the absence of a broad selective milieu. It is more probable that significant preadaptations were present in early hominids that served as a behavioral base from which the "breakthrough" adaptations (53) of later hominids could progressively develop. We are therefore in search of a novel behavioral pattern in Miocene hominoids that could evolve from typical primate survival strategies, but that might also include important elements of other mammalian strategies, that is, a behavioral pattern that arose by recombination of common mammalian behavioral elements and that increased survivorship and birthrate.

In her essay on mother-infant relationships among chimpanzees, van Lawick-Goodall (54) noted two primary causes of mortality among infants: "inadequacy" of the mother-infant relationship and "injuries caused by falling from the mother." An intensification of both the quality and quantity of parenting would unquestionably improve survivorship of

the altricial chimpanzee infant. The feeding and reproductive strategies of higher primates, however, largely prevent such an advancement. The mother must both care for the infant and forage for herself. A common method of altricial infant care in other mammals is sequestration of offspring at locations of maximum safety. Nests, lodges, setts, warrens, dreys, dens, lairs, and burrows are examples of this strategy. A similar adaptation in primates is usually not possible, however, because the need to forage requires both mother and infant to remain mobile. The requirement of mother-infant mobility is a significant cause of mortality and is at the same time the most important restriction on primate birth spacing.

Many primates display significant sex differences in foraging. Diet composition, selection of food items, feeding time, and canopy levels and sites differ in some species (55). In at least *Pongo pygmaeus* and *Colobus badius*, males often feed at lower canopy levels than females (56-58). In the gelada baboon, all-male groups "tended not to exploit quite the same areas as the reproductive units thus reducing indirect competition for food" (59). Clutton-Brock (55) notes that an increased separation of males from female-offspring foraging sites is advantageous where (i) animals feed outward from a fixed base, (ii) the adult sex ratio is close to parity, and (iii) feeding rate is limited by search time rather than by handling time, which is the time spent both preparing and consuming food. Similar feeding differences by sex are found in birds and other mammals (60).

It is reasonable to assume that Miocene hominoids traveled between food sources on the ground and that these primates would be best characterized as omnivores (12). These are ecologically sound assumptions. Increased seasonality coupled with already occurring local biotic variation (edaphic grasslands, savannah, woodland, forest) (8, 12, 39-41) would have presented variable and mosaic conditions. Occupation of heterogeneous ("patchy") environments and use of variable food sources favors a generalist strategy, whereas reliance on a homogeneous diet requires high food concentrations (61, 62). The time spent searching for food is greatest among generalists who live in food-sparse environments (63). In short, Miocene ecological conditions support the view that feeding rate would have been more dependent on search time than handling time.

Greater seasonality and the need to increase both birthrate and survivorship would also favor at least partial separa-

tion of male and female day ranges since this strategy would increase carrying capacity and improve the protein and calorie supply of females and their offspring. Terrestriality, however, would require a centrifugal or linear displacement of males, as opposed to vertical stratification in canopy feeding. Given the Miocene conditions described above, such separation could become marked especially in the dry season. If such separation were primarily due only to an increase in the male day range, moreover, the range of the female-offspring group could be proportionately reduced by progressive elimination of male competition for local resources. This separation would be under strong positive selection. Lowered mobility of females would reduce accident rate during travel, maximize familiarity with the core area, reduce exposure to predators, and allow intensification of parenting behavior, thus elevating survivorship (64). Such a division of feeding areas, however, would not genetically favor males unless it specifically reduced competition with their own biological offspring and did not reduce their opportunities for consort relationships. Polygynous mating would not be favored by this adaptive strategy because the advantage of feeding divergence is reduced as the number of males is reduced. Conversely, a sex ratio close to parity would select for the proposed feeding strategy. Such a ratio would obtain if the mating pattern were monogamous pair bonding. In this case, males would avoid competition with their bonded mates and biological offspring (by using alternative feeding sites) and not be disadvantaged by physical separation, that is, there would be no loss of consort opportunity. In short, monogamous pair bonding would favor feeding divergence by "assuring" males of biological paternity and by reducing feeding competition with their own offspring and mates.

Such a system would increase survivorship and would also favor any increase in the reproductive rate of a monogamous pair so long as feeding strategy was sufficient to meet the increased load on the sources of protein and calories. One element of feeding among forest chimpanzees is the "food call" sometimes made by males upon discovery of a new food source (65). In the proposed system, however, selection would not favor this behavior; instead, selection would favor a behavior that would benefit only the male's own reproductive unit. The simple alternative to the food call would involve collecting the available food item or items and returning

Table 1. Relative reproductive values of Old World primates calculated from Eq. 4 (see text) and multiplied by 10 for clarity.

