THE PATTERN OF HUMAN EVOLUTION: Studies on Bipedalism, Mastication, and Encephalization

Henry M. McHenry

Department of Anthropology, University of California, Davis, California 95616

INTRODUCTION

The recent and sudden proliferation of hominid fossil discoveries sparks new interest in human evolution, especially in the early part of the story. In the last decade the sample of pre-three-million-year-old australopithecines has multiplied by more than a hundredfold. A decade ago almost the entire East African Plio-Pleistocene hominid fossil record fit in a few cookie tins in a small safe; it now fills an entire room. Instead of isolated bits we now have samples of populations with most skeletal parts represented.

What follows is an account of recent refinements and revisions of our understanding about the pattern of human evolution, specifically the tempo and mode of the evolution of hominid bipedalism, the human dental configuration, and encephalization. Taxonomy, ecology, behavior, dating, and other topics have been reviewed recently elsewhere (14, 15, 16, 35, 72, 95, 98, 110, 204, 248, 255–257, 258, 286).

For over a century the prevailing view among evolutionists has been that bipedalism preceded encephalization (167). Lamarck (123), Haeckel (73), and Darwin (39) made this clear. The last decade of hominid fossil discoveries has made some surprising refinements in this view. Perhaps the most dramatic discovery is the pattern revealed by the 3.7 to 3.0 m.y. old *Australopithecus afarensis:* bipedalism is established, yet absolute brain size is about one third that of modern *Homo sapiens* and teeth are intermediate between pongid and hominid (110). Does this imply a complete mosaic? When and how did bipedalism evolve and was it completely established before the human pattern of dentition originated? When and through what

151

stages did human dentition evolve? Did *relative* brain expansion only occur in the last 3 m.y.? Why did it expand, and is there paleoneurological evidence of reorganization? Remarkable progress in human evolutionary studies over the last decade brings clearer answers and new questions.

BIPEDALISM

The last decade has been extraordinarily successful in terms of the number and quality of discoveries of Plio/Pleistocene hominid postcrania. When the author began research on this collection about a decade ago there were less than three dozen hominids known with postcrania and most of these were isolated scraps (160). Now the number stands closer to 300, spans a greater time range, and includes complete elements and a partial skeleton (181, 254).

The South African sites have produced a slow but steady flow of new hominid postcrania and several important new studies of the old material. The year 1972 saw the publication of *Early Hominid Posture and Locomotion* by John Robinson, who described and analyzed the old material in great detail (218). He proposed that the robust australopithecines were inefficient bipeds who retained tree-climbing adaptations in the hindlimb. The South African gracile hominids of Sterkfontein and Makapansgat, in his view, were efficient bipeds whose postcrania resembled later members of the genus *Homo*. Even though these views have attracted few supporters (148–151, 156, 162, 164, 167), the book stands as an invaluable source of information about these important hominids. Reanalyses of the shoulder (23, 184, 268, 270), elbow, (160, 167, 170, 175, 227–231), wrist (143, 144, 181), and metacarpals (47, 144, 218) of the South African australopithecines reveal how strikingly primitive or unique these hominids were in their forelimb. New studies of the hindlimb show that these creatures were bipedal (17, 26, 31, 32, 41–43, 46, 50, 76, 142, 148–151, 154–156, 159, 160, 162–178, 181, 212, 213, 218, 243, 254, 267, 269, 295–298, 300), but the morphology of the hip and ankle is uniquely different from *H. sapiens* (31, 32, 160, 163–167, 174, 176–178, 183, 186–190, 192, 218, 243, 246, 262, 271, 300, 303, 304). The meaning of these hindlimb differences is still subject to an unresolved and often contentious debate (148–151, 153–156, 181, 188–190, 262, 296–298, 300). New attempts to estimate body size of these South African hominids result in different estimates [ranging from 18 kg (151) to 37 kg (288) for *A. africanus* and 36 kg (168) to 80 kg (218) for *A. robustus*]. The author is most comfortable with 35 kg for *A. africanus* and 44 kg for *A. robustus*, with both species showing greater variability than *H. sapiens*, which probably reflects greater sexual dimorphism [females about two-thirds the size of males (160, 163, 168, 171, 181)].

A great leap in the quality and quantity of postcranial material came in the early 1970s with the collections from East Turkana, Kenya (129). The material provided fodder for new academic wars between those who recognized two patterns of postcranial morphology (and possibly gait) between 1.8 and 1.3 m.y. ago (41, 43, 45, 46, 176, 178, 290, 293) and those who considered all the material as undiagnostically different from *Homo* except in features related to muscularity and parturition (148–151, 155, 156, 289). The study of the East Turkana postcrania is made difficult by the fact that the two or more species that inhabited that lake shore between 1.8 and 1.3 m.y. ago did not leave their taxonomically diagnostic elements (skulls and teeth) associated with their postcrania, so one can never be sure a given femur is *A. boisei* or *H. habilis* or something else (129). The richness of the East Turkana material made appreciation of variability much easier: there is an extraordinary range of sizes and shapes of each element. The concurrent work at Omo produced a nearly complete ulna, together with other postcrania, which further confirmed the primitiveness of the forelimb in at least one species at 2 m.y. (66, 96, 180). Not all early hominid forelimbs were primitive, however. The Kanapoi humerus found in 1967, which is believed to be from beds that are 4 m.y. old, is perfectly modern in all details (160, 161, 170, 175, 203, 227–231). The 2 to 1.5 million-year-old Olduvai postcrania show the same variability: some elements are modern looking and some retain many primitive features (9, 40–44, 46, 49, 145, 146, 185–193, 212, 213, 244, 245, 291).

The discoveries at East Turkana were spectacular for the 1.8 to 1.3 m.y. range, but nothing could overshadow Hadar, Ethiopia, for the 3 to 3.5 m.y. age (105–111). Early knees added proof of bipedalism in human evolution predating *A. africanus* (105–111). Lucy appeared in 1974 with her 40% complete adult skeleton dating back to 3 or 3.5 m.y. ago (106, 108–111). The discovery of the First Family at the 333 location, which slightly predates Lucy, added a population of 13 individuals who apparently died together at the same time (106, 109–111). Some features of these *A. afarensis* postcranial remains include: 1. their striking resemblance to *A. africanus* despite diagnostically different dentitions and crania (181); 2. their adaptation to bipedality at this early date (110); 3. the primitiveness of some aspects of their limbs (181, 262); 4. the total lack of any diagnostic knuckle-walking adaptations in their hands (110); 5. the small size of the female (23 kg) compared to the male (51 kg) (171); and 6. the long pubis forming an oval-shaped birth canal which was wide from side to side but restricted from front to back (152). The last point means that theories on the lateral support system and its relationship to parturition and encephalization need revision (148–152, 156, 166, 167). It was once thought that the differences between the australopithecine and modern human hips were due to the demands of

the ever increasing brain size of the newborn in human evolution (135–137), which led to a lengthening of the load arm relative to the power arm of the gluteal abductors in the frontal plane (side to side) (156). The reconstructed Lucy (AL 288) pelvic girdle shows that the changes in the evolution of the human hip were not so much in the frontal plane as in the front-to-back dimension. Whatever the specifics of pelvic remodeling are, however, there is clearly a relationship between birth canal size and brain size in hominid evolution (114, 115, 135, 136, 138–140). A commitment to bipedalism in *A. afarensis* seems obvious from the extraordinary footprints found in the 3.8–3.6 m.y. ashes of Laetoli, Tanzania, showing all the features of modern hominids including a convergent big toe, heel strike, arches, and human-like proportions (25, 48, 125–127, 282). An additional set of footprints of a later hominid has been found at East Turkana (10).

Fossils are not all that is new in the study of bipedalism, however. Refined laboratory techniques of electromyography (67a, 99, 100, 242, 260–267), kinesiology (34, 267), and biomechanics (233, 234, 241) have yielded crucial information for the interpretation of hominid and hominoid locomotion leading to reinterpretations of what may have changed during those early years of our family. Energetic measures of locomotion of bipedal and quadrupedal gaits have cleared up many false impressions about the sequence of events leading to our ancestor's first steps (64, 65, 75, 157, 197, 219, 240, 250–252, 259).

This new evidence has led to many new interpretations of evolution of hominid bipedalism. Critical evaluation must concentrate on just a few of the most influential of these ideas, since they are the ones which get into textbooks and most pervasively influence general theories on human evolution.

One such influential theory is the idea that *Australopithecus* was identical to *Homo* in its postcrania except for features related to muscularity and parturition (289). This implies that the postcranium of *Australopithecus* had already evolved a long way from the last common ancestor of apes and man, having retained no trace other than muscularity and changes due to parturition of its nonhominid antecedents. But the case for primitive retentions and uniqueness is strong. From shoulder to toe some species of *Australopithecus* do have plesiomorphic (primitive) and automorphic (uniquely derived) traits not shared by the genus *Homo*. For example, the recently reconstructed shoulder of *A. africanus* from Sterkfontein has a plesiomorphic configuration of glenoid which sits at a pongid-like angle relative to the spine and axillary border (270). In its unreconstructed state it had phenetic affinities with *Pan* not *Homo* (23). The distal humerus of *A. robustus* also has many phenetic affinities to the apes and not *Homo* (170, 175). Details of the wrist such as the posterior position of the trapezoid facet on the capitulum or the lack of a third metacarpal styloid process in *A.*

africanus are clearly primitive (i.e. found in catarrhine primates in general but not in *Homo*) (143, 181). The shape of the *A. robustus* thumb metacarpal is strongly curved, robust, and unlike *Homo* in overall shape (217). The ulna is strongly curved and has *Pan*-like features not generally found in *Homo* (69, 96, 180). The australopithecine forelimb appears slightly longer relative to the hindlimb than is generally true of *Homo* (109). The foot phalanges are relatively long and curved in *A. afarensis* (106, 262).

