REVISION OF THE WEEVIL GENUS *TYLODERMA* SAY (COL.: CURCULIONIDAE) IN MEXICO, CENTRAL AMERICA, SOUTH AMERICA, AND THE WEST INDIES

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ABSTRACT

Forty-four species of *Tyloderma* are known to occur in Mexico, Central America, South America, and the West Indies. A redescription of the genus is provided, and the species are keyed and placed in 11 species groups, which also are defined. Twenty-five new species are described, and two species-group names are synonymized: *T. foveostriatum* Voss is a junior synonym of *T. innotatum* Hustache (which is given here specific rank); and *T. metallicum* Voss is a junior synonym of *T. aeneum* Hustache. Lectotypes are designated for *T. aeneum*, *T. cupreum* Hustache, *T. inaequale* Voss, *T. innotatum*, *T. nigromaculatum* Hustache and *T. obliquatum* Hustache. A description or redescription of each species is included, and some important taxonomic characters, including the male phallus, and female 8th sternite and spermatheca are illustrated. Information is presented on plant associations and natural enemies. Complete distributional records are included for all species which are exclusively Neotropical, and the distributions of all species are mapped.

A SELFISH THEORY OF HUMAN ORIGINS[1]

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ABSTRACT: Selection for relatively larger brains via partly neotenic development explains the origin of many unique human traits. Larger brains with greater memory and reasoning capacity have been a pervasive trend in primate evolution; they have enabled primates and, later, hominids in particular to compete successfully with species that otherwise would displace them. Neotenic development not only increases relative brain size but also promotes a bipedal stance and canine reduction; other human traits followed as secondary consequences of these. Some unique aspects of hominid physiology developed from a strategy of finding food during the hottest part of the day, when most predators slept. The controlled use of fire had more significance for the developing uniqueness of this primate lineage than did tool-making. Language, a belief in an afterlife, love, division of labor, and strong individual and group identity, with religion, war, and awareness of more than immediate kinship, as consequences, were products of juvenile personalities and larger memories. Fire provided safety from predators and led to an unusual concentration of social interactions and subsequently to some behaviors unusual for primates.

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Most theories on the origin of unique human traits claim that either males or females, but rarely both, created the selective pressures that led to the changes in stance, brain size, and cultural behavior that separate them so distinctly from their closest primate relatives. For example, males stood upright to launch missiles at predators or prey (e.g., Washburn and Lancaster, 1968; Fifer, 1987) or to bring nutritional gifts to females to help feed more helpless young in exchange for sex (e.g, Isaac, 1978; Lovejoy, 1981; Hill, 1982; Fisher,1982; Parker, 1987). Alternatively, females arose on two legs to gather vegetable food with tools and to carry it back to a home base, and thus were the sex most responsible for the change (e.g., Linton, 1971; Tanner and Zihlman, 1976; Zilhman, 1978; Fedigan, 1986), perhaps with an important contribution from their children (Zeller, 1987). One modeller, though, has reasonably postulated little sexual differentiation in productive activities (obtaining surplus food with tools) among the early hominids [Leibowitz (1983), as discussed in Fedigan (1986)]. Common to all of these theories is the sharing of 'technologically' procured food as the foundation of the earliest hominid societies and causal to the evolution of unique human traits.

I sketch here a different theory of human origins which has a number of points that have not been raised before. The theory is based on selfishly, i.e., individually, motivated behavior. Simply, the need for finding another meal challenged the human lineage enough to explain its divergence from the apes. Altered social systems and tool-making abilities emerge later in human evolution as

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consequences, rather than causes for their uniqueness. Initially, humans probably retained the social system of their arboreal ancestors, whether one similar to that of chimps or different [see Tanner (1981), Fedigan (1982), or Kinzey (1987)]. If so, males and females probably foraged separately, as they do in most apes, and they did not share food extensively or live in concentrated groups. Trees were too scattered in the relatively open habitats that early hominids are thought to have invaded (e.g., Wolpoff, 1980) for concentrated gatherings. Thus, they used them at night (or alternatively, a cliff ledge) for protection from predators until they learned to control fire. Early hominids show a greater degree of sexual dimorphism than did later ones (Frayer and Wolpoff, 1985), but that does not say much about the social organization of the earliest hominids: an orang- or gorilla-type organization is even as likely as some other given the considerable differences seen between the social structure of these extant highly dimorphic primates.

In overview, selection for increased intelligence aided our ancestors in finding suitable food for an ape in an environment increasingly harsh for them. This selection is evident in the steady and relatively rapid increase in brain size that began at least four million years ago with the concurrent appearance of a bipedal stance. Brain enlargement is not typically emphasized as initially important in hominid evolution because it has been an underlying pattern of the primate radiation (Gould, 1977) and the earliest hominids did not have absolutely larger brains than do chimps. For their smaller size, however, the brains of the earliest australopithecines were significantly larger than those of chimps (see below).

As Gould (1977) has emphasized, brain enlargement was achieved by neotenic development: a retardation in development that enabled the brain to enlarge by delaying birth. Each significant amount of increase in brain size during the four million years of recorded hominid evolution has apparently been associated with new abilities, as far as we can judge from archaeological remains.

Although archaeological evidence continues to increase, piecing together the probable behavior of human ancestors has become no easier. In the beginning hominids were more like their nearest relatives, whose behavior can perhaps hint at a model. However, the several species of apes have themselves evolved since our several sequential phyletic divergences from their ancestors, and their social organizations today differ so much from each other that it is dangerous to use any of them uncritically to model our own ancestral behavior (see discussion in Kinzey, 1987). There are similarities and when a critical phyletic and adaptive analysis is done it will probably let us reconstruct our early ancestral behavior better than we can now do. Very near the present, hunter/gatherer societies can serve as adequate models although they too vary appreciably in many ways. There remains a very large expanse in between, where hominids made the transition from apes to recognizable humans, that is difficult to interpret. Any living counterparts are unlikely (see also Potts, 1987). Nevertheless, sequences can be inferred from what fossil and archaeological remains do exist. The following is a summary of arguments which I develop more fully in a forthcoming book along with critical evaluation of the controversies that surround most of the aspects I merely touch upon here.