Annual survivorship	Reproductive values		
	Old World monkeys*	Chimpanzees†	Man‡
.90	17	4	2
.92	23	7	4
.94	31	13	9
.96	42	25	24
.98	58	50	64

*Maximum life potential = 20; sexual maturity = 4; birth space = 2 (49, 50, 103). †Maximum life potential = 40; sexual maturity = 10; birth space = 3 (46, 54, 103). ‡Maximum life potential = 60; sexual maturity = 15; birth space = 2.5.

them to the mate and offspring. Contrary to the opinion that such behavior would be altruistic, it would not be so in the proposed system, because it would only benefit the biological offspring of the male carrying out the provisioning and thus would be under powerful, direct selection. If this behavior were to become a regular component of the male's behavioral repertoire, it would directly increase his reproductive rate by correspondingly improving the protein and calorie supply of the female who could then accommodate greater gestational and lactation loads and intensify parenting (66). The behavior would thus achieve both an increase in survivorship and a reduction in birth space. It would allow a progressive increase in the number of dependent offspring because their nutritional and supervisory requirements could be met more adequately.

Behaviors associated with similar reproductive strategies are in fact present in other primates. In both the Callitrichidae and Aotinae, extensive paternal care of the young constitutes a critical part of reproductive strategy in some species (67, 68). Among callitrichids, the social unit is usually an adult male and female, plus one to several subadults. Maternal care is largely restricted to suckling and grooming, the male being responsible for subadults at all other times. The modal birth is dizygotic twins (55, 68). It is likely that this system is a partitioning of care in response to the high protein and calorie requirements of these small species. Male care during foraging tends to equilibrate the high caloric load imposed on females by lactation and gestation of two (and sometimes three) offspring—the process of twinning being an obvious demographic adaptation of elevated birthrate. As Hershkovitz (68) notes: "survival of a population [of callitrichids] in the wild depends on close synchronization between cyclical

nutritional requirements for young and old and the seasonal changes in the quality and quantity of available food." This same statement could be as well applied to early hominids, especially given increased Miocene seasonality and the need for a decrease in birth spacing. The altricial infants of Miocene hominoids, however, would have required reduced mobility and therefore prevented a callitrichid strategy of male care, with the simplest solution being the male provisioning model proposed above.

The Origin of Bipedality

Provisioning is, of course, the primary parental care strategy of most canids and birds (69-71). Both groups exhibit direct male involvement similar to that described for callitrichids. Their offspring are normally immature at birth, immobile, and require constant provisioning and parenting. In some species, a sexual division of labor, like that posited here for early hominids, is observed. Female hornbills (Bucerotidae), for example, depend totally on male provisioning for their survival and that of their offspring. Monogamous pair bonding is characteristic of 90 percent of bird species (70, 72) and is the most common mating system in provisioning canids (69). Both groups, as a fundamental feature of reproductive strategy, commonly sequester their offspring at home bases (73).

One critical difference separates provisioning in birds and canids from that suggested for early hominids. Birds and canids can carry in their mouths or regurgitate (or both) a significant proportion of their body weight. Oral carrying would have been inadequate for early hominids, however, and a strong selection for bipedality, which would allow provisions to be carried "by hand," would thus accompany provisioning behavior (74).

Chimpanzees are fully capable of short-range bipedal walking and a variety of hindlimb stances (75), but because they lack the pelvic and lower limb adaptations characteristic of hominids, bipedal walking leads to rapid fatigue (23). It appears likely that the skeletal alterations for bipedality would be under strong selection only by consistent, extended periods of upright walking and not by either occasional bipedality or upright posture. While primitive material culture does not impose this kind of selection, carrying behavior of the type suggested above, does. It is likely that the need to carry significant amounts of food was a strong selection factor in favor of primitive material culture (76). Al-

though it is not a significant shift from primitive tools of the type used by chimpanzees today, such as "termite sticks" and "leaf sponges," to simple and readily available natural articles that could be used to enhance carrying ability, it is a significant shift from such primitive and occasional tool use to the stone tools of the basal Pleistocene. Development of such tools is most likely to have followed an extended period of more primitive material culture, which was not critical to survival. It has been suggested frequently that the earliest tools were weapons. However, the progressive development of more advanced stone tools from rudimentary weapons is unlikely. A prolonged and extensive period of regular and habitual use of simple (primitive) carrying devices could eventually allow the coordination and pattern recognition necessary for a more advanced reliance on material culture.

The sequential evolution of behavior proposed in this article has a high probability of mirroring actual behavioral events during the Miocene. In most higher primates, male fitness is largely determined by consort success of one sort or another (77). Male enhancement of offspring survival is for the most part indirect and is expressed more in terms of demic or kin selection by general behaviors such as territory defense or predator recognition and repulsion (78). Females are solely responsible for true parenting and their ability in this is under strong selection. However, progressive intensification of higher primate K strategy elevates parenting requirements and lowers reproductive rate. The most obvious, and perhaps only, additional mechanism available with which to meet this "demographic dilemma" is an increase in the direct and continuous participation by males in the reproductive process. Whatever the actual sequence of events, whether as posed above or by some alternative order, such additional investment would improve survivorship and favor a mating structure that intensified energy apportionment to the male's biological offspring. Two mating patterns satisfy this latter requirement: polygyny (one male and several females) or monogamy. The former, however, requires male energy to continue to be devoted to maintaining consorts, and a pool of competing males is ensured by polygynous structure itself, thereby directing it away from direct enhancement of survivorship.