Could these and other australopithecine traits of the forelimb imply a terrestrial locomotor behavior other than bipedalism? With available evidence from the hindlimb the answer is an unequivocable no. All diagnostic hindlimb specimens of *Australopithecus* show a complete reorganization for bipedalism, and forelimbs show no sign that they were used as a quadrupedal prop. The australopithecine hip is clearly incompatible with quadrupedalism (151). So what do the plesiomorphic traits of the forelimb imply? Perhaps some or all species of *Australopithecus* were more arboreal than *Homo* (23, 218). An alternative is that the adoption of bipedalism led to relatively rapid reorganization of the hindlimb, but a slower change in the forelimb resulting in the retention of many primitive features.

Another influential view sees *Australopithecus* becoming extinct on its own side branch without evolutionary connection to *Homo* (10, 11, 189, 190, 303). One version of this theme is expounded by Oxnard and colleagues: using sophisticated methods of analysis, they report that the *Australopithecus* postcrania are so unlike *Homo* that an evolutionary connection is unlikely (10, 11, 145, 146, 183–193, 303, 304). For example, the pelvic blades are rotated differently, the shoulder is unlike modern *Homo sapiens* (10, 11, 185, 190), and the talus of the foot is not like any living biped (10, 11, 145, 146, 186–193). These and other conclusions are derived from elegant and complex anatomical analyses which are more free from observer bias than other approaches and take into account variability and other factors that influence anatomical analyses. Those workers in the majority (i.e. those who believe *Australopithecus* was bipedal like *Homo* and ancestral to *Homo*) tend to ignore the challenge. Some criticism has been leveled at aspects of their approach, however (26, 28, 169, 292). Perhaps the source of much of the disagreement comes from equating phenetic resemblance or dissimilarity with taxonomic and phylogenetic affinity without dissecting out shared primitive traits from shared derived traits (55, 56, 59, 226, 248, 249). One should expect *Australopithecus* to share numerous primitive traits with its last common ancestor with the pongid evolutionary lineage, but taxonomic and phylogenetic affinities should be based solely on shared derived traits. A relatively long ischial shank or splayed iliac blades do link *Australopithecus* with Pongidae, but these are primitive retentions overshadowed by the much more taxonomi-

cally, phylogenetically, and functionally relevant traits such as lowered iliac blades, bipedally adapted knees, and feet with convergent big toes, short toes, and arches.

Theories on the origin of bipedalism itself are by their very nature important and speculative. They are important because they involve the first change that differentiated the hominid evolutionary lineage from the rest of the animal kingdom. They are speculative because they require reconstruction of so many unknowns, especially the morphology, behavior, and ecology of the last common ancestor and the first hominid. Darwin's view of the origin of bipedalism remains useful (39): bipedalism arose when our ancestors came "... to live somewhat less on trees and more on the ground," which was due to "... a change in its manner of procuring subsistence, or to a change in the conditions of its native country" (p. 135). More specific causes for the adoption of upright posture have been proposed such as carrying (78, 79, 80, 120, 153), display or warning (147, 216, 280), new feeding adaptations (57, 112), tools (120, 276–279), or a combination of these (221, 232). A conservative view is that the hominid ancestor maintained the typical hominoid foraging regime in a Miocene habitat in which food was becoming more and more widely dispersed and required greater terrestrial travel to harvest (81, 219, 220). Bipedalism could easily have been the mode of terrestrial travel for this arboreally adapted hominoid, as it is in all of the modern species of lesser apes, since modern hominoids are equally efficient as bipeds or as quadrupeds at normal speeds (251). Given the added advantage of free forelimbs, bipedalism for a small hominoid seems likely. An objection to this model is that bipedalism could only arise under special circumstances because it is presumably an inefficient way for a mammal to get about (153). Such an objection misses two important points, however: 1. our Miocene hominoid ancestor was probably *not* an efficient quadruped since modern hominoids are inefficient quadrupeds (251), and 2. hominid bipedalism is as efficient as average mammalian quadrupedalism at normal speeds (219). The first point was proved by Taylor & Rowntree (251), who tested two chimpanzees for energetic efficiency during bipedalism and quadrupedalism and found the surprising result that the two patterns used about the same amount of energy. Both gaits used 50% more energy than the average quadrupedal mammal. Such a result makes sense because the hominoid body is adapted to a certain style of arboreal locomotion which makes terrestrial gait energetically costly (251, 253). The second point is confirmed by recalculating the energy expenditure of humans and chimpanzees walking at normal speeds: the human energetic cost is about average for the mammals, but the chimpanzee still uses about 50% more energy per body weight (219). The adoption of bipedalism by a Miocene hominoid need not be taken as such an unlikely

event, especially given the fact that all lesser apes today are habitual bipeds (34, 267) and bipedalism can easily be adopted by modern chimpanzees in the wild (12).

A far more elaborate view is presented by Lovejoy (153) using information from a wide spectrum of sources including mammalian demography, ecology, and social behavior. At the core of the theory is the notion that bipedalism evolved in response to selection pressures on food carrying by monogamous males who provision their home-bound mates and their dependent infants. Unlike chimpanzees, so the theory goes, early hominids could produce more than one infant per 5.6 years per female as long as the faithful male would share in rearing responsibilities. Any complex hypothesis like this, especially one about hominid origins, will receive its share of petty criticisms of details which may add up to rejection of the whole edifice unfairly. On the other hand, complex hypotheses should be compatible with most relevant information available. The scenario is not likely to win over many anthropologists, ecologists, or primatologists familiar with mammalian and human mating systems; all available evidence indicates that early hominids were polygynous and not monogamous and that male provisioning of immobile females and offspring was unlikely. The living descendants of these early hominids are certainly not strictly monogamous; only about 20% of human societies today have laws prohibiting polygyny and these are usually recent and commonly broken in practice (97). Among all monogamous primates, sexual dimorphism is nearly absent, but in *A. afarensis* it is pronounced (106) (males may be nearly twice the weight of females), as one might expect in a polygynous species (141). All monogamous primates are highly territorial, with the adult male and female and their offspring forming the exclusive territorial unit (1, 287). *A. afarensis* apparently lived in much larger groups, as indicated by the 333 site of Hadar where apparently 13 individuals died together 3.5 m.y. ago (106). No monogamous primate species is known to have a male who provides food for the female and her offspring (287). Among modern hunters and gatherers the female does more than her share of the food gathering even while carrying an infant. Among the !Kung San (Bushmen) the female walks an average of almost 5000 miles in the first 4 years of a child's life while carrying the infant (132). The average female gathers an estimated 12,000 calories per day in food while the male averages only about 7,230 calories (97, 122). Nor is paternal care of infants limited to monogamous primates (20, 97). Decrease in birth spacing is hardly a sufficient cause for the origin of monogamy and paternal care. As Hrdy & Bennett (97) point out, a polygynous male with two females giving birth every 6 years would produce 1.6 babies for every one that a single female would produce with 5 year birth intervals.

MASTICATION

Evolutionists studying hominid dentition live at an exciting time, and we can appreciate their euphoria over the discovery of *A. afarensis* (105–111, 286). In so many traits this species fills the gap between the pongid and hominid patterns, proving that bipedalism preceded the evolution of many of the distinctive human dental adaptations.

The strikingly primitive pattern of the *A. afarensis* dental apparatus is clear when compared with Le Gros Clark's description of the total morphological pattern which distinguishes the dentitions of hominids and pongids (24). He asserted that these traits have high taxonomic relevance. In the intervening three decades, most authorities have agreed (21). All of the species of *Australopithecus* except *A. afarensis* clearly have the hominid pattern (24). *Australopithecus afarensis* fills the gap: in some respects it is hominid, in some respects pongid, and in others unique (106, 128, 281, 284, 285).

Of Le Gros Clark's total morphological pattern of hominid versus pongid dentitions, the most strikingly pongid characters of *A. afarensis* include straight postcanine dental rows, diastema, conical-shaped canines with sharp points, anterior and posterior attrition facets on the canines, canine cingulum and small talonid, strong canine sexual dimorphism, oblique first lower premolar, and very small metaconid on the first lower premolar (105–111, 128, 283–286).

One completely unanticipated and often overlooked peculiarity of *Australopithecus* is postcanine megadontia. Early describers may have occasionally mentioned the fact that the teeth appeared large relative to body weight, but usually mastication was studied by one set of experts and postcrania by another. Jolly (112, 113) and Wolpoff (288) were two of the first to explicitly examine the relationship. Pilbeam & Gould (209) put the study on firmer quantitative grounds in which they showed that all *Australopithecus* species had enormous cheek teeth relative to estimated body weight. They argued that relative to body weight, cheek tooth area in *modern* hominoids is relatively constant. One can explain the difference in size of cheek teeth in *Pan, Homo,* and *Gorilla* merely as an artifact of body size. Although their conclusion that all australopithecines are scaled variants of the same animal has been criticized (27, 29, 30, 116, 294), it is clear that all species of *Australopithecus* are way above modern hominoids in relative cheek tooth size. This is true for *A. afarensis* as well. The diagnosis of this species contained the statement that the species had relatively smaller cheek teeth (104), but this is true only relative to front teeth and not to body weight. Even without estimating body weight the relation holds; there are several australopithecine individuals with associated jaws and

postcrania (AL 288, TM 1517, Sts 7) in which general body size can be compared directly to tooth size for the same individual. Relative to post-cranial size, the cheek teeth of *A. afarensis, africanus,* and *robustus* are enormous compared to other hominoids. By analogy, Pilbeam & Gould (209) and others (58, 112, 113, 145, 274, 275, 288) make a case for a diet for *Australopithecus* especially high in vegetation. Bone crushing (247) and seed eating (112) seem unlikely from recent scanning electron microscope studies of enamel wear (222, 223, 272, 273). Meat was certainly part of the human diet by 2 million years ago (19, 98). Some dietary differences may have existed between species of early hominids (72).

