



On New Perspectives on Ape and Human Evolution

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socioeconomic formation is a fundamental category of historical materialism. It is capable of being promoted both as a method and as an alternative research concern to Gjessing's, because, given the correspondences between forces of production and components of the superstructure, the probability is great that the areas of the economic basis of society which are inaccessible to archaeology—namely, relationships of production—conformed to those which have been identified in comparisons with more recent society (on the methods and their bases, see Grünert 1974, among others).

In conclusion, a detail: Considering the justifiable zeal with which Gjessing has applied the proper designation "Saame" (Sameh) instead of "Lapps," he ought to use the proper designation "Nenzen" in place of the obsolete and discriminatory "Samoyed."]

On New Perspectives on Ape and Human Evolution

by MAXINE R. KLEINDIENST

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Therefore I wonder whether the reality behind the nomenclatural mystification on the status of the "Australopithecines" is that we all are still so much indoctrinated by pre-darwinian creeds and Weltanschauung that we are still unable to refrain from reserving a special seat in the universe for Man. [Kortlandt 1972:55–56]

That is the essence of science: ask an impertinent question and you are on the way to the pertinent answer. [Bronowski 1973:719]

I was asked to comment on Kortlandt's *New Perspectives on Ape and Human Evolution* (reviewed in CA 15:427–48), but having written a brief note did not submit it. While I am fundamentally in sympathy with his attempt to view the ancestors,¹ and their nearest relatives, as parts of diverse evolving ecosystems within naturally bounded regions, I have no sympathy with the "classic" strategy of relegating problems to blanks on the map. The major weakness is that Kortlandt is firmly impaled on the paradox of the Principle of Uniformitarianism. (I was unable to decide whether or not his oft-repeated statement that "apes can't swim" is entirely facetious.)² Committing the fallacy of projecting direct modern analogues into the past, however, is sometimes necessary and, in any case, is common practice in the reconstructive sciences. Consequently, these comments are as much related to the December 1974 issue of CURRENT ANTHROPOLOGY and to the general literature as to Kortlandt's work, although it follows that I think he should not have allowed himself to be so easily dissuaded from his earlier "dehumanization" hypothesis (cf. Kortlandt, CA 15:445).

For several years, reading the literature on human evolution,

¹ The term, suggested by A. F. C. Haldemann, will be used instead of "early man." No accepted usage distinguishes the subdiscipline of archeology which studies the relatively recent prehistoric past from that which studies the remote past. There are essential differences in method and approach; the most important is that numerous assumptions based on actualistic principles are valid only for the recent past, concerned with the cultural remains of modern *Homo sapiens sapiens*. "Paleo-archeology" will be used here to denote the study of the remote past and the cultural remains of earlier hominids.

² F. D. Burton (personal communication) states that the actual situation is that "apes don't swim"—i.e., there seems to be no clear physiological reason for their reluctance to do so.

[The above comment was sent to Gutorm Gjessing, and he decided not to respond.—EDITOR.]

References Cited

- ENGELS, F. 1969. "Karl Marx, 'Zur Kritik der politischen Ökonomie,'" in *K. Marx und F. Engels, Werke* 13:468–77. Berlin: Dietz.
- GRÜNERT, H. 1974. Bemerkungen zu Geschichte, Stand und Bedeutung der Zusammenarbeit von Archäologie und Ethnographie in der Ur- und Frühgeschichtsforschung. *Ethnographisch-Archäologische Zeitschrift* 15:255–71.
- GUHR, G., K.-H. OTTO, and H. GRÜNERT. 1962. Die Ur- und Frühgeschichtsforschung im Rahmen der Gesellschaftswissenschaften. *Ethnographisch-Archäologische Zeitschrift* 3:13–58.
- MARX, K. 1969. "Zur Kritik der politischen Ökonomie," in *K. Marx und F. Engels, Werke* 13:3–160. Berlin: Dietz.

I have felt that there might be something wrong with the way the whole picture has been viewed. Too many pieces in the puzzle are contradictory, and there is too much detailed special argument attempting to make them fit. Most often the "morphological" view is at variance with the behavioral arguments, which are now facilitated in physical anthropology, as in paleo-archeology, by new technology. Without presenting an extensive review (much of the relevant literature is cited in CA 15[4]), there is, for instance, the biochemical evidence indicating recent splitting of the African ape and human lines, as few as 1.5 million years ago (Sarich 1968, Goodman 1974), while Kortlandt (1972:31–34) and others (Uzzell and Pilbeam 1971) attempt to push the event much farther into the past in order to adjust to morphological assignments. There is the statement by Pilbeam and Gould (1974) that allometry shows australopithecines to be "variants of the 'same' animal," different from but in some way ancestral to *Homo*, while Oxnard (1974) sees essential functional-behavioral differences between australopithecines and *Homo* and suggests that they are entirely separate lines.

In particular, one circumstance has increasingly appeared to me to be paradoxical, and intriguing. Even given Simons's (1972:234,241–53; Simons and Pilbeam 1965) and Pilbeam's (1969; 1972:371)³ assignments of dryopithecine ancestors to African apes—which have recently been questioned (Andrews 1974:190)—there are *no* fossil ancestors assigned to the African apes for something on the order of *14 million years* (or more) of geological time (using van Couvering's [1972] correlations). The "classic" explanation, which I have seen advanced most recently by Krantz (1973), is that they lived in forest habitats and therefore didn't get fossilized. Given the amount of bone-hunting carried out in Africa, and especially in East Africa, during the past 60 years, this seems a gap in the fossil record which calls for attention, and a better explanation. Other "forest-habitat" animals have been preserved (among them dryopithecines, pigs, monkeys, bovids, elephants). Further, the habitats of modern apes do not entirely rule out fossilization even in wet forests. For instance, Schultz (1961:82–83) suggests that sick or injured primates seek caves or fissures as places of shelter; these might present situations for fossilization and preservation in any habitat. More than once in paleontological research this kind of gap has been discovered to be not a lack of fossil evidence, but a lack of recognition of existing fossils as what they were within the correct evolving lineage.

One fossil which may be relevant to the issue is Olduvai

³ Pilbeam (1972:371) states that "there is a reasonable probability that *Dryopithecus africanus* and *D. major* are ancestral respectively to the chimpanzee, *Pan troglodytes*, and to *Gorilla gorilla*." But on the next page he says that from Fort Ternan come "several specimens of *Dryopithecus* . . . more similar to Asian later Miocene species than to earlier Miocene African forms. . . ."

Gorge H34, from site JK2, in Bed III, dated on paleomagnetic evidence to over .7 million years. L. S. B. Leakey originally identified these specimens as possibly belonging to a "giant ground-living monkey" (Kleindienst 1964) and then filed them away in a box labeled "Proconsul." When the femur was viewed as hominid by M. D. Leakey, others suggested that it was "pathological" (another "classic" explanation), bird, or carnivore (M. D. Leakey, personal communication). All of this suggests that something about these fossils does not fit the prevailing preconceptions. They are primate, and, particularly if all the specimens (a femur fragment, a tibia fragment, two incisors, one phalanx) assigned by the excavators are considered (Kleindienst 1975), this might be an ancestral ape rather than a hominid.