In their synthesis of the evolution of mating systems, Emlen and Oring (72) stress three factors common to polygynous mating structure. (i) One sex is

predisposed to assume most, or all, of the parental care. (ii) Parental care requirements are minimal. (iii) A superabundant food resource enables a single parent to provide full parental care. As has been noted above, however, survivorship of offspring must have been critical to Miocene hominoids; further female parenting is negated by the mobile feeding strategy; hominoid males may be considered an "untapped pool" of reproductive energy; and Miocene ecological conditions required a generalist feeding strategy. Conditions were prime for the establishment of male parental investment and a monogamous mating structure. Finally, it should be pointed out that only among primates in which the male is clearly and directly involved in the parenting process should monogamy be found. This is exactly the case, as this mating structure is found only in gibbons, siamangs, and the New World taxa discussed above (55).

Human Sexual Behavior and Anatomy

The highly unusual sexual behavior of man may now be brought into focus. Human females are continually sexually receptive (79) and have essentially no externally recognizable estrous cycle; male approach may be considered equally stable. Copulation shows little or no synchronization with ovulation (80). As was pointed out above, the selective emergence of a monogamous mating structure and male provisioning would require that males not be disadvantaged in obtaining consorts. Provisioning in birds and canids is normally made possible by highly restricted breeding seasons and discrete generations—the female normally is impregnable for only brief periods during which parental care is not required. The menstrual cycle of higher primates (81), however, requires regular male proximity for reproductive success. The progressive elimination of external manifestations of ovulation and the establishment of continual receptivity would require copulatory vigilance in both sexes in order to ensure fertilization. Moreover, copulation would increase pair-bond adhesion and serve as a social display asserting that bond. Indeed, any sequestration of ovulation (82) would seem to directly imply both regular copulatory behavior and monogamous mating structure. It establishes mathematical parity between males restricted to a single mate and those practicing complete promiscuity, and the balance of selection falls to the offspring of pair-bonded males, since their energetic capacity for provisioning

(and improved survivorship and reproductive rate) is maximized.

Man displays a greater elaboration of epigamic characters than any other primate (8, 59, 83, 84). Frequently, our sexual dimorphism is tacitly accepted as evidence for a polygynous mating structure because marked sexual dimorphism is most often a product of elaboration of characters of attraction, display, and agonistic behavior in males of polygynous species. Among primates, the degree of sexual dimorphism corresponds closely to the degree of male competition for mates (56, 59, 83). Yet human sexual dimorphism is clearly not typical as is even made clear by the fossil record. In their discussion of *A. afarensis*, Johanson and White (17, 85) note that although this species shows "marked body size dimorphism, the metric and morphological dimorphism of the canine teeth is not as pronounced as in other extant, ground-dwelling primates. This implies a functional pattern different from that seen in other primates and may have significant behavioral implications." There can be no doubt that large male canines are part of the "whole anatomy of bluff, threat, and fighting" (6). The reduction and effective loss of canine dimorphism in early hominids therefore serves as primary evidence in favor of the proposed behavioral model (86). But it is important to stress that while canine dimorphism was undergoing reduction, other forms of dimorphism were apparently being accentuated, as judged from their expression in modern man, who remains the most epigamically adorned primate.

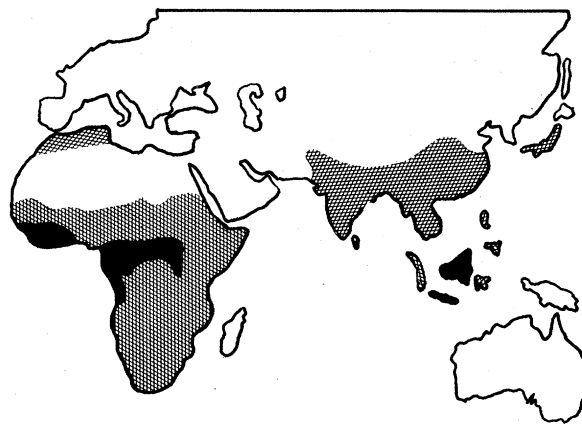
Since man displays a highly unusual mating structure, it is perhaps not surprising that his epigamic, or perhaps parasexual, anatomy is equally unusual and fully explicable by that mating structure. If pair bonding was fundamental and crucial to early hominid reproductive strategy, the anatomical characters that could reinforce pair bonds would also be under strong positive selection. Thus the body and facial hair, distinctive somatotype, the conspicuous penis of human males, and the prominent and permanently enlarged mammae of human females are not surprising in light of Mayr's (87) observation that in "monogamous species such as herons (egrets) in which the pair bond is continuously tested and strengthened by mutual displays, there has been a 'transference' of the display characters from the males to the females with the result that both sexes have elaborate display plumes." In man, however, marked epigamic dimorphism is achieved by elaboration of parasexual characters in both males and females,