The last decade has also witnessed the rapid accumulation of fossil homi-noids of the Middle to Late Miocene, particularly those classified in the family Ramapithecidae (2–8, 51–54, 122, 194, 195, 205–208, 210, 235–239). As defined by Pilbeam (205–208), this family includes genera such as *Ramapithecus, Sivapithecus, Gigantopithecus,* and possibly other genera. These new fossils show that there was a whole radiation of Middle to Late Miocene hominoids characterized by their heavy chewing mechanisms. The mandibular corpus is thick and deep, the cheek teeth are relatively large, bunodont, and have much thicker enamel than is characteristic of the living African great apes. The faces are short, which gives leverage advantage to power of the bite, and the attachment areas for the muscles that move the jaw are rugose and heavy. If the postcrania is correctly classified (none of it was directly associated with gnathic elements), then it is clear that these forms were also postcanine megadonts like *Australopithecus* (205–207).

Surprisingly, the great increase of Ramapithecine gnathic material recov-ered in the last decade has not led to unanimity of opinion about the phylogenetic position of *Ramapithecus.* Some view *Ramapithecus* as the first member of Hominidae (117, 235–239), implying that the human evolu-tionary lineage diverged from the rest of Hominoidea before 16 m.y. Others place *Ramapithecus* on a side branch to extinction (33, 71, 179, 225, 301), noting that the genetic similarity between great apes and people (18, 225) precludes such an early differentiation of Hominidae. A compromise might be that an open-country adapted *Ramapithecus*-like form is the common ancestor of both great apes (or just African great apes) and people (207, 299). This compromise view is unlikely for several reasons, however: 1. the hominoid forelimb and trunk is a uniquely derived complex which is adapted for arboreal life (253–255) and only secondarily and still energeti-cally inefficiently adapted to the terrestrial locomotion required for open-country life (251); 2. the many similarities among the dentitions of living great apes which are different from *Ramapithecus* would have to have evolved in parallel two or three separate times; 3. the resemblances in the masticatory apparatus of *Australopithecus* and *Ramapithecus* are most

probably the result of parallel evolution in that they represent a similar and separate hominoid solution to open-country life (33, 71, 179). The face of Ramapithecidae aligns this group more closely to *Pongo* (173, 208).

More detailed studies of hominoid dentitions may never resolve the issue of the status of *Ramapithecus* because hominoid teeth are so conservative (3). Faces and postcrania may be the most important elements to establish hominoid phylogeny. The author's and Corruccini's efforts to sort the teeth phylogenetically using multivariate analysis and cladistics lead to the conclusion that the common ancestor of *Pan, Gorilla,* and *Australopithecus* was unlikely to be *Ramapithecus* (33, 179). By this analysis the 5 to 5.5 m.y. old Lothagam jaw fragment is the earliest known fossil hominid with derived traits which are shared by later members of Hominidae (202).

ENCEPHALIZATION

Early evolutionists were mindful of the idea that the human brain evolved after many other human features had been established (39, 73, 123). Few predicted the completeness of the mosaic, however (167). Bipedalism almost completely preceded encephalization as did the evolution of most human dental features: Bipedal hominids lived on this earth for at least 2 m.y. before encephalization really began in earnest. Only in the last 2 m.y. has endocranial volume tripled in absolute size and doubled in relative size.

The last decade has brought an avalanche of new evidence. The claim that brain size in some 1.8 to 1.6 m.y. old East African hominids was significantly larger than brain size in *Australopithecus* (124) was dramatically confirmed by the discovery of the 1470 skull (129–131). Several useful reviews of hominid paleoneurology and encephalization have been published recently (61, 62, 70, 74, 86, 101, 102, 182, 215). Reliable endocranial volumes of all possible new Plio/Pleistocene hominids have been published by a single skilled investigator whose work forms the cornerstone of hominid paleoneurology today (82–92). Table 1 presents these endocranial volumes of the Plio/Pleistocene hominids with some comparative examples and body weight estimates made by the author from studies of the original postcranial fossils (168, 171). Also shown are two measures of relative brain size. The values for *A. afarensis* are based on early reports of the estimated cranial capacities of two *A. afarensis* endocranial casts which are approximately 380 cc and 450 cc (106, 118). Body weight estimates based on regression analyses (168, 171) for small *A. afarensis* postcrania (AL 288) and large postcrania (AL 333-3) are 23.0 kg and 51.2 kg, respectively.

Table 1 also presents two measures of relative brain size. The encephalization quotient (E. Q.) is the actual endocranial volume divided by the scaled body weight times 0.12 (101). The scaling coefficient is 0.67 which

Table 1 Endocranial volume, estimated body weight, and encephalization coefficients for fossil hominids and living comparisons

TAXA	Endocranial volume (cc)	Estimated body weight	E.Q.[a]		C.C.[b]	
			Actual E.Q.	As a percent of *H.s.*	Actual C.C.	As a percent of *H.s.*
F. oregonensis[c]						
(mountain lion)	107	28.8	1.0	14	10.1	10
P. troglodytes[d]	395	45.0	2.6	38	33.6	34
A. afarensis	415[e]	37.1[f]	3.1	45	36.9	37
A. africanus	442[g]	35.3[f]	3.4	49	40.0	40
A. robustus	530[h]	44.4[f]	3.5	51	45.2	46
H. habilis	636[i]	48.0[f]	4.0	58	53.3	54
H. erectus[d]	1,050	53.0	6.2	90	86.0	87
H. sapiens[d]	1,230	57.0	6.9	100	99.1	100

[a] Encephalization quotient (101–104).
[b] Constant of cephalization (77).
[c] A carnivore which has a relative brain size close to the mammalian mean (214).
[d] From Pilbeam & Gould (209).
[e] From Johanson & Edey (106).
[f] Calculated from McHenry (168, 171).
[g] From Holloway (82).
[h] From Holloway (83).
[i] From Holloway including O.H. 7, 13, 25; KNM-ER 1470, 1805, 1813 (84–92).

fits the relationship between brain and body weight in a large sample of living mammals (70), although recent research shows the coefficient may be higher (158). The constant of cephalization (77) is the actual endocranial volume divided by the body weight scaled to the 0.23 power, which usually fits closely related animals better than does the 0.67.

One interesting fact to emerge from the study of these endocranial volumes and their size relative to scaled body weight is how long hominid brains stayed at a very small size. From almost 4 to about 2 m.y. absolute and relative brain size changed insignificantly. The relative endocranial volume of *A. afarensis* was only slightly above the level seen in *Pan* today, particularly if body weight is scaled by the coefficient 0.23 (constant of cephalization). What emerges is an image of a creature with a brain size much more like any other member of the suborder Anthropoidea (where E. Q. = 2) than like *H. sapiens.* These were creatures with all the constraints of the animal world without language or agriculture. It is a false bias to treat them as humans.

Although it is clear from available evidence that a revolution in brain-size increase occurred about 1.8 m.y. ago, the relationship between time and endocranial volume is difficult to assess. A simple double logarhithmic relationship (133, 134) is inappropriate (69). The evolution of brain size

since 2 m.y. appears gradual (35) but may in fact be punctuated with periods of rapid encephalization and periods of stasis (69, 302).

Studies of the reshaping of the brain in human evolution based on endocranial casts have been fraught with difficulty and controversy (61–63, 70, 86, 89, 93, 94, 101–104, 201). Especially difficult have been attempts to distinguish uniquely hominid shape characteristics. Dart's (36–38) early claim for a caudal position of the lunate sulcus in the Taung endocranial cast (hominid-like) is apparently based on incorrect identification of that sulcus (61, 62, 94). Other claimed shape differences also may not be valid such as relative height of the cortex and angle of the orbital surface of the frontal lobe (62, 86). For a review of this controversy the reader is advised to consult especially the works of Falk (61–63), Holloway, (85–94), Jerison (101–104), and Passingham (198–201). A recent review by Falk (61) concludes that "Features that distinguish hominid from pongid brains seem to be the result of allometry (i.e. determined by brain size) rather than the result of selection for qualitatively different neurological features" (61, p. 93). The details of neural reorganization can best be studied by comparative neurology of living animals, although careful studies of the exterior shape of endocranial casts are valuable (89).

The reason for encephalization in human evolution is not obvious. A concise review is given by Falk (61), who lists warfare (211), language (39, 63), tools and labor (39, 60, 119), hunting (80, 121), and heat stress (67) as five recent favorites. Caspari (22) and Sacher (224) suggest a relationship between encephalization and longevity. Gabow emphasizes population structure and culture (68). Although some or all of these "prime movers" may have been involved, language emerges as the most likely (61, 63, 196).

CONCLUSIONS AND SUMMARY

Over the last decade, the enormous proliferation of new information about the origin and evolution of human bipedalism, mastication, and encephalization has changed many old views, confirmed others, and added unanticipated details to knowledge about the pattern of human evolution. A few highlights reviewed here include:

1. As predicted by early evolutionists before evidence was available, bipedalism preceded encephalization in human evolution, although the extent to which the two features evolved separately is a surprise revealed by new discoveries of *A. afarensis* fossils and footprints. Adaptation to walking upright with a striding gait in this 3.6 m.y. old hominid is obvious, yet its relative brain size is only just above that of the modern chimpanzee.

2. The human dental pattern evolved at yet another rate as revealed by *A. afarensis.* An overall resemblance to *Homo* is clear, especially in the

somewhat reduced size of the canine, but in numerous other respects this earliest human species spanned the gap between pongid and hominid dentitions.

3. Although *Australopithecus* is a committed biped, it still retains a surprising number of primitive traits of the forelimb which link it to the common ancestor of apes and people. There are also many unique features of the hindlimb.