The articles in CA 15[4] devoted to various aspects of problems in human (and African ape) evolution, and the literature at large, appear to accept a certain view of the past—to be within a certain "paradigm" (cf. Tuttle, CA 15:398): (1) Morphology takes precedence over other evidence. (2) While the ancestors did not look or act like modern humans, ancestral apes looked and acted like modern apes (this despite disclaimers). (3) Bipedal primates diverged from ancestral quadrupedal primates (alternatively, arboreal primates). (4) Once bipedal, primates remained bipedal. Essentially the models proposed fall into two classes: those that view apes and hominids as deriving from a common, remote ancestor with australopithecines in the hominid line, and those which view australopithecines as a separate line, more closely related to hominids than to apes, which became extinct.

As someone who is interested in putting behavior on the stones rather than on the bones, but who regrets the present lack of adequate knowledge of processes which would allow combination of the two into testable behavioral hypotheses, I think there are sufficient grounds for at least asking my bio-behavioral colleagues to consider what I have come to think of as the "unmentionable alternative hypothesis." (I think it is theologically, rather than biologically, unmentionable.) A third class of model, not now acknowledged,⁴ is that australopithecines (rather, assigned fossils) are not representatives of a bipedal "experiment that failed" and became extinct (Oxnard 1974:9); they—or some of them—are the ancestral African apes.

As the australopithecine lineages (if there are two) came to occupy increasingly divergent ecological niches from those preempted by the culturally adapting, bipedal, diurnal, carnivorous/omnivorous hominids, they increasingly adjusted to arboreal and/or climbing modes of behavior and "ape" behavior patterns. The knuckle-walking specialisation of African apes can be seen as explained by Tuttle (CA 15:397; cf. Simons 1972:236) and/or as a logical adjustment of a specialized form of bipedalism to quadrupedalism. At the logical extreme, it is possible to view the robust australopithecines as potential ancestral gorillas and the gracile forms as potential ancestral chimpanzees. The final divergence of ape and hominid lines may indeed be as recent as the biochemical evidence suggests. This alternative hypothesis would reconcile some of the apparent contradictions, although it certainly transgresses the entrenched views of ape and human evolution, of the relationships of morphology to generic connections, and of the directionality that is assumed to be "known": for example, that predicated on the supposed "reduction" of canines (Washburn and Avis 1958; Washburn and Howell 1961; Kortlandt 1972:63; Washburn and Ciochon 1974),⁵ or the

⁴ Australopithecines were previously so assigned (e.g., Simpson 1945), but on morphological grounds and little fossil evidence. It is primarily interpretations of bipedalism that removed them to the hominid line (Clark 1955:110,152; Robinson 1972).

⁵ I can envisage a small-canined primate that wanted to eat meat and marrow from large bones turning to the use of stone artifacts; but small canines do not predicate the behavior. I find it

direction of change in other morphological features. However, it seems easier to allow dryopithecines to disappear in Africa over 14 million years (cf. Pilbeam 1972; Krantz 1973) than to get rid of australopithecines in 1 million years.

If the scant, and controversial, material reported by L. S. B. Leakey from Fort Ternan (1971 [1968]) is accepted as archeological evidence, stone use and the dietary implications of smashed bones indicate that a primate was at least an occasional carnivore/scavenger in middle-Miocene times (some 14 million years ago). Todd and Blumenberg (CA 15:383–85) summarize the case for its being *Ramapithecus*, as Leakey suggested, but do not refer to archeological evidence. What this evidence and later archeological occurrences do show is that the culturally adapting ancestors ate meat and marrow. The consequences of hunting behavior (which I do not limit to "large" animals) have been discussed at length (e.g., Dart 1949, 1953; Washburn and Avis 1958; Spuhler 1959; Oakley 1961; Campbell 1966:172–74,200–204; Krantz 1968; Laughlin 1968; Washburn and Lancaster 1968; Cachel 1973; Brown and Lahren 1973), but the essential behavioral question is *why?* What do these foods offer, nutritionally, that would induce a primate to seek them out and to become, in effect, a diurnal carnivore? (Cachel [1973] has discussed the availability of a niche for a diurnal carnivore in the late Cenozoic of Africa.) There may be specific conditions that make meat and fat first a desirable part of a primate's diet and then a necessity (F. D. Burton, personal communication; cf. Suzuki 1973).

There is a long gap in the paleo-archeological record as well—Fort Ternan should be redug as an archeological site, as should other paleontological sites. There are the few early occurrences in the Omo Valley (Bonafille, Chavaillon, and Coppens 1970; Chavaillon 1970; Howell 1972:349; Merrick et al. 1973).⁶ By the time of the archeological occurrences at East Rudolf, ca. 2.6 million years ago (Isaac, Leakey, and Behrensmeier 1971, Brock and Isaac 1974, Isaac 1974), the selection and transportation of stone raw materials and the manufacture of stone artifacts associated with smashed bone indicate an intelligent, bipedal primate that was a hunting and/or scavenging carnivore/omnivore. This presence is only confirmed by the recent osteological finds (R. E. F. Leakey 1973). The evidence from Lower and Middle Bed I at Olduvai Gorge, ca. 1.8 million years (M. D. Leakey 1971:21–60), indicates primate behavior which involved bone smashing, plus more sophisticated selection and transportation of stone materials, much more than casual use and manufacture of artifacts, and stone structures—and which may already be dependent upon the use of artifacts. However, contrary to still prevalent assumptions (as previously expressed by such investigators as Campbell [1966:203], Steward [1968:331], and Washburn and Lancaster [1968]), the economic role specialization of "hunting and gathering" should not necessarily be envisaged (cf. Livingstone 1969); hunting, home bases, and centralized food-sharing are also compatible with the matrifocal or female-based "living group" units that characterize some nonhuman primates and other animals.⁷ The importance of the fact that females may have been dependable providers should not be overlooked when considering the problem of

difficult to see how the implications of stone artifact use or manufacture produce selective pressure against large canines.

⁶ I regard the archeological occurrences from the early South African cave sites as insecurely dated (cf. Isaac 1974) and as not being in primary archeological context. They do offer corroborative archeological evidence for the geographic extent of culturally adapting behavior.

⁷ F. D. Burton has contributed much discussion on this point. I know that at least one (female) anthropologist has stated this in print. I apologize to whoever it was; I could not relocate the reference. The term "living group," to refer to groups of unknown size and composition represented by some archeological occurrences, is adopted from N. Howell and R. B. Lee.

bringing males permanently into the family circle. Nor need the ancestors necessarily be seen as "social" carnivores, composed into living groups involving either "gangs" or "bands"; we should imagine that all adaptive strategies have been tried in the past 3+ million years of cultural behavior and consider how to discriminate among them.

The event in the archeological record marked by the first appearance of large flakes in intractable raw materials—artifacts classed as "Lower Acheulian" in the upper part of Middle Bed II in the Olduvai sequence (M. D. Leakey 1971:124–55) and in the Peninj Group in the Natron Basin (Isaac 1965, 1967)—is not well dated. At Peninj it appears to fall between 1.0 and 1.5 million years, with a likelihood of being closer to 1.5 (Isaac 1974:513; Isaac and Curtis 1974). Since we do not know how, or for what, the artifact forms manufactured on large flakes were used (Kleindienst and Keller 1974), the implications of their appearance are unclear. Is it only coincidental that this would be within the time range of the latest date for ape-human divergence indicated by the biochemical method?