Partial and selective developmental retardation (neoteny) best explains directly or indirectly most unique hominid traits, including relative large brains, a bipedal stance and reduced canines. The latter have often been given special significance in our social organization, but I interpret their reduction in size as a product of neoteny that was subsequently advantageous as an aid to eating. Indeed, Leutenegger & Shell (1987) give evidence that sexual dimorphism in body size was more pronounced in earlier hominids than was canine dimorphism. As they show, the usual situation in apes and other groups of primates is for the sexual dimorphism of canines to increase disproportionately with an increase in body-size dimorphism. Neoteny initially reduced only canine dimorphism, so early male hominids began to look like females despite being more than twice the body mass; both became juvenile in appearance though not in size. The canines maintain deep roots that predict a longer canine at full development. Retarded development [alternatively, crowding by enlarged molars (Jungers, 1978)] possibly kept the canines short and other uses followed. A short but deeply rooted canine is an extremely useful tool. Think how often you use them in impatience when an appropriate tool cannot be found. Evidence suggests that they were so used later in our evolution if not earlier (e.g., Wolpoff, 1980). No direct early selection need be postulated; a correlated response of retarded development or differential enlargement of other teeth may be sufficient to account for them. Other hypotheses that attempt to explain canine reduction are seriously flawed.

Behavioral and cultural adaptations can be interpreted as consequences of larger brains coupled with physical traits such as bipedal locomotion. The story is not linear but I organize it around three major events: Bipedal locomotion on the ground, increased brain size with the evolution of consciousness, and the controlled use of fire.

Bipedalism

The most striking departure of the earliest hominids from their relatives is a morphological shift toward sustained, bipedal striding and running. Brain enlargement is not nearly so obvious because the earliest hominids were smaller than chimpanzees and thus their brains were not absolutely larger. Relative brain expansion between modern chimpanzees and the australopithecines was about 20% to 45% as estimated from the unfortunately few data given by McHenry (1982) and Hofman (1984). These values are based on allometrically scaling the species to the same body size. Pigmy chimps are also moderately neotenic but their brains are only about 7% larger than those expected from similar-sized adult common chimps (Hofman, 1984). Reorganization of the brain may also have been significant (Halloway, 1983) although this is highly controversial (Falk, 1985, but see Deacon (1988a,b) for better evidence at a perhaps later stage).

Small apes in trees often walk bipedally along main branches. On the ground, their bipedal movement rather than quadrupedal is characteristic (Tuttle, 1974; Prost, 1980). The instigator of our upright posture while bipedal may have been neotenic development, because juvenile primates have a head that sits more upright on its spine. The neotenic pigmy chimps are more bipedal than their relatives when on the ground (Zihlman et al., 1978). Several arboreal Miocene apes were morphologically preadapted for sustained bipedal locomotion on the ground (Tuttle, 1974; Aiello, 1981), no doubt because they strode the branches of trees on two legs rather than four. Vertical climbing and leaping among small apes selects for structural traits that favor a bipedal mode of locomotion on the ground. Bipedalism does not need any strong selective forces of descent to the ground to evoke it. Morphological evidence fails to support knuckle-walking for even the earliest hominids (Johansen and White, 1979; Tuttle, 1974; Bush et al., 1982) although biochemical evidence would be easier to interpret if they used this locomotion. The matter is still highly controversial, but most sorts of biochemical evidence suggests that gorillas diverged before chimps and humans (e.g., Weiss, 1987). Hominids probably did not stand upright after moving habitually on all fours; they merely descended from trees on their two hind limbs and stayed that way. Reasons for remaining upright on the ground, if an ape is morphologically so predisposed to begin with, are more numerous than reasons to bend over to use the hands as well as the feet in walking:

-- Walking upright reduces the amount of sunlight that strikes the body directly; an average of 60% less surface area is exposed to the direct rays of the sun (Wheeler, 1984). For an ape that chooses to be active when the sun is highest, as our early ancestors may well have done (see below), an upright posture is decidedly advantageous. In the tropical climates in which hominids evolved, an upright stance, with greater exposure to prevailing breezes, further cooled the body when they were active during the hottest part of the day.

-- Often accustomed to well-amputated lawns, we might not appreciate the possibility that the early hominids probably found most food in brushy habitats through which they climbed more than strode. Walking along a tree branch was probably easier than climbing through a bramble patch. Hands are useful for pushing aside vegetation that might strike the face. The earliest hominids were shorter standing erect than the grass in many savanna habitats; on all fours, they were decisively shorter. Grass brushing across the face can be uncomfortable, so why choose such annoyance if not necessary? Swatting flies may have been another advantage of walking upright. Ungulate dung, so prevalent in open areas, attracts flies, which on a warm day can be a nuisance to any animal. A chimp might even find stumbling briefly on its hind legs a lesser evil than these buzzing insects.

