

Ramapithecus and Hominid Origins¹

by Milford H. Wolpoff

ACCORDING TO THE BACONIAN (i.e., inductivist) view of how science proceeds, the changing interpretations of *Ramapithecus* over the last two decades should reflect a shifting data base. As more data have been recovered, presumably the hypotheses regarding their interpretation have correspondingly changed to encompass a more complete (and more revealing) data set. Because it has been contended at various times that *Ramapithecus* is the earliest hominid,² these changing interpretations should have resulted in different theories of hominid origins.

In this paper, I argue that this does not describe what has

¹ For permission to examine the specimens in their care, I am very grateful to P. Andrews, L. de Bonis, C. K. Brain, D. J. Johanson, G. H. R. von Koenigswald, M. Kretzoi, M. Leakey, R. E. F. Leakey, J. Melentis, M. Pickford, D. Pilbeam, Wu Rukang, P. V. Tobias, and A. C. Walker. I thank R. Ciochon, R. Corruccini, D. W. Frayer, L. O. Greenfield, W. Jungers, R. Kay, F. B. Livingstone, M. Russell, and L. Shepartz for help in preparing the manuscript. This research was supported by NSF grant BNS 76-82729.

² By "hominid" I specifically mean those taxa in the lineage leading to *Homo sapiens*, and any collateral branches of this lineage, after the divergence of this lineage from the one leading to the African apes.

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The present paper was submitted in final form 14 I 82.

actually happened. Instead, it has been shifting hypotheses that have altered the interpretation of the data base. The shifting hypotheses have been about hominid origins and not about *Ramapithecus* at all, because by and large the importance of *Ramapithecus* has historically been in the claim that it represents the earliest hominid. This argument is very Popperian in that it regards the interpretation of data as a consequence of theoretical framework and the function of new data recovery mainly as a potential refutation of current hypotheses (Wolpoff 1976b, 1978). Unlike Popper (1957), or at least the interpretations that have been given to his works (Halstead 1980, but see Popper 1980), I regard evolutionary theory as a falsifiable *scientific* theory, and specific evolutionary hypotheses such as those concerning hominid origins as *scientific* hypotheses because they are potentially refutable. The changing interpretations of *Ramapithecus* reflect just such a series of refutations.

Thus, whether or not *Ramapithecus* is a hominid, a hominid ancestor, or a collateral branch to the hominids, it is my contention that a complex interplay of theory, analysis and interpretation, and accumulating discoveries has wedded the interpretation of *Ramapithecus* to the problem of human origins.

RAMAPITHECUS AND DARWIN'S THEORY

The Darwinian theory of hominid origins has remained very powerful, and in one way or another it has influenced virtually every attempt to hypothesize about this event. Darwin posited what we would call a positive feedback relationship between what he viewed as the four critical elements that distinguish humans from the African apes: bipedalism, tool use, canine reduction, and the expansion of the brain. He hypothesized a fundamental adaptive shift associated with the origin of the human line, in which an arboreal adaptation was exchanged for a terrestrial one and a primarily frugivorous diet was replaced by one emphasizing meat obtained by hunting. The tools attained their importance through their use in hunting and in defense. Bipedalism evolved as an adaptation for freeing the hands during locomotion so that tools and weapons could be carried and used easily. Canines diminished in size as tools replaced their functions in cutting, slashing, and social displays. Lastly, expanding brain size resulted from selection for more complex cooperative behavior and language, both of which were viewed as critical to the adaptations just discussed.

The initial interpretation of *Ramapithecus* as a hominid ancestor was completely within this Darwinian framework, just as were the initial interpretations of *Australopithecus africanus* (Dart 1925) and *Gigantopithecus blacki* (Wu 1962). Thus, the characteristics Lewis (1934) emphasized in his hominid interpretation of the *Ramapithecus* maxillary remains were the parabolic dental arcade, small canines that were transversely

expanded, lack of a functional diastema, and a small degree of maxillary prognathism. Because a small canine and features related to it represent the only characteristics in a maxilla that can be related to the Darwinian theory, attention was focused on the interpretation of their morphology.

When Simons (1961) resurrected the *Ramapithecus* argument, he emphasized the same canine-related features, even removing from the taxon one mandible that did not fit the functional model because of its sectorial P_3 . In a subsequent publication (1964) assigning a number of mandibles to the taxon, one of the primary criteria he used was an inward turning of the corpus at the M_1 position, indicating a parabolic arcade and a short snout. These interpretations were fully consistent with the canine-reduction aspect of Darwin's model.

Similarly, Leakey's (1962) publication of the *Kenyapithecus* maxilla emphasized the small canine seemingly associated with it (the tooth was found several feet away), although his discussion indicated that the tooth was probably used in cutting. While *Kenyapithecus* was not regarded as a hominid in this publication, its detailed resemblance to the *Ramapithecus* palates was noted. In a later publication, Leakey (1967) formally allocated *Kenyapithecus* to the hominids, emphasizing the vertically short canine crown and roots, the small shovel-shaped incisor crowns, and (what he termed) the arcuate shape of the dental arcade. Moreover, like Dart he sought evidence for the behavioral implications of the reduced canine, ultimately claiming evidence for artificially smashed bone at Fort Ternan (Leakey 1968) as an indication that tools were being used.

The interpretive framework for these materials was probably most explicitly stated in a paper by Pilbeam (1966). *Ramapithecus* was claimed to be "completely hominid in known parts" (p. 3); the hominid characteristics were found mainly in the features associated with canine reduction described above. Moreover, Pilbeam argued that since the small canines were ineffective in agonistic behavior and group defense, "presumably, weapon use was established by this time" (p. 3). Finally, because "food must have been prepared for chewing by non-dental means; hands were probably used extensively and perhaps tools as well. . . . The evidence, admittedly circumstantial at present, suggests a primate perhaps already bipedal and fully terrestrial" (p. 3).

With reduced canines, tool use, and (provisionally) bipedalism included in the *Ramapithecus* paradigm, there remained only increased intelligence to complete the predictions of Darwin's hypothesis. Indirect arguments suggesting improved intellectual capacities for the species were presented by Simons (1972) with an analysis of differential molar wear. He claimed that *Ramapithecus* differed from contemporary dryopithecines in showing a greater difference in wear between the adjacent molars (a steeper wear gradient). The steeper gradient was interpreted to indicate a longer period of time between successive molar eruptions and consequently delayed maturation of *Ramapithecus* offspring. The maturational delay presumably permitted the learning of more complex behaviors during childhood.

In sum, *Ramapithecus* was considered a hominid because the known remains fit the applicable aspects of Darwin's model. Thus, it was possible to use the model to speculate or interpret within the framework of interrelations that it provided. The arguments and interpretations indicating tool use, bipedalism, and more complex behavior clearly followed.

The inductivist interpretation would suggest that Darwinian-based arguments were ultimately dismissed because new data suggested a new theory about the phylogenetic status of *Ramapithecus*. Indeed, the period of the earlier 1970s in which this framework was effectively questioned was also a period of intensive fossil discovery. However, for several reasons I do not believe that the two phenomena are causally related.

The fit of the *Ramapithecus* data to the Darwinian model involved much more interpretation than actual analysis. The

canine, for instance, was regarded as small and reduced long before a canine was found (the Fort Ternan specimen), and even when a canine was recovered and showed the morphology of a honing tooth, its "small size and reduction" were still emphasized. It did not require new materials to question these interpretations. Following the original paper by Lewis (1934), Hrdlička (1935) systematically rejected the morphological arguments supporting the hominid interpretation, and other workers showed that the relative sizes of the canines and the incisors do not differ from those of some of the Africa pongids (Wolpoff 1971a, Yulish 1970). The reconstruction of the dental arcade as parabolic was questioned (Frayer 1976) and ultimately shown to be incorrect (Vogel 1975, Greenfield 1978). The evidence for a steep molar wear gradient in *Ramapithecus* was questioned (Greenfield 1974), and in any event the presence of steep gradients in primate species without delayed maturation had already been shown (Mann 1968, Wolpoff 1971b). The questions described above (as well as others from this period [see von Koenigswald 1972, Robinson 1967]) were not raised because new materials were discovered; their basis was in the original specimens and their interpretations. However, historically it was too early for criticism to be effective, and these objections were not widely noted. First, the Darwinian hypothesis of hominid origins had to be replaced by another.

RAMAPITHECUS AND JOLLY'S THEORY

Publication of Jolly's "seed-eaters" hypothesis (1970) received widespread attention (Jolly 1973) and was generally (although not universally) well accepted among paleoanthropologists. Although Robinson (1963) had earlier argued that the masticatory apparatus of the "*Paranthropus*" remains from South Africa indicated a vegetarian adaptation in what he regarded as a little-modified descendent of the original australopithecine stock, it was Jolly who publicized a formal evolutionary hypothesis indicating mechanisms that connected hominid origins with a diet-oriented masticatory shift and the behaviors associated with it.

Indeed, while Jolly also focused on "*Paranthropus*" (and OH 5 from East Africa) in support of his ideas, it soon became clear that the earlier *Australopithecus africanus* evinced the same masticatory adaptation (Wolpoff 1973). The model was immediately applied to the interpretation of *Gigantopithecus bilaspurensis* (Simons and Ettl 1970), which was then still considered an "aberrant ape" (Pilbeam 1970). The application to *Ramapithecus* was somewhat slower.

Jolly's model linked canine reduction, upright posture and finally bipedalism, the development of thumb opposability, the appearance of language, the development of single-male groups, and the evolution of a masticatory apparatus adapted for powerful grinding and crushing to a dietary and behavioral adaptation emphasizing the exploitation of seeds and other small objects. Jolly did not deal with brain-size (or, more generally, behavioral-complexity) increases, since, by the end of the 1960s, it was evident that Pliocene *Australopithecus* had an essentially ape-sized brain. Moreover, Jolly did not accept the arguments for delayed maturation (Mann 1968) or for neural reorganization (Holloway 1966), so in essence he had nothing to explain. For these reasons, and because the early hominid dietary adaptation involved plant foods rather than meat (as Darwin had suggested), neither culture nor tool use played a role in his hominid-origins model (much to the apparent relief of some of the more paleontologically oriented paleoanthropologists).

Interpretation of an adaptation combining small-object feeding, powerful masticatory apparatus, and terrestriality found its way into the *Ramapithecus* discussions as new materials were discovered and older specimens reanalyzed. This inter-

pretation was clear in the reconstruction and analysis of the Fort Ternan individual (Andrews and Walker 1976) and helped mitigate the effects of the narrow, parallel-sided dental arcade and associated mandible with a sectorial P_3 on the hominid interpretation of the specimen (although this process actually took some time, during which the premolar in question was "semi-sectorial" or "incipiently bicuspid" [Simons 1976]).

By the earlier 1970s, the molars of already known *Ramapithecus* specimens had been reexamined and evidence found that was interpreted to show powerful mastication in this form (Simons and Pilbeam 1972), including thick enamel, interproximal attrition, and a steep molar wear gradient (the alternative to the delayed-maturation interpretation). Other features now brought into focus were the flat, deep face, vertical incisors, and heavily buttressed mandible (especially at the symphysis).

Newly discovered specimens were interpreted in a framework that itself was changing (Wolpoff 1975). Description of the Çandır mandible (Andrews and Tekkaya 1976), for instance, emphasized the buttressing of the mandibular corpus and symphysis and shortening of the anterior face, while the shape of the dental arcade confirmed the Fort Ternan reconstruction. However, the sectorial P_3 was still being regarded as "molarized" (Simons 1976). While the Pyrgos mandible was the only one known of the Greek specimens, it was described as extraordinarily australopithecine-like (Walker 1976), with an "arcuate" mandibular arcade (Simons 1978), although the (remains of) large molars and a thick mandibular body were also given some attention. The numerous more recent discoveries of much more complete Greek specimens have been interpreted somewhat differently (de Bonis and Melentis 1977, 1978).

The Hungarian finds from Rudabánya (Kretzoi 1975) were viewed as *Ramapithecus*-like forms, although not actually allocated to *Ramapithecus*. Indeed, Kretzoi (1976) found greater similarities between *Rudapithecus* and early *Homo* than between *Rudapithecus* and *Australopithecus*. Simons (1976) disagreed on both points, allocating this form to *Ramapithecus* and noting the dental and gnathic adaptations for powerful mastication. At the same time, he compared the canine form and wear on the RUD 12 maxilla with the Hadar australopithecine palate AL 200 as well as with *Gigantopithecus*. The ground was shifting for the functional interpretation of the *Ramapithecus* canine; it no longer was incisiform (as it was in the middle of the decade [see Conroy and Pilbeam 1975]), but with the recovery of the Hadar australopithecines it could still be related to the hominids. In a similar manner, once analysis of australopithecine dental arcades showed that they were not parabolic (Genet-Varcin 1969), this condition was no longer claimed to characterize *Ramapithecus* (Simons 1977, Simons and Pilbeam 1978).