The paleo-archeological problems would be simplified if only one lineage need be seen as culturally adapting, although this cannot be presumed to be the case. African prehistorians have taken the new dating methods, and other new technology, as a means of release from prior presumptions of generic relationships based on morphology. We are attempting to ask, and test, processual behavioral hypotheses. Therefore:

Where *are* the ancestral African apes for 14 (maybe 18) million years?

Maybe it *is* time to try another paradigm?

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In 1963 (*a,b*), Jane Goodall published her discovery that the chimpanzees at the Gombe Stream ate meat. The anthropological world met this report with joy. This piece of evidence seemed critical to the evolving savanna model of hominisation. To go from the forest chimpanzee as ancestor to the savanna baboon as model required merely the attribution of a behaviour suddenly verified in the former to the latter.

Early reports of meat-eating, primarily by baboons, had already established the model (Dart 1953). Subsequent reviews (Dart 1963) and reports (DeVore and Washburn 1963) made at the time of Goodall's discovery were submerged in the more dramatic event, but invaluable for the confirmation of the model. These reports of meat-eating were disappointing; the frequency was low and predatory behaviour either not apparent (DeVore and Washburn 1963) or not fully described (Dart 1963). It was with relief, then, that anthropologists received subsequent announcements that meat-eating in baboons showed predatory behaviour, at least in part (Altmann and Altmann 1970). Meat-eating has more recently been observed in a variety of cercopithecoids (e.g., Struhsaker 1967, Home-wood 1975). Implicit in the later baboon reports was the view that earlier researchers had not attended to such observations with sufficient diligence, this accounting for the discrepancy between earlier and later work. Van Lawick-Goodall (1965) and Teleki (1973) had seen actual hunting behaviour in the chimpanzees. DeVore and Washburn (1963) had noted that, in the Nairobi Game Park baboons, meat-eating was merely part of their opportunistic food habits; they literally tripped over the prey. Altmann and Altmann (1970:167) discussed their observations, stating,

... it is not always true that baboon predation is fortuitous, that they merely stumble upon their prey and do not hunt it. If one

considers the major phases or components of hunting, including stalking or searching, attacking or chasing, killing, and eating, it becomes clear that the extent to which baboons "hunt" depends upon numerous factors, including particularly the species of prey.

It is perhaps relevant that primatology in the late '60s and early '70s was just starting to explore variability within primate species. Although in developing the New Systematics in the 1950s biological scientists had formally rejected typology, zoologists, psychologists, and anthropologists were still, throughout the '60s, assuming that a description of one local population of a primate species would stand for the species. The majority of models developed to explain variability were based on ecological principles. Such speculation provoked the recrudescence of the defunct nature-nurture dichotomy as opponents to the ecological models invoked phylogeny as decisive in variations. Behaviour itself was viewed as derivative of morphology in a particular environment—never as generative of subsequent adaptations. The behaviour *had* to be ancient. "These repetitive records extending temporally over the past century and spatially . . . leave no doubt whatever about the flesh protein needs and consequent carnivorous propensities of Southern African baboons" (Dart 1963:53).

As "perpetual" behavior (Dart 1963:53), "consistent but very minor" (DeVore and Washburn 1963:363), the meat-eating behaviour of baboons suited models of hominisation. Two related factors were ignored: that behavioural flexibility is a hallmark of the Primate Order and that there is a distinction between actual and potential behaviours. Potential is discussed by students of evolution in terms of "preadaptations"—traits that apparently suddenly appear. Since traits cannot suddenly appear (*pace* Lamarck), they must have lain dormant, and their manifestation indicates that the organism was already preadapted. Feeding behaviour is such a trait. Despite the insistence of paleontologists that the masticatory apparatus implies the food sources, organisms with apparently specialized dentition are known to be more flexible in their diet. The carnassials of carnivores do not preclude their dependence on vegetable and fruit matter. The potential for meat-eating is unquestionable in primates, opportunistic omnivores derived from insectivorous forms. The question before us is whether or not the current *frequencies* of meat-eating and hunting behaviour are constant, recurrent, or a new response in the history of these primate species.

My speculation is that the present frequencies are a response to environmental exigencies. The destruction of nonhuman primates' environments as human encroachment proceeds, with not only the transformation of the ecology from forest to farm (or city?), but an increase in the density of another species within their domain, has created a stressful situation. Techniques and strategies for exploitation of the environment may no longer suffice in the face of this pressure, and the animals can no longer simply go elsewhere. In this context, it is perhaps significant that cannibalism has been observed amongst the Gombe chimps. Bygott (1972:411) writes: "The data are at present insufficient to indicate whether infant-eating in chimpanzees is aberrant behaviour, or a rarely-seen adaptive response to social or ecological pressures."

Cannon (1966:239) suggests that there are two kinds of stress, physical and psychogenic. In the former, effects are "determined largely by biochemical processes, the typical response . . . characterized by negative balances of nitrogen, potassium, and phosphorus; disturbed carbohydrate utilization; fatty changes in the liver; tendency to ketosis. . . ." In the latter, stress "comprises a group of reactions integrated or intermediated through the central nervous system. It manifests itself as fear, worry, anxiety, tension, hostility. . . ."

With so little information on nutrition in primates, it seems parsimonious to suggest that protein content underlies meat-eating behaviour in nonhuman primates. The references cited

concur in this assumption. Entering the trophic ladder at a higher level affords the absorption of proper protein for immediate use without expenditure or conversion of primary sources, but that benefit would probably not suffice. Documentation on what part of the prey is eaten with what frequency is sparse, but it is certainly not only muscle that is sought. The value of the prey may as easily lie in its lipid or mineral content. Indeed, Stoltz and Saayman (1970) and Dart (1963) note predation upon sheep and lambs, ostensibly "for the milk in their stomachs" (Dart 1963:50). Yet the lining of the stomachs of these animals is particularly rich in the bacteria responsible for available B vitamins (Tyler 1964).

It is my suggestion that meat-eating enhances adaptation in a stress situation. Cannon (1966:240) notes: "In view of the many metabolic processes which may be influenced by stress, it is apparent that nutritional processes also become an important part of many, if not most, stress reactions." Meat-eating may either facilitate neuronal transmission, permitting meat-eating species dependent on behaviour patterns as their primary adaptive mechanism to function, or operate directly on the system to decrease the effects of the full expression of the stress syndrome (Selye 1959, Ratcliffe 1968), debilitation and exhaustion. In understanding the physiological value of this aspect of nonhuman primate nutrition and the changes in behaviour associated with it, we may arrive at a better perspective on the development of meat-eating behaviour in early human ancestors.