4. Sexual dimorphism in body size was stronger in *A. afarensis* than in *Homo,* implying a polygynous mating system if the universal pattern seen in living primates is true of this extinct species.

5. The pelvic girdle of *Australopithecus* was relatively narrow from front to back having a narrow conjugate diameter of the birth canal and laterally splayed iliac baldes. The pelvic girdle became more rounded in *Homo,* possibly as a result of selection for a wider birth canal for larger-headed newborn, but also possibly for added efficiency of bipedal gait.

6. There are so many shared derived traits linking early *Australopithecus* with early *Homo* that it is very likely that these forms were in an ancestral-descendant relationship.

7. The origin of hominid bipedalism may not have involved extraordinary events, but could have arisen as an energetically efficient mode of terrestrial locomotion for a small-bodied hominoid moving between arboreal feeding sites.

8. The evolution of human dentition passed through an unexpected stage of postcanine megadontia in which cheek teeth expanded enormously relative to body size. This pattern may have evolved from a similar pattern in the Middle to Late Miocene Ramapithecidae, but more likely was an independent acquisition from a smaller toothed, forest-adapted hominoid.

9. Only in the last 2 million years has relative brain size increased rapidly in human evolution beginning with the appearance of *Homo habilis.* The pattern of this increase through time is not necessarily gradual nor is it demonstrably punctuated.

10. Reorganization of the hominid brain in evolution is nearly impossible to demonstrate from fossil endocranial casts. Comparative neurology of extant hominoids is a more likely source of information about reorganization. Language is the most likely single feature involved in both encephalization and neural reorganization in hominid evolution.

Literature Cited

1. Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., Sherman, P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In *Evolutionary Biology and Human Social Behavior,* ed. N. A. Chagnon, W. I. Irons, pp. 402–35. North Scituate, Mass: Duxbury
2. Andrews, P. 1978. Taxonomy and relationships of fossil apes. In *Recent Advances in Primatology,* ed. D. J. Chivers, K. A. Joysey, pp. 43–56. London: Academic
3. Andrews, P. 1981. Species diversity and diet in monkeys and apes during the Miocene. In *Aspects of Human Evolution,* ed. C. B. Stringer, pp. 25–61. London: Taylor & Francis
4. Andrews, P., Evans, E. N. 1979. The environment of *Ramapithecus* in Africa. *Paleobiology* 5(1):22–30
5. Andrews, P., Molleson, T. I. 1979. The provenance of *Sivapithecus africanus. Bull. Br. Mus. Nat. Hist. (Geol.)* 32(1): 19–23
6. Andrews, P., Tekkaya, I. 1976. *Ramapithecus* in Kenya and Turkey. *Proc. 9th Congr. I.P.P.S.* 6:1–14
7. Andrews, P., Tobien, H. 1977. New Miocene locality in Turkey with evidence on the origin of *Ramapithecus* and *Sivapithecus. Nature* 268:699–701
8. Andrews, P., Walker, A. 1976. The primate and other fauna from Fort Ter-

nan, Kenya. In *Human Origins: Louis Leakey and the East African Evidence,* ed. G. Ll. Isaac, E. R. McCown, pp. 279–304. Menlo Park, Calif: Benjamin
9. Archibald, J. D., Lovejoy, C. O., Heiple, K. 1972. Implications of relative robusticity in the Olduvai metatarsus. *Am. J. Phys. Anthropol.* 37:93–96
10. Ashton, E. H. 1981. Primate locomotion: some problems in analysis and interpretation. *Philos. Trans. R. Soc. London Ser. B* 292:77–87
11. Ashton, E. H. 1981. The Australopithecinae: their biometrical study. *Symp. Zool. Soc. London* 46:67–126
12. Bauer, H. R. 1977. Chimpanzee bipedal locomotion in the Gombe National Park, East Africa. *Primates* 18(4): 913–21
13. Behrensmeyer, A. K., Laporte, L. F. 1981. Footprints of a Pleistocene hominid in northern Kenya. *Nature* 289: 167–69
14. Boaz, N. T. 1979. Hominid evolution in eastern Africa during the Pliocene and early Pleistocene. *Ann. Rev. Anthropol.* 8:71–85
15. Boaz, N. T., Howell, F. C. 1977. A gracile hominid cranium from Upper Member G of the Shungura Formation, Ethiopia. *Am. J. Phys. Anthropol.* 46: (1):93–108
16. Brain, C. K. 1981. *The Hunters or the Hunted? An Introduction to African*

Cave Taphonomy. Chicago: Chicago Univ. Press

17. Brain, C. K., Vrba, E. S., Robinson, J. T. 1974. A new hominid innominate bone from Swartkrans. *Ann. Transvaal Mus.* 29(5):55–63

18. Bruce, E. J., Ayala, F. J. 1979. Phylogenetic relationships between man and the apes: electrophoretic evidence. *Evolution* 33(4):1040–56

19. Bunn, H. T. 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291:574–77

20. Busse, C., Hamilton, W. J. III. 1981. Infant carrying by male chacma baboons. *Science* 212:1281–83

21. Campbell, B. G. 1972. Conceptual progress in physical anthropology: fossil man. *Ann. Rev. Anthropol.* 1:27–54

22. Caspari, E. W. 1979. Evolutionary theory and the evolution of human brain. In *Development and Evolution of the Brain,* ed. M. E. Hahn, C. Jensen, B. C. Dudek, pp. 9–28. New York: Academic

23. Ciochon, R. L., Corruccini, R. S. 1976. Shoulder joint of Sterkfontein *Australopithecus. S. Afr. J. Sci.* 72:80–82

24. Clark, W. E. LeGros. 1964. *The Fossil Evidence for Human Evolution.* Chicago: Univ. Chicago Press. 2nd ed.

25. Clarke, R. J. 1979. Early hominid footprints from Tanzania. *S. Afr. J. Sci.* 75:148–49

26. Corruccini, R. S. 1975. Morphometric assessment of australopithecine postcranial affinities. *Syst. Zool.* 24(2):226–33

27. Corruccini, R. S. 1976. Multivariate allometry and australopithecine variation. *Evolution* 30(3):558–63

28. Corruccini, R. S. 1978. Morphometric analysis: uses and abuses. *Yearb. Phys. Anthropol.* 21:134–50

29. Corruccini, R. S., Ciochon, R. L. 1979. Primate facial allometry and interpretations of australopithecine variation. *Nature* 281:62–64

30. Corruccini, R. S., Henderson, A. M. 1978. Multivariate dental allometry in primates. *Am. J. Phys. Anthropol.* 48:203–8

31. Corruccini, R. S., McHenry, H. M. 1978. Relative femoral head size in early hominids. *Am. J. Phys. Anthropol.* 49(1):145–48

32. Corruccini, R. S., McHenry, H. M. 1980. Hominid femoral neck length. *Am. J. Phys. Anthropol.* 52(3):397–98

33. Corruccini, R. S., McHenry, H. M. 1980. Cladometric analysis of Pliocene hominids. *J. Hum. Evol.* 9:209–21

34. Cortright, G. W. 1976. A kinematic analysis of gibbon bipedalism. *Am. J. Phys. Anthropol.* 44(1):172 (Abstr.)

35. Cronin, J. E., Boaz, N. T., Stringer, C. B., Rak, Y. 1981. Tempo and mode in hominid evolution. *Nature* 292:113–22

36. Dart, R. A. 1925. *Australopithecus africanus:* The man-ape of South Africa. *Nature* 115:195–99

37. Dart, R. A. 1926. Taung and its significance. *Nat. Hist.* 26:315–27

38. Dart, R. A. 1967. *Adventures with the Missing Link.* Philadelphia: Institutes Press

39. Darwin, C. 1872. *The Descent of Man and Selection in Relation to Sex.* New York: Appleton. 2 vols.

40. Day, M. H. 1969. Femoral fragment of a robust australopithecine from Olduvai Gorge, Tanzania. *Nature* 221:230–33

41. Day, M. H. 1973. Locomotor features of the lower limb in hominids. *Symp. Zool. Soc. London* 33:29–51

42. Day, M. H. 1974. The interpolation of isolated fossil foot bones into a discriminant function analysis—a reply. *Am. J. Phys. Anthropol.* 41(2):233–35

43. Day, M. H. 1974. Development of hominid locomotion. *Nature* 251:9–10

44. Day, M. H. 1976. Hominid postcranial material from Bed I, Olduvai Gorge. See Ref. 8, pp. 363–74

45. Day, M. H. 1976. Hominid postcranial remains from the East Rudolf succession. In *Earliest Man and Environments in the Lake Rudolf Basin,* ed. Y. Coppens, F. C. Howell, G. Ll. Isaac, R. E. F. Leakey, pp. 507–21. Chicago: Univ. Chicago Press

46. Day, M. H. 1978. Functional interpretations of the morphology of postcranial remains of early African hominids. In *Early Hominids of Africa,* ed. C. J. Jolly, pp. 311–45. London: Duckworth

47. Day, M. H., Scheuer, J. L. 1973. A new hominid metacarpal from Swartkrans. *J. Hum. Evol.* 2(6):429–38

48. Day, M. H., Wickens, E. H. 1980. Laetoli Pliocene hominid footprints and bipedalism. *Nature* 286:385–87

49. Day, M. H., Wood, B. A. 1968. Functional affinities of the Olduvai hominid 8 talus. *Man* 3:440–55

50. de Arsuaga, J. L. 1981. Iliac angular measurements in *Australopithecus. J. Hum. Evol.* 10:293–302

51. deBonis, L., Bouvrain, G., Melentis, J. 1975. Nouveaux restes de primates hominoïdes dans le Vallésien de Macédoine (Grèce). *C. R. Acad. Sci. Paris* 281D:379–82