With the addition of the Çandır and *Rudapithecus* specimens to the *Ramapithecus* sample, it became generally accepted that *Ramapithecus* combined a short face, thick molar enamel, a nonparabolic dental arcade (with varying degrees of posterior divergence), a relatively thick corpus and symphysis, and widely divergent zygomatic processes in a pattern that so clearly indicated powerful mastication (Wolpoff 1974, Hylander 1979) that at least one researcher described the complex as most resembling a miniature hyperrobust australopithecine (Walker 1976). At the same time, the canine function was seen to be pongid-like (although also like that of the earliest hominids). With the acceptance of Jolly's model, some of the criticisms of one decade were incorporated into the interpretations of the next.

Thus, by the closing years of the last decade, a firm case was being made that *Ramapithecus* showed the dental and gnathic adaptations of a powerful masticator and could be considered a hominid because it fit Jolly's model of hominid origins (Simons and Pilbeam 1978). These characteristics (in contrast to those emphasized by Darwin) related to an adaptive shift involving

terrestrial small-object feeding in semiopen or open ecozones (Pilbeam 1979). This interpretation took most of the decade to develop fully because the anterior teeth were never really de-emphasized until the discoveries at Rudabánya and Hadar allowed a rather different comparison to sustain the hominid interpretation.

In all, this was truly a case in which (to paraphrase Samuel Butler) the foundations were changed while the superstructure remained the same. The focus shifted from the front to the back of the jaw, and *Ramapithecus* remained a hominid.

Although Jolly's hypothesis was about hominid origins and the examples it drew upon were Pliocene *hominids*, it was the application of this model to *Ramapithecus* that carried the seeds of its destruction. Three factors have combined to set the stage for questioning whether the seed-eaters hypothesis can account for *hominid* origins.

First, a set of morphological characteristics indicating a powerful masticatory complex appears in a variety of mammals. Long before the hypothesis was published, the dental and gnathic characteristics associated with powerful grinding and crushing were recognized in a species whose diet was clearly not small objects. This complex, (perhaps mistakenly) referred to as the "T complex" because of Jolly's analogy using *Theropithecus*, was earlier described in the giant panda (Sicher 1944) in a comparison with bears that parallels Jolly's comparison of *Theropithecus* and *Papio*. Indeed, in his discussion of this bamboo-eating species, Davis (1964) found the closest analogy to be with "*Paranthropus robustus*." A similar morphological complex characterizes some of the leaf-eating ceboids (Kinzey 1974). The point is that, in living forms, the dental/gnathic complex described by Jolly does not necessarily indicate small-object feeding, let alone a terrestrial adaptation. It does not necessarily lead to hominization. Consequently, the same argument must apply to the interpretation of *Ramapithecus* as well as of other fossil primates. Thus, for instance, White (1975) indicates the possibility of a giant-panda-like diet for *Gigantopithecus* and suggests that the pandas may have replaced this primate. Kay (1981) describes an alternative dietary interpretation for the *Ramapithecus* specimens themselves (nut eating) that involves neither a terrestrial adaptation nor any of the aspects of hominization hypothesized by Jolly. These arguments tend to remove some of the cause-and-effect aspects of the seed-eaters hypothesis by showing that a morphological adaptation to powerful grinding and crushing does not require a diet of seeds or grains. Moreover, there is an ample variety of other difficult-to-masticate food sources that early or pre-hominids might have utilized (Coursey 1973, Wolpoff 1973, Kay 1981).

Second, Jolly's hypothesis has always been weak in its explanation of how other basal hominid features might have followed from small-object feeding. For instance, whatever the validity of the argument that small canines remove the restriction of canine interlock and allow free lateral movement of the jaws, the argument can only account for canine reduction; it does not account for the change in canine form and function in the hominids. Bipedalism, too, has never been adequately explained by this hypothesis, and attempts to do so (Wrangham 1980) have been less than convincing. Finally, not all workers are as willing as Jolly to regard culture, tool making, and expanded behavioral complexity as hominid attributes that evolved after hominids originated. It is not clear that these lack all causal relation to hominid origins. Thus, while small-object feeding could account for some of the features found in the earliest Pliocene hominids, it does not necessarily account for others.

Third, the focus on this dental/gnathic complex resulted in renewed support for the earlier claims that *Ramapithecus* was similar, or identical, to the other Asian hominoids (Frayer 1976, 1978; Greenfield 1974, 1975, 1977, 1979) because many of these earlier claims were based on the same diet-related characteris-

tics but these features were not regarded as especially important under the Darwinian hypothesis. The special similarities (if not identity) of *Ramapithecus* and *Sivapithecus* (Andrews and Tekkaya 1980; Greenfield 1977, 1980; Frayer 1978; Pilbeam 1979), the combined mandibular morphology of both taxa in one species of *Ouranopithecus* (de Bonis and Meletis 1980), and the likelihood that these hominoids were markedly dimorphic (Frayer 1976, Greenfield 1979, Pilbeam 1979, Wolpoff 1980) suggest that at the very least the paradigm for the genus *Ramapithecus* must be expanded to include more specimens and a wider range of variation. The features that assumed importance in the newer interpretation, which was a consequence of the framework provided by the seed-eaters hypothesis, were widespread, and when sexual dimorphism was taken into account it became far from clear how many species were actually involved in what has increasingly come to be regarded as a single adaptive radiation (Wolpoff 1980) that might be referred to by the nontaxonomic term "ramapithecine" (see also Kay and Simons 1982). By many accounts, the ramapithecines would include specimens allocated to *Ramapithecus*, *Kenyaipithecus*, *Sivapithecus*, *Ankarapithecus*, *Rudapithecus*, *Bodvapiithecus*, *Ouranopithecus*, "*Hemianthropus*," and *Gigantopithecus* (Pilbeam 1979, Kretzoi 1975, Wolpoff 1980).

An adaptive radiation can result from the appearance of a new adaptation, with consequences that allow a previously unutilized set of niches to be entered (Simpson 1953). Rapid speciation almost invariably follows (Stanley 1979), and the resulting taxonomic group soon becomes highly diversified. In the ramapithecines, the common element in the remains now known for the group is the masticatory apparatus, adapted for a diet requiring powerful or prolonged grinding and crushing. It is likely that this reflects the novel adaptation that was the basis of the subsequent radiation. The exploitation of otherwise unusable dietary resources would allow adaptation to new ecozones because this dental/gnathic adaptation is not an adaptive specialization; it acts to expand the range of available resources.

Apart from the masticatory complex, other common elements are difficult to identify because few skeletal parts besides jaws and teeth have been found. Moreover, features unique to the ramapithecines cannot always be clearly distinguished from shared primitive features (such as the retention of marked sexual dimorphism) because little is known of the ancestral condition. Recent evidence suggests that the ramapithecines evolved from a *Proconsul* or *Proconsul*-like form of approximate *P. nyanzae* size (Pickford 1982).

Temporal and geographic considerations alone suggest the existence of a fairly large number of ramapithecine species. Of greater importance is the number of lineages in the adaptive radiation. Although workers such as Pilbeam (1979) have indicated five or more, the fact is that no ramapithecine-bearing locality has provided evidence of more than two contemporary lineages, and in many cases the data can be interpreted to show only one. This could be a consequence of the generalizing aspects of the masticatory morphology underlying the radiation. Instead of more finely subdividing the new niche, competition between the emerging ramapithecines seems to have promoted their rapid spread. The resulting pattern emphasizes allopatric more than sympatric species proliferation in a manner similar to the distribution of baboons and baboon-like forms such as *Theropithecus*, but the extent of allopatric species proliferation may have been markedly greater than in these cercopithecoids.

The evidence of variation within the ramapithecine adaptive radiation tends to be obscured by two circumstances. First, gross size would appear to be the most dramatic variant in the recognized ramapithecine forms (molars, for instance, range from smaller than *Homo sapiens* to *Gigantopithecus* size). The problem this creates is one of separating variation due to scaling from that due to other factors. Even so, the adaptive importance of size variation over this range should not be under-

stated. Second, because jaws and teeth are the most usual fossil remains, most comparisons are limited to the very adaptive complex that forms the basis of the radiation and consequently would not be expected to show dramatic adaptive differences within it.

In the context of this common adaptive pattern there are, however, important morphological variants. For instance, enamel thickness varies continuously from the extremely thick condition in *Ouranopithecus*, *Gigantopithecus*, and "*Hemianthropus*" to a thinner expression in some of the Rudabánya forms. Even at individual sites this feature varies considerably. Thus at Rudabánya the larger specimens (*Bodvapiithecus*) have quite thick enamel, while the smaller ones range from this thickness to a thinner condition such as that seen at its extreme in RUD 12. Kay and Simons (1982) probably had this specimen in mind as the basis for their claim that molar enamel at Rudabánya is thin and consequently that *Rudapithecus* should be allocated to the European dryopithecines rather than to the ramapithecines. However, RUD 12 lies at the low end of a range of marked variation in enamel thickness, even within the *Rudapithecus* remains. Similarly, marked variation can be found in the deeply incised molar wrinkles that characterize some of the ramapithecine specimens. As in the case of enamel thickness, the variation is one of frequency between samples. Cingulum expression represents yet another varying feature. Variation can be seen in the development of the P₃ metaconid, which ranges from complete absence to the full development of an equal-sized cusp. Kay and Simons (1982) report that the frequency of P₃ metaconid enlargement observable in some of the ramapithecine specimens (excluding *Gigantopithecus*) is comparable to that observed in chimpanzees and orangs (although not gorillas). However, they further claim that the degree of development in some of the ramapithecine specimens exceeds that which they have observed in these living apes. This forms part of their argument for a special relationship between the ramapithecines and the hominids. Yet, the fact is that this feature is quite variable in the radiation, ranging from the gorilla condition (no metaconid) to the *Homo*-like bicuspid form of the *Gigantopithecus* premolars, with cusps of equal size.

Few nondental features allow comparison of the ramapithecine forms. The distal humeri from Hungary and Pakistan differ notably; the Fort Ternan humerus could represent a third variant, but its association with the African ramapithecine is uncertain. On the other hand, the cranial remains from Hungary, Pakistan, Greece, and the People's Republic of China are surprisingly similar.

The relation of the adaptive radiation of the ramapithecines to hominid origins will be discussed below. The acceptance of the notion of a ramapithecine adaptive radiation provides the third basis for questioning the seed-eaters model as a hypothesis about *hominid* origins. This is because the ramapithecine adaptive radiation was highly successful in terms of geographic range and survivorship of the taxonomic group. It has recently become evident that there were at least two nonhominid Pleistocene survivors.

RAMAPITHECUS AND THE LATE-DIVERGENCE HYPOTHESIS

The idea of a fairly recent divergence between humans and apes is hardly new. Early contentions of a late divergence were influenced by the very short estimates of the earth's age that preceded a full understanding of radioactive decay. The late-divergence hypothesis as presented by Greenfield (1980, 1982) specifically focuses on the divergence between humans and the African apes, emphasizing that there were two different divergence points in the evolution of the recent hominoids. This distinction is an important one.

Late divergence between humans and African apes and an

earlier separation of *Pongo* have been supported morphologically, genetically, biochemically, and, most recently, paleontologically.

Morphologically, it has long been recognized that the chimpanzee is the most human-like of the pongids (Huxley 1861, 1863; Gregory 1930; Simpson 1963; Washburn 1968), and the idea of a very *Pan*-like ancestor for the hominid line has been maintained for decades (Schwalbe 1923, Coolidge 1933, Gregory 1934, Weinert 1944, Washburn 1968, Zihlman et al. 1978, Zihlman 1979, among others [although not necessarily like *Pan paniscus* (McHenry and Corruccini 1981, Johnson 1981)]). This special relationship is one important aspect of the late-divergence hypothesis: the morphological data provide information about divergence sequence, although not absolute date.

These morphological comparisons are independently supported by genetic analysis. Chromosome banding studies show an especially close relation of *Homo*, *Pan*, and *Gorilla*, with *Pongo* somewhat divergent (Miller 1977, Yunis, Sawyer, and Dunham 1980). The comparison of protein coding sequences indicates an extraordinary genetic similarity between *Homo* and *Pan* (King and Wilson 1975). These genetic comparisons reveal less difference between the two genera than is common between sibling species. The extent of similarity far exceeds the minimum necessary to show that the relationship is genuine (Doolittle 1981). Taken at face value, these data would tend to indicate recent divergence as well as extreme closeness of relationship for the African hominoids and a more distant relation and earlier divergence for *Pongo*.

Biochemical analysis also supports the particular closeness of relationship of *Homo*, *Gorilla*, and *Pan*. In a recent series of summaries for numerous genetic systems (Goodman 1976, Dene, Goodman, and Prychodko 1976), it was found that immunodiffusion studies, nucleotide replacements, and the analysis of various proteins consistently show humans, chimpanzees, and gorillas to be more closely related to each other than any of these are to orangutans. Thus, the divergence sequence suggested earlier on the basis of morphology is supported.