Reply

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Kleindienst's socratic nonconformity contributes to a badly needed bombardment of current stereotypes in paleoanthropology, but she overshoots the mark by trying to overkill. Furthermore, she underestimates the amount of factual data available on her subject matter. Briefly, the following points should be made:

1. The "classic" explanation of the absence of ancestral African apes for either 14 or 18 million years (depending on the assumed status of "*Kenyapithecus wickeri*") postulates that they lived in forest habitats and consequently were not fossilized. This idea is indeed sheer nonsense. Any alternative explanation should, however, consider the following facts: (a) Dryopithecine remnants have been found by the hundreds—in habitats that varied from dense tropical rain forests and mountain forests through different types of mosaic landscapes, parklands, woodlands, grass savannas cut by gallery forests, and steep-sided valleys in rocky habitats to marshlands, swamp forests, and oak forests in the warm-temperate zone; in an area ranging from Spain to China to East Africa; and in deposits covering a time span of at least 8 and probably 10 million years (for references, see Kortlandt 1972). (b) The geographical range of the common species of chimpanzee (*Pan troglodytes*), corrected for recent extermination by man in suitable habitats and for recent destruction of habitats by man, consists of about 40% predominantly savanna, woodland, and dry-forest vegetation belts, about 55% predominantly rain- and swamp-forest vegetation belts, and about 4% typical mountain-forest zones (for references, see Kortlandt 1972 and unpublished data). (c) Our contemporary chimpanzees live in a variety of local habitats almost as wide as that of the dryopithecines in former times, excluding, however, open marshlands and oak forests. There are neither comparative anatomical

nor paleoecological data to suggest any temporary narrowing of their ecological niche during the last 10–12 million years. On the contrary, their advanced arboreal locomotor specializations seem to have evolved *much* later than in the Asian apes (see also Kortlandt 1975). Thus their ancestors must have always been extremely eurytopic creatures. (d) Those chimpanzees which today live in savannas, woodlands, and mosaic landscapes spend much of their time (both day and night) in periodically flooded, riverine, and swampy types of forest, i.e., in habitats that offer excellent chances of fossilization. Furthermore, the pygmy chimpanzee (*Pan paniscus*) lives largely in a periodically flooded river-basin area. Thus the chances of fossilization of chimpanzees in all these types of habitat definitely appear better than those of humans under wildlife conditions. Since, however, their (apparent) ancestors have never been found in *any* of the many fossil-rich deposits in East and South Africa dating from either 14 or 18 million years ago (again depending on the assumed status of "*Kenyapithecus*"), we can only conclude that these ancestors probably did not live there in those times. In West and Central Africa, on the other hand, such deposits from that time span are quite scarce. (e) Most Plio-Pleistocene hominid fossils and artefacts from East Africa were deposited in lake and river shore zones, i.e., at sites where shore forests were close by, except in (semi-) desertic habitats. Such forests were opened up and secondarized by large herbivores on their way to drinking water, and hence constituted excellent chimpanzee habitats, similar to what can be observed at present, e.g., in the Rwenzori National Park in Uganda (formerly the Queen Elizabeth National Park). Yet no ape remnants have been found at such hominid fossil sites. (f) In optimum habitats, chimpanzees can reach population densities of up to 4, or even 7, individuals per square km (Reynolds and Reynolds 1965, Sugiyama 1968). Human population density in the Lower Paleolithic has been estimated as never exceeding 0.004 individuals per square km (Deevey 1960). Consequently one would expect that, for each hominid fossil in a fluvial deposit with traces of gallery forest, about a thousand ape fossils would have been found. Yet there are none at all (except, possibly, for two or three doubtful cases which have not yet been adequately described). Even if Deevey's figure is rather low (as is suggested by some other estimates of Lower Paleolithic population densities; Braidwood and Reed 1957, Nougier 1954), the absence of (proto-) chimpanzees in East Africa would still be highly significant by statistical criteria, at least for the last 4–5 million years. To find these apes, therefore, one has to look for good sites in West and Central Africa. And even if in the future some kind of (proto-) chimpanzee were to be found at a hominid site in East Africa, we would still be pretty sure that it would represent only a dead-ending sideline of their evolution elsewhere. This is the inevitable implication of the plain fact that, within their present-day natural range, in those areas where these apes are strictly protected by religion, they belong to the most abundant mammal species among the fauna which live at potentially fossiliferous sites. Thus we must locate their original homeland in a virtually fossil-blank subcontinent. (g) For the gorilla and the orangutan, the chances of fossilization of their ancestors were very, very much lower, both because they are forest apes and because they are rare species. Yet, Pleistocene orangutan fossils have been found in Sumatra, Borneo, and China.

2. The possibility that our contemporary chimpanzees and gorillas descended from some sort of australopithecine about 1 or 1½ million years ago can be ruled out for a number of reasons: (a) Paleontologically speaking, the australopithecines have always been quite conservative creatures. This is emphasized by the skeleton from the Awash area, 3 to 4 million years old, recently unearthed by Johanson and Taieb (not yet published). (b) The dryopithecines and the gigantopithecines appear to have been conservative as well, judging from the fossils known to date. (c) The selection pressures upon the

chimpanzee locomotor apparatus appear to be surprisingly low. Many apes that have been shot in the wild show the traces of healed limb fractures (Schultz 1937, 1969). Seriously crippled chimpanzees have survived for years at the Beni, Budongo, Gombe, and Kanka-Sili observation sites (Kortlandt 1975). One of them, "Grandad," at the Beni site, still copulated successfully after having been handicapped for four years at the least. Such cases seem never to have been observed among any large non-ape (i.e., non-climbing, non-weapon-using) mammals. Chimpanzee evolution, therefore, must have been slow compared to that of other mammals. (d) Nor are there any special reasons for presuming that the Pleistocene climatic fluctuations exerted a stronger selection pressure upon the African apes than upon other African mammals. On the contrary, their eurytopic behavioural versatility greatly facilitated their survival under changing conditions. This is emphasized, furthermore, by the wide geographical distribution of the pygmy chimpanzee (*Pan paniscus*) in the periodically flooded forests between the Congo-Lualaba and Kasai Rivers (sites mapped by G. Vandebroek, unpublished).

3. Kleindienst's quotations of the $1\frac{1}{2}$ million years' datings of the African ape-hominid phyletic divergence as calculated by Sarich (1968) and by Goodman (1974) are incorrect, because the figures have been taken out of their proper context: (a) Sarich assumed that "the amount of [albumin molecular] change has been directly proportional to the amount of time elapsed" (p. 106), but his results would have been much more consistent with the available paleontological datings if he had assumed that the amount of change had been proportional to the number of generations elapsed. It is surprising that neither Sarich himself, nor his critics Simons (1969) and Read and Lestrel (1970), have noticed this. Admittedly, in a later paper based on more extensive data and a revised calculation model, Sarich and Wilson (1973) found that there were no indications of a generation-time-dependent slowdown in albumin evolution when comparing different primate lineages. Their conclusion was that "it remains difficult if not impossible to reconcile the growing body of protein and nucleic acid data with a divergence time of more than about 5 million years ago between man and African apes" (p. 1146). Many other data, however, suggest that it is more realistic to assume that the rate of evolution of proteins and DNA has decelerated in proportion to the increase of the length of the generation cycle (Goodman and Moore 1971, Goodman et al. 1974, Kohne 1970, Kortlandt 1972, Lovejoy, Burstein, and Heiple 1972). (b) Goodman's (1974: 219) figure of $1\frac{1}{2}$ million years ago for the African ape-hominid divergence should be taken *not* as the result of an attempt at dating, but as the outcome of an attempt to test and evaluate a new calculation technique based upon globin codon sequences, assuming only for the purpose of the test that no deceleration had taken place. One of the results of this test was a date of $20\frac{1}{2}$ million years ago for the Old World monkey-ape divergence, whereas the current estimates from fossil evidence lie in the 40-million-years range. From these and other considerations Goodman (pp. 217-22) ultimately concluded that "molecular evolution must have been markedly decelerated [particularly] in the *Hominioidea*" because of several sets of factors. (c) It is illuminating here to quote the figures for the African ape-hominid divergence as calculated by those authors who have tried to account for the deceleration in protein evolution: (1) Goodman and Moore (1971): about 11 million years, based on immunological distances and two calibration points from fossil evidence (*Tupaiidea* and *Cercopithecoidea*); (2) Lovejoy, Burstein, and Heiple (1972): 12-14 million years, based on immunological distances, DNA hybridization, neocortex sizes, ages of menarche, and three calibration points from fossils (*Tupaiidea*, *Prosimii*, and *Aegyptopithecus*); (3) Kortlandt (1972): 12-15 million years, based on immunological distances, organizational levels, lengths of life cycles, and one fossil calibration point (*Propliopithecus*). The