-- All else being equal, a standing hominid can see farther than a bent one. Eyes or cameras placed farther from the ground can scan a larger view. Our surveillance technology, used to ensure the safety of our social groups, has gained increasing height over the millenia, from four-foot individuals to satellites. Whether upright hominids saw anything of significance is debatable. For example, in tall-grass savannas, they may not have been able to see over the grass. Even were they able to, their predators were likely concealed. While standing tall improves distance viewing, it decreases ability to detect subtle hints of food on the ground. Bipedal walking does not inhibit moving in a bent posture when searching the ground for food. Little is lost, and a lot may have been gained. Although we may not need to seek special selective advantages for bipedalism, they no doubt influenced subsequent hominid evolution:

-- Hands were available to carry food while searching for more. If our unique traits were forged in a drier habitat where food was more scarce, a biped that eats while searching has a potential advantage. Occasionally discovering a transportable excess of food might have led it to carry this back to the nesting place at night to eat the next day or to seek a shaded or safer place to eat it at that moment. (As I discuss below, distant transport of excess food applies particularly to meat but many vegetable foods can be economically carried reasonable distances.) However, since safe nesting places at night were probably a scarce resource, other individuals were undoubtedly present; they likely either solicited or stole the excess food depending on their relative social status or size. The ability to gather excess food can foster both admired human traits (sharing, provisioning) and undesired ones (theft). It need not have been an important aspect of early hominid biology and I suspect it was not regularly practiced, and thus was not an important influence on social structure, until after the use of fire (see below).

-- Upright posture has been argued to curtail development of the visually conspicuous estrous swellings that typify chimpanzees and some other primates: with the genital organs now partly between the legs, they are somewhat less visible and enormous swellings might interfere with bipedal walking (Tanner, 1981). I disagree, because enough tumescence of the female genital region can be achieved to make them quite visually conspicuous without restricting locomotion. Afterall, the genitals of females are homologous to those of males so if the latter can have large genitals, why not females? Female hyenas mimic males (see Gould, 1981b) and certain populations of humans have unusually large and conspicuous labia minora (see Gould, 1982). Bushy pubic hair obscures seeing human female genitals after sexual maturity, let alone seeing any small changes in tumescence that may occur over the menstrual cycle or with sexual readiness. Because among apes only chimpanzees have such enormous announcements of sexual readiness, the ancestral hominid probably lacked them as well. With an initial social organization that may have been more like that of gorillas or orangs, because of the high degree of sexual size dimorphism, than like that of chimpanzees, the earliest hominids may not have had any reason to advertize so blatantly their sexual readiness. Although olfactory signalling of estrus seems to have persisted in humans, its relative influence on the timing or frequency of copulation is still not clear (e.g., Money, 1981: Manson, 1986). A bipedal stance made sniffing of the genital region awkward though not impossible (Tanner, 1981), but other modes of pheromone dispersal, such as axillary and pubic hair, are thought to have evolved to overcome this difficulty (e.g., Guthrie, 1976). At present it does not seem likely that bipedalism much altered signalling of sexual receptivity in hominid females. A great deal of what we observe in human sexual behavior now may be attributed more to current social convention than to an evolutionary inheritance.

-- An upright posture caused a shift in the position of the vagina that favored ventro-ventral copulations over dorso-ventral ones (see Gould, 1975, or Gallup and Suarez, 1983), with some interesting consequences (see Sheets-Johnstone, 1989). In the dorso-ventral position a female cannot move with the male; she is passive with respect to the copulatory act. Ventro-ventral couplings, in contrast, enable each partner to thrust. Active participation by the female may have selected for longer penile size in males: if she moves in synchrony with a male, a longer penis is required to maintain contact. Among primates, human males have longer penises for their size (Short, 1976). The ability of the female to participate actively during copulation enhanced her ability to achieve orgasm [an ability potentially available to most female mammals (see Jolly, 1985)] and thus derive pleasure from the activity. The consequences of this potential were probably not realized until relatively late in our evolution, when freedom from the threat of predators gave us leisure to enjoy sex (see below).

-- Bipedal walking did not necessarily reduce the ability of an infant to cling to its mother even though its feet were less designed for gripping and an upright posture produces more sway in the upper body (it might have been like clinging to the upper branch of a tree). Arms were available for support, although an infant as precocial at birth as chimps are (a state that probably existed until the emergence of modern humans: see Trinkaus, 1986) had reasonable ability to cling to its mother's hair by its own efforts until further neoteny at some stage reduced body hair. However, as scalp hair increased in thickness (and possibly in length as a response to bipedal wanderings into the open at midday: see below), a precocial infant still had hair to grip with its hands but also a waist to grip with its legs and an occasional support from a mother's hand. Older infants could "piggy-back" a ride with arms around the neck or scalp hair with at least as much safety as an infant ape rides upon its mother's back.

Large Brains

Although bipedalism certainly influenced some human traits, the increase in brain size was more significant for the acquisition of most hominid traits, particularly when coupled with bipedalism, a trait that neoteny also partially caused. Brain increase has been a general trend in vertebrate and particularly in primate evolution. As mentioned above, primates got brainier over time, in part as a developmental consequence of retarded development. Did it really help them survive? If so, how?

The first primates originated early in the mammalian radiation at the end of the Cretaceous (Van Valen and Sloan, 1965). As dinosaurs vanished and flowering plants and insects flourished, the earliest primates found a rich source of food in the terminal branches of trees. With grasping fingers instead of paws, they could sneak quietly along a branch and grasp an insect before it was aware of its danger (Cartmill, 1974). A hand that can cling to a branch while the other is reaching for a fruit suspended from a branch that will not bear one's weight is also useful. Hands had an advantage until wings proved superior. Birds and bats can move more rapidly through the canopy of a forest than primates can. They can scan for and locate fruiting trees more rapidly. A larger brain that remembered the position and timing of fruiting trees could possibly compete. Once it finds the trees it can feed while keeping winged competitors at bay by a swipe of the hand.