Biochemical studies have also been used to calibrate a divergence "clock" for this sequence (Sarich and Wilson 1967, Sarich 1974, Sarich and Cronin 1976). This "clock" seems to provide direct evidence for a very late *Pan-Homo* divergence (estimates based on this procedure have ranged between 3,500,000 and 5,500,000 years ago). However, the techniques that result in these estimates give divergence times for other species that are at significant variance with virtually any interpretation of the fossil record (Uzzell and Pilbeam 1971, Jacobs and Pilbeam 1980, Read and Lestrel 1972, Radinsky 1978, Walker 1976 and references therein). Moreover, there have been an extraordinary number of criticisms of the molecular "clock" (Lovejoy, Burstein, and Heiple 1972, Lovejoy and Meindl 1973, Read 1975, Read and Lestrel 1970, Jukes and Holmquist 1972, Corruccini et al. 1980, Goodman 1974, Fitch and Langley 1976, Jukes 1980). Probably the best way to summarize the very disparate points raised is that the "clock" simply *should not* work. This conclusion supports the paleontological analyses that claim the clock *does not* work when applied to divergence times over broad time spans. Consequently, although biochemical evidence seems to support a late *Pan-Homo* divergence, I believe that this is a red herring and that the molecular "clock" does not support any divergence time, just as other independent evidence for late *Pan-Homo* divergence does not support the molecular "clock." However, while specific divergence *dates* may be rejected, I do not believe it is possible to dismiss the implications of the biochemical evidence for divergence *sequence* (Greenfield 1982).

Finally, paleontological evidence also supports the contention of an especially close relation between the hominid line and the ancestors of the African apes. The relationship has long been recognized for *A. africanus* (Clark 1947), and the discovery of an even closer approach to the chimpanzee condition in *A.*

afarensis (Johanson and White 1979) is not surprising. While the Pliocene fossil evidence can provide no more than a minimum divergence date (4,000,000 years), the number of primitive and specifically chimpanzee-like features in the known crania support the contention of a late divergence.

In sum, these data strongly support the notion that the divergence of the lineage leading to *Pongo* from the lineage leading to *Homo*, *Pan*, and *Gorilla* was earlier than the divergence of these three African hominoids from each other. The data further suggest that the later (African) divergence may have been fairly recent.

The effect of the late-divergence hypothesis on the interpretation of the ramapithecines is a consequence of the earlier divergence proposed for *Pongo*. This became evident when two of the Pleistocene survivors of the ramapithecine adaptive radiation were first recognized as such. One of these, *Gigantopithecus*, survived into the Middle Pleistocene, where contemporaneity with hominids has been established (Hsu, Wang, and Han 1975). The other survivor is *Pongo*.

Once again, the assertion that *Pongo* evolved from a ramapithecine was not initially established from recently discovered data, although the interpretations and implications of this contention are recent. Gregory and Hellman (1926) noted a number of morphological similarities between *Sivapithecus* and *Pongo* molars and suggested an ancestral relationship. Of course, they did not regard *Sivapithecus* as a ramapithecine (*Ramapithecus* had yet to be recognized). The dental similarities can now be shown to extend throughout the ramapithecine remains and include, in addition to those noted by Gregory and Hellman, the following variably expressed features: (1) enamel thickness; (2) deeply incised wrinkles that persist after crown morphology has been worn away (especially in the Lufeng ramapithecines and "*Hemianthropus*" but also sporadically in the remains from Pakistan and Hungary); (3) asymmetric heteromorphic lateral maxillary incisor size and form; and (4) central maxillary incisors that change in angulation during life so that in younger individuals a lingual wear plane typically extends from the tip to the base.

Newly discovered ramapithecine cranial remains also support the hypothesis of a ramapithecine ancestry for *Pongo*. In particular, the face and partial cranium from Pakistan (GSP 15000) reveal a suite of extraordinarily *Pongo*-like details (Pilbeam 1982). Specific resemblances include the facial profile, high hafting of the braincase on the face (a vertically oriented masticatory system), morphology of the zygomatic (especially size and position of the zygomatic foramen), orbit shape, palate shape and the form of the incisive and palatine foramina, relative I² size, and the form of the articular eminence of the glenoid fossa. The lower face and palate from Turkey (MTA 2125) have been similarly described: "the closest comparisons in most cases were with the orang-utan" (Andrews and Tekkaya 1980:94). The upper face from Rudabánya (RUD 44) is also characterized by *Pongo*-like features, including relative orbit heights, a very wide outer-orbital area, and marked converging anterior temporal ridges. Finally, *Pongo*-like features seem to characterize the newly discovered Lufeng crania (Wu 1981). As in the Rudabánya remains, the most marked resemblances are in the upper face and frontal, including the marked temporal ridges, the wide outer-orbital pillars, and the shape of the orbits and supraorbitals (Xu and Lu 1980).

Interestingly, Kay and Simons (1982) argue against a special affinity to *Pongo* in the ramapithecine facial remains, although their discussion omits the most complete, Lufeng and GSP 15000. Their contention is mainly based on the Turkish face, MTA 2125, and involves arguments that I regard as less than convincing. For instance, in claiming the specimen is not as prognathic as *Pongo*, they use as a measure of maxillary prognathism what is actually one of relative alveolar height

(alveolar height/palate breadth at M2), bearing no relation to how *prognathic* the premaxilla might be, independent of its relative size. Similarly, they admit to the marked maxillary incisor heteromorphy in the Turkish specimen but feel it does not align it with *Pongo* because the incisor heteromorphy in this living ape was presumably attained by relative I¹ expansion (this was calculated relative to molar size and therefore potentially confuses I¹ expansion with molar reduction). Besides positing an ad hoc explanation for what appears to be a simple relationship, this argument ignores the important morphological similarity of I² form in MTA 2125 and other specimens to that in *Pongo*. I would argue, in contrast, that the central and lower portions of the known ramapithecine faces do in fact show specific resemblances to *Pongo*'s. On the basis of the faces from Rudabánya, Ravin, Turkey, Pakistan, and Lufeng, these similarities would seem to include the incisor heteromorphy (metric and morphological), the changing incisor wear plane beginning with the very marked angulation characteristic of young individuals, the premaxillary prognathism as measured by the angulation of the premaxilla, and the strong superior-medial angulation of the canine roots. However, as I have said, I believe that an even stronger resemblance between these faces and *Pongo*'s is shown in the upper face and frontal as represented at Rudabánya, Pakistan, and Lufeng.

Kay and Simons conclude that the Turkish face shows some resemblances to those of all of the extant pongids. While I believe that there are more specific relations with *Pongo* than they admit, I would support this basic conclusion. To the general ancestral features they discuss might be added the variable characteristics of the ramapithecine dentitions described above, including cingulum development, molar wrinkling, enamel thickness, and P₃ metaconid expression. The fact is that ramapithecine variation in these facial and dental features would potentially allow the ancestry of every living hominoid group to be found.

However, in this context, the specific resemblances of *all* of the ramapithecine faces to *Pongo*'s have unavoidable implications for the hypothesis that the ancestry of *Pongo* is to be found within the ramapithecine adaptive radiation. Of course, only one of the ramapithecine lineages could be ancestral to this living ape; on the basis of the present evidence (especially the new material from China and Pakistan) and the argument of geographic proximity, this almost certainly would be an Asian lineage. However, if one of the ramapithecines is ancestral to *Pongo*, the implications are far-reaching for the entire adaptive radiation.

There are two hypotheses about how the ramapithecines may be related to hominids, depending on when the ramapithecines appeared relative to the split between the line leading to *Pongo* and the line leading to the African hominoids and subject to the constraints of the data discussed above.

If the split between the African hominoids and the line leading to *Pongo* occurred *before* the ramapithecines evolved, then the ramapithecines must be uniquely associated with either the *Pongo* line or the African hominoid line. The evidence for the ancestry of *Pongo* among the ramapithecines indicates that if this hypothesis were correct, no ramapithecines contributed to hominid ancestry because they were on the *Pongo* side of the split (Andrews 1982). It would then follow that the numerous dental and gnathic similarities of the earliest hominids (especially *A. afarensis*) with the ramapithecines would have to be interpreted as parallel independent acquisitions. This is far from impossible, since most of the similarities are in the dental/gnathic complex associated with powerful mastication and, as noted above, this complex has appeared again and again in unrelated forms as a common response to a similar adaptation. Thus, this interpretation cannot be easily dismissed. On the other hand, it was exactly this sort of evidence that led to the contention of a ramapithecine adaptive radiation. If the same criteria were applied to the jaws and teeth of *A. afarensis*, the

functional interpretation of the morphology of this extraordinarily megadont early hominid form would suggest the same conclusion, namely, that *A. afarensis* is part of or closely related to the ramapithecine adaptive radiation. Indeed, this is how R. E. F. Leakey (1976) interpreted the Hadar female AL 288-1. Thus, I consider this first hypothesis to be the far less likely one (Wolpoff 1981). Indeed, unless one is willing to postulate a fairly extensive amount of parallel or even convergent evolution in the hominoids, it can probably be rejected.

If the split between the African hominoids and the line leading to *Pongo* took place *within* the ramapithecines, some sort of ramapithecine ancestry for hominids as well as for *Pongo* is implied. Thus one could account for the fundamental aspects of both of the sets of interpretations that have developed in the last decade: the relationship of the ramapithecines to *Pongo* and the similarities of the ramapithecines to the earliest hominids. Indeed, an alternative way of stating this hypothesis is that the earliest hominids are part of the ramapithecine adaptive radiation.

Under this hypothesis there is a ramapithecine ancestry for the African apes (as discussed by Greenfield 1977), but these forms diverged markedly from the ancestral condition because of their specific dietary adaptations, with effects on their dental morphology and function described by Kay (1975, 1981) and Maier and Schneck (1981). At the same time, however, it would account for the specific resemblances of *Australopithecus* and *Pan* by presuming a late divergence between them.

This hypothesis thus necessarily posits a specific ramapithecine ancestor for the hominids, a species which is *also* ancestral to *Pan* and *Gorilla*. It is possible that one of the Eurasian ramapithecines represents this ancestor, but I suspect that the limited evidence now available does not allow a decision as to which (if any) of these lineages is the most likely (Wolpoff 1980). Traditional comparisons have emphasized the hominid-like aspects of the smaller species (albeit as a hominid and not as a common ancestor of the hominids and African apes), such as *Ramapithecus* or *Rudapithecus*, but detailed dental morphology and size considerations could argue for one of the larger forms (*Sivapithecus*, *Ouranopithecus*). However, Middle Miocene geography would suggest the possibility that none of the Eurasian forms represent this ancestor.

If an African ramapithecine is a more likely candidate for this ancestor, the situation is little improved. There are virtually no hominoid fossils known between the Fort Ternan ramapithecines and *A. afarensis*; Lukeino, Ngorora, and Lothagam could be interpreted as either ramapithecines or early hominids, although there are substantial similarities between Lothagam and the mandibles from Laetoli. It is possible that the Fort Ternan ramapithecine represents or is closely related to the common ancestor of the African hominoids. On the other hand, it may be too early. The fact is that the date of the split between the African and Eurasian forms is unknown, and this split could be later than the Fort Ternan remains. Thus, in my view there is no ramapithecine ancestor for the African hominoids that can be identified unambiguously at this time. While it is possible that one of the Eurasian forms is this ancestor, I believe it more likely that, as the African fossil record spanning the later Miocene is better explored, a suitable ramapithecine lineage (perhaps beginning with Fort Ternan) will be found.

I predict that when found the Late Miocene African ramapithecine will be identifiably similar and fairly closely related to the known Eurasian remains. Craniodentally it will resemble *A. afarensis*, although with much more projecting and more sexually dimorphic canines. It will *not* resemble a chimpanzee to a significantly greater extent than *A. afarensis* does, and it will especially not resemble a pygmy chimpanzee. It is likely that at the time of the human-African-ape divergence, character displacement and other consequences of competition had initially greater effects on the apes than on the human line.

Thus, I suggest that the last common ancestor of the African apes and humans was probably as different from living apes as it was from living humans. No living ape, even an enculturated one such as described by Kortlandt (1972), could form an adequate model for this ancestral form, any more than a living human group could.

Such an ancestral species would be expected to retain the dental/gnathic complex associated with powerful or prolonged chewing. At the same time, one might expect the more elongated cranial form also emphasizing anterior dental loading that characterizes the African apes in contrast to the shortened, more vertically oriented form of *Pongo* crania. If one were to describe this hypothetical ramapithecine cranium as a chimpanzee-like vault with a ramapithecine face and dentition (with the consequent molar-loading-related superstructures on the vault), this description would be fairly close to the known cranial remains of *A. afarensis* (Johanson 1980).

The locomotor complex of this ramapithecine might be expected to reflect an at least partly arboreal adaptation (climbing, arm hanging) without the brachiating specializations of the African apes or their associated knuckle-walking quadrupedalism. This is suggested by a number of comparisons, including the lumbar elongation of the australopithecines (STS 14 has six functional lumbar) combined with the arm-hanging abilities inherent in the human upper torso and even more markedly expressed in *Australopithecus*.