52. deBonis, L., Melentis, J. 1977. Un nouveau genre de primate hominoïde dans le Vallésien (Miocène supérieur) de Macédoine. *C. R. Acad. Sci* 284D: 1393–96

53. deBonis, L., Melentis, J. 1977. Les primates hominoïdes du Vallésien de Macédoine (Grèce). Étude de la machoire inférieure. *Géobios* 10(6):849–85

54. deBonis, L., Melentis, J. 1978. Les primates hominoïdes du Miocène supérieur de Macédoine. Étude de la machoire supérieure. *Ann. Paleontol. Vertébr.* 64(2):185–202

55. Delson, E. 1977. Catarrhine phylogeny and classification: principles, methods and comments. *J. Hum. Evol.* 6:433–59

56. Delson, E., Eldredge, N., Tattersall, I. 1977. Reconstruction of hominid phylogeny: a testable framework based on cladistic analysis. *J. Hum. Evol.* 6: 263–78

57. DuBrul, E. L. L. 1962. The general phenomenon of bipedalism. *Am. Zool.* 2:205–8

58. Dunbar, R. I. M. 1976. Australopithecine diet based on a baboon analogy. *J. Hum. Evol.* 5(2):161–68

59. Eldredge, N., Tattersall, I. 1975. Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. *Contrib. Primatol.* 5:218–42

60. Engels, F. 1973. The part played by labour in the transition from ape to man. In *Selected Works,* ed. K. Marx, F. Engels, 3:66–77. USSR: Moscow Progress Publ.

61. Falk, D. 1980. Hominid brain evolution: the approach from paleoneurology. *Yearb. Phys. Anthropol.* 23:93–108

62. Falk, D. 1980. A reanalysis of the South African australopithecine natural endocasts. *Am. J. Phys. Anthropol.* 53(4): 525–40

63. Falk, D. 1980. Language, handedness, and primate brains: did the australopithecines sign? *Am. Anthropol.* 82(1):72–78

64. Fedak, M. A., Pinshow, B., Schmidt-Nielsen, K. 1974. Energy cost of bipedal running. *Am. J. Physiol.* 227(5): 1033–44

65. Fedak, M. A., Seeherman, H. J. 1979. Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* 282:713–16

66. Feldesman, M. R. 1979. Further morphometric studies of the ulna from the Omo Basin, Ethiopia. *Am. J. Phys. Anthropol.* 51(3):409–16

67. Fialkowski, K. R. 1978. Early hominid brain evolution and heat stress: a hypothesis. *Stud. Phys. Anthropol.* 4: 87–92

67a. Fleagle, J. G., Stern, J. T. Jr., Jungers, W. L., Susman, R. L., Vangor, A. K., Wells, J. P. 1981. Climbing: a biomechanical link with brachiation and with bipedalism. *Symp. Zool. Soc. London* 48:359–75

68. Gabow, S. L. 1977. Population structure and the rate of hominid brain evolution. *J. Hum. Evol.* 6(7):643–65

69. Godfrey, L., Jacobs, K. H. 1981. Gradual, autocatalytic and punctuational models of hominid brain evolution: a cautionary tale. *J. Hum. Evol.* 10: 255–72

70. Gould, S. J. 1975. Allometry in primates, with emphasis on scaling and the evolution of the brain. *Contrib. Primatol.* 5:244–92

71. Greenfield, L. O. 1980. A late divergence hypothesis. *Am. J. Phys. Anthropol.* 52(3):351–66

72. Grine, R. E. 1981. Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microscope analysis of occlusal events. *S. Afr. J. Sci.* 77:203–30

73. Haeckel, E. 1868. *Natürliche Schopfungsgeschichte.* Berlin: Reimer

74. Hahn, M. E., Jensen, C., Dudek, B. C., eds. 1979. *Development and Evolution of Brain Size. Behavioral Implications.* New York: Academic

75. Hayes, K. C., Winter, D. A., Norman, R. W. 1977. Energetics of bipedal locomotion. *Yearb. Phys. Anthropol.* 20: 481–90

76. Heiple, K. G., Lovejoy, C. O. 1971. The distal femoral anatomy of *Australopithecus. Am. J. Phys. Anthropol.* 35: 75–84

77. Hemmer, H. 1971. Beitrag zur Erfassung der Progressiven Cephalisation bei Primaten. In *Proc. 3rd Congr. Primatol. Zürich, 1970,* ed. J. Beigert, W. Leutenegger 1:99–107. Basel: Karger

78. Hewes, G. W. 1961. Food transport and the origin of hominid bipedalism. *Am. Anthropol.* 63(4):687–710

79. Hewes, G. W. 1964. Hominid bipedalism: independent evidence for the food-carrying theory. *Science* 146:416–18

80. Hewes, G. W. 1973. Primate communication and the gestural origin of language. *Curr. Anthropol.* 14:5–24

81. Hockett, C. F., Ascher, R. 1964. The human revolution. *Curr. Anthropol.* 5:135–47

82. Holloway, R. L. 1970. New endocranial values for the Australopithecines. *Nature* 227:199–200

83. Holloway, R. L. 1972. New australopithecine endocast, SK 1585, from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 37:173–86

84. Holloway, R. L. 1973. New endocranial values for the East African early hominids. *Nature* 243:97–99

85. Holloway, R. L. 1974. The casts of fossil hominid brains. *Sci. Am.* 231(1):106–15

86. Holloway, R. L. 1975. *The role of human social behavior in the evolution of the brain.* 43rd James Arthur Lecture on the Evolution of the Brain, pp. 1–45. New York: Am. Mus. Nat. Hist.

87. Holloway, R. L. 1975. Early hominid endocasts: volumes, morphology, and significance for hominid evolution. See Ref. 261, pp. 393–415

88. Holloway, R. L. 1976. Paleoneurological evidence for language origins. *Ann. NY Acad. Sci.* 280:330–48

89. Holloway, R. L. 1979. Brain size, allometry, and reorganization: toward a synthesis. In *Development and Evolution of Brain Size*, ed. M. E. Hahn, C. Jensen, B. C. Dudek, pp. 59–88. New York: Academic

90. Holloway, R. L. 1980. Within-species brain-body weight variability: a reexamination of the Danish data and other primate species. *Am. J. Phys. Anthropol.* 53(1):109–22

91. Holloway, R. L. 1980. The O.H. 7 (Olduvai Gorge, Tanzania) hominid partial brain endocast revisited. *Am. J. Phys. Anthropol.* 53(2):267–74

92. Holloway, R. L. 1981. The endocast of the Omo L338y-6 juvenile hominid: gracile or robust *Australopithecus? Am. J. Phys. Anthropol.* 54(1):109–18

93. Holloway, R. L. 1981. Exploring the dorsal surface of hominoid brain endocasts by stereoplotter and discriminant analysis. *Philos. Trans. R. Soc. London Ser B* 292:155–66

94. Holloway, R. L. 1981. Revisiting the South African Taung australopithecine endocast: the position of the lunate sulcus as determined by the stereoplotting technique. *Am. J. Phys. Anthropol.* 56(1):43–58

95. Howell, F. C. 1978. Hominidae. In *Evolution of African Mammals*, ed. V. J. Maglio, H. B. S. Cooke, pp. 154–248. Cambridge: Harvard Univ. Press

96. Howell, F. C., Wood, B. A. 1974. Early hominid ulna from the Omo basin, Ethiopia. *Nature* 249:174–76

97. Hrdy, S. B., Bennett, W. 1981. Lucy's husband: what did he stand for? *Harvard Mag.* 83(6):7–46

98. Isaac, G. L., Crader, D. C. 1981. To what extent were early hominoids carnivorous? An archaeological perspective. In *Omnivorous Primates*, ed. R. S. O. Harding, G. Teleki, pp. 37–103. New York: Columbia Univ. Press

99. Ishida, H., Kimura, T., Okada, M. 1975. Patterns of bipedal walking in anthropoid primates. *Symp. 5th Congr. Int. Primatol. Soc., 1974*, pp. 287–301. Tokyo: Jpn. Sci. Press

100. Ishida, H., Okada, M., Tuttle, R. H., Kimura, T. 1978. Activities of hindlimb muscles in bipedal gibbons. In *Recent Advances in Primatology*, Vol. 3, Evolution, ed. D. J. Chivers, K. A. Joysey, pp. 459–62. London: Academic

101. Jerison, H. J. 1973. *Evolution of the Brain and Intelligence.* New York: Academic

102. Jerison, H. J. 1975. Fossil evidence of the evolution of the human brain. *Ann. Rev. Anthropol.* 4:27–58

103. Jerison, H. J. 1976. Paleoneurology and the evolution of the mind. *Sci. Am.* 234(1):90–101

104. Jerison, H. J. 1977. Should phrenology be rediscovered? *Curr. Anthropol.* 18:744–46

105. Johanson, D. C., Coppens, Y. 1976. A preliminary anatomical diagnosis of the first Plio/Pleistocene hominid discoveries in the Central Afar, Ethiopia. *Am. J. Phys. Anthropol.* 45(2):217–34

106. Johanson, D. C., Edey, M. A. 1981. *Lucy: The Beginnings of Humankind.* New York: Simon & Schuster

107. Johanson, D. C., Lovejoy, C. O., Burstein, A. H., Heiple, K. G. 1976. Functional implications of the Afar knee joint. *Am. J. Phys. Anthropol.* 44(1):188 (Abstr.)