Hands were probably the most important innovation for the prosimian way of life; a larger brain only helped living in the three-dimensional world of trees. Among vertebrates in general, arboreal species have larger brains than their closest relatives (e.g., Eisenberg, 1981). A large brain has some strong disadvantages. It lengthens the time of development at all stages of life while increasing the energy needed to support this highly active organ (Hofman, 1983). To be brainy requires finding more food while slowing down the rate at which one reproduces. It is puzzling why increased brain size has evolved unless it does have strong adaptive advantages. One observable trend in vertebrate evolution is that an increase in body size is accompanied by a decrease in relative (but an increase in absolute) brain size (e.g., Jerison, 1973). Larger body size reduces reproductive potential, so reducing relative brain size helps to compensate. High reproductive potential is advantageous, as anyone concerned with controlling mice, rabbits, or other pests realizes. Yet brain increase has been a recurring trend in primate evolution. Once birds (previously occupying different niches) and bats evolved to compete with the niche prosimians had carved for themselves, those species that got brainier had an advantage and survived. They have persisted even if not particularly numerous. Human dominance of the energy control on Earth attests to a shaky superiority of brain versus reproductive control. Too often human populations are severely decimated by pests with higher reproductive potential that have become able to get around their controls. The story of primate and human evolution centers on the value of larger brain size. Most of the other unique human traits are simply consequences of a neotenic development that produced juvenile mammals with relatively larger brains. I briefly summarize the advantages that relatively larger brains gave primates at each major stage of their evolutionary history subsequent to the early prosimian radiation discussed above.

-- Prosimians were faced with a pirating of their main resource by swifter bats and birds. They can't develop wings readily to meet their competitors on their own ground, so their descendants take an offensive stance. With larger brains achieved by both an increase in body size and neotenic trends in development, primates remember where trees are in fruit (insects are abandoned with the increase in body size as a less profitable food). If they get there in time, they can dominate food supply by sheer size. Thus, the continued success of the primate lineage was being secured by the larger monkeys as the smaller prosimians were being competively challenged by birds and bats. Prosimians still maintain high diversity in Madagascar, where monkeys never invaded (Le Gros Clark, 1971). This fact renders the actual culprit in prosimian decline uncertain; it may have been both the swifter birds and bats and the brainier monkeys, or maybe the latter alone.

-- Monkeys diverged in their radiation, with the brainier lineage adhering to the ancestral pattern of eating fruit. Old World monkeys (Cercopithecidae) wandered out into open areas and experimented with greens for a diet (Andrews, 1981). As a consequence, they developed defenses against the toxins that most plants produce. Many of them also evolved a stomach somewhat like a ruminant's, where microorganisms ferment the otherwise indigestible cellulose of their diet and remove some toxins (Langer. 1988). They could tolerate eating greener fruit than apes when they went back to the forest in a natural expansion of their niche and so partly outcompeted them there (Andrews, 1981). Memory no longer helped the apes because if monkeys ate available fruit earlier, it was no longer around when the apes remembered that it should be optimally ripe. Monkeys had one disadvantage. Their journey into open terrestrial environments fixed upon them a quadrapedal mode of locomotion. In trees they walk along the limbs on all fours and are less successful at reaching fruit suspended from the terminal branches. Many arboreal monkeys have concentrated on leaves rather than fruit.

-- The ape lineage reflected the prosimian radiation except for considerable enlargement in body size and relative brain size: they still reached for fruit at the terminal branches of trees and did so with a variety of locomotory patterns and sizes, as did the prosimians. Competitive pressure from monkeys forced apes to find food in a different way. Most didn't, so their large radiation in the Miocene has dwindled to only a few. The most speciose group of apes are now the small gibbons, which swing through the forests with greatly elongated arms and reach for food at the end of branches, where monkeys have difficulties getting to. The other forest apes got larger and so could coexist with monkeys by sheer body mass. The ape that became the ancestor of hominids moved into the open, where they could compete with terrestrial monkeys by having a different way of obtaining food, coupling the advantages of large relative brain size with those of bipedal locomotion.

The bipedal choice left hands unencumbered by locomotory constraints; they could be otherwise used for more than food gathering. They eventually were, but the initial and continued success of the hominid lineage depended more on their larger brains than their bipedality. Initially, larger brains with greater memory capacity aided them in exploiting resources in more open habitats. They could remember the positions of plants that produce tubers during the lean dry season even though the exposed parts had vanished. When dwindling forests in a drying climate crowded the native primate habitat, new abilities to find another meal elsewhere were valuable to continued existence. On the savanna, as in the forest, a superb topographic memory may have made the difference between going hungry or finding food. The ability to remember minute structural details of a landscape preceded the superb communicatory abilities of humans as the major cause for success of a larger brain that necessarily slowed reproductive rate. Memory initially as well as later enhanced the survival of our ancestors (Parker and Gibson, 1979). Hominids were not particularly unique at this stage of their evolution but were possibly more flexible and skilled at finding hidden food when hunger gave an advantage to the brainier. As an analogy, consider the many small advantages of a photographic memory, all else being equal, even in a society which relies on various extensions of brains for memory retention and retrieval.

Finding hidden sources of food in an open, seasonally dry habitat was only one advantage of a better memory. As small and physically defenseless animals, brainy hominids probably soon learned that their predators slept during the middle of the day. What better defence for the defenceless than avoidance, and what better time to seek food than the middle of the day if one can tolerate the heat? An upright stance and increased ability to sweat enhanced the ability of hominids to be active for sustained periods of time during the hottest part of the day (see Carrier, 1984). Being cowards thereby led to an ability to outrun potential prey; thus commenced the life of a predator in a primarily herbivorous lineage.

Becoming predatory may also be attributed to selection for larger brains. Adequate brain development requires a diet relatively high in protein. Meat is a highly desired food for most primates although it is debatable whether they actively seek it. The fact that other primates are a major source of meat might mean only that they are the easiest to capture (they have no better escapes than their erstwhile predators), although this fact has generated some provoking theories (e.g., Goodall, 1986). With larger brains our lineage needed more energy (particularly protein) to support their growth and development and with larger brains they may have been better at acquiring it. Learning the habits of potential predators or prey as well as the location of buried tubers may have enhanced finding meat, either on the hoof or recently dead. For example, vultures are visual signals that some animal had recently died.