approximate coincidence of the results obtained by three different methods may not be taken as an indication of the validity and reliability of these methods, but it does show that Kleindienst's tentative idea is far beyond any reasonable margin of plausibility. (I have, however, not been able to survey all the recent literature on this topic.) These datings also imply, on the other hand, that the alleged status of *Ramapithecus* (including *Kenyapithecus wickeri*) as an exclusively hominid ancestor (e.g., Simons 1968, 1972) is shaky. Moreover, the new reconstructions by Genet-Varcin (1969), Vogel (1975), and Walker and Andrews (1973) have at least reopened the possibility that *Ramapithecus* (*Kenyapithecus*) represents the common African ape-hominid ancestor. If so, the fossil gap of 18 million years for the African apes would be reduced to 14 million years. This is still a rather large gap, but it does not justify exotic assumptions on ape and human phylogeny.

4. It is a fact that the anthropoid apes cannot swim. Many zoos have had sad experiences which prove this. I have myself observed two cases in which chimpanzees would have drowned in a 5-foot-deep moat if they had not been rescued by an attending scientist. Their behaviour underwater was striking and dramatic: instead of simply trying to walk quadrupedally to the nearby shore, they stood upright and made little jumps while alternately extending one or the other hand helplessly into the air. Furthermore, those chimpanzees in captivity which are familiar with water tend to stop entering it as soon as the level reaches their bellies. Wildlife observations by old-timers in Africa suggest that the risk of incidents with crocodiles may explain this caution. The same is suggested by the effect exerted by rivers on monkey speciation and geographical distribution in Africa.

Summing up, I would like again to emphasize that while there is a lot of pertinent data available to paleoanthropology, the paleoanthropologists themselves are often insufficiently aware of their existence. Most of us are so intensively involved in the relentless pursuit of solid evidence in special fields, not to mention other commitments, that we hardly ever have the time and serenity to step back for a while and survey the battlefield of scientific progress from a wider perspective. Yet this is what we all badly need to do. More specifically, since teeth, bones, and stone tools are nothing more than the fossilized traces of an adaptive process in a particular niche of a particular ecosystem, what we must have in paleoanthropology is an integration of the "classic" kinds of research on these traces with the new ecosystem research that has resulted from ecological and behavioural fieldwork. It is, after all, the changing ecosystem which has caused the evolution of the organisms that constitute the system.

Burton quotes Dart's (1963) statement on (presumed) flesh protein needs in savanna-dwelling baboons, but she does not enter into the scientific background of this issue, e.g., the questions whether only one or both of the australopithecines preyed on live animals, whether one or both were scavengers, whether their protein needs may have been different, whether the bone accumulations on the australopithecine sites have resulted partly or wholly from extraordinary geological circumstances, etc. (Compare the different data and opposing views in, e.g., Brain 1958, 1970; Dart 1949, 1957, 1964; and Robinson 1956, 1963, 1972.) Thus the real issues at stake are circumvented.

She writes that "zoologists, psychologists, and anthropologists were still, throughout the '60s, assuming that a description of one local population of a primate species would stand for the species." Actually, Kooij's and my systematic data-collecting work on the differences between savanna-dwelling, rock-dwelling, and forest-dwelling species and social groups of primates started in 1957 and was published in 1959 and 1963. The latter work summarizes extensively (among other things) the results obtained from 39 carefully scrutinized and analysed reports containing evidence for predatory be-

haviour (including incipient forms) in primates in the wild and from 77 similar reports on such behaviour in primates in captivity, mainly in zoos. Burton ignores this work, although it was published in the same volume as (and only four pages after) Dart's. His paper was based on only 14 reports (including one of doubtful reliability) from only 6 areas. Furthermore, he did not enter deeply into the behavioural and ecological mechanisms involved, whereas we tried as thoroughly as possible to analyze the various phylogenetic, geographic, climatic, nutritional, and other ecological factors that might explain the data available to us. For example (Kortlandt and Kooij 1963:81, 83):

Predatory behaviour . . . is not a very common phenomenon in zoo Primates. Rather, it is a peculiarity with certain individuals, and a fashion with certain groups. Furthermore, an interesting feature is the frequent occurrence of predatory behaviour in an *incipient* and *incomplete* form. . . . The frequent occurrence of such incipient predatory activities, together with the fact that full predatory behaviour occurs in only a minority of zoo Primates, suggests that carnivorous behaviour in Primates—rather than being a part of the normal behaviour of everyday life—represents some kind of “emergency potentiality” that may be activated under exceptional ecological circumstances (e.g. when the normal sources of proteins are being depleted). Such an emergency pattern can be useful in areas where great seasonal and annual variations in the food supply occur, i.e. particularly in savanna and deciduous forest habitats (see Dart—this volume). . . .

Since a relatively large number of respondents have been quoted here, one might imagine that carnivorous behaviour is an everyday activity in wild Primates. But this is not so. Some respondents with many years of field experience have never seen it, others only a few times; still others report that it is a seasonal and/or local phenomenon, or is caused by prolonged drought and food scarcity, etc. Thus, the field data support our impression, from zoo data, that the potentiality in non-anthropoid Primates to exercise predatory activities should be interpreted as an emergency measure for special needs, or under special ecological conditions.

Normally, the vertebrate prey that is caught, killed and consumed by wild Primates consists of small and practically defenceless animals. . . . However, the savanna-inhabiting baboons of the eastern part of Africa, in those areas where they are carnivorous, prey mainly on such medium-sized animals as young antelope, hare, fowl, etc. Similarly, the savanna-inhabiting chimpanzees of Tanganyika prey on young antelope and hare (Goodall). . . . Conversely, the forest chimpanzees observed by the senior author in the Congo certainly did not taste and barely noticed the live hen chicks, small dead birds, and dead snakes which he had placed along their path; of the respondents who had investigated large numbers of stomach contents of forest-dwelling chimpanzees, only one reported vertebrate remains (Merfield). . . . Thus it seems that a constant rain-forest habitat will discourage predatory habits, or at least will discourage preying on larger-sized prey, whereas a savanna habitat with large climatic fluctuations will promote it. . . . All the twenty-six reports we received on predatory behaviour in baboons refer to the area east of the Nile and the 29th meridian, ranging from the Red Sea Hills (Sudan) in the north to the Kruger Park in the south, except one case reported from the 26th meridian in Southern Rhodesia, and possibly one report from Katanga. . . . This area . . . includes the only locality where chimpanzees are known to prey on medium-sized animals, and it includes also nearly all the localities where the fossil remains and artifacts of australopithecines have been found. . . .