108. Johanson, D. C., Taieb, M. 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260:293–97

109. Johanson, D. C., Taieb, M., Coppens, Y., Roche, H. 1978. Expédition internationale de l'Afar, Éthiopie (4e et 5e campagnes 1975–1977): nouvelles découvertes d'Hominidés et découvertes d'industries lithiques pliocènes à Hadar. *C. R. Acad. Sci.* 287:237–40

110. Johanson, D. C., White, T. D. 1979. A systematic assessment of early African hominids. *Science* 203:321–30

111. Johanson, D. C., White, T. D., Coppens, Y. 1978. A new species of the genus *Australopithecus* (Primates:

Hominidae) from the Pliocene of Eastern Africa. *Kirtlandia* 28:1–14

112. Jolly, C. J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5:5–27

113. Jolly, C. J. 1972. Changing views of hominid origins. *Yearb. Phys. Anthropol.* 16:1–17

114. Jordaan, H. V. F. 1976. Newborn: adult brain ratios in hominid evolution. *Am. J. Phys. Anthropol.* 44(2):271–78

115. Jordaan, H. V. F. 1976. Newborn brain: body weight ratios. *Am. J. Phys. Anthropol.* 44(2):279–84

116. Kay, R. F. 1975. Allometry and early hominids. *Science* 189:63

117. Kay, R. F. 1981. The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthropol.* 55:141–51

118. Kimbel, W. H. 1978. Characteristics of fossil hominid cranial remains from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 50:454

119. Kochetkova, V. 1978. *Paleoneurology.* Washington DC: Winston

120. Kortlandt, A. 1967. Use of the hands in chimpanzees in the wild. In *Use of the Hands and Communication in Monkeys, Apes and Early Hominids,* ed. B. Rensch, pp. 59–102. Bern/Stuttgart: Huber

121. Krantz, G. S. 1968. Brain size and hunting ability in earliest man. *Curr. Anthropol.* 9:450–51

122. Kretzoi, M. 1975. New ramapithecines and *Pliopithecus* from the lower Pliocene of Rudabanya in north-eastern Hungary. *Nature* 257:578–81

123. Lamarck, J. B. P. A. 1809. *Philosophie Zoologique.* Paris

124. Leakey, L. S. B., Tobias, P. V., Napier, J. R. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202:7–9

125. Leakey, M. D. 1978. Pliocene footprints at Laetolil, Northern Tanzania. *Antiquity* 52(205):133

126. Leakey, M. D. 1981. Tracks and tools. *Philos. Trans. R. Soc. London Ser. B* 292:95–102

127. Leakey, M. D., Hay, R. L. 1979. Pliocene footprints in the Laetolil beds at Laetoli, Northern Tanzania. *Science* 278:317–23

128. Leakey, M. D., Hay, R. L., Curtis, G. H., Drake, R. E., Jackes, M. K., White, T. D. 1976. Fossil hominids from the Laetolil Beds. *Nature* 262:460–66

129. Leakey, M. G., Leakey, R. E., eds. 1978. Koobi Fora Research Project, Vol. 1. *The Fossil Hominids and an Introduction to Their Context,* 1968–1974. Oxford: Clarendon

130. Leakey, R. E. F. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* 242:447–50

131. Leakey, R. E. F. 1976. New hominid fossils from the Koobi Fora formation in Northern Kenya. *Nature* 261:574–76

132. Lee, R. B. 1979. *The !Kung San.* New York: Cambridge Univ. Press

133. Lestrel, P. E. 1976. Hominid brain size versus time: revised regression estimates. *J. Hum. Evol.* 5(2):207–12

134. Lestrel, P. E., Read, D. W. 1973. Hominid cranial capacity versus time: a regression approach. *J. Hum. Evol.* 2(5):405–11

135. Leutenegger, W. 1972. Newborn size and pelvic dimensions of *Australopithecus. Nature* 240:568–69

136. Leutenegger, W. 1973. Gestation period and birth weight of *Australopithecus. Nature* 243:548

137. Leutenegger, W. 1973. Encephalization in australopithecines: a new estimate. *Folia Primatol.* 19:9–17

138. Leutenegger, W. 1973. Maternal-fetal weight relationships in primates. *Folia Primatol.* 20:280–93

139. Leutenegger, W. 1974. Functional aspects of pelvic morphology in simian primates. *J. Hum. Evol.* 3:207–22

140. Leutenegger, W. 1976. Allometry of neonatal size in eutherian mammals. *Nature* 263:229–30

141. Leutenegger, W. 1977. Sociobiological correlates of sexual dimorphism in body weight in South African australopiths. *S. Afr. J. Sci.* 73:143–44

142. Leutenegger, W. 1977. A functional interpretation of the sacrum of *Australopithecus africanus. S. Afr. J. Sci.* 73:308–10

143. Lewis, O. J. 1973. The hominid os capitatum, with special reference to the fossil bones from Sterkfontein and Olduvai Gorge. *J. Hum. Evol.* 2:1–12

144. Lewis, O. J. 1977. Joint remodelling and the evolution of the human hand. *J. Anat.* 123(1):157–201

145. Lisowski, F. P., Albrecht, G. H., Oxnard, C. E. 1974. The form of the talus in some higher primates: A multivariate study. *Am. J. Phys. Anthropol.* 41(2):191–215

146. Lisowski, F. P., Albrecht, G. H., Oxnard, C. E. 1976. African fossil tali: further multivariate morphometric studies. *Am. J. Phys. Anthrop.* 45(1):5–18

147. Livingstone, F. B. 1962. Reconstructing

man's Pliocene pongid ancestor. *Am. Anthropol.* 64:301–95

148. Lovejoy, C. O. 1974. The gait of australopithecines. *Yearb. Phys. Anthropol.* 17:147–61

149. Lovejoy, C. O. 1975. Biomechanical perspectives on the lower limb of early hominids. See Ref. 261, pp. 291–326

150. Lovejoy, C. O. 1976. *The locomotor skeleton of basal Pleistocene hominids.* 9th Congr., Union Int. Sci. Préhist. Protohist., Nice, pp. 145–76

151. Lovejoy, C. O. 1978. A biomechanical review of the locomotor diversity of early hominids. In *Early Hominids of Africa,* ed. C. J. Jolly, pp. 403–29. London: Duckworth

152. Lovejoy, C. O. 1979. *A reconstruction of the pelvis of AL288 (Hadar Formation, Ethiopia).* Presented at Ann. Meet. Am. Assoc. Phys. Anthropol., 48th, San Francisco

153. Lovejoy, C. O. 1981. The origin of man. *Science* 211:341–50

154. Lovejoy, C. O., Heiple, K. G. 1970. A reconstruction of the femur of *A. africanus. Am. J. Phys. Anthropol.* 32: 33–40

155. Lovejoy, C. O., Heiple, K. G. 1972. The proximal femoral anatomy of *Australopithecus. Nature* 235:175–76

156. Lovejoy, C. O., Heiple, K. G., Burstein, A. H. 1973. The gait of *Australopithecus. Am. J. Phys. Anthropol.* 38: 757–80

157. Margaria, R., Cerretelli, P., Aghemo, P., Sassi, G. 1963. Energy cost of running. *J. Appl. Physiol.* 18:367–70

158. Martin, R. D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293:57–60

159. Mayer, P. J., van Gerven, D. P. 1978. Evidence of hip dislocation in hominid SK 50 and its bearing on assessments on hip extension. *Man* 13(1):52–54

160. McHenry, H. M. 1972. *The postcranial anatomy of early Pleistocene hominids.* PhD thesis. Harvard Univ., Cambridge, Mass.

161. McHenry, H. M. 1973. Early hominid humerus from East Rudolf, Kenya. *Science* 180:739–41

162. McHenry, H. M. 1973. Australopithecine anatomy. *Science* 181:738–39

163. McHenry, H. M. 1974. How large were the australopithecines? *Am. J. Phys. Anthropol.* 40:329–40

164. McHenry, H. M. 1975. The ischium and hip extensor mechanism in human evolution. *Am. J. Phys. Anthropol.* 43(1):39–46

165. McHenry, H. M. 1975. A new pelvic fragment from Swartkrans and the relationship between the robust and gracile australopithecines. *Am. J. Phys. Anthropol.* 43:245–62

166. McHenry, H. M. 1975. Biomechanical interpretation of the early hominid hip. *J. Hum. Evol.* 4(5):343–56

167. McHenry, H. M. 1975. Fossils and the mosaic nature of human evolution. *Science* 190:425–31

168. McHenry, H. M. 1975. Fossil hominid body weight and brain size. *Nature* 254:686–88

169. McHenry, H. M. 1975. A view of the hominid lineage. *Science* 189:988

170. McHenry, H. M. 1976. Multivariate analysis of early hominid humeri. In *The Measures of Man,* ed. E. Giles, J. S. Friedlaender, pp. 338–71. Cambridge: Peabody Mus. Press, Harvard Univ.