Regular meat-eating, whether from predatory or scavenging activity, has been definitely associated with only one of two lineages of bipedal apes (see Wolpoff, 1980). That which seemed to eat meat also had a larger brain size than earlier hominids. Other traits indicate it was also more neotenic. Evidence from teeth simply suggests that one lineage adapted to a diet of tougher vegetable food by evolving stronger and larger teeth whereas the other used tools to macerate their food instead. Chimpanzees and other animals sometimes use tools to extract otherwise unavailable food (see King, 1986). They do not, however, regularly make or store tools for such purposes. Modifying a part of the environment to enhance future extracting ability suggests a greater power of abstraction, an awareness that the environment could be manipulated to enhance survival. A greater memory capacity of Homo habilis may have been decisive to this new ability.

The presence of tools and foreign stones to make more tools at sites of bone accumulation (see Potts, 1984) suggest an incipient consciousness in H. habilis. These hominids came to realize that it was both easier and safer to carry back carcasses or parts thereof to an adequate supply of good stone tools with which to cut off rapidly edible meat. The presence of uncut, foreign stone that seems to have been carted from some distance implies a greater degree of consciousness than yet shown by any ape, consciouness being a knowledge of future intent based on past events that gave success. Cache sites were a way that hominids could be successful scavengers/hunters in a highly competitive world where their strength and speed ranked them near the bottom for their size.

Hominids had one advantage over other predators/scavengers attracted to a carcass or kill: if they were there first, they could quickly cut off limbs and rapidly run off with them. Hyenas often drag parts of carcasses away to hide for later consumption (Kruuk, 1972), but such a process is necessarily slow. Although not particularly fast, hominids developed unusual stamina and thus could run for longer distances during the heat of the day than other predators (Carrier, 1984). They were also likely to be first at a carcass, spotting it by buzzards, in the middle of the day. Most predators, with the exception of hunting dogs (Lycaon), which had entered Africa only about that time (see Malcolm, 1980), were sleeping off their luck of the previous night or early morning. Nevertheless, unlucky and hungry predators were undoubtedly about and soon would show up at a carcass. The cache site was no safer than the carcass itself, but the hominids had some time to cut off meat with the aid of abundant tools and retreat to the safety of trees before they were located. Whether the hunters often obtained enough to take back with them to the waterhole by which they spent the night with other members of the social group will likely remain unknown. Presumably they sometimes struck big and had far more than they could eat then. Once back with others they undoubtedly shared. Meat spoils fast in a hot climate and its very desirability induces others to take it by force or by stealth. Presumably the hunters could gain more by judicial sharing. Back then meat, rather than gold, could 'buy' what was available (perhaps sex or prestige).

Fire

Awareness that one can manipulate the environment enhances finding and preparing the next meal. For a long time little happened until our ancestors discovered how to control fire. Before then they were confined to trees or cliffs during much of the day when predators were seeking prey. A hungry predator is not going to be deterred by a few rocks launched at it by several or even dozens of puny hominids. It could undoubtedly get one and leave. Weapons that are effective against prey or predator appear only rather late in human evolution. The earliest tools seem to be simply tools (see Isaac, 1986). Fire, however, frightens as well as fascinates many animals; it both attracts and repels. With it our ancestors can keep potential predators (competitors) at a distance. Because they have arms, a group of 'hunters' can carry a relatively large carcass (scavenged or killed) back to a place where they were safe. Vigilance was required because any large kill attracts potential scavengers. Possibly our association with dogs stemmed from an incipient domestication initiated by the use of fire. Attraction to fire led to familiarization with hominids; they became less feared when they did not attack. Athough it is hard to make 'friends' with squirrels and birds in the city, consistent feeding and cautious approach can lead a squirrel to accept food from one's hand. Domestication was probably as profitable for the recipient as for our ancestors. Dogs were probably better at locating prey and hominids at killing it (at least later in our evolution).

Fire finally freed hominids from a fear of predators and provided leisure to exploit their growing consciousness. It probably had more influence on their social structure than any other single event in their history. With it they could finally become fully terrestrial animals; retreat to trees or cliffs at night was no longer necessary to protect them against predators. Fear of the dark was banished with light, and the generated heat enabled them to invade parts of the world formerly too cold. The effective day was lengthened and hominids now had more time for socializing in a close group than one scattered in the trees with approaching dusk. Individuals can become better acquainted and lifelong friendships better forged. With growing memory from larger brains, individuals began to obtain more distinct personalities based on their past actions. Dominance was no longer a matter of who was stronger at this moment in time; it became increasingly a matter of who generally had better success at leadership. An ageing or somewhat wounded leader of the hunt may retain his rank despite physical weakness.

The importance of fire to the transition from ape to human is central because it enabled hominids to control their physical environment, to shape it to suit their physical inadequacies, to invade lands where no other primate had ever gone before. Without it, hominids still gained consciousness or sapience and that lent our ancestors success in direct competition with better-endowed predators. Without it, hominids would probably have been stuck at being just another animal species with a limited geographic range and subject to the usual environmental changes that affect the survival of other species. Without it, hominids could never have eliminated their competition as they are currently in the process of doing (along with a great deal more besides). Fire had far-reaching social and intellectual consequences that I only briefly summarize below.