rather than in males alone. Their display value is clearly cross-sexual and not intrasexual as in other primates. It should be stressed that these epigamic characters are highly variable and can thus be viewed as a mechanism for establishing and displaying individual sexual uniqueness, and that such uniqueness would play a major role in the maintenance of pair bonds (59). This is especially important when other epigamic features of man (pubic, axillary, and scalp hair), which have been elaborated in both sexes, are considered. Such characters may also contribute to individual sexual uniqueness (88). Redolent individuality is clearly the most probable role of axillary and urogenital scent "organs" (eccrine and apocrine glands plus hair), which are unique among mammals (89). An objection that might be voiced in response to these suggestions is that such auxiliary pair-bond "enhancers" are eclipsed by the paramount role of culture in the mating practices of non-technological societies. Quite the contrary, the more that culture can be shown to dominate the mating structure and process of recent man, the more ancient must be the anatomical-physiological mechanisms involved in the formation and maintenance of pair bonds (90).

Higher Primate Paleogeography

The present-day geographic distributions of Old World monkeys and apes are shown in Fig. 3. The great apes are markedly restricted and occupy only minor areas where minimal environmental changes have taken place since the early Miocene. Yet the fossil record shows that their lineal ancestors (dryopithecines, *sensu lato*) spread throughout the Old World following the establishment of a land bridge and forest corridor between Africa and Eurasia about 16 to 17 million years ago, and that they enjoyed considerable success after their colonization of Europe and Asia (41, 91). Old World monkeys, on the other hand, were much less abundant during this period (92). After the middle and late Miocene, however, a marked reduction in dryopithecine numbers occurred. While this cannot be deduced from the sparse fossil record of the late Miocene and early Pliocene, the distribution of extant descendants of the dryopithecines is ample evidence of their relict status. Today, Old World monkeys are clearly the dominant and successful group, having replaced the dryopithecines and their descendants during the last 12 million years (91). One hominoid group did survive

Fig. 3. Approximate distribution of extant Old World monkeys (hatched) and pongids (gorilla, chimpanzee, orangutan) (solid) (38, 58, 102, 103).



and remain relatively abundant—the Hominidae. It is probable that the hominoid trends of prolonged longevity and increased parental investment are the key to the replacement of most pongid taxa by Old World monkeys, which are reproductively more prosperous. If only a portion of Miocene hominoids made the adaptations described above, two distinct groups would subsequently result. One group might counter the "demographic dilemma" according to the model suggested in this article; a second group could survive by occupying habitats with minimal environmental hazards. Hominids, being more demographically resistant to environmentally induced mortality, would be more capable of expanding into novel and varied habitats, especially mosaics, and of competing with the radiating Old World monkeys. Conversely, the extant pongids are by implication descendant of populations progressively more restricted to highly favorable forest conditions, where minimal seasonality in food supply, low predation pressure, and limited size of the home range would be in effect. These differences in habitat preference would result in a more extensive fossil record for hominids than pongids, both by virtue of the geographic expansion of hominids and as a consequence of the occupation of habitats with more favorable conditions of fossilization. It is therefore quite possible that the sivapithecines (*sensu lato*) of the middle and late Miocene, which already evince dental modifications adumbrating those of late Pliocene hominids (12), may have contained primitive emergent hominids, at least behaviorally, if not phylogenetically.

The Nuclear Family

Man's most unique character is without question his enormous intelligence, and its evolutionary pathway has fascinated all who have attempted to explain

the human career. Hunting and toolmaking are most frequently cited as "primal causes" for the Pleistocene acceleration in hominid brain development. Yet have these not figured so prominently because they leave ubiquitous evidence—the archaeological record? Other human behaviors at least as critical to survival (especially reproductive behavior) are not "fossilized." It is now clear that man probably remained an omnivore throughout the Pleistocene and that hunting may have always been an auxiliary food source (93).

As Reynolds (94) stressed, intense social behavior would seem the most likely single cause of the origin of human intelligence if one origin must be isolated. Tools are used to manipulate the environment and are thus a vehicle of intelligence, not necessarily a cause. Chimpanzees occasionally use tools (a behavior that has fascinated many early hominid theorists), but tools are not critical to their survival. Primates, which are the most intelligent mammals, have achieved evolutionary success primarily by their social and reproductive behavior, which is their most developed ordinal character. It seems reasonable therefore to propose that a further elaboration of this adaptive strategy is the most likely "cause" of early hominid success and the further development of intelligence.