In sum, I believe the evidence best supports the late-divergence hypothesis presented by Greenfield (1980). I would suggest that an adaptation for foods requiring powerful or prolonged chewing arose among one of the *Proconsuls* and that, because this provided the basis for utilizing a much wider range of dietary resources, a very successful adaptive radiation of hominoids resulted. With the geographic spread of the ramapithecines, the radiation was split into Eurasian and African branches (the *Pongo*-African hominoid split) and perhaps into European and Asian branches as well. I predict that the eventual discovery of more complete remains will demonstrate a much wider adaptive range within this radiation than the analysis of the dental/gnathic complex now indicates. It would appear that the western portion of the Eurasian ramapithecines became extinct while there were at least two Pleistocene survivors to the east: *Gigantopithecus* and *Pongo* (the so-called giant-orang teeth and the "*Hemianthropus*" specimens³ from South China may represent a third Pleistocene survivor).

Relatively little is known of the African ramapithecine branch. Genetic evidence relating *Pan* and *Homo* and the morphological relations of *Pan* and *A. afarensis* indicate that during the late Miocene one of the African ramapithecine lineages further split into lines leading to the adaptively specialized African apes and a hominid line.

RAMAPITHECUS AND HOMINID ORIGINS

While I have argued that none of the ramapithecines are hominids, I propose that the earliest hominids were a special form of ramapithecine. I believe this is a distinction with a

³ The confusion of "*Hemianthropus*" teeth with *Australopithecus* teeth (von Koenigswald 1957) is a consequence of their similar size and shared primitive characteristics, related to the basal ramapithecine masticatory adaptation. These teeth are actually worn versions of the thick-enameled dental remains that have been attributed to "giant oranges." Even in Asian Middle Pleistocene deposits, it is often difficult to distinguish worn orang postcanine teeth from worn hominid teeth. Since there are no remains other than dental known for this third form (giant oranges, "*Hemianthropus*"), exactly what is represented is unclear. However, size extends completely into the *Gigantopithecus* range, and there also

difference because it brings a different focus to the problem of hominid origins than is usually applied.

This difference is the result of two recent changes in interpretation. The first is a swing away from the earlier notion of australopithecines as fully human beings (albeit with somewhat diminished mental capacities) advanced by workers such as Clark (1967, perhaps in reaction to Zuckerman) and Isaac (Isaac and Isaac 1975; see also Leakey and Lewin 1977). The second is the recognition, after a decade of behavioral studies, that the African apes, and by implication the latest common ancestor of these apes and humans, are far more hominized than was once believed. As a result, the ramapithecines can be viewed as more human-like while the earliest humans can be viewed as more ramapithecine-like without the contradictions that have historically been associated with this convergence of views.

An example of the first change is the way the importance of brain size has changed from the Darwinian expectation that dramatic improvement of mental capacity was a critical underlying factor in hominid origins. The available evidence now suggests that marked brain-size increase was *not* a rapid event directly associated with hominid origins. The evolution of modern brain size (and presumably the cultural/behavioral changes that came with it) has taken most of the Pleistocene. Evidently, only moderate or even minimal endocranial expansion can be associated with hominid origins. Holloway (1980) has published figures for Jerison's encephalization quotient for a sample of *Pan*, where $EQ = \text{brain weight}/0.12 * \text{body weight}^{.666}$. The midsex value for *Pan* is 2.96. Using the midsex cranial capacity for *A. africanus* which I have determined (443 cc) and an approximate midsex body weight average of 40 kg (Wolpoff 1973) produces an EQ of 3.20. These data, with the evidence for neural reorganization (Holloway 1966, 1976), suggest that while some brain-related changes may have been associated with hominid origins, their magnitude was small compared with subsequent Pleistocene changes. The extent of actual change was probably even smaller and will be better estimated when data for the earlier species *A. afarensis* are available.

At the same time, the progressive hominization of the ramapithecines has brought the realization that hominid origins may not have involved the specific origins of hominid features. The changes surrounding this event appear to have been more concerned with emphasis and importance than with the appearance of evolutionary novelties. For example, the evidence for chimpanzee tool making that has accumulated over the past two decades increases the likelihood that the (African ramapithecine) common ancestor of hominids and the African apes was a tool maker. Yet, this contention seems to be contradicted by the numerous assertions that stone tools do not pre-date 2,500,000 years ago. The absence of any stone tools associated with *A. afarensis* has been taken to mean that tool making originated after hominid origins and thus did not play a role in the event (see, for instance, Lovejoy 1981). I believe this is an apparent contradiction stemming from a confusion between tool making and *stone* tool making that has existed over the last decade. Perhaps this confusion is a result of the difficulty of unambiguously identifying utilized or rudimentarily flaked stone (the ghost of the Kafuan is still with us), or perhaps it is a reaction to the enthusiastic interpretations of Dart or to the observed manufacture of nonlithic tools by chimpanzees. Whatever the case, it is probably a mistake to treat the two as synonymous in terms of their timing and their effects on the

appears to be considerable morphological overlap. Thus, at least the dental evidence suggests that it may be a third lineage, contemporary with and intermediate between *Pongo* and *Gigantopithecus*.

course of hominid evolution. Undoubtedly, stone tool making was critical in hominid evolution. Its development may well have been associated with the divergence of the two hominid lineages of the earliest Pleistocene and the marked and rapid development of features associated with further hominization in one of them. Nonetheless, it is likely that the manufacture of tools made of perishable materials and the use of unmodified stone long preceded the development of recognizable lithics. The potential adaptive importance of nonlithic tools could hardly be overstated (Wolpoff 1980). In view of the fact that this behavior is shared with *Pan* (see van Lawick-Goodall 1973, McGrew, Tutin, and Baldwin 1979, Teleki 1974, Harding and Teleki 1981), its origin likely pre-dates the hominid-African-pongid divergence, and changes in the importance of this behavior are a potentially critical aspect of hominid origins. If so, this does not at all mean that tool making was unimportant in the events leading to and following hominid origins, but rather that it did not originate then.

A similar example can be found in the changing views of diet and diet-related behavior in the course of hominid origins. The seed-eaters hypothesis, or something like it, would seem to pertain to *hominoid* rather than to *hominid* origins. Yet, this does not mean that powerful mastication was *unimportant* in the process of hominid origins. This adaptive complex simply did not originate then. Darwin emphasized the causal influence of hunting in his model of adaptive change in the earliest hominids. Applying Jolly's model to the earliest stages of hominoid evolution and taking the continued evolution of the powerful masticatory apparatus in subsequent hominid evolution (Wolpoff 1980) into account, it appears likely that organized hunting did not play a preeminent role in the earliest stages of hominization. Once again, however, this does not imply that organized hunting played *no* role in hominid origins, especially since most of the elements of organized hominid hunting appear in chimpanzee behavior (Galdikas and Teleki 1981). Like tool making, this behavior was probably characteristic of the ancestral African ramapithecine form.

One might say, in the end, that the gap between humans and their (presumably more apelike predivergence) ancestors has been successfully bridged from both directions.

In many respects, the model I am suggesting is very Darwinian in its scope, although not in its detail. Yet, in my view the main difference from Darwin's emphasis involves a distinction between *origins* and *importance*. Of the elements discussed by Darwin, it is possible that only bipedalism actually originated at the time when the hominids became a distinct lineage. Tool making and the beginnings of organized hunting may have preceded this event, while significant expansion of the brain and functional change in the canine probably followed it. Similarly, the development of a powerful masticatory apparatus seems to have preceded the event.

Thus, I contend the ramapithecine ancestor of the hominids and the African apes had already undergone a number of changes that are generally regarded as hominization. Shared characteristics of the living hominoids combined with the paleontological evidence discussed here indicate that this ramapithecine form was behaviorally complex, a tool user and a rudimentary tool maker, an omnivore utilizing a wide variety of dietary resources ranging from difficult-to-masticate foods to protein obtained through organized hunting and systematically shared by at least part of the social group, an incipient biped (the behavior was possible but not morphologically efficient), and just possibly a more complex communicator than is generally thought, utilizing a limited but symbolic-based open communication system. Hominid origins would seem to have involved as much a shift in the importance of these characteristics as the origin of uniquely hominid ones.

In sum, I propose that the continued reanalysis of *Ramapithecus* has ultimately affected the acceptable model of hominid origins, just as the reverse has been the case. In my view this

continued reanalysis has resulted in the contention that the ramapithecines were not hominids, but the earliest hominid was a ramapithecine. Many of the interpretations and implications of Jolly's model have been focused on the problem of hominoid, rather than hominid, origins. Finally, this reanalysis, along with the last decade's advances in pongid behavioral studies and fossil hominid recovery, renews the focus on a modified Darwinian model for the origin of our lineage.

AN ECOLOGICAL MODEL OF HOMINID ORIGINS

There clearly were changing interrelated ecological adaptations associated with hominid origins. These changes are best discussed in the context of the fact that the effects on the African *pongid*⁴ lineage (or lineages) were at least as great as on the hominids. It is critical to remember that *hominid* origins are also *African ape* origins.

The actual speciation event separating hominid and (African) ape lineages will probably always remain unknown, since it need not be directly associated with any of the adaptive changes that followed. The genetic isolation and ultimate speciation of ramapithecine populations was not necessarily a consequence of adaptive divergence (although this is always a possibility). However, following this event the adaptive shifts in the lineages could be interpreted as the result of subsequent competition between them.

This suggested model for divergence makes no assumptions about the niche of the ancestral ramapithecine species. The group may have been primarily arboreal or largely terrestrial prior to the speciation event. I believe that actual finds, ecological associations, and analysis of the locomotor skeleton (when discovered) will ultimately provide the data needed to resolve this question. However, given the consequences of competition following speciation, one credible hypothesis is that the initial niche was a broad one, involving dense to fairly open parklands with some utilization (perhaps seasonal) of even more densely forested localities. Besides best fitting a dietary regime indicated by the masticatory complex, such a hypothesis would allow one to view the initial results of competition as dividing the niche occupied by the parent ramapithecine species into two narrower and less overlapping adaptive zones. These would be the more open parklands grading into savanna (hominids) and the denser woodlands grading into forest (African apes). The effects of subsequent competition on the differing adaptations outlined by this initial division would presumably be continued niche divergence that proceeded until the adaptive zones were sufficiently separate significantly to reduce competition over limiting resources. This model ties the appearance of a terrestrial, open-grasslands adaptation in the hominids to a *combination* of competitive exclusion *and* opportunism allowed by the expanded dietary resource base available to a hominoid species with both a powerful masticatory apparatus and rudimentary tool and weapon use. The model implies that there is no necessary link between the specific development of a powerful masticatory apparatus and any terrestrial adaptation (*contra* Pilbeam 1979). Moreover, it suggests a ramapithecine adaptation to ecological circumstances that would support any of the several models of preadaptations for bipedalism that have been recently proposed (Tuttle 1974a, Post 1980, Stern and Susman 1981).

As I reconstruct the divergence process, apes presumably reduced competition through dietary (and eventually dental/

⁴ If this model is correct, "pongid" is no longer an appropriate name for this African group, since the Pongidae are named after *Pongo* and it is my contention that *Pongo*, *Pan*, and *Gorilla* no longer form a natural group by themselves (they would only if *Homo* were included). Their relationship is one of *grade*, and therefore they should be referred to together by a nontaxonomic term such as "great apes."

gnathic) specialization and locomotor changes (true brachiation, knuckle walking) allowing an effective woodland/forest adaptation (Andrews 1981). Precluded from these ecozones by competition, the hominid adaptation was to more open regions. Building on their ramapithecine inheritance, a combination of powerful masticatory apparatus, the probably rapid development of efficient bipedalism, the use of rudimentary tools and weapons (digging sticks, clubs), and a series of social changes possibly related to the recognition of extended kinship relations (Wolpoff 1980, Allen et al. 1982) allowed a wide range of difficult-to-gather and difficult-to-masticate foods to help form the basis of an effective adaptation to a unique open-country niche. One would suspect that dietary items included seeds and grains, nuts, roots, and hunted, gathered, and scavenged protein during the dry season (Coursey 1973, Peters 1979). Wet-season food resources cover a much wider potential range and do not necessarily involve difficulties in acquisition or mastication.