It is unfortunate that the time of origin of the controlled use of fire is so uncertain. Equivocal evidence places its origin at about 1.4 million years ago, solid evidence, at only 0.5 million years (see James, 1989). Within that nearly million-year span Homo erectus showed significant increase in brain size. Later populations of erectus had brains that overlapped in size those of modern humans. Did it really take a very large increase in brain size (about double the mass between habilis and late erectus) for hominids to realize that they could control and use fire to their advantage? At present we don't know, but future finds may clarify the issue. The exceedingly slow cultural change of Homo erectus suggests that they, like habilis before them, still lived in trees and led much the same way of life. They were larger and more successful hunters with somewhat more elaborate tools, but they still lacked projectile weapons or other compound tools (see Butzer, 1977). The controlled use of fire did not definitely appear much before the first sapiens (in the broad sense) about 400,000 years ago (see James 1989), and thus its consequences may have been experienced only by the later erectus populations. Although fire undoubtedly provided the context for the accelerated late Pleistocene (Upper Paleolithic) cultural change (which is either coincidentally or causally associated with the appearance of anatomically modern humans), it did not immediately trigger a revolution. What did still baffles our imaginations although the answer perhaps lies amidst the increasing accumulation of facts about human history and biology. Some of the direct consequences of fire on the material and social lives of hominids include the following:

A home base with a protective fire encouraged hunters to bring all meat to that base, where females and young were present. Although the hunters may still have eaten the best of the spoils, the leftovers were available to women and perhaps to the infirm, children and camp scavengers. Skins and bones were initially thrown aside as useless. Children ever seek interesting things to explore in their leisure time. Large cardboard boxes discarded from refrigerators or other large objects often provide endless sorts of diversions for the young. Imagine playing hide and seek among discarded skins and discovering they kept one dry in the rain. Children probably had somewhat more leisure time with longer days created by fire and the preservation of food (they did not have to spend all their safe waking hours foraging). Only in agricultural or industrial societies can a lot of useful work be found for children (see Zeller, 1987).

Fire not only preserved food but kept competitors away from the store. Bones with fragments of meat that are hard to remove (e.g. vertebrae) were probably tossed aside. If unclaimed by camp scavengers the meat may have had a chance to dry in the sun. Women about camp or children may have noticed fewer flies or maggots upon such meat. Someone hungry may have tried eating it and found it still tasteful. Eventually a connection between drying meat and long-term preservation may have occurred. Meat preservation significantly improved the survival probabilities of our ancestors. A series of large kills could be saved to cover a series of failures. Banking to avoid theft serves much the same purpose. Microbes were a major thief of hard-won meat in those days, and they are still our competitors (Janzen, 1977).

With fire about as protection, our ancestors may have discovered that cooking meat made it both tasty and easier to eat. The soft parts harden but the tough parts soften with dry heat. More than taste, cooking meat kills certain important parasites such as tapeworms and trichinid worms. Those populations that preferred their meat barbecued probably enjoyed better health and so prospered. Most of the vegetable foods we currently eat provide little nutrient value without cooking (see Stahl, 1984), although soaking seeds in water and letting them sprout releases more nutrients (a technique that may have been discovered long before the controlled use of fire). The real contribution of gathered plant food to the diet of early Paleolithic humans, when hunting was reasonably established, is not well understood. Certainly many plants provided essential nutrients not found in meat and almost anything can still a rumbling stomach when hungry. Women with their somewhat reduced mobility, imposed by pregnancy or clinging young, probably stayed near camp to tend fires, to gather fuel, to preserve meat, to cure skins, to gather available edible vegetables, and to perform endless other tasks the hunters had no time, inclination, or energy to consider while preparing for or recovering from a hunt of large animals. Parenthetically, it is only after the use of fire that evidence for regular big-game hunting exists (see Wolpoff, 1980), and with it a division of labor between the sexes.

Interaction of Fire, Brains, and Bipedalism: Emergence of Unique Human Traits

Positive evidence for the emergence of traits that we regard as truly human (aside from large brains, tool-making, and bipedalism), appear in the fossil record long after the controlled use of fire. This evidence more or less coincides with the appearance of anatomically modern humans and disappearance of archaic ones (see White, 1982; Mellars, 1989: Mellars and Stringer, 1989). The controlled use of fire initiated a new way of life for a brainy primate with a juvenile personality, but at some point a new element entered that changed our ancestors in a significant way (e.g., see Tudge, 1989). When hominids became human is an academic question until we can decide upon a definition for humanity. Nevertheless, one form of hominid becomes associated with positive evidence for the traits that we think make us different from other animals.

Although archaic Homo sapiens had as large brains as anatomically modern humans, if not larger (Neanderthals), they lack the art and evidence of individuality that distinguish the later group. They may not have been able to speak (or sing) as well as later humans, but convincing (though somewhat controversial: Gargett, 1989) evidence that they bury their dead, does support existence of some type of language: abstract thoughts such as a belief in an afterlife can be communicated only through language. Although I cannot fully support it (see Trinkaus, 1986, for some evidence), a premature time of birth in anatomically modern humans as a side effect from pelvic narrowing to improve long-distance running (and thus hunting ability), may well have led to greater brain power. Studies have shown that exposure to more complex environments during early infancy increases cortex mass and the number of neural connections (Rosenzweig et al., 1972; Wallace, 1974). A month or so of life outside the womb during the period of brain expansion likely contributed to a rise in "intelligence". Perception of individuality is perhaps the trigger that separated science and art as well as populations and also enhanced technological control at some expense to the quality of life.

I cover below some of the consequences of the contolled use of fire by a brainy, bipedal primate. When these attributes appeared is not particularly at issue here. If Neanderthals were really like modern humans in individualistic drive, I feel sorry for them. Yet our species may be picking up the past in more ways than fashion. When we can communicate so instantly with the world, human differences erode and individuals begin to solve the problem of their individual uniqueness. Back to fire.

-- Fire enabled our ancestors to make fuller use of their intellects. The discoveries of household economy mentioned above were a product of opportunity and a brain that could take advantage of it. A larger brain has greater memory capacity, all else being equal. Correlations or patterns in the environment are very much the product of memory. Repeated associations suggest causations that induce experimentation. If they hold and are useful, they are adopted. Given the leisure that fire presented and larger memories that tied past events together to suggest a causation or a future happening, symbolic communication emerged as a necessity. Gestural and simple vocal communication are adequate for activity that occurs in the present. Symbolic communication is needed when one is attempting to express a correlation of past events with the present and relate it to the future. One cannot point to something seen in the past or indicate where that is likely to be tomorrow.