It is of interest to explore one further effect of the proposed model on early hominid social structure. The strong maternal and sibling ties of higher primates are now well documented (47, 54, 94, 95). The matrifocal unit of chimpanzees continues throughout the life of the mother, as do sibling ties. In the proposed hominid reproductive strategy, the process of pair bonding would not only lead to the direct involvement of males in the survivorship of offspring, in primates as intelligent as extant hominoids, it would establish paternity, and thus lead to a gradual replacement of the

matrifocal group by a "bifocal" one—the primitive nuclear family (84, 96). The effects of such a social unit on survivorship and species success could be profound. It could lead to a further shortening of birth space, which would accelerate the reproductive rate and amplify sibling bonds. Reduction of birth space would allow coincident protraction of the subadult (learning) period (97). Behaviors that in other primates are common causes of infant death (for example, agonistic buffering) (78) would be largely eliminated, while those that might improve survivorship (for example, adoption) (46, 98) would be facilitated. The age until which an orphaned chimpanzee does not survive the death of its mother is "around 5 years of age, but may stretch another 3 to 4 in special circumstances" (46). Survival of a second parent may have been a crucial reproductive advance in early hominids (99). Primi-parous females are much less adept than multiparous mothers. Drickamer (50) found that in free-ranging *Macaca mulata* "between 40 and 50% of the infants born first or second to a female did not survive their first year, but by the fourth infant born to the same female only 9% died during the first 12 months." Lancaster (100) notes that: "Recent field and laboratory workers have shown that in many species of mammals, and especially in monkeys and apes, learning and experience play vital roles in the development of the behavior patterns used in mating and maternal care." The effect of intensified parenting, protracted learning, and enhanced sibling relationships would have a markedly beneficial effect upon survivorship. Such projections of the behavior of developing hominids are certainly not new, but they have not received their due emphasis. Can the nuclear family not be viewed as a prodigious adaptation central to the success of early hominids? It may certainly be considered as being within the behavior repertoire of hominoid primates, provided that the reproductive and feeding strategies commensurate to its development were themselves under strong selection. This brief review of the fossil record and some primate behavioral and ecological adaptations would seem to strongly favor the correctness of this view.

Conclusion

It is a truism to say that even late Pliocene hominids must have been unusual mammals, both behaviorally and anatomically. As was pointed out above, emphasis in models of human origin has

traditionally been on singular, extraordinary traits of later human evolution. The model proposed in this article has placed greater emphasis on a fundamental behavioral base from which these unusual adaptations could be directionally selected.

The proposed model accounts for the early origin of bipedality as a locomotor behavior directly enhancing reproductive fitness, not as a behavior resulting from occasional upright feeding posture. It accounts for the origin of the home base in the same fashion as it has been acquired by numerous other mammals. It accounts for the human nuclear family, for the distinctive human sexual epigamic features, and the species' unique sexual behavior. It accounts for a functional, rudimentary material culture of long-standing, and it accounts for the greater proportion of r-selected (45) characters in hominids relative to other hominoids. It accounts for these characters with simple behavioral changes common to both primates and other mammals and in relatively favorable environments, rather than by rapid or forced occupation of habitats for which early hominoids were clearly not adaptively or demographically equipped. It is fully consistent with primate paleogeography, present knowledge of higher primate behavior patterns (as well as those of other mammals), and the hominid fossil record.

If the model is correct, the conventional concept that material culture is pivotal to the differentiation and origin of the primary characters of the Hominidae is probably incorrect. Rather, both advanced material culture and the Pleistocene acceleration in brain development are sequelae to an already established hominid character system, which included intensified parenting and social relationships, monogamous pair bonding, specialized sexual-reproductive behavior, and bipedality. It implies that the nuclear family and human sexual behavior may have their ultimate origin long before the dawn of the Pleistocene.