The primary hominid adaptation was, of course, behavioral, with the morphological changes coming as a consequence. Some of the elements of this behavioral change probably involved shifts in the emphasis and adaptive importance of preexisting behaviors such as the manufacture and use of tools. Others, however, were fundamental and perhaps novel. These involve what may have been a dramatic restructuring of socially defined roles and the consequent social expectations. For instance, Mann (1972) has emphasized the shifts in regulatory behavior that must have followed from the replacement of canines by tools in social displays and the consequent loss of physiological control (i.e., late canine eruption in males) over the initiation of adult behavior. Recent studies of labor division in chimpanzees (Galdikas and Teleki 1981) help call attention to the hominid shift in provisioning strategy and behavior already posited by Isaac (1978). Isaac's contention is that the use of a home base reflects reciprocal provisioning, and the recent studies of chimpanzee provisioning suggest that such reciprocity must have resulted from the appearance of two new elements for this behavior. Female chimpanzees are known to share foods, and regular male provisioning of females (although not necessarily along lines of biological relationship) usually occurs when there is an episode of hunting. The important elements introduced to this pattern by the emerging hominids almost certainly were the female provisioning of males and the orientation of provisioning networks along lines of biological relationships. If it were posited that early hominid females regularly gathered difficult-to-masticate foods as part of the developing grasslands adaptation, such a shift in provisioning strategy would fit the morphological evidence of increasing masticatory power in the early hominid evolutionary sequence. Interestingly, recent analysis of microscopic cut marks on animal bones from Olduvai (Lewin 1981) suggests that the animal skins were salvaged and possibly used as rudimentary containers (to carry gathered plant foods to a home base?).

The social basis for such a shift in provisioning has recently been discussed by Lovejoy (1981), who posits the appearance of monogamy as the binding mechanism for reciprocal provisioning and suggests that shorter birth spacing resulting from the improved diet for monogamous pairs underlay the population expansion of the emerging grasslands-adapted hominids. While monogamy is probably neither necessary nor perhaps even sufficient to account for this critical change in provisioning strategy (Allen et al. 1982), some form of social role definition based on kinship relations almost certainly evolved as its basis. Moreover, the potential complexity of relations in such a social pattern combined with the requirements of reciprocal food sharing would render the development of an open communication system very advantageous (cf. Isaac 1978, Wolpoff 1980, Holloway 1969, and others). The comparative paleoneurology of australopithecine endocasts provides some direct (although limited) supportive evidence for the contention of an early appearance for hominid language (Holloway 1976).

Thus, in sum, there are reasons to suggest that a number of recognizably cultural elements were associated with hominid origins and/or the subsequent adaptive changes that occurred early in the evolution of our lineage. While these behavioral changes must remain the most contentious element of any theory of human origins, their importance as primary causal factors in the sequence of observable morphological, demographic, and adaptive changes underlies the continued attempts to use the available comparative and interpretive data to delimit the conditions surrounding their appearance and evolution.

Judging from its expression in *A. afarensis*, bipedalism would also appear to have been an early critical aspect of the developing hominid adaptation. The main advantages of bipedal locomotion—freeing the hands, carrying, and long-distance energy-efficient stride—probably all played a role in what was very likely a rapid locomotor shift. Arguments about whether carrying babies was more important than carrying clubs (e.g., Lovejoy 1981) miss the entire point of this locomotor change; a *group* of early hominids could carry *all* of the items that have been deemed important in the various arguments about the origin of bipedalism.

The *A. afarensis* dentitions show that, unlike the appearance of bipedalism, the change in the canine cutting complex was more gradual. Individuals in this earliest hominid species show canine and premolar wear indicating a range including chimpanzee-like honing (White 1981), occlusal chiseling (Wolpoff 1979, Wolpoff and Russell 1981), and flat grinding (Taieb, Johanson, and Coppens 1975). There is a corresponding polymorphism in the form of the P_3 , ranging from single-cusped forms (sectorial [Coppens 1977]) to a bicuspid morphology with equal-sized cusps (Johanson 1980) and including all of the variants between. Thus, while the functional change in the cutting complex may have begun with hominid origins, it required continued selection to attain the modern condition, in which the canine is morphologically and functionally incisor-like and the P_3 is incorporated into the grinding dentition.

It is tempting to suggest that the gradualness of this change reflects the gradualness with which tools replaced the cutting functions of the canine, but this argument is essentially circular and requires independent confirmation. Moreover, I have hypothesized (1979) that the development of the bicuspid P_3 crown, with a ridge connecting the two cusps, may have provided a means of retaining a form of the cutting function of the canine while reducing its projection and overlap. This would presumably be an intermediate step in the process of functional change in the anterior cutting complex. Whatever the case, the association of this change with tool use remains an unsettled issue.

Finally, just as brain-size expansion associated with complex behavior and cooperation were important in Darwin's model (we would term these developments "cultural" today), I believe that the origin of the cultural adaptation was probably critical in this modification of it. Behavioral interpretations without obvious morphological correlates are very difficult to assess, and the relevant morphological data (relative brain size, endocast analysis) have not been published for the earliest hominid species. Nevertheless, the later species *A. africanus* shows evidence of both limited brain-size expansion and neural reorganization, as well as delayed maturation, and it is surely short of a wild leap of faith to hypothesize that these correlates of cultural behavior had their origin in the social changes associated with the hominid adaptations to open country. Indeed, the specific elements suggested by Darwin, cooperation and language, may well have played a critical role in the group adaptations to this ecozone. Two decades of baboon studies have shown the importance of structured cooperative behavior in the savanna adaptations of this species, and the ramapithecine ancestor of the hominids probably brought a much more

complex repertoire to the behavioral basis of the hominid adaptation, judging from the behavioral complexity of the African apes.

Whether or not culture (meaning structured learned behavior) actually originated with the hominids or developed as part of their successful open-country adaptation, its effects are demonstrable in the morphology of *A. africanus*. This early hominid species had already embarked on an evolutionary pathway that was and has remained unique.

CONCLUSIONS

I remarked at the beginning that the complex historical interplay between theories of hominid origins and the interpretations of *Ramapithecus* has affected the development of both. In many respects, what I have described is a full circle in which modified versions of the original hominid-origins theory and the original interpretation of *Ramapithecus* can be sustained, but not quite in the way they were first presented, while incorporating the bulk of the discoveries, interpretations, and criticisms that have appeared along the way. In the circumscribing of this circle, it is clear that the development of one could not have preceded without the development of the other, which is to say that there are neither factless theories nor theoryless facts.

If *Ramapithecus* itself was not a hominid, there is a great likelihood that the earliest hominid was a ramapithecine. If all of the details of Darwin's theory of hominid origins are not fully correct, virtually every one of them must still be accounted for by any current origins hypothesis. If Jolly's model cannot be applied to hominid origins, a modification of it may have critical importance in the interpretation of hominoid origins, and in any event the dental/gnathic complex he described for hominids was there at their beginning and played an important role in their earliest adaptive changes.

Of the participants in the intertwined developments of the last few decades, if it can be said that none were completely right it is also true that few were completely wrong, at least in the context of the model I have presented. Moreover, the interpretations that can be sustained in one form or another far outnumber those that must be completely rejected. In all, the historical development of human-origins theories and ramapithecine interpretations presents a satisfying contrast to the Piltdown fiasco and reflects the scientific aspect of paleoanthropological studies in a most positive manner.

Comments

by L. DE BONIS

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19 III 82

This article has three parts: (1) a review of ideas on the phyletic status of *Ramapithecus* and their relationship to opinions about the origin of man, (2) a proposal of phyletic relationships between fossil and recent higher primates, and (3) personal views on an ecological model of hominid origins.

I agree completely with the first, which is a good analysis of the bias caused by a priori hypotheses about the origins of *Homo*. Wolpoff points out that there have been mistakes not only in interpretations, but also in observations. The lower third premolar of *Ramapithecus*, considered more or less sectorial depending on the opinion of the same writer at different times, is a good example. Another example, this one showing the influence of values on interpretations, is the idea that *Ramapithecus* was probably monogamous because of the presumed weakness of the canines (Kay 1982).

Wolpoff, following Pilbeam's (1982) ideas, considers *Sivapithecus* a good ancestor for *Pongo*, whose tooth enamel is relatively thick. This is a fairly good possibility, but whether the characters shared by *Sivapithecus* and *Pongo* are derived or not is difficult to answer. Wolpoff does not accept the view that all the ramapithecines are ancestral to (or a sister group of) *Pongo* alone. He thinks, as I do, that the overall similarities between some of them and the archaic Plio/Pleistocene hominines are a result of relationship. He admits, however, that ramapithecines are also a stem group for the African apes, whose tooth enamel is very thin. This would be a full reverse evolution toward a dentition very similar to that of *Dryopithecus*. Is this a parsimonious hypothesis? It does not seem so to me. Wolpoff attempts a phylogeny which fits pretty well with the late divergence between man and African apes suggested by the so-called molecular clock, but he cites a number of articles which claim that molecular biology cannot give the time of divergence, but only biological distances between living animals. Why should the ramapithecines not be considered a polyphyletic group (in the sense of Henning 1966)? The same trend and adaptation to a new ecological niche (a more open environment) give the same results (thickness of enamel and powerful masticatory apparatus) in two different lineages. This would explain the lack of a developed honing complex in some ramapithecines (*Ouranopithecus* or *Gigantopithecus*). In this case, we would have to assume that the divergence from the African apes occurred before the late Miocene. The evolutionary history of the higher primates will become clearer when we know more about the anatomy of the skull and especially of the limb bones.

I have little to say on the last part, which concerns the behavior of the ramapithecines, the possibility of tool making before stone tools, and the possible competition in some ecozones between the African apes and the ancestors of man, but perhaps now people will be encouraged to interpret new fossils along the lines of this ecological model. . . .

by JOHN G. FLEAGLE

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Wolpoff has provided an urgently needed perspective on the all too rapidly changing interpretations of the ape-human divergence. Because of the extensive journalistic influence in paleoanthropology today, we read at very regular intervals that a recently discovered fossil or new theory has overturned all current views of human evolution and completely revised our understanding of human origins. If that were actually the case, it would reflect very poorly indeed on the general credibility of paleoanthropology as a scientific discipline. Fortunately, as Wolpoff clearly demonstrates, our understanding of primate and human evolution is not so capricious and lightly conceived. The arguments of Gregory, Hellman, and Lewis (1938) that the "ramapithecines" from the Miocene of India and Pakistan have the most hominid-like dentitions of all known dryopithecines remain true today (Kay and Simons 1982). The changing "interpretations" have, as Wolpoff emphasizes, come mainly in the theoretically inspired elaborations such as tool use, bipedalism, and delayed maturation, for which there has, unfortunately, never been any significant fossil evidence. If *Ramapithecus* has indeed remained slippery enough to maintain a position beneath a continually changing early-hominid theoretical superstructure, it is because this superstructure has only rarely dealt with the meager morphological evidence we actually have had for *Ramapithecus*. As Wolpoff argues, all of these extrapolations could be seen as testable hypotheses awaiting the needed fossil or other evidence.

While I strongly support Wolpoff's emphasis on viewing

both theories and interpretations in paleoanthropology as testable hypotheses, I would also emphasize that new fossils are only one source of new data that can test and hence refine such hypotheses. As Wolpoff's own model (?hypothesis) clearly illustrates, many of our changing views on *Ramapithecus* and hominid origins have indeed come about from an increased data base, especially in primate ecology, comparative anatomy, demography, and statistical analysis, as well as new Plio/Pleistocene hominids.

My main comments on the scenario he has proposed for hominid origins concern his suggestion that the hominid-African ape ancestor was less suspensory and more bipedal than modern African apes. If hominids are actually more closely related to African apes than to Asian apes as Wolpoff believes and most of the biomolecular and some morphometric data indicate (Oxnard 1981), from a neontological perspective it is more parsimonious to assume that the suspensory behaviors (Fleagle 1976) and associated morphological adaptations (e.g., Tuttle 1974b, Washburn 1968) shared by orangutans and African apes are primitive for the group. The distinctive hominid features, even those which appear primitive (e.g., Wood-Jones 1929), are probably specializations. The derivation of hominids from a pongid-like ancestor is a long-standing issue in physical anthropology that has never been satisfactorily resolved (Fleagle and Jungers n.d.) largely because any solution involves considerable parallel evolution and the critical fossil evidence of either fossil pongids or intermediate forms remains lacking. Nevertheless, in my opinion, the available fossil evidence supports a more pongid-like ancestor than Wolpoff suggests. The ramapithecine postcranial remains show no evidence of bipedalism, incipient or otherwise, and indicate that at least one species had a large, grasping hallux (Pilbeam et al. 1980). Furthermore, although early *Australopithecus* from East Africa were definitely bipedal (Lovejoy 1981), they show more than vestigial adaptations for suspensory behavior in both proportions (Jungers n.d.) and osteological details throughout the skeleton (Stern and Susman 1982). Even a perfectly modern biped like *Homo habilis* retained many suspensory adaptations in its hand (Susman and Creel 1977, Susman and Stern 1982). There is increasing evidence that suspensory behavior (including climbing) is not so antithetical to bipedalism as many earlier and recent paleoanthropologists have maintained, but in many ways is preadaptive for such behavior (Fleagle et al. 1981). I agree with Wolpoff that the late Miocene ancestor will probably show a different mosaic of primitive and derived features than a *scala naturae* approach to human evolution would predict; uniqueness of fossil primates is the rule rather than the exception in primate evolution (Fleagle and Jungers n.d., Fleagle and Simons n.d.). However, until we find the African ape-hominid ancestor and recognize it as such, we probably shouldn't endow it with more hominid characteristics than we have morphological evidence to support.

by DAVID W. FRAYER

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In the past, hominid origins seemed rather straightforward. Some forest apes became more terrestrial, moved onto the open plain, and developed the morphological and cultural features we associate with the australopithecines. Those that remained in the forest were the ancestors of the African and Asian apes. Although an oversimplification, this kind of reconstruction can no longer be supported, as Wolpoff's article demonstrates. Given the continued repetition of the unsupportable "facts" about "Ramapithecus" in virtually every textbook, it will be interesting to see how long it will take for this paper to have an impact.