Burton states: “My speculation is that the present frequencies [of meat-eating and hunting behaviour in African monkeys, baboons, and chimpanzees] are a response to environmental exigencies,” which she attributes to “the destruction of nonhuman primates’ environments.” The first half of this speculation has, however, already been formulated in more or less synonymous terms not only in the article by Kortlandt and Kooij just quoted, but also in Dart (1953:215; 1963:51), Potter (1949, quoted in Dart 1963:51), and my Précis in CA 15:430. Thus it is not Burton's speculation. Nor

is it a speculation. I refer to the evidence produced in these publications. The second half of Burton's suggestion is disproved, at least partly, by data from sites in national parks and game reserves where no overforaging of plants and fruit occurs. The stress-physiological aspects proposed by Burton deserve consideration by experts in this field. The indications suggesting a higher frequency of egg-eating and meat-eating among savanna-dwelling chimpanzees as compared to their forest-dwelling conspecifics (reviewed by Kortlandt 1972) and the preference for eating the brains of prey (Teleki 1973) make a case for specific dietary needs for certain proteins, vitamin B12, phosphorus, etc., but alternative explanations cannot be ruled out. Unfortunately, quantitative research on food-intake by wild primates (e.g., McGrew 1974) has hardly gotten off the ground because most students of primate behaviour are too romantic to be interested in ecosystem analysis. The absence of a (published) faunal inventory and a vegetation study of the Gombe Stream National Park speaks for itself. The time appears not yet to be ripe for shifting from behavioural bookkeeping to ecological system analysis in primate fieldwork.

During the last 15 years it has become more and more obvious that the motivational factors and functional survival values underlying “hunting” and “predatory” behaviour in primates constitute an extremely complicated matter. In chronological order, and referring only to chimpanzees, the progress of sophistication becomes obvious if one compares the thinking reflected in Kortlandt (1959), Kortlandt and Kooij (1963), Kortlandt (1967), van Zon and van Orshoven (1967), van Lawick-Goodall (1968), Kortlandt and van Zon (1969), Bygott (1972), Kortlandt (1972), Teleki (1973), Wrangham (1974), Bygott (1974), Wrangham (1975), and Kortlandt (1974, unpublished, available on request). It has been Burton's bad luck not to have been able to participate in this dialogue between the Amsterdam and Cambridge teams. No one will blame her for that. One wonders, however, how we can improve the scientific communication system so that our colleagues all over the world can better profit from such local scientific developments. I may repeat here the same words with which I ended the preceding review discussion (CA 15:446): What I have learned from this is that we badly need an adequate information-retrieval system, preferably worldwide, to give us better access to those fields of knowledge which lie outside the realm of what is currently considered to constitute anthropology, but which are nevertheless immediately pertinent to our discipline, or may one day come to be.

References Cited

- ALTMANN, S., and JEANNE ALTMANN. 1970. *Baboon ecology*. Basel: Karger.
- ANDREWS, P. 1974. New species of *Dryopithecus* from Kenya. *Nature* 249:188–90.
- BONNEFILLE, R., J. CHAVAILLON, and Y. COPPENS. 1970. Paléontologie.—Résultats de la nouvelle mission de l'Omo (3^e campagne 1969). *Comptes Rendus de l'Académie des Sciences de Paris* 270:924–27.
- BRAIDWOOD, R. J., and C. A. REED. 1957. The achievement and early consequences of food production: A consideration of the archeological and natural-historical evidence. *Cold Spring Harbor Symposia on Quantitative Biology* 22:19–31.
- BRAIN, C. K. 1958. *The Transvaal ape-man-bearing cave deposits*. Transvaal Museum Memoir 11.
- . 1970. New finds at the Swartkrans australopithecine site. *Nature* 225:1112–19.
- BROCK, A., and G. L. ISAAC. 1974. Paleomagnetic stratigraphy and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. *Nature* 247:344–48.
- BRONOWSKI, J. 1973. The hidden structure. *The Listener*, May 31, pp. 714–19.
- BROWN, C., and S. A. LAHREN. 1973. More on hunting ability and increased brain size. *CURRENT ANTHROPOLOGY* 14:309–10.
- BYGOTT, J. D. 1972. Cannibalism among wild chimpanzees. *Nature* 238:410–11.