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14. A convincing and more detailed argument is provided by Jolly (8).
15. Whether or not the early evolution of material culture did in fact proceed in a gradualistic manner is difficult to establish. A punctuated equilibrium model is equally applicable to the early artifact record, and it is not unlikely that material culture proceeded at variable rates.
16. Contrary to popular opinion, there is no evidence whatsoever that early hominids hunted. Bipedality is probably the mode of locomotion least adapted to hunting, unless sophisticated technology is available (or unusually high levels of intelligence, or both). The evidence made available by *A. afarensis* is particularly striking. Further australopithecine evolution from that species is documented by a reduction of the anterior dentition and further enlargement of the grinding teeth. Artifacts do not appear until 2 million years ago, and when they do appear it is difficult to interpret them as hunting implements. In short, if the evidence made available by the fossil record is to be used in reconstructing early hominid evolution, one of its clearest implications is that hunting was not a dietarily significant behavior. See also (8, 41, 62, 91, 102).
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 48. A female chimpanzee reaches sexual maturity at about age 10 years. Using the average span of 5.6 years between successful births (46) gives a required life expectancy of about 21 years (a chimpanzee infant usually dies after his mother's death if it is not at least 4 years old). The authors (46, p. 577) conclude similarly that "The mean generation span, or elapsed time between birth of a female and birth of her median offspring, is about 19.6 years for a sample of ten Gombe females with three or more recorded births." Their most realistic estimate of achieved reproduction is three to four "offspring that are successfully raised to sexual maturity" (46, p. 580).
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- portantly, the adoption of bipedality would mean the loss of most or all of the prehensibility of the infant foot, which is an important grasping organ in the chimpanzee infant. This, in turn, selects for a more secure infant carrying ability in the mother and thus bipedality. This form of selection can clearly not be viewed as the initial selective force for bipedal locomotion, but in conjunction with others, would certainly contribute to the total selective pattern.
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 57. Clutton-Brock (56) notes that "although sex differences in feeding behavior are common among primates there is little evidence to suggest that they have evolved to minimize feeding competition between the sexes." Yet for the two species just cited this may indeed be the case. *Colobus badius* uses a more generalist feeding strategy than its sympatric congeners, has a larger number of adult males within the troop [T. T. Struhsaker and J. F. Oates, in (58), pp. 165-186] and has the highest population density of any Old World monkey [T. H. Clutton-Brock, in (58), pp. 503-512]. It is clearly true of the orang (64).
 58. R. W. Sussman, Ed., *Primate Ecology: Problem Oriented Field Studies* (Wiley, New York, 1979).
 59. J. H. Crook, in (40), pp. 231-281.
 60. R. K. Selander, in (40), pp. 180-230; *Condor* **68**, 113 (1966); G. E. Hutchinson, *The Ecological Theater and the Evolutionary Play* (Yale Univ. Press, New Haven, Conn., 1965).
 61. This forms the basis for an additional criticism of the hominid model proposed by Jolly (8). Gelada baboons are highly specialized feeders whose feeding rate is largely limited by handling time.
 62. "Although nutritional factors alone would not preclude the possibility that early hominids were dietarily quite specialized, [from] the available archaeological evidence and [from] what is known of the dietary patterns of living gatherer-hunters and chimpanzees, it appears unlikely that all early hominids were almost exclusively carnivorous or herbivorous. It is more reasonable to suggest that the diet fell within the broad range of today's gatherer-hunter diets, but that within the wide spectrum of this adaptation, local environmental resources and seasonal scarcity may have forced some individual populations to become more dependent on vegetable or animal tissue foods than others" [A. E. Mann, personal communication: see "The evolution of hominid dietary patterns" in *Primate Dietary Patterns*, R. S. O. Harding and G. Teleki, Eds. (Columbia Univ. Press, New York, in press)].
 63. E. R. Pianka, *Evolutionary Ecology* (Harper & Row, New York, 1974), and references therein.
 64. D. A. H. Orr [in (58), p. 320] comments with respect to the orang-utan: ". . . orang social organization might easily be explained as follows: In order not to overload the food supply, orangs disperse themselves in the jungles. Females carrying infants or tending young juveniles can best survive if they don't have to move far. Young orangs could also best learn the jungle in a restricted, familiar area. . . . Adult males are unencumbered by young and can more easily move over wider areas. This means that they compete with females for food only for short periods of time, and thus do not overload her food supply and force her to move over wider areas."
 65. V. Reynolds and F. Reynolds, in *Primate Behavior*, I. DeVore, Ed. (Holt, Rinehart & Winston, New York, 1965), pp. 368-424; J. Van Lawick-Goodall, *Anim. Behav. Mono.* **1**, 161 (1968); Y. Sugiyama, *Primates* **9**, 225 (1968); *ibid.* **10**, 197 (1969). See R. W. Wrangham [in *Primate Ecology*, T. H. Clutton-Brock, Ed. (Academic Press, New York, 1977), pp. 504-538] for further discussion on the possible functions of the "food call."
 66. Such loads can become intense (up to 1.5 times normal resting basal metabolic rate in females) [O. W. Portman, in *Feeding and Nutrition of Nonhuman Primates*, R. S. Harris, Ed. (Academic Press, New York, 1970), pp. 87-116]. The modern human preparation for lactation is an average accumulation of 9 pounds subcutaneous fat [D. B. Jelliffe and E. F. P. Jelliffe, *Human Milk in the Modern World* (Oxford Univ. Press, Oxford, 1978)]. A major birth interval limitation in hominoid primates may well be the lactational loads placed on the mother (in contradistinction to the needs of the infant)