As a start to the revision, unlike Wolpoff, I would like to

see the name "ramapithecine" dropped (Greenfield 1979 has already presented a valid case for sinking the genus "Ramapithecus"). As is implicit in Wolpoff's article, nearly every description of the genus and every model proposed for its origin is fraught with overinterpretation, pigeonholing of "essential" morphological features, and predetermination that "Ramapithecus" was the hominid ancestor. Continued use of the name "ramapithecine" will only confound new interpretations by confusing the old arguments with the new ones that arise. Given the new discoveries in Pakistan (Pilbeam 1982, Andrews 1982) and China (Xu and Lu 1980, Wu 1981), it might be better to start over with a new nomenclature.

The reinterpretation of the Eurasian "ramapithecines" as ancestral to *Pongo* or other nonaustralopithecine forms, combined with the serological and chromosome banding studies, creates real difficulties for the notion of the hominid taxonomic status of "Ramapithecus." In particular, as Wolpoff argues, the Eurasian forms may now best be seen as analogies to the African hominid ancestors. Since it appears that oranges split off some 10,000,000 to 8,000,000 years ago, it could be argued that all the Eurasian forms are on a sidebranch. What is left as a common ancestor to the hominoids is the handful of material from Fort Ternan. Although I have not seen the originals, from casts and descriptions mainly of the mandible and two maxillary halves this material is gnathically and dental similar to the later Eurasian forms. In particular, it has large molars and thick enamel (Andrews and Tekkaya 1976:11-12). Consequently, if this form or something like it is the common ancestor of the hominoids, then modern African apes show a deviation from this pattern back to the *Proconsul* condition, while hominoids and *Pongo* retain the pattern. The alternative is that all the "ramapithecines" (including the Fort Ternan material) are an extinct sidebranch and that something like the earlier *Proconsul* forms persisted and diverged very late. I prefer this option. However, in either case and for any other phylogenetic scheme that is proposed, there is considerably more parallelism in hominoid evolution than has been assumed.

More critical, however, is the validity of the models proposed for the origin of hominids themselves. Although I basically agree about the importance of the various components of Wolpoff's ecological model, the fundamental question is why not even one of the Eurasian forms evolved into a hominid. These forms come in a variety of sizes, have all the precursor dental and gnathic adaptations (presumably indicating similar types of diets), were probably at least semiterrestrial, and lived in a range of habitats from closed to open. Although Wolpoff's model does well in accounting for the origin of hominids, it does not cover the alternative Eurasian situation. If hominids went through a "ramapithecine" stage, what kept the Eurasian forms from arriving at the same hominid outcome? Clearly, a lot more work, especially fieldwork in the Mid-Late Miocene of Africa, is needed before we can reach some consensus about hominid origins.

by LEONARD O. GREENFIELD

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From my perspective, human-origin theories (such as the Darwinian model or the seed-eaters hypothesis) have, or should have, been proposed and tested on the basis of the most up-to-date phylogenetic information. This is because the specific course of evolutionary events is revealed by stratophenetic evidence (fossils in a temporal sequence). Because knowledge of the phylogeny of the extant great apes and man has recently increased (assuming that the late-divergence hypothesis

is the more accurate one), there has been a change in origin theory. Thus if the late-divergence hypothesis is correct (and the face from Pakistan recently described by Pilbeam has increased its credibility while reducing confidence in the competing early-divergence hypotheses), then we can expect further improvements in its accuracy to result in still more accurate origin theories.

In Wolpoff's discussion of the adaptations which led to the *Sivapithecus* radiation (I use this term synonymously with his "ramapithecines"), there is probably too much emphasis on dental and dietary adaptation (although some bias is unavoidable because of the nature of the fossil record). I agree with him that the masticatory apparatus of *Sivapithecus* suggests that the included taxa were equipped to masticate an expanded range of dietary items (they probably were dietary generalists). This contention is also supported by the observation (unquantified) that despite a wide ecological, temporal, and geographic range there is surprisingly little morphological variation (in dental systems) among *Sivapithecus* species (for example, closely related living and extinct baboon taxa exhibit a much wider morphological range). However, equally likely is the possibility that the basis for the adaptive radiation included not only the ability to masticate diverse dietary items, but also an expanded neocortex with a corresponding increase in the capacity to realize a wider range of learned behaviors (this latter adaptation taken to extremes in humans). A hallmark of the living great apes and man is greater mentation than is seen in other extant higher primates. It could be expected, therefore, that their last common ancestor, *Sivapithecus*, was also of the same grade. Of course, this is a (somewhat) testable hypothesis, because the new cranial remains (and any future cranial finds) should reveal whether *Sivapithecus* possessed the external neocortical features (as seen in endocasts) common to *Pongo*, *Pan*, *Gorilla*, and *Australopithecus/Homo* as well as an estimate of its brain-mass/body-mass proportions.

by KENNETH H. JACOBS

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Nearly ten years have passed since the last major review of hominid-origins models (Jolly 1973). In that time, a burgeoning fossil record has forced the abandonment of several dearly held notions regarding pongid and hominid phylogeny. Wolpoff's article provides some much needed perspective on both the development of earlier models and the constraints within which attempts to develop new models must operate.

His historical review of the ebb and flow of competing origins models is especially timely and could ideally serve as an object lesson guiding the formulation and evaluation of new models. Unfortunately, the very history Wolpoff discusses gives little cause for optimism. There is far more to "Popperian" science than the recognition of the interplay between data and the models organizing their collection and interpretation. A vital factor is the requirement that models be subjected to constant critical scrutiny; that a set of data fits a given model is significant only if no other model can adequately accommodate those data. Instead, paleoanthropology has traditionally tried to cajole new data into a preferred existing framework. Only rarely are the data recognized as being intractable, provoking a frantic groping for a new, all-encompassing framework. In this sense, the history of our developing understanding of hominid origins converges on the rather more pessimistic Kuhnian model.

Acceptance of *Australopithecus* as a hominid had less to do with its congruence with a model of hominid origins than with its exhibiting a set of distinctive hominid features that had been identified long before any evolutionary scheme sought to

interrelate them. Indeed, only with this acceptance was it finally possible to flesh out Darwin's model. Similarly, Simons's resurrection of *Ramapithecus*-as-hominid relied solely upon its putative resemblance to *Australopithecus*, a resemblance thought to be sufficient to consider congeneric status for the two (Simons 1964: 535). The completely secondary relevance of origins models to this argument is clearly illustrated by the ease with which *Ramapithecus* underwent a "terrestrial dental shift" away from inferred tool using, coinciding of course with the same shift in *Australopithecus*. Only the expanded fossil record finally forced the recognition that the phenetic similarities between the two forms were either wholly illusory or primitive retentions.

All of this would be mere historical nit-picking were it not for the fact that we are currently in a unique position. *Australopithecus afarensis*, by demonstrating the association of a small brain, essentially sivapithecine dento-gnathic complex, and lack of stone tools in a bipedal primate, has been the most important factor in wiping the slate virtually clean of prior origins models. The potential for generating and rigorously testing competing models is unparalleled. The only model explicitly stimulated by *A. afarensis* is Lovejoy's (1981), dealt with only briefly by Wolpoff. It is compelling in its breadth of scope and frustrating in its focus on features not amenable to fossilization. Still, it threatens to become as widely accepted and ardently clung to as earlier models. Some have questioned Lovejoy's insistence on monogamy as an essential part of a provisioning scheme (Hrdy and Bennett 1981, Allen et al. 1982), while Isaac (1981) presages Wolpoff's comments regarding the potential role of nonlithic tools. The alternative model presented here by Wolpoff, involving adaptive divergence and character displacement in emerging African pongid and hominid lineages, is vague and in fact only a rephrasing of Bock's (1979) general model of allopatric/neosympatric speciation.

This is not meant to detract from Wolpoff's contribution. At a time when new introductory texts continue to echo the claim of *Ramapithecus* as the earliest hominid, his clear exposition of the complexity of the issues involved is most welcome. The true value of this article, however, would be to stimulate a far more concerted effort to consider the full range of possible models that are compatible with the known fossil hominid record.

by R. PROTSCH

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Because of the incredible wealth of information and the wide scope of Wolpoff's paper, I must restrict myself to a commentary on the paper as a functioning unit rather than going into detail.

Wolpoff presents an expansive but at the same time very precise and clear overview of the most important elements and consequences of *Ramapithecus* in the context of hominid evolution. He effectively shows the varying degrees to which facts are made, or preferentially selected, to fit theory and vice versa. I am in full agreement that this is an important phenomenon throughout the sciences.

Essentially Wolpoff is not presenting any information that has not been available for some time. For instance, the ancestry of *Pongo*, *Pan*, *Gorilla*, and the hominids is known to fall into a time period somewhere between 16,000,000 and 7,000,000 years ago. Within this time span, ramapithecine morphology is quite diverse and found in a wide range of geographical and formally diverse ecological settings. However, the perspective Wolpoff creates is a unique and remarkably clear picture of *Ramapithecus* and hominid origins. Considering the wealth of information that has come to light in recent years and the number of hypotheses and theories related to it, it is very im-

portant that all the information on *Ramapithecus* has been collected, ordered, and discussed.

The only thing I find disturbing in the paper, and of course it is inevitable in an overview of this type, is the speculation about cultural, behavioral, and ecological aspects: White's (1975) panda replacement of *Gigantopithecus*, theories of bipedalism based on not yet available facts about the locomotor skeleton, Lovejoy's (1981) proposal about the appearance of monogamy and the relative importance of food-carrying vs. baby-carrying, the question of changing provisioning strategy (Isaac 1978), the lack of factual evidence of nonlithic tool use by ramapithecines, and the validity of judging the role of organized hunting on the basis of chimpanzee behavior (Galdikas and Teleki 1981). For the most part, Wolpoff recognizes the questionable or superficial character of such speculations. Again, details of this type are part of the historical development of hypotheses related to the ramapithecines and demonstrate his thoroughness in examining the material.

I have to disagree with Wolpoff on the question of important morphological variants such as enamel thickness. Contrary to his observation, the Rudabánya material shows a quite uniform thickness in both the smaller and the larger specimens, including RUD 12 (Xirotiris and Protsch, in preparation).

There should also be some reservation about the immediate acceptance of the naming of *A. afarensis* (see Day 1980, Protsch 1981).

Wolpoff predicts that ramapithecine forerunners for the earliest hominids will be found (possibly excluding the Fort Ternan specimen). He is cautious in his suggestion that the finds from Ngorora, Lukeino, and Lothagam (I would also include Kanapoi and Chemeron) are either ramapithecines or early hominids; I don't think that there is much doubt about their being hominids (Protsch 1981).

Two things come to mind in reflecting upon Wolpoff's article: A great many informative details and theories are discussed with appropriate thoroughness, and the shift of importance related to the timing of events and hypotheses is consistently emphasized. I feel that he has created a remarkably clear image of how events pertaining to *Ramapithecus* and the evolution of hominids could have occurred. His article is an important contribution to our ideas on hominid and pongid (African ape) evolution.

by G. PHILIP RIGHTMIRE

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Discoveries of later Miocene "apes" have been accumulating at an encouraging rate, and in the last few years we have acquired a more comprehensive understanding of the environmental settings in which these primates lived. As a consequence, interpretations of the significance of Miocene hominoid taxa have been changing, as a number of workers have modified their views to accommodate this new information. Whether such shifts in paleontological thinking are in fact closely linked to the recovery of fresh material is questioned by Wolpoff, and there will be objections to some of his assertions as to how science has progressed. However, one can hardly take issue with the contention that theory and the analysis of new fossils have wedded the interpretation of *Ramapithecus* to the problem of human origins. *Ramapithecus* itself now seems less convincing as an early hominid, but the morphology of *Australopithecus afarensis* does point toward an (unknown?) ramapithecine as the common ancestor of hominids and probably the African apes as well.

Only a few years ago, it was rather widely agreed that while ramapithecines exhibited some apelike features, the pongids of today were much more likely to be evolved from earlier to middle Miocene hominoids best represented by species of *Pro-*

consul in eastern Africa. These dryopithecines, with large, sexually dimorphic canines and thin-enamelled cheek teeth not enlarged relative to body size, were recognized as primitive but similar dentally to apes. Ties with the African apes were considered most likely, although most authorities stopped short of postulating direct ancestor-descendant relationships between *Pan* or *Gorilla* and species known from earlier Miocene localities.