171. McHenry, H. M. 1976. Early hominid body weight and encephalization. *Am. J. Phys. Anthropol.* 45(1):77–84

172. McHenry, H. M. 1978. Fore- and hindlimb proportions in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 49(1):15–22

173. McHenry, H. M., Andrews, P., Corruccini, R. S. 1980. Miocene hominoid palatofacial morphology. *Folia Primatol.* 33:241–52

174. McHenry, H. M., Corruccini, R. S. 1975. Multivariate analysis of early hominid pelvic bones. *Am. J. Phys. Anthropol.* 43(2):263–70

175. McHenry, H. M., Corruccini, R. S. 1975. Distal humerus in hominid evolution. *Folia Primatol.* 23:227–44

176. McHenry, H. M., Corruccini, R. S. 1976. Fossil hominid femora and the evolution of walking. *Nature* 259: 657–58

177. McHenry, H. M., Corruccini, R. S. 1978. Analysis of the hominoid os coxae by Cartesian coordinates. *Am. J. Phys. Anthropol.* 48:215–26

178. McHenry, H. M., Corruccini, R. S. 1978. The femur in early human evolution. *Am. J. Phys. Anthropol.* 49(4): 473–88

179. McHenry, H. M., Corruccini, R. S. 1980. Late Tertiary hominoids and human origins. *Nature* 285:397–98

180. McHenry, H. M., Corruccini, R. S., Howell, F. C. 1976. Analysis of an early hominid ulna from the Omo Basin, Ethiopia. *Am. J. Phys. Anthropol.* 44(2):295–304

181. McHenry, H. M., Temerin, A. 1979. The evolution of hominid bipedalism:

evidence from the fossil record. *Yearb. Phys. Anthropol.* 22:105–31

182. Oakley, D. A., Plotkin, H. C. 1979. *Brain, Behaviour and Evolution.* New York: Methuen

183. Oxnard, C. E. 1966. Some functional osteometric features of the primate innominate bone. *Proc. Int. Primatol. Soc. Frankfurt,* pp. 59–60

184. Oxnard, C. E. 1968. A note on the fragmentary Sterkfontein scapula. *Am. J. Phys. Anthropol.* 28:213–18

185. Oxnard, C. É. 1968. A note on the Olduvai clavicular fragment. *Am. J. Phys. Anthropol.* 29:429–32

186. Oxnard, C. E. 1972. Some African fossil foot bones: a note on the interpolation of fossils into a matrix of extant species. *Am. J. Phys. Anthropol.* 37:3–12

187. Oxnard, C. E. 1973. Some problems in the comparative assessment of skeletal form. *Symp. Soc. Stud. Hum. Biol.* 11:103–25

188. Oxnard, C. E. 1973. *Form and Pattern in Human Evolution: Some Mathematical, Physical, and Engineering Approaches.* London/Chicago: Univ. Chicago

189. Oxnard, C. E. 1975. The place of the australopithecines in human evolution: grounds for doubt? *Nature* 258:389–95

190. Oxnard, C. E. 1975. *Uniqueness and Diversity in Human Evolution.* Chicago: Univ. Chicago Press

191. Oxnard, C. E. 1978. The Olduvai foot. *Anat. Rec.* 190:499–500

192. Oxnard, C. E. 1979. Relationship of *Australopithecus* and *Homo:* another view. *J. Hum. Evol.* 8:427–32

193. Oxnard, C. E., Lisowski, F. P. 1980. Functional articulation of some hominoid foot bones: implications for the Olduvai (Hominid 8) foot. *Am. J. Phys. Anthropol.* 52(1):107–18

194. Ozansoy, F. 1970. *Ankarapithecus meteai,* pongidé fosile aux trais humains du Pliocène de Turquie. *Turk. Tarih Kurumu. Belleten* 34:3–15

195. Pairó, M. C., Hürzeler, J. 1969. Catálogo comentado de los Póngidos fósiles de España. *Acta Geol. Hisp.* 4(2):44–48

196. Parker, S. T., Gibson, K. R. 1979. A developmental model for the evolution of language and intelligence in early hominids. *Behav. Brain Sci.* 2:367–408

197. Parsons, P. E., Taylor, C. R. 1977. Energetics of brachiation vs. walking: a comparison of a suspended and inverted pendulum mechanism. *Physiol. Zool.* 50:182–88

198. Passingham, R. E. 1975. The brain and intelligence. *Brain Behav. Evol.* 11:1–15

199. Passingham, R. E. 1975. Changes in the size and organisation of the brain in man and his ancestors. *Brain Behav. Evol.* 11(2):73–90

200. Passingham, R. E. 1978. Brain size and intelligence in primates. See Ref. 100, pp. 85–86

201. Passingham, R. E. 1981. Broca's area and the origins of human vocal skill. *Philos. Trans. R. Soc. London Ser. B* 292:167–75

202. Patterson, B., Behrensmeyer, A. K., Sill, W. D. 1970. Geology and fauna of a new Pliocene locality in northwestern Kenya. *Nature* 226:918–21

203. Patterson, B., Howells, W. W. 1967. Hominid humeral fragment from early Pleistocene of northwestern Kenya. *Science* 156:64–66

204. Peters, C. R. 1979. Toward an ecological model of African Plio-Pleistocene hominid adaptations. *Am. Anthropol.* 81(2):261–78

205. Pilbeam, D. 1978. Rethinking human origins. *Discovery* 13(1):2–9

206. Pilbeam, D. 1978. Rearranging our family tree. *Hum. Nat.* 1(6):38–45

207. Pilbeam, D. 1979. Recent finds and interpretations of Miocene hominoids. *Ann. Rev. Anthropol.* 8:333–52

208. Pilbeam, D. 1982. New hominoid skull material from the Miocene of Pakistan. *Nature* 295:232–34

209. Pilbeam, D., Gould, S. J. 1974. Size and scaling in human evolution. *Science* 186:892–901

210. Pilbeam, D. R., Rose, M. D., Badgley, C., Lipschutz, B. 1980. Miocene hominoids from Pakistan. *Postilla* 181:1–94

211. Pitt, R. 1978. Warfare and hominid brain evolution. *J. Theor. Biol.* 72: 551–75

212. Preuschoft, H. 1971. Body posture and mode of locomotion in early Pleistocene hominids. *Folia Primatol.* 14:209–40

213. Preuschoft, H. 1978. Recent results concerning the biomechanics of man's acquisition of bipedality. See Ref. 100, pp. 435–58

214. Quiring, D. P. 1950. *Functional Anatomy of the Vertebrates.* New York: McGraw-Hill

215. Radinsky, L. 1974. The fossil evidence of anthropoid brain evolution. *Am. J. Phys. Anthropol.* 41:15–28

216. Ravey, M. 1978. Bipedalism: an early warning system for Miocene hominoids. *Science* 199:372

217. Rightmire, G. P. 1972. Multivariate analysis of an early hominid metacarpal from Swartkrans. *Science* 176:159–61

218. Robinson, J. T. 1972. *Early Hominid Posture and Locomotion.* Chicago: Univ. Chicago Press

219. Rodman, P. S., McHenry, H. M. 1980. Bioenergetics and the origin of hominid bipedalism. *Am. J. Phys. Anthropol.* 52(1):103–6

220. Romer, A. S. 1959. *The Vertebrate Story.* Chicago: Univ. Chicago Press. 4th ed.

221. Rose, M. D. 1976. Bipedal behavior of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. *Am. J. Phys. Anthropol.* 44(2):247–62

222. Ryan, A. S. 1979. Wear striation direction on primate teeth, a scanning electron microscope examination. *Am. J. Phys. Anthropol.* 50(2):155–68

223. Ryan, A. S. 1981. Anterior dental function in *Australopithecus afarensis* and in Neanderthals: dietary and behavioral implications. *Am. J. Phys. Anthropol.* 54:271–72

224. Sacher, G. A. 1975. Maturation and longevity in relation to cranial capacity in hominid evolution. See Ref. 261, pp. 417–41

225. Sarich, V. M. 1973. Just how old is the hominid line? *Yearb. Phys. Anthropol.* 17:98–112

226. Schaeffer, B., Hecht, M. K., Eldredge, N. 1972. Phylogeny and paleontology. *Evol. Biol.* 6:31–46

227. Senut, B. 1978. Étude comparative des piliers de la palette humérale. Deuxième partie. *Cah. Anthropol.* 4:1–20

228. Senut, B. 1979. Comparison des hominidés de Gomboré 1 B et de Kanapoi: Deux pièces du genre *Homo? Bul. Mém. Soc. Anthropol. Paris* 6:111–17

229. Senut, B. 1980. New data on the humerus and its joints in Plio-Pleistocene hominids. *Coll. Antropol.* 4(1):87–93

230. Senut, B. 1981. Humeral outlines in some hominoid primates and in Pliopleistocene hominids. *Am. J. Phys. Anthropol.* 56(3):275–84

231. Senut, B., Le Floch, P. 1981. Divergences des pilliers de la palette humérale chez les Primates hominoïdes. *C. R. Acad. Sci. D* 292(10):665–69

232. Sigmon, B. A. 1971. Bipedal behavior and the emergence of erect posture in man. *Am. J. Phys. Anthropol.* 34:55–60

233. Sigmon, B. A. 1974. A functional analysis of pongid hip and thigh musculature. *J. Hum. Evol.* 3:161–85

234. Sigmon, B. A. 1975. Functions and evolution of hominid hip and thigh musculature. See Ref. 261, pp. 235–52

235. Simons, E. L. 1976. The nature of the transition in the dental mechanism from pongids to hominids. *J. Hum. Evol.* 5:511–28

236. Simons, E. L. 1977a. Ramapithecus. *Sci. Am.* 236(5):28–35

237. Simons, E. L. 1977b. The fossil record of primate phylogeny. In *Molecular Anthropology,* ed. M. Goodman, R. E. Tashian, pp. 35–62. New York: Plenum

238. Simons, E. L. 1981. Man's immediate forerunners. *Philos. Trans. R. Soc. London Ser. B* 292:21–41

239. Simons, E. L., Pilbeam, D. R. 1978. Ramapithecus (Hominidae, Hominoidea). In *Evolution of African Mammals,* ed. V. J. Maglio, H. B. S. Cooke, pp. 147–53. Cambridge: Harvard Univ. Press

240. Smith, E. A. 1979. Human adaptation and energetic efficiency. *Hum. Ecol.* 7(1):53–74

241. Stern, J. T. Jr. 1972. Anatomical and functional specializations of the human gluteus maximus. *Am. J. Phys. Anthropol.* 36:315–40

242. Stern, J. T. Jr., Susman, R. L. 1981. Electromyography of the gluteal muscles in *Hylobates, Pongo,* and *Pan:* implications for the evolution of hominid bipedality. *Am. J. Phys. Anthropol.* 55:153–66

243. Steudel, K. 1978. A multivariate analysis of the pelvis of early hominids. *J. Hum. Evol.* 7(7):583–95

244. Susman, R. L., Creel, N. 1979. Functional and morphological affinities of the subadult hand (O.H. 7) from Olduvai Gorge. *Am. J. Phys. Anthropol.* 51(3):311–32