- and any improvement in feeding strategy could "support" a reduction in birth space on this basis.
67. G. Mitchell and E. M. Brandt, in *Primate Socialization*, F. E. Poirier, Ed. (Random House, New York, 1972), pp. 173-206; H. Kummer, *Primate Societies* (Aldine, Chicago, 1971).
 68. P. Hershkovitz, *Living New World Monkeys* (Univ. of Chicago Press, Chicago, 1977), vol. 1.
 69. H. C. B. Grzimek, Ed., *Animal Life Encyclopedia* (Van Nostrand Reinhold, New York, 1975), vol. 12.
 70. D. Lack, *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968). Monogamy is especially characteristic of long-lived (K-selected) birds [J. W. F. Davis, *J. Anim. Ecol.* 45, 531 (1976); A. Mills, *ibid.* 42, 147 (1973); J. C. Coulson, *ibid.* 35, 269 (1966)].
 71. J. F. Eisenberg, *Handb. Zool.* 10, 1 (1966).
 72. S. T. Emlen and L. W. Oring, *Science* 197, 215 (1977).
 73. Such sequestration is common among rodents as well with perhaps its most classic expression in castorids, which are comparatively K-selected (requiring 3 to 4 years to mature sexually) and live in stable family groups.
 74. A second, also important, element of food-handling behavior may have been pre-mastication. Reduction of birth space would have required an earlier reinitiation of ovulation, which would in turn have required a reduction of mechanical stimuli to the mechanoreceptors of the nipple and areola (and thereby a reduction in prolactin levels) [R. C. Kolodny, L. S. Jacobs, W. H. Daughaday, *Nature (London)* 238, 284 (1972)], and hence an earlier age of weaning. Parental pre-mastication would have facilitated such behavior, at the same time enhancing parental bonds (see discussion of the nuclear family). This could have also increased the rate of dental wear and have been an auxiliary selection component of the dentognathic changes characteristic of early hominids.
 75. H. R. Bauer, *Primates* 18, 913 (1977).
 76. R. E. Leakey and R. Lewin, *People of the Lake* (Doubleday, New York, 1978); G. Hewes, *Am. Anthropol.* 63, 687 (1961).
 77. R. L. Trivers, in (40), pp. 136-179; R. P. Michael and D. Zumpe, *J. Reprod. Fertil.* 21, 199 (1970); T. E. Rowell, in *Social Communication Among Primates*, S. Altman, Ed. (Univ. of Chicago Press, Chicago, 1967), pp. 15-32; I. Devore, in *Sex and Behavior*, F. Beach, Ed. (Wiley, New York, 1965), pp. 266-289; see (36, 67).
 78. S. H. Hrdy, in *Advances in the Study of Behavior*, J. S. Rosenbalt, R. A. Hinde, E. Shaw, C. Beer, Eds. (Academic Press, New York, 1976), vol. 6, pp. 101-158.
 79. D. C. Johanson, personal communication.
 80. R. A. McChance, M. C. Luff, E. E. Widdowson, *J. Hyg.* 37, 571 (1937); J. R. Udry and N. M. Morris [*Nature (London)* 220, 593 (1968)] did find such a relationship, but it is a moot point since with sequestration of ovulation and its external manifestations, copulation would require female initiation.
 81. F. A. Beach, *Psychol. Rev.* 54, 297 (1947); M. A. Chance, in *Culture and the Evolution of Man*, M. F. Ashley Montagu, Ed. (Oxford Univ. Press, New York, 1962), pp. 84-130.
 82. J. Lancaster, personal communication.
 83. D. Morris, *The Naked Ape* (Cape, London, 1967).
 84. F. A. Beach, in *Human Evolution: Biosocial Perspectives*, S. L. Washburn and E. R. McCown, Eds. (Benjamin-Cummings, Menlo Park, Calif., 1978), pp. 123-154.
 85. In other primates that are monogamous, there is little sexual dimorphism. All of these, however, live in territorial family groups [A. Jolly, *The Evolution of Primate Behavior* (Macmillan, New York, 1972)] and there is therefore no intragroup competition for mates. Strong sexual dimorphism is usually a consequence of either differential competition for mates or differential exploitation of resources (56, 60). In *A. afarensis*, according to the proposed model, dimorphism would be favored on the latter basis. Small female body size would reduce caloric-protein requirements, while large body size would increase male mobility and predator resistance.
 86. This is not meant to imply that it was a cause of canine reduction, but only that the process could occur by a combination of relaxation of selection on large male canine size and a positive selective mechanism for reduced canines. The latter is most likely to be found in the concurrent dentognathic changes of greater molar dominance and general anterior tooth reduction (8, 17).
 87. E. Mayr, in (40), p. 97.