Much of this abstract symboling may have been related to hunting, but I suspect not. Human curiosity needed an outlet. Potentially meaningful patterns conceived by an individual need confirmation by peers to become meaningful and useful, and thus the need for a way to communicate them. A larger memory provides a larger past and thus a larger set of data amongst which to find patterns, many of which may have had no direct survival value at the time. Later they did. At times society has ignored science as irrelevant to immediate human concerns, but in a broad sense it may have been the basis of our language and a cause for improvement of our material culture. In art and music language is irrelevant; their symbolism lacks the time component of a verbal language. Their message is more emotional and more immediate than the abstractions of science. In art there is no directional correlation between past and future. They capture the essence of a present mood rather than a logical potential of the future. Evidence of art does not necessarily mean existence of language. The latter probably preceded the former, mainly because evidence of burial preceded indications of art. The existence of burial suggests communication of abstract ideas.

-- Memory invaded dreams. Past events recurred with vivid imagery yet they became jumbled with current events. Did past events have something to say about what is troubling now? Did a mother long dead appear in a dream that gave direction to future acts? Such dreams disturb us now. Why not our ancestors? In those dreams, individuals that have died reappear because they are a part of our memories. The more significant an impact certain individuals have on one's life, the more they emerge in one's dreams. One can observe death, but at night that individual lives on. It invades the mind in situations that never really existed, so they are not just memories of the past. That individual still lives and might be indicating future events. There is a spirit land where one goes upon death; one does not truly die but can return as an insubstantial image. The more impact individuals made in life, the more they resided in the memories of their contemporaries and the more they lived on in the stories they told to their children. There really is quasi-immortal life: that carried by the orally transmitted and recorded memory of our descendants. Such memory has survival value. Wisdom of creative individuals is not forgotten and may influence the life of a society for many millenia. Continuity of culture is not destroyed when a particularly strong leader dies. Continuity of a band may benefit after the death of an inspired leader until another as equally as talented can take its place. Poetry may have originated as a means to keep memory alive. It is easier to memorize words that have cadence and rhyme and succinct sharp imagery. The earliest recorded literature is poetic in nature.

Dreams give rise to an afterlife and thus to reverence for the remains of the recent dead. Burial signifies that hominids probably had such a conception by the Middle Paleolithic (see Garrett, 1989). More controversial is whether burial signifies the existence of a spoken language. I suspect it does, because to reach such a conclusion as the existence of an afterlife, individuals had to relate their dreams to others. Gestures and simple vocalizations are simply not adequate to explain dreams.

-- Fire led to more cohesion and less fission among early humans. It concentrated the activities of a group that formerly had dispersed among several trees for rest and safety at night. Now groups up to 30 or so clustered about the same fire and were in continual contact. Dispersal to obtain food occurred during the day but at other times a fire drew individuals together into more intimate contact than experienced by any other primate. With larger memories, individuals obtained more distinct personalities. As mentioned above, history now enters into the social structuring of a society. Individuals are judged not simply on what they are now but on what they have been in the past. Current status probably rested as much on past laurels then as it does now.

Concentration of individuals has both benefits and drawbacks. Individuals can learn to know one another better but tensions mount as crowding grows. Increasing loss of body hair as a result of neoteny rendered grooming among individuals less necessary but that same neoteny produced a juvenile seeking of affection. Our ancestors evolved themselves into a bind -- requiring less (for ectoparasite removal) but wanting more physical stimulation from others. Grooming in chimps grades into massages in hominids that might culminate in copulatory acts within or between sexes. Preferred grooming partners were probably friends, those individuals with whom daily troubles were shared. Such friends were most likely of the same sex but, as estrus lost its imperative, females may have sought such grooming from male as well as female friends. Female equality has deep roots, as does homosexuality. Intellectual compatibility more than a breeding imperative influenced our choice of a partner with whom to release tensions by means of behaviors that can be construed as sexual or juvenile in nature, depending on one's inclination. Strong affection or a personal bonding to an individual that is considered as a form of 'love' was more likely homosexual than heterosexual in origin, simply because it reflected mental rather than hormonal drives. This 'love' can be interpreted as a more intense friendship that involves physical as well as intellectual and emotional sharing. Among many other animals, homosexual behavior has been observed in other apes, particularly the bonobos, which are the most neotenous of the great apes. Our greater indulgence in non-reproductive sexual behaviors (substitutes for grooming) may simply reflect our more neotenous nature. We have childlike personalities that need constant affection and reassurance to face a world in which our behavior is uncertain. Behavior has become more choice and less genetic in origin and inquisitive minds find more questions than answers. Affection from those one loves reassures that one's behavioral choices are acceptable.

-- Fire meant a consistent sharing of meat with women and children because the hunters could bring large game to a place of safety. In return for meat, females helped the hunters in many ways, as mentioned above. A one-to-one pairing between a male and female for economic efficiency may have begun with the use of fire but only during interglacials or in unglaciated regions (most of the Earth) was such an arrangement ideal. The earlier hunters had herds of large game animals to pursue. The hunt was a cooperative effort of all males of the social group and the spoils available to all. It was a communal society in which individual differences in contribution were not tallied, except in leadership roles, in legend, or perhaps a special food from a kill. All worked for the good of the group and individual success was recognized in continual survival (although in communes some individuals are recognized as 'leaders' and others as 'followers', but leaders benefit only when their group flourishes). In Europe after the latest glaciation, forests replaced steppes and tundra. Game no longer roamed in large herds but foraged in isolation. Hunting became an activity for an individual or a pair (plus dogs?). Division of the meat and skin became asymmetric, with the hunter and his dependents getting the better share. When hunters work alone, a female to help out may have made a crucial difference. Although sexual activities may still have been highly promiscuous, a female tended to pair with a male for the economic benefits. Is hunting the oldest profession?