More recently, with the description of important new specimens from Pakistan and sites in Europe, attention has shifted from the dryopithecines toward the ramapithecines as the group from which modern apes may be derived. In particular, it has become apparent that at least some of the megadont, thick-enamelled ramapithecines resemble *Pongo*, cranially as well as dentally. This case has been made by Pilbeam (1982) and more forcefully by Andrews (1982) in respect to the face and mandible of GSP 15000 from the Potwar Plateau. The Pakistan specimen is attributed to *Sivapithecus indicus*. Wolpoff argues that other ramapithecines also show orang-like features, but here there is some difference of opinion. The extent to which species of *Sivapithecus* or *Ramapithecus* may resemble African pongids rather than living Asian apes is still uncertain, pending more complete study of the material available. There is, however, a growing consensus that the ramapithecines are broadly related to apes as well as to humans, and Wolpoff's suggestion that a late Miocene ramapithecine may be ancestral to *Pan*, *Gorilla*, and hominids is hardly heretical. Many workers will agree with much of what he has to say.

by VINCENT SARICH

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Wolpoff tends to reflect establishment views as to the proper nature of paleoanthropological endeavor. I believe these views to be maladaptive. Perhaps the best recent antidote to them is an article by Patterson (1981), which ends with the following sentences:

As this review shows, the belief that paleontology alone should, or can, determine relationships is a myth. So too is the Haeckelian belief that ontogeny alone will do the trick, for it is negated if neoteny or other forms of secondary loss ever occur. What remains is the unity of the comparative method, in which paleontology can hold its own by acknowledging its debt to neontology, and by repaying that debt in contributing what it alone can: age of groups, paleobiogeographical data, and new character combinations that can reverse decisions on homology and polarity, so testing, and perhaps on rare occasions overthrowing, theories of relationship.

I can read Wolpoff's closing sentence, "In all, the historical development of human-origins theories and ramapithecine interpretations presents a satisfying contrast to the Piltdown fiasco and reflects the scientific aspect of paleoanthropological studies in a most positive manner," in contrast, only as unconscious satire. Whatever else may ultimately come of the *Ramapithecus* fiasco, it will never be seen as an example of how to do paleoanthropology—except, perhaps, by those who fail to see that direct evidence from the past will never make more than a small, though vital, contribution to understanding the present and how it got to be that way.

This view of course stands in marked contrast to the strong recent tendency of paleontologists in general, and paleoanthropologists in particular, to see themselves in the role of final arbiters of evolutionary questions. This has been compounded by their remarkable success in persuading the community of interest to accept this view of their role. All this would not be so serious if these would-be final arbiters acted as if they had an even moderately realistic view of the relative amounts

of information available from studies of living forms as compared with those found in the fossil record. That this is not the case can easily be seen by comparing, for example, Le Gros Clark's *Antecedents of Man* with the more recent efforts of Simons and Szalay and Delson on the same subject. If you essentially leave out the comparative anatomy and, more recently, biochemistry of living forms, you have discarded more than 99% of your data base, and it is thus not surprising that the paleoanthropological community has taken so long even to approach a resolution of the *Ramapithecus* mess. By essentially ignoring the evidence from living forms, they have unconsciously put themselves in the position of the drunk looking for his coin underneath the lamppost because that's where the light is. The problem is that the fossil light can be mighty feeble and only rarely shines in a helpful place. Thus what we should be asking is not what the paleoanthropologists did with *Ramapithecus*, but what they, as intelligent scientists, should have done with the totality of the information available to them. Unfortunately the emphasis was on the dentition and not on the implications of an origin 15,000,000 years ago of the hominid line for other lines of evidence. The marked upper-body similarities among the living hominoids, clearly a derived feature not present in the fossil record of 15,000,000 to 20,000,000 years ago, then have to be explained as parallelisms or convergences. Here the anatomy of living forms combined with the relevant fossil record gave a picture of hominoid evolution inconsistent with an early separation of the hominid line—yet that picture was essentially ignored in favor of one based on some very subjective and equivocal interpretations of very scrappy Miocene dentitions. About the same time (mid- to late '60's), the marked behavioral similarities between ourselves and chimpanzees in particular were becoming ever more difficult to ignore, and one might think this would have given the early-divergence advocates some pause—yet this was just the period when the *Ramapithecus*-is-a-hominid position seems to have hardened. Finally, of course, some very disturbing molecular data and interpretations also made their appearance at about this time. It is awkward for Wolpoff's narrative of the triumph of paleoanthropology that Allan Wilson and I had shown as long ago as 1967 the essential impossibility of a hominid line with a 13,000,000-year-old *Ramapithecus* on it—and that we did it in a biochemistry laboratory without a single fossil in it—but he rises to the challenge. First there is a lengthy listing of some of the articles which have, over the years, expressed disagreement with our suggestion of a 4,000,000–5,000,000 years ago separation of *Homo*, *Pan*, and *Gorilla* lineages. Is there any indication that these objections have been answered? No. Is there a critical analysis of the molecular-clock hypothesis? No. What there is is an apparent acceptance of the “where there's smoke, there must be fire” dictum and then the remarkable statement:

Probably the best way to summarize the very disparate points raised is that the “clock” simply *should not* work. . . . Consequently, although biochemical evidence seems to support a late *Homo-Pan* divergence, I believe this is a red herring, and that the molecular “clock” does not support any divergence time, just as other independent evidence for a late *Pan-Homo* divergence does not support the molecular “clock.”

This is surely parody, yet Wolpoff is serious in preferring a lengthy, tortuous fossiliferous path to an answer provided long ago to anyone who thought to look beyond teeth to functioning organisms. The logic of the biochemistry laboratory only confirmed that answer; it did not invent it.

It is the whole organism—muscles, joints, behavior, molecules, and, yes, even teeth—that evolved. The evolutionary scenario we reconstruct is tested at each step along the path by requiring that it be consistent with all the available evidence. This is a very rigorous test. The object lesson ought to be how easily the solution to the “*Ramapithecus* problem”

came when one remembered that it was whole organisms that lived, died, and changed over time and how slowly it came when the basic concern was with the bits and pieces which are directly comparable in the fossil record and living forms.

by JEFFREY H. SCHWARTZ

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Wolpoff's contribution is the fourth of a recent spate of articles concentrating on *Sivapithecus*, *Ramapithecus*, *Pongo*, and hominid origins. The more morphologically oriented of these (Andrews 1982 and Pilbeam 1982) conclude that, because recent finds of more complete craniofacial specimens of *Sivapithecus* are remarkably orangutan-like in distinctive (= phylogenetically significant) features, this presumed primitive hominid, and ramapithecines in general, have nothing to do with hominid origins. Thus, such features as low-cusped cheek teeth and thick molar enamel, which are also possessed by *Pongo* and ramapithecines (see below), arose in parallel and are therefore not diagnostically hominid as has been supposed. Kay's (1981) contribution and Wolpoff's are largely scenarios defending presumed phylogenetic hypotheses rather than rigorous presentations of such hypotheses. In Kay's, the hypothesis is that higher-cusped-cheek-toothed and thin-molar-enamelled dryopithecines gave rise to a low-cusped-cheek-toothed and thick-molar-enamelled clade in which *Pan* and *Gorilla* secondarily derived the common (and, thus, presumably primitive) primate condition retained by the dryopithecines. In Wolpoff's more elaborate scheme, the underlying phylogenetic hypothesis is essentially the same, but the necessary “reversion” in dental characteristics in *Pan* and *Gorilla* is not discussed. Although all four of these scholars may take issue with details of each other's formulations, each has explicitly (Wolpoff, Andrews) or implicitly maintained as the basic hypothesis the notion that the African “apes” and hominids are more closely related to each other than either is to *Pongo*. Thus, if ramapithecines look craniofacially like orangutans, then either the hominid dental features evolved in parallel and ramapithecines have nothing to do with proper hominids or we must, as Wolpoff has attempted, construct a scenario that accommodates new information.

What I find a bit disconcerting is that none of these scholars has even entertained as a possible alternative hypothesis the obvious: that *Pongo*, and not *Pan* or *Gorilla*, shares with hominids (including ramapithecines) these unique dental character complexes because these taxa shared a common ancestor not shared with *Pan* or *Gorilla*. Within the low-cusped-cheek-toothed and thick-molar-enamelled clade there are nested different, smaller clades, one of which is *Sivapithecus* and *Pongo* as sister taxa. I have earlier hinted at this hypothesis (Schwartz 1981) and recently found (Schwartz n.d.) that major foramina configurations of the palate support it (= are shared by the same taxa united by hominid dental features).

I find unconvincing the argument that because some ramapithecines do not have the “diagnostic” thick molar enamel this can and does happen frequently in parallel. How do we know that low-cusped cheek teeth and thick molar enamel are a developmental unit? We don't. Their distribution among primates, however, appears relatively limited, and thus one can suggest that primitively thin-molar-enamelled taxa such as *Rudapithecus* are united with other low-cusped cheek-toothed and dentomorphologically similar taxa as a clade, within which is a clade of thick-molar-enamelled taxa. Thin-molar-enamelled and higher-cusped cheek-toothed *Pan* and *Gorilla* are the sister taxa of this clade.

As a morphologist, I find no difficulty in readjusting to a different hypothesis. I am not swayed by blanket statements of how similar *Pan* and hominids are because most of the sim-

ilarities appear to be primitive retentions, and I am so far unpersuaded by karyological and biochemical studies for similar reasons as well as others (see, e.g., Holmquist 1976, Williams 1962). Perhaps it is time to rethink and rigorously test those hypotheses that have been elevated to the level of the known.

by IAN TATTERSALL

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Although somehow he and his students emerge as the heroes of the story, Wolpoff's review of the changing interpretations of *Ramapithecus* provides a reasonably balanced account of how, in one particular area of paleoanthropology, expectation has colored interpretation to an extent that could be considered remarkable were it not a good example of what has become more or less the standard practice for paleontology as a whole. One might note, however, that the process that Wolpoff describes fits much better the Kuhnian paradigm than the Popperian one he claims.

Perhaps the single most significant aspect of Wolpoff's view of earlier theories of the importance of *Ramapithecus* in hominid evolution is his recognition that virtually all have been conceived and expressed at the level of what has been called the evolutionary "scenario" (even if he chooses not to employ the term). As Wolpoff explicitly recognizes, such formulations are highly complex and consist of a variety of different types of input which feed back on each other in an elaborate way. It is fair enough, then, for Wolpoff to dismiss earlier ideas as "less than convincing" simply on the grounds that they do not meet his personal criteria of plausibility; this is the only basis upon which scenarios can be evaluated, and it has been noted elsewhere (Tattersall and Eldredge 1977) that scenarios are limited only by the imagination of the author and the credulity of the audience. But since Wolpoff is at pains to emphasize his belief that evolutionary statements should be scientific in the sense that they be potentially refutable, it is disappointing that he rejects one set of scenarios only to replace it by another, without at first addressing himself to the more fundamental, more limited—and yes, more tedious—level of analysis to which testable evolutionary statements are restricted.

This having been said, however, it cannot be denied that Wolpoff's discussion at his chosen level is both interesting and stimulating. Since it is pointless to criticize scenarios without knowledge of the simpler and more testable hypotheses on which they should be based, I will refrain from general comment on Wolpoff's scenario beyond noting that a long succession of "ifs" gives way gradually to a series of rather concrete claims based on them. However, I cannot resist one specific comment.

Wolpoff's discussion is particularly useful in emphasizing that the suite of characters, behavioral and morphological, that severally or together are generally thought to distinguish hominids from apes in fact consists of a mix of plesiomorphies and apomorphies. This important point has been widely overlooked, although it reflects what amounts to a general property of all species. However, Wolpoff ruins the impact of this crucial observation by returning repeatedly to a concept of "hominization"—a ghastly term with more than a ring of orthogenesis to it—that depends on just such a character set. If, as Wolpoff rightly asserts, the origin of a monophyletic family Hominidae is to be found in a single speciation event (which would in itself eliminate "hominization" as a "process"), then "hominization" cannot be defined in terms of the acquisition of a suite of characters unless all of those characters stemmed uniquely from that event. And this we know not to be the case. The sooner we eliminate "hominization," together with

all its connotations, from our vocabularies, the better off we shall be.

by MICHAEL J. WALKER

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The views that (a) ramapithecines were forerunners of both the subfamily Ponginae and the Hominidae and (b) "a special form" of ramapithecine sired the latter are presented as scientific propositions open to the possibility of refutation should the inconveniently missing links turn out to be different from expectations—or fail to turn up altogether. No less a name than Popper is invoked to lend weight to the scientific *bona fides* of these formulations. Wolpoff shortchanges us and does Sir Karl a disservice. The first proposition is a "motherhood" catch-all so general as to embrace even the most unpleasant primate surprises the fossil record may hold in store, while *mutatis mutandis* judicious taxonomic tinkering could bring the most recalcitrant ramapithecine into line with it. The second proposition is not Popperian, but, being a possible consequence of the first, a deductivist inference. Moreover, Wolpoff's appeals to refutability are not at all the same thing as Popperian scientific formulations which permit attempts to falsify them within the accessible data they address themselves to. (I once heard a parson say heaven was a scientific theory we would be able to verify or refute in the hereafter. . . .) While there exist critics of Popper who cannot be ignored, it behooves scientists who invoke him not to abuse his principles.