 88. Modern man displays a remarkable number of morphological traits that may be considered epigamic (hair color and type, lip size and form, corporal hair patterning, eyebrows, facial countenance, and so forth). Attempts have been made to correlate some of these with geographic variables, but they have been largely unsuccessful. An alternative explanation is that disruptive selection acts to maximize the variability of these features within populations, thereby enhancing the distinctiveness of potential and actual mates in establishing and maintaining pair bonds. The subsequent geographic isolation, whether partial or complete, of a population could then have resulted in a truncation of expression and apparent uniqueness of some features that maintained their epigamic significance in the population (for example, the epicanthic eye fold). The obvious polygenic basis of such traits and their reappearance in unrelated populations (Bushman, Lapps, infant Euroamericans) indicate that their expression is a consequence of elevated frequencies of genes that may be universal in *H. sapiens*, but below an expressive threshold in some populations.
 89. W. Montagna, in *Biological Anthropology*, S. H. Katz, Ed. (Freeman, San Francisco, 1975), pp. 341-351.
 90. Further evidence of the age of pair bonding is provided by the absence of strong canine dimorphism in *A. afarensis* (17). The only other Old World higher primates without canine dimorphism are the gibbon and siamang, which are monogamous (6).
 91. E. Delson, in *Approaches to Primate Palaeobiology*, F. S. Szalay, Ed. (Karger, Basel, 1975), pp. 167-217.
 92. ——— and P. Andrews, in *Phylogeny of the Primates*, W. P. Luckett and F. S. Szalay, Eds. (Plenum, New York, 1976), pp. 405-446.
 93. R. B. Lee, in *Man the Hunter*, R. B. Lee and I. DeVore, Eds. (Aldine, Chicago, 1968), pp. 30-48. The provisioning model proposed here effectively accounts for the origin of hunting by means of a progressive elaboration of provisioning behavior (that is, collecting → scavenging + collecting → hunting + scavenging + collecting) without the requirement that hunting be critical to human evolution at any point. The similarity in social behavior between canids and early humans has often been cited and attributed to hunting. It is more likely that such similarities take origin in reproductive strategy (pair bonding, intratrop cooperation, provisioning, male involvement in sub-adult care, and so forth) and that hunting merely represents one food procurement method that satisfies the economic requirements of the social system. There are numerous carnivores that do not display this form of reproductive strategy, and there are some rodents that do but, of course, do not hunt (73).
 94. V. Reynolds, *The Biology of Human Action* (Freeman, San Francisco, 1976).
 95. J. H. Kaufmann, *Ecology* 40, 500 (1965); M. Yamada, *Primates* 4, 43 (1963); C. B. Koford, *Science* 141, 356 (1963).
 96. The term bifocal is preferable to nuclear family because the latter carries manifest connotations from its application to Western and non-Western modern human cultures, none of which are implied by its use here.
 97. A. E. Mann's extensive studies of dental development and wear in australopithecines ["Some palaeodemographic aspects of the South African australopithecines" (*Univ. Penn. Publ. Anthropol.* 1, 1975)] indicate a prolonged period of development was established by about 2.5 million years ago. K. R. McKinley's survivorship calculations based upon Mann's data [*Am. J. Phys. Anthropol.* 34, 417 (1971)] led him to conclude that australopithecines show a hominid rather than a nonhuman primate "birth spacing pattern." While these calculations require a number of assumptions about the origin and nature of the death assemblages at Swartkrans and Sterkfontein, they are strong evidence that a major demographic shift was fully developed by 2.0 to 2.5 million years ago which included an extended period of sub-adult dependency.
 98. H. Kummer, in *Social Communication Among Primates*, S. Altman, Ed. (Univ. of Chicago Press, Chicago, 1967), pp. 63-72; D. S. Sade, in *ibid.*, pp. 99-115; see (47, 54).
 99. M. H. Wolpoff, cited in *Mosaic* 10, 28 (1979).
 100. J. B. Lancaster, in *Primate Socialization*, F. E. Poirier, Ed. (Random House, New York, 1972), pp. 83-104.
 101. C. O. Lovejoy, R. S. Meindl, T. R. Pryzbeck, T. S. Barton, K. G. Heiple, D. Kotting, *Science* 198, 291 (1977).
 102. A. H. Schultz, *The Life of Primates* (Universe, New York, 1969).
 103. J. R. Napier and P. H. Napier, *A Handbook of Living Primates* (Academic Press, New York, ed. 3, 1970).
 104. I thank G. J. Armelagos, T. Barton, B. Campbell, T. Gray, F. C. Howell, K. Jacobs, D. C. Johanson, B. Kimbel, A. E. Mann, R. S. Meindl, R. P. Mensforth, M. H. Wolpoff, P. Shipman, A. C. Walker, T. D. White, and S. Ward, who read earlier versions of this paper and provided valuable comments. I thank D. C. Johanson, C. J. Jolly, J. Lancaster, R. S. Meindl, and T. D. White for valuable discussions about its content. I thank T. Barton for discussions and advice with respect to the quantitative approach used, L. Don Carlos and R. P. Mensforth for research assistance, and R. S. Meindl for listening to endless anecdotes about the behavior of canids, rodents, and birds.