Later, when personal possessions or wealth became a human attribute, women became more valuable entities than simply willing partners. With language, kinship could be tallied and kin were to benefit more than non-kin (see below for a discussion of the origin of kinship). Females can inherit or marry into possessions. They became an item of wealth, a possession that lost its function. For the few with wealth, slaves or servants did the tasks a female once performed. Now, she merely represented a transfer of possessions, including delivery of undoubted heirs. Virginity became as valued as beauty or money. Our promiscuous nature, developed out of need for companionship as we realized our uniqueness from the rest of the living world, was ineffectively suppressed as wealth and control over the world became more important. Equality returns somewhat as we have finally mastered our control of the world and realize we are lonely once more. We seek the heavens for other conscious minds while attempting to speak with chimps. With too many humans to feed and with better survival, females are no longer breeding machines. They have been reluctantly admitted to have intelligence (Gould, 1981a) and should be as free as males to enjoy the pleasure of sex. Breeding is no longer a prime directive. Unwanted children alone could keep humans thriving for the next several centuries. With superb survival, a very low birth rate is sufficient and perhaps desirable.

-- Kinship dominates studies of our own species. We keep close track and usually avoid incest. Those most familiar to one are those one might want to 'groom' most. Incest leads to pregnancy and frequently disastrous offspring. Exceptionally excellent ones can be expected as well, but as the bad seemed to outweigh the better, incest avoidance became a nearly universal practice. Why keep track of our relatives? Sometimes we do not even like them, so why acknowledge them? Why leave possessions to kin who may waste their inheritance rather than to an unrelated kindred spirit who might appreciate and make good use of it? What do kin have that non-kin lack? I suspect familiarity and thus a share in one's memories. An individual with which one grows up becomes a part of one's memory, a part of oneself. Genetic identity is less important than familiarity. If personality is inherited, socially or biologically, one may like kin better on the average than strangers. Our ancestors had little idea of genetics but the consciousness that led them to speech also led them to an awareness of a pattern of birth defects and resemblances. Perhaps the resemblance of sire and first offspring (given a virgin bride) promoted the habit of leaving possessions to such an individual, one reborn and one likely to behave as one had.

-- Fire promotes unity in several ways and yet divides by that same unity. It provides a safe haven from predators as well as releasing our dreams. It invokes a unity of spirit amongst those who sit around it. Flame-induced trances evoke memories and recall the dead to the living. At some point our large memory banks caused us to realize that we were different, not just from other species and not just from other social groups, but also from one another. Personal distinction became a goal. Group distinction often aided that goal. We became a species of societies where membership is desired and not-to-belong becomes a sort of death. Family ties have similarities to religious ones. They evoke the same emotions to unite the members. One works for a larger identity than one's self whose goal thereby incorporates the personal goal. The recognition of individuality that initially divided humans into 'them' and 'us' continues to divide. Deviants simply fracture off to start a new society, to become hermits, or to find somewhere else to live. Earth has become too small to contain our differences. We exterminate alternative versions of ourselves as readily as other species when they get in our way. We either need more worlds to contain our splintered identities or we need to realize that we are essentially the same despite the differences.

Given group identity, the ability to accumulate wealth, greed, and the burden of the past, war was inevitable. Whenever another had something desirable, simply take it rather than bargain and trade. 'They', not 'us', are expendable. Expansion genetically favors one's potential success. Societies can expand without war, but the latter is perhaps the most direct way to do so and was the one favored by our ancestors in recorded history and ethnography. As individuals, stealing can become acceptable behavior; as nations, it is our patriotic duty to do so or to prevent 'others' from taking what belongs to 'us'. What do 'others' have that 'we' seek to gain? A history of war is needed to provide a precise answer. Expansion of living space or patchily distributed essential resources are common excuses, but any and all, have been used. Simple retaliation or capture of a free wife can be an excuse to eliminate others too like us but not part of our group. Maybe even hair or eye color can discriminate 'us' from 'them'. Similarity breeds more antagonism, because the similar are more likely to be successful at obtaining whatever is desired. Similarity breeds contempt or at least more superficial differences to fault. Basically, the same process that generates diversity among living organisms promotes diversity and antagonism among human groups. The main difference is that one is driven by a biological imperative; the other, by rationality. 'We' are right and 'they' are wrong.

In Conclusion

Large brains have brought us far -- from plucking insects at the end of branches to plucking 'others' from the skies. Despite the slowing down of reproduction engendered by larger brains, we still threaten to ruin Earth with the pollution brought on by our overcrowding. Vast expanse of population not only depletes the Earth, it directly leads to stress (Bornstein and Bornstein, 1976). The long story of our history is one of the steady success of larger, more juvenile brains punctuated with other biological or cultural acquisitions. A bipedal stance gave us a competitive advantage over better endowed predators which we avoided when we learned to work while others slept. Making stone tools to hasten dismembering a carcass or digging up roots gave us the idea we could transform Earth to suit our needs. With fire, we have largely succeeded to the point of our discomfort. With technological mastery came the concept of love when one bewildered juvenile turned to another for comfort. Our memories have brought us a lot although wisdom may have escaped us thus far. Our brains have ceased to increase in absolute size but we continue to extend our childhood and thus the time of creative thought. Although the matter is controversial, modern humans may have differed from archaic ones like the Neanderthals by a premature birth forced upon them by a more delicate skeleton better suited for sustained running. Exposure to a complex environment before the brain has finished maturing ensures greater neuronal connectiveness and thus greater intelligence. Greater technological skill demanded more time to master, so the young were forced to school. Discoveries of adults become the toys of the next generation. Our children achieve what we could only imagine. Within the memories of a few we have gone from the first sustained flight in air to the moon. We have also fought two wars that involved most of the world. We become ever more bewildered children, uncertain where our brains have led us.

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