- . 1974. Agonistic behaviour and dominance in wild chimpanzees. Unpublished Ph.D. thesis, Cambridge University, Cambridge, England.
- CACHEL, S. 1973. A new view of speciation in *Australopithecus*. Paper presented at the IXth International Congress of Anthropological and Ethnological Sciences, Chicago, preprint no. 0027.
- CAMPBELL, B. 1966. *Human evolution*. Chicago: Aldine.
- CANNON, P. 1966. "Nutrition and stress," in *Food and civilization: A symposium*, pp. 238–49. Springfield: Thomas.
- CHAVAILLON, J. 1970. Découverte d'un niveau oldowayen dans la basse vallée de l'Omo (Ethiopie). *Compte Rendu des Séances Mensuelles de la Société Préhistorique Française* 1:7–11.
- CLARK, W. E. LE GROS. 1955. *The fossil evidence for human evolution: An introduction to the study of paleoanthropology*. Chicago: University of Chicago Press.
- DART, R. A. 1949. The predatory implemental technique of *Australopithecus*. *American Journal of Physical Anthropology*, n.s., 7:1–38.
- . 1953. The predatory transition from ape to man. *International Anthropological and Linguistic Review* 1:201–18.
- . 1957. *The osteodontokeratic culture of Australopithecus prometheus*. Transvaal Museum Memoir 10.
- . 1963. The carnivorous propensity of baboons. *Symposia of the Zoological Society of London* 10:49–56.
- . 1964. "The ecology of the South African man-apes," in *Ecological studies in southern Africa*. Edited by D. H. S. Davis, pp. 49–66. The Hague: Junk.
- DEEVEY, E. S. 1960. The human population. *Scientific American* 203:195–204.
- DEVORE, I., and S. WASHBURN. 1963. "Baboon ecology and human evolution," in *African ecology and human evolution*. Edited by F. C. Howell and F. Bourlière, pp. 335–67. Chicago: Aldine.
- GENET-VARCIN, E. 1969. *À la recherche du Primate ancêtre de l'homme*. Paris: Boubée.
- GOODALL, J. 1963a. My life among wild chimpanzees. *National Geographic* 124:272–308.
- . 1963b. Feeding behaviour of wild chimpanzees. *Symposia of the Zoological Society of London* 10:39–48.
- GOODMAN, M. 1974. Biochemical evidence on hominid phylogeny. *Annual Review of Anthropology* 3:203–28.
- GOODMAN, M., and G. W. MOORE. 1971. Immunodiffusion systematics of the Primates. I. The Catarrhini. *Systematic Zoology* 20:19–62.
- GOODMAN, M., G. W. MOORE, J. BARNABAS, and G. MATSUDA. 1974. The phylogeny of human globin genes investigated by the maximum parsimony method. *Journal of Molecular Evolution* 3:1–48.
- HOMWOOD, K. 1975. Monkey on a river bank. *Natural History* 84(1):68–73.
- HOWELL, F. C. 1972. "Pliocene/Pleistocene Hominidae in eastern Africa: Absolute and relative ages," in *Calibration of hominoid evolution*. Edited by W. W. Bishop and J. A. Miller, pp. 331–68. Toronto: University of Toronto Press.
- ISAAC, G. L. 1965. The stratigraphy of the Peninj Beds and the provenance of the Natron australopithecine mandible. *Quaternaria* 7:101–30.
- . 1967. "The stratigraphy of the Peninj Group—Early Middle Pleistocene formations west of Lake Natron, Tanzania," in *Background to evolution in Africa*. Edited by W. W. Bishop and J. D. Clark, pp. 229–57. Chicago: University of Chicago Press.
- . 1974. Stratigraphy and patterns of cultural change in the Middle Pleistocene, July 2–11, 1973, Burg Wartenstein, Austria. *CURRENT ANTHROPOLOGY* 15:508–14.
- ISAAC, G. L., and G. H. CURTIS. 1974. Age of early Acheulian industries from the Peninj Group, Tanzania. *Nature* 249:624–27.
- ISAAC, G. L., R. E. F. LEAKEY, and A. K. BEHRENSMEYER. 1971. Archeological traces of early hominid activities, east of Lake Rudolf, Kenya. *Science* 173:1129–34.
- KLEINDIENST, M. R. 1964. "Summary report on excavations at site JK 2, Olduvai Gorge, Tanganyika, 1961–1962," in *Annual report of the Antiquities Division for the year 1962, Appendix 2*, pp. 4–6.
- . 1975. Excavations at site JK2, Olduvai Gorge, Tanzania, 1961–1962: The geological setting. *Quaternaria* 17. In press.
- KLEINDIENST, M. R., and C. M. KELLER. 1974. Toward a functional analysis of handaxes and cleavers: The evidence from eastern Africa. Paper presented at the 7th annual conference of the University of Calgary Archaeology Association, "A Symposium on Primitive Technology and Art," November 15–17, Calgary, Alta.
- KOHNE, D. E. 1970. Evolution of higher-organism DNA. *Quarterly Review of Biophysics* 33:327–75.
- KORTLANDT, A. 1959. *Tussen mens en dier*. Groningen: Wolters.
- . 1967. "Experimentation with chimpanzees in the wild," in *Neue Ergebnisse der Primatologie—Progress in Primatology*. Edited by D. Starck, R. Schneider, and H.-J. Kuhn, pp. 208–24. Stuttgart: Fischer.
- . 1972. *New perspectives on ape and human evolution*. Amsterdam: Stichting voor Psychobiologie.
- . 1974. Das sogenannte Raubtierverhalten der Schimpanzen. Vortrag, IV. Ethologentreffen. MS.
- . 1975. "Ecology and paleoecology of ape locomotion." *Proceedings of the 5th International Congress of Primatology, Nagoya, 1974*. In press.
- KORTLANDT, A., and M. KOOLJ. 1963. Protohominid behaviour in Primates. *Symposia of the Zoological Society of London* 10:61–88.
- KORTLANDT, A., and J. C. J. VAN ZON. 1969. "The present state of research on the dehumanization hypothesis of African ape evolution." *Proceedings of the 2d International Congress of Primatology, Atlanta, 1968*, vol. 3, pp. 10–13. Basel: Karger.
- KRANTZ, G. S. 1968. Brain size and hunting ability in earliest man. *CURRENT ANTHROPOLOGY* 9:450–51.
- . 1973. The double descent of man. Paper presented at the IXth International Congress of Anthropological and Ethnological Sciences, Chicago, preprint no. 2004.
- LAUGHLIN, W. S. 1968. "Hunting: An integrating biobehavioral system and its evolutionary importance," in *Man the hunter*. Edited by R. B. Lee and I. DeVore, pp. 304–20. Chicago: Aldine.
- LEAKEY, L. S. B. 1971 (1968). "Bone smashing by late Miocene Hominidae," in *Adam or ape: A sourcebook of discoveries about early man*. Edited by L. S. B. Leakey, J. Prost, and S. Prost, pp. 443–47. Cambridge: Schenkman.
- LEAKEY, M. D. 1971. *Olduvai Gorge: Excavations in Beds I and II, 1960–1963*. Cambridge: Cambridge University Press.
- LEAKEY, R. E. F. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* 242:447–50.
- LIVINGSTONE, F. 1969. Genetics, ecology, and the origins of incest and exogamy. *CURRENT ANTHROPOLOGY* 10:45–61.
- LOVEJOY, C. O., A. H. BURSTEIN, and K. G. HEIPLE. 1972. Primate phylogeny and immunological distance. *Science* 176:803–5.
- MCGREW, W. C. 1974. Tool use by wild chimpanzees feeding upon driver ants. *Journal of Human Evolution* 3:501–8.
- MERRICK, H. V., J. DE HEINZELIN, P. HAESAERTS, and F. C. HOWELL. 1973. Archaeological occurrences of early Pleistocene age from the Shungura Formation, Lower Omo Valley, Ethiopia. *Nature* 242:572–75.
- NOUGIER, L.-R. 1954. Essai sur le peuplement préhistorique de la France. *Population* 9:214–74.
- OAKLEY, K. P. 1961. "On man's use of fire, with comments on tool-making and hunting," in *Social life of early man*. Edited by S. L. Washburn, pp. 176–93. Viking Fund Publications in Anthropology 31.
- OXNARD, C. E. 1974. *Australopithecus vs. the computer*. *University of Chicago Magazine* 67:8–12.
- PILBEAM, D. 1969. *Tertiary Pongidae of East Africa: Evolutionary relationships and taxonomy*. Peabody Museum Bulletin (Yale) 31.
- . 1972. "Evolutionary changes in the hominoid dentition through geological time," in *Calibration of hominoid evolution*. Edited by W. W. Bishop and J. A. Miller, pp. 369–80. Toronto: University of Toronto Press.
- PILBEAM, D., and S. J. GOULD. 1974. Size and scaling in human evolution. *Science* 186:892–901.
- RATCLIFFE, H. L. 1968. Environment, behaviour and disease: Observations and experiments at the Philadelphia Zoological Gardens. *Transactions and Studies of the College of Physicians and Surgeons of Philadelphia*, Series 4, 36:7–21.
- READ, D. W., and P. E. LESTREL. 1970. Hominid phylogeny and immunology: A critical appraisal. *Science* 168:578–80.
- REYNOLDS, V., and F. REYNOLDS. 1965. "Chimpanzees of the Budongo Forest," in *Primate behavior*. Edited by I. DeVore, pp. 368–424. New York: Holt, Rinehart and Winston.
- ROBINSON, J. T. 1956. *The dentition of the Australopithecinae*. Transvaal Museum Memoir 9.
- . 1963. "Adaptive radiation in the australopithecines and the origin of man," in *African ecology and human evolution*. Edited by F. C. Howell and F. Bourlière, pp. 385–416. Chicago: Aldine.
- . 1972. *Early hominid posture and locomotion*. Chicago: University of Chicago Press.
- SARICH, V. M. 1968. "The origin of the hominids: An immunological approach," in *Perspectives on human evolution*. Edited by S. L. Washburn and P. C. Jay, pp. 94–121. New York: Holt, Rinehart and Winston.
- SARICH, V. M., and A. C. WILSON. 1973. Generation time and genomic evolution in Primates. *Science* 179:1144–47.
- SCHULTZ, A. H. 1937. Proportions, variability, and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Human Biology* 9:281–328.
- . 1961. "Some factors influencing the social life of primates in general and of early man in particular," in *Social life of early man*. Edited by S. L. Washburn, pp. 58–90. Viking Fund Publications in Anthropology 31.
- . 1969. *The life of Primates*. London: Weidenfeld and Nicolson.