245. Susman, R. L., Stern, J. T. Jr. 1979. Telemetered electromyography of flexor digitorum profundus and flexor digitorum superficialis in *Pan paniscus* and implications for interpretations of the O.H. 7 hand. *Am. J. Phys. Anthropol.* 50(4):565–74

246. Suzman, I. M. 1976. The affinities and functional anatomy of the Makapansgat juvenile ilia. *Proc. 73rd Congr. S. Afr. Assoc. Adv. Sci.* 2:100–9

247. Szalay, F. S. 1975. Hunting-scavenging protohominids: a model for hominid origins. *Man* 10:420–29

248. Szalay, F. S., Delson, E. 1979. *Evolutionary History of the Primates.* New York: Academic

249. Tattersall, I., Eldredge, N. 1977. Fact, theory, and fantasy in human paleontology. *Am. Sci.* 65(2):204–11

250. Taylor, C. R., Caldwell, S. L., Rowntree, V. J. 1972. Running up and down

hills: some consequence of size. *Science* 178:1096–97

251. Taylor, C. R., Rowntree, V. J. 1973. Running on two or four legs: which consumes more energy? *Science* 179:186–87

252. Taylor, C. R., Schmidt-Nielsen, K., Raab, J. L. 1970. Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219(4):1104–7

253. Temerin, L. A. 1980. The evolution of the orang-utan. *Nature* 288:301

254. Thompkins, R. J. 1977. Early hominid postcrania and locomotor adaptations. *Kroeber Anthropol. Soc. Pap.* 50:85–104

255. Tobias, P. V. 1978. The earliest Transvaal members of the genus *Homo* with another look at some problems of hominid taxonomy and systematics. *Z. Morphol. Anthropol.* 69(3):225–65

256. Tobias, P. V. 1980. The natural history of the helicoidal occlusal plane and its evolution in early *Homo. Am. J. Phys. Anthropol.* 53(2):173–88

257. Tobias, P. V. 1980. "Australopithecus afarensis" and *A. africanus:* Critique and an alternative hypothesis. *Paleontol. Afr.* 23:1–17

258. Tobias, P. V. 1981. The emergence of man in Africa and beyond. *Philos. Trans. R. Soc. London Ser. B* 292:43–56

259. Tucker, V. A. 1975. The energetic cost of moving about. *Am. Sci.* 63(4):413–19

260. Tuttle, R. 1974. Recent thinking on human evolution. IV. Darwin's apes, dental apes, and descent of man—normal science in evolutionary anthropology. *Curr. Anthropol.* 15:389–98

261. Tuttle, R. H. 1975. Knuckle-walking and knuckle-walkers: a commentary on some recent perspectives on hominoid evolution. In *Primate Functional Morphology and Evolution,* ed. R. H. Tuttle, pp. 203–12. The Hague: Mouton

262. Tuttle, R. H. 1981. Evolution of hominid bipedalism and prehensile capabilities. *Philos. Trans. R. Soc. London Ser. B.* 292:89–94

263. Tuttle, R. H., Basmajian, J. V. 1975. Electromyography of *Pan gorilla:* an experimental approach to the problem of hominization. *Symp. 5th Congr. Int. Primatol. Soc., 1974,* pp. 303–14. Tokyo: Jpn. Sci. Press

264. Tuttle, R. H., Basmajian, J. V., Ishida, H. 1975. Electromyography of the gluteus maximus muscle in *Gorilla* and the evolution of hominid bipedalism. See Ref. 261, pp. 253–69

265. Tuttle, R. H., Basmajian, J. V., Ishida, H. 1978. Electromyography of pongid gluteal muscles and hominid evolution. See Ref. 100, pp. 463–68

266. Tuttle, R. H., Basmajian, J. V., Ishida, H. 1979. Activities of pongid thigh muscles during bipedal behavior. *Am. J. Phys. Anthropol.* 50(1):123–36

267. Tuttle, R. H., Buxhoeveden, D. P., Cortright, G. W. 1979. Anthropology on the move: progress in experimental studies of nonhuman primate positional behavior. *Yearb. Phys. Anthropol.* 22:187–214

268. Vallois, H. V. 1977. Interpretation of the scapula of *Plesianthropus transvaalensis. J. Hum. Evol.* 6(8):675–79

269. Vančata, V. 1978. Reconstruction of the locomotor behavior of the earliest hominids. *Anthropologie* 16(3):271–76

270. Vrba, E. S. 1979. A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *Am. J. Phys. Anthropol.* 51(1):117–29

271. Walker, A. 1973. New *Australopithecus* femora from East Rudolf, Kenya, *J. Hum. Evol.* 2:545–55

272. Walker, A. C. 1981. *Dietary hypotheses and human evolution.* Presented at Ann. Meet. Am. Assoc. Adv. Sci., Toronto

273. Walker, A. 1981. Diet and teeth. *Philos. Trans. R. Soc. London. Ser. B* 292:57–64

274. Wallace, J. H. 1975. Dietary adaptations of *Australopithecus* and early *Homo.* In *Paleoanthropology, Morphology and Paleoecology,* ed. R. H. Tuttle, pp. 203–23. The Hague: Mouton

275. Ward, S. C., Molnar, S. 1980. Experimental stress analysis of topographic diversity in early hominid gnathic morphology. *Am. J. Phys. Anthropol.* 53(3):383–96

276. Washburn, S. L. 1950. The analysis of primate evolution with particular reference to the origin of man. *Cold Spring Harbor Symp. Quant. Biol.* 15:67–78

277. Washburn, S. L. 1960. Tools and human evolution. *Sci. Am.* 203(3):3–15

278. Washburn, S. L. 1967. Behavior and the origin of man. *Proc. R. Anthropol. Inst.* 3:21–27

279. Washburn, S. L., Moore, R. 1980. *Ape into Human.* Boston: Little, Brown

280. Wescott, R. W. 1967. The exhibitionistic origin of human bipedalism. *Man* 2:630

281. White, T. D. 1977. New fossil hominids from Laetolil, Tanzania. *Am. J. Phys. Anthropol.* 46(2):197–230

282. White, T. D. 1980. Evolutionary implications of Pliocene hominid footprints. *Science* 208:175–76

283. White, T. D. 1980. Additional fossil hominids from Laetoli, Tanzania: 1976–1979 specimens. *Am. J. Phys. Anthropol* 53(4):487–504

284. White, T. D. 1981. On the evidence for "anterior dental cutting" in Laetoli hominids. *Am J. Phys. Anthropol.* 54(1):107–8

285. White, T. D. 1981. Primitive hominid canine from Tanzania. *Science* 217: 348–49

286. White, T. D., Johanson, D. C., Kimbel, W. H. 1981. *Australopithecus africanus:* its phyletic position reconsidered. *S. Afr. J. Sci.* 77:445–70

287. Wittenberger, J. F., Tilson, R. L. 1980. The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst.* 11:197–232

288. Wolpoff, M. H. 1973. Posterior tooth size, body size, and diet in South African gracile australopithecines. *Am. J. Phys. Anthropol.* 39(3):375–94

289. Wolpoff, M. H., Lovejoy, C. O. 1975. A rediagnosis of the genus *Australopithecus. J. Hum. Evol.* 4:275–76

290. Wood, B. A. 1975. Evidence on the locomotor pattern of *Homo* from early Pleistocene of Kenya. *Nature* 251: 135–36

291. Wood, B. A. 1974. Olduvai Bed I postcranial fossils. A reassessment. *J. Hum. Evol.* 3:373–78

292. Wood, B. A. 1976. Controversial morphometrics. *Nature* 262:331–32

293. Wood, B. A. 1976. Remains attributable to *Homo* in the East Rudolf succession. In *Earliest Man and Environments in the Lake Rudolf Basin,* ed. Y. Coppens, F. C. Howell, G. Ll. Issac, R. E. F. Leakey, pp. 490–506. Chicago: Univ. Chicago Press

294. Wood, B. A., Stack, C. G. 1980. Does allometry explain the differences between "gracile" and "robust" australopithecines? *Am. J. Phys. Anthropol.* 52(1):55–62

295. Zihlman, A. L. 1967. *Human locomotion: A reappraisal of the functional and anatomical evidence.* PhD thesis. Univ. Calif., Berkeley

296. Zihlman, A. L. 1971. The question of locomotor differences in *Australopithecus. Proc. Int. Congr. Primatol., 3rd,* 1:54–66

297. Zihlman, A. L. 1978. Interpretations of early hominid locomotion. In *Early Hominids of Africa,* ed. C. J. Jolly, pp. 361–77. London: Duckworth

298. Zihlman, A. L., Brunker, L. 1980. Hominid bipedalism: then and now. *Yearb. Phys. Anthropol.* 22:132–62

299. Zihlman, A. L., Cronin, J. E., Cramer, D. L., Sarich, V. M. 1978. Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature* 275:744–46

300. Zihlman, A. L., Hunter, W. S. 1972. A biomechanical interpretation of the pelvis of *Australopithecus. Folia Primatol.* 18:1–19

301. Zihlman, A. L., Lowenstein, J. M. 1979. False start of the human parade. *Nat. Hist.* 88(7):86–91

302. Zindler, R. E. 1978. On the increase of cranial capacity in mankind's lineage: augments and elaborations. *J. Hum. Evol.* 7(4):295–305

303. Zuckerman, S. 1970. African cousins. In *Beyond the Evory Tower.* New York: Taplinger

304. Zuckerman, S., Ashton, E. H., Flinn, R. M., Oxnard, C. E., Spence, T. F. 1973. Some locomotor features of the pelvic girdle in primates. *Symp. Zool. Soc. London* 33:71–165