- SIMONS, E. L. 1968. A source for dental comparison of *Ramapithecus* with *Australopithecus* and *Homo*. *South African Journal of Science* 64:92-112.
- . 1969. The origin and radiation of the Primates. *Annals of the New York Academy of Sciences* 167:319-31.
- . 1972. *Primate evolution: An introduction to man's place in nature*. New York: Macmillan.
- SIMONS, E. L., and D. R. PILBEAM. 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthropeoidea). *Folia Primatologica* 3:81-152.
- SIMPSON, G. G. 1945. *The principles of classification and a classification of mammals*. Bulletin of the American Museum of Natural History 85.
- SPUHLER, J. N. 1959. "Somatic pathways to culture," in *The evolution of man's capacity for culture*. Edited by J. N. Spuhler, pp. 1-13. Detroit: Wayne State University Press.
- STEWART, J. H. 1968. "Causal factors and processes in the evolution of pre-farming societies," in *Man the hunter*. Edited by R. B. Lee and I. DeVore, pp. 321-34. Chicago: Aldine.
- STOLTZ, L. P., and G. S. SAAYMAN. 1970. Ecology and behaviour of baboons in the northern Transvaal. *Annals of the Transvaal Museum* 26(5):99-143.
- STRUHSAKER, T. T. 1967. Behavior of vervet monkeys (*Cercopithecus aethiops*). *University of California Publications in Zoology* 82:1-64.
- SUGIYAMA, Y. 1968. Social organization of chimpanzees in the Budongo Forest. *Primates* 9:225-58.
- SUZUKI, A. 1973. The origin of hominid hunting: A primatological perspective. Paper presented at the IXth International Congress of Anthropological and Ethnological Sciences, Chicago, preprint no. 0210.
- TELEKI, G. 1973. *The predatory behavior of chimpanzees*. Lewisburg: Bucknell University Press.
- TYLER, C. 1964. *Animal nutrition*. London: Chapman and Hall.
- UZZELL, T., and D. PILBEAM. 1971. Phyletic divergence dates of hominoid primates: A comparison of fossil and molecular data. *Evolution* 25:615-35.
- VAN COUVERING, J. A. 1972. "Radiometric calibration of the European Neogene," in *Calibration of hominoid evolution*. Edited by W. W. Bishop and J. A. Miller, pp. 247-71. Toronto: University of Toronto Press.
- VAN LAWICK-GOODALL, J. 1965. New discoveries among Africa's chimpanzees. *National Geographic* 128:272-308.
- . 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1:161-311.
- VAN ZON, J. C. J., and J. VAN ORSHOVEN. 1967. Enkele resultaten van de Zesde Nederlandse Chimpanse-Expeditie. *Vakblad voor Biologen* 47:161-66.
- VOGEL, C. 1975. "Remarks on the reconstruction of the dental arcade of *Ramapithecus*," in *Antecedents of man and after*. Edited by R. H. Tuttle. The Hague: Mouton. In press.
- WALKER, A., and P. ANDREWS. 1973. Reconstruction of the dental arcades of *Ramapithecus wickeri*. *Nature* 244:313-14.
- WASHBURN, S. L., and V. AVIS. 1958. "Evolution of human behavior," in *Behavior and evolution*. Edited by A. Roe and G. G. Simpson, pp. 421-36. New Haven: Yale University Press.
- WASHBURN, S. L., and R. L. CIOCHON. 1974. Canine teeth: Notes on controversies in the study of human evolution. *American Anthropologist* 76:765-84.
- WASHBURN, S. L., and F. C. HOWELL. 1961. "Human evolution and culture," in *Evolution after Darwin, Vol. 2, The evolution of man*. Edited by S. Tax, pp. 35-56. Chicago: University of Chicago Press.
- WASHBURN, S. L., and C. S. LANCASTER. 1968. "The evolution of hunting," in *Man the hunter*. Edited by R. B. Lee and I. DeVore, pp. 293-303. Chicago: Aldine.
- WRANGHAM, R. W. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour* 22:83-93.
- . 1975. The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Unpublished Ph.D. thesis, Cambridge University, Cambridge, England.

On the Evolution of the Brain and Intelligence

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Jerison's book (reviewed CA 16:403-26) represents a fascinating and maybe unique approach to an ancient problem that appeals to philosophers, theologians, and economists as well as biologists—the place of man in nature. He analyzes the evolution of the brain in vertebrate phylogeny on the basis of its quantitative parameters, as known from the endocasts of fossil animals. In this context, the brain is viewed as the "organ" of mind, and its setting within an evolutionary perspective may serve to outline the history of emerging intelligence in the organic world. Thus Jerison attempts to assess the role of enlarged brains in evolution and the selective pressure toward the enlargement of this organ and behavioral capacities.

The law he derives from his research is "The brains of all animals have evolved in ways appropriate to life in their niches or adaptive zones, in accordance with the principle . . . that describes the relationship to behavior of the structure of the brain as an organ of the body." Doubts as to the meaning of this statement are impossible: Jerison is straightforward and unambiguous. His approach is not trivial, for it connects—or tries to connect—behavior and evolution, brain and taxonomic lineages, in a correct, "vertical" perspective, the paleontological one, and not in the usual way, horizontally. In this way the functional changes in the brain during its evolution can be seen to involve processes in no way distinct from those of the rest of

the body except for the specificity and complexity of the neural mechanisms.

Another interesting point is the author's criticism of the oversimplified theories on encephalization, which sometimes seem teleological.

Like any new and original contribution to human thought, Jerison's book is sometimes even more valuable for the doubtful solutions it sets forth than for the convincing ones. For example:

1. The role of the perceptual apparatus is stressed, but the action of motor skill in evolution and the correlative brain enlargement is not sufficiently assessed. This is relevant in many instances; e.g., the "hand" of anthropoids is not only a perceptual epicritical organ, but also a refined tool.

2. The parallelism between brain size and intelligence and the concept of "additive neurons" are perhaps not sufficient to explain the "redundancy" of higher vertebrates' brains. Redundancy is a double-edged weapon, because while enlargement of the brain seems to correlate with an improvement in "intelligence," it remains doubtful what the quantitative relation is between sensorimotor performance and the critical volume for such performance. The outstanding example is the modern anthropologists' jaunt across the Brain Rubicon toward new cellular, molar, molecular shores. Moreover, the brain contains more glia than neurons, and during its enlargement the neuron-to-glia ratio is not fixed. Thus it remains unclear how many "extra neurons" are to be found in an enlarged brain.

3. In some instances, the dependent variable of the system called forth to explain pressures for enlarged brains—the ecological niche—is altogether an "independent variable" deduced from uncertain speculations.

On the whole, the above criticisms are not intended to destroy, but, as far as possible, to strengthen the vigorous