Certainly, ranging over three continents and in diverse habitats, ramapithecines are unlikely to have contributed to hominid origins alone. Given the stone tool-making potential of *Pongo* (Wright 1972), anthropocentric egos may feel attracted to Wolpoff's first proposition; at least it allows skills to be kept within the (super) family. But there are snags. Wolpoff admits that his view implies late divergence between the Hominidae and the Ponginae, especially in Africa. Given evidence for bipedal hominids from Hadar and Laetoli about 3,500,000 years ago, this divergence must have taken place between that time and the upper limit for *Ramapithecus* in the late Miocene, probably between 6,000,000 and 4,000,000 years ago—unless the "special form" of *Ramapithecus* differed from others in being bipedal. Now, Wolpoff regards "the lumbar elongation of the australopithecines (STS 14 has six functional lumbar)" as suggesting that their ramapithecine progenitor was adapted to an "arboreal" habitat. Yet later on he feels that *Pan* and *Gorilla* represent arboreal ramifications and the hominids non-arboreal descendants of ramapithecine forerunners, despite the evidence that *Pan*, *Gorilla*, and *Pongo* manage quite well in the jungle with only three or four lumbar vertebrae, while man walks quite adequately in treeless landscapes with five (only rarely four or six). It is likely that STS 14 is a quirk of population sampling—all the same, "primitive" primate lumbar elongation apparently is more appropriate in bipedal than in quadrupedal descendants of ramapithecines. Were there, then, two ramapithecine groups, one with elongated lumbar regions (bipedal?) and one with short lumbar regions (quadrupedal and arboreal?)? Inferences about an early divergence come from yet other genetically controlled differences. Schultz (1930: esp. 322–25) pointed out that variability in sacral segment numbers is much less in man than in populations of cadavers of every major anthropoid group inspected. This suggests a long period of bipedalism in hominid phylogeny. The differences in densities and effectiveness of both sweat glands and hairs when man is contrasted with other pongids might also be a pointer to different behavioural patterns when bipedal omnivores are contrasted with quadrupedal herbivores.

Wolpoff highlights the tautologous relationship (without, as I have shown, being able to escape it) that exists in palaeontology between classification and evolutionary interpretation. He is right to remind us that just when Frayer (1974) was indicating the incompatibility of Darwin's hypothetical hominid ancestor and *Ramapithecus*, Jolly's seed-eating hypothesis gave *Ramapithecus* a new lease of life in that role. The trouble in palaeontology is that classification is not an independent, objective procedure vis-à-vis the theory of evolution by natural selection. Even the most parsimonious interpretations of the data cannot avoid falling headlong into muddles caused by confusing deductions from the (unfalsifiable) theory with inferences from morphological considerations of bones. As Popper might have said, explaining away the data is not the same thing as explaining them. One-and-a-half cheers for Wolpoff for raising some interesting ideas. I shall reserve the other one-and-a-half until they are brought into line with scientifically robust propositions.

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Wolpoff joins the growing troop of paleoanthropologists shifting from the long-held belief in an early divergence of apes and hominids—about 20,000,000 years ago, with *Ramapithecus* as the first hominid—to a growing conviction that hominids and African apes diverged from a common ancestor in Africa about 5,000,000 years ago. The biochemical evidence for this late divergence began emerging in the 1960s but was hotly denied by many anthropologists, including Wolpoff. By now the molecular data and their correct predictions—chimplike African hominids at 3,500,000 years—have become so compelling that many former proponents of *Ramapithecus*-as-hominid have quietly abandoned that position, without, however, admitting that biochemistry had anything to do with it. On the contrary, they stoutly maintain, as Wolpoff does, that they deduce a recent divergence from the same morphological evidence of teeth and bones that formerly was seen as proof of an early divergence.

It is obvious to anyone reading the literature on human evolution over the past two decades that these anthropologists are now looking at the world of human origins through biochemical glasses while boasting of their 20/20 vision, especially in hindsight. Wolpoff says that dating by "molecular clocks" cannot be right and *should not* work, and therefore the fact that it happens to be right about the ape-human split is a "red herring." This syllogism is fairly typical of his deductive logic. Just as the biochemical data are right for the wrong reasons, it appears to Wolpoff that those who (like himself) held that *Ramapithecus* was hominid were wrong for the right reasons—namely, the shape and size of the teeth. Wolpoff writes: "If *Ramapithecus* itself was not a hominid, there is a great likelihood that the earliest hominid was a ramapithecine." No African ramapithecine is known younger than 12,000,000 years and no hominid more than 5,000,000, but Wolpoff stretches this taxon across 7,000,000 fossil-free years in order to establish the continuity he needs to be correct in retrospect.

According to Wolpoff, "Of the participants in the intertwined developments of the last few decades, if it can be said that none were completely right it is also true that few were completely wrong, at least in the context of the model I have presented." In the context of that model, no one could possibly be completely right or wrong, because it is like a bride decked out in something old, something new, something borrowed, something blue, something purple, something orange, etcetera. He has provided her with a hominoid phylogeny derived from molecular data, while denying the validity of the

molecules, and a behavioral scenario derived from the familiar "chimpanzee model" of hominid origins, without mentioning chimpanzees, and the enigmatic mother of us all turns out to be a veiled ramapithecine, just as the paleoanthropologists have always maintained. She was a most remarkable progenitor: if African, she must be credited with a 7,000,000-year gestation time; if Asian, she gave birth first to *Pongo* 10,000,000 years ago and remained steadfastly ramapith until she could breed hominids, chimpanzees, and gorillas 5,000,000 years ago in Africa. Wolpoff should be congratulated on having created a "model" so flexible and so contradictory that verification or falsification is rendered hopeless from the start. He has summed it up well: "In many respects, what I have described is a full circle in which modified versions of the original hominid-origins theory and the original interpretation of *Ramapithecus* can be sustained, but not quite in the way they were first presented, while incorporating the bulk of the discoveries, interpretations, and criticisms that have appeared along the way."

Finally, in his last sentence, without prior warning, Wolpoff rushes Piltdown onstage like a *deus ex machina* to rescue paleoanthropologists from their ramapithecine dilemmas: "In all, the historical development of human-origins theories and ramapithecine interpretations presents a satisfying contrast to the Piltdown fiasco and reflects the scientific aspect of paleoanthropological studies in a most positive manner." Unlike Wolpoff, we are struck by the parallels rather than the contrasts between the Piltdown and *Ramapithecus* histories. In both cases, a large number of paleoanthropologists accepted a new "human ancestor" on the basis of shaky dental and gnathic evidence. In both cases, the controversy between believers and nonbelievers raged for decades and was finally resolved by biochemical evidence—for Piltdown by demonstration that the fluoride and collagen concentrations of the jaw and skull were quite different and indicative of relatively recent burial, for *Ramapithecus* by molecular data suggesting so recent an ape-human divergence that *Ramapithecus* could not have been hominid—as has subsequently been borne out by finds of an orang-like face and arboreally adapted limb bones.

Reply

by MILFORD H. WOLPOFF
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CA commentary provides a unique forum for discussion in paleoanthropology, and this is why I felt it important to bring to the journal a problem I believe should be widely discussed (a shorter, earlier version of this paper will appear in a book edited by R. Ciochon and R. Corruccini). While somewhat disappointed that the paper did not elicit more response, I am very grateful to those who did submit their comments. I believe the resulting exchange of ideas will help clarify both the points I have tried to make and the substantial issues that they raise.

I find it interesting that very few have questioned my historical interpretation, most of the discussion revolving about the model that I presented in the later part of the paper. While some of the respondents seem basically to agree with most of this model, other responses are more critical. Yet the points raised are so different and the alternative perspectives suggested here and elsewhere (see Kay 1982) cover so wide a range that I find myself in very much of a middle-of-the-road position.

Both Jacobs and, more explicitly, Walker question whether the model of hominid origins I present is sufficiently scientific, in a Popperian sense. Jacobs, who seems unjustifiably pessimistic about everything, contrasts Popper and Kuhn without

recognizing that, while Popper discussed how science *should* proceed, Kuhn demonstrated how the Popperian approach to science *actually works*. Curiously, he dismisses my model as too vague and as a restatement of Bock's more general one (actually, it is a direct rendition of Mayr's [1963] and a restatement of my own [1971c: 605]), although I believe I have been specific enough in my predictions (for instance, the form of the as yet undiscovered late Miocene African ramapithecine) and explicit enough in my assumptions for refutations to be easily identifiable. Instead, Jacobs embraces Lovejoy's (1981) model, although this reduces the explanation of the origin and initial adaptations in our lineage to a single cause for which there can *never* be *any* fossil evidence. Actually, Lovejoy's model is not an "alternative" to mine, since if correct it could be incorporated within it (removing only the single-cause contention), as I have pointed out elsewhere (1980), while if incorrect (see Allen et al. 1982) it can hardly detract from it.

Walker confuses the Popperian approach with the Hennigian interpretation of it, stating, for instance, that Popperian scientific formulations "permit attempts to falsify them within the accessible data they address themselves to." My understanding of a scientific hypothesis is that it must be potentially refutable. It seems to me that generating predictions about as yet unknown fossils creates one of the rare potentials for refutation in a field that suffers from the limitation that it attempts to account for events that happened only once.

Tattersall raises two knotty issues that I did not address, both of course from his own perspective. He also comments on the fact that I have not reduced my analyses to testable hypotheses, in the Hennigian sense (although recognizing that the paper was not written at this level). He is quite right about this, and my not doing so was quite purposeful; this is the very sort of problem for which I believe a cladistic approach must be circular. The fact is that if a *Proconsul* species is the last common ancestor of the hominoids there is a very different set of plesiomorphies than if a ramapithecine is the last common ancestor. If these are taken as alternative hypotheses, completely different cladistic analyses of the hominoids follow from them, with differing suites of shared derived features, different (and in each case substantial) parallelisms, and different resultant phylogenetic relationships. The problem is, which is correct? Is maximizing the number of shared derived features a better criterion than choosing the most acceptable parallelisms (as both Frayer and Schwartz seem to prefer)? When a cladistic analysis involves taxa that are potentially ancestral to other taxa analyzed, it is difficult to avoid circularity.

A second point Tattersall raises stems from an argument inherent in the punctuated-equilibrium approach. If one accepts this model, as he does, then, as he remarks, a character set descriptive of a taxon must originate with it. However, I am much more of a gradualist, having found from my own experience that major evolutionary changes can accumulate during the continuous evolution of a lineage. Thus, features can (and do) change *after* a speciation event, and I find "hominization" an appropriate term for this process in our lineage. The fundamental difference between these models, in my view, is not whether major changes can (and do) occur during speciation events, but whether major changes can *also* occur as the result of gradual evolution.

The problem of acceptable parallelisms is also raised in comments by de Bonis (see also 1982), Frayer, Schwartz, and Walker. The main concern seems to be about parallelisms between the African apes and *Proconsul* that are necessitated by this model. Interestingly, however, the suggested revisions are quite different, and none of these commentators deals with the alternative parallelisms his revised model would generate. De Bonis suggests regarding the ramapithecines as a polyphy-

letic group with a separate preramapithecine divergence for the African apes, while Frayer contends that no ramapithecine is ancestral to either hominids or the African apes. Both of these could credibly fit the divergence sequence indicated by morphological, biochemical, and genetic analysis of the living forms, but each raises even more serious problems of parallelisms than it solves. Moreover, there is much to be said for the contention that the alleged parallelisms (or, alternatively, if de Bonis and Frayer are correct, primitive retentions) between *Proconsul* and the African apes are more apparent than real. Certainly, morphological details of the cranium, mandible, and postcranial skeleton are very derived in the African apes, and recent studies indicate the same conclusion for many aspects of dental morphology (Kay 1975, Maier and Schneck 1981). The sticking point seems to be mainly thin enamel, which by itself is not in my view convincing enough to accept these alternatives.

Schwartz takes a very different approach to these same considerations, arguing that *Pongo* is the hominoid most closely related to the hominids. I believe this is unlikely; while a few derived features do unite *Homo* and *Pongo*, the weight of the morphological evidence and virtually all of the biochemical evidence (which, unlike Schwartz, and *contra* statements by Zihlman and Lowenstein, I am quite willing to accept) indicates a closer relation between the African hominoids than between any of these and the Asian hominoids.

Walker also raises a problem of parallelism, focusing on lumbar vertebrae number although misinterpreting both my arguments and the functional morphology of the region. I did not claim that the (hypothesized) common ancestor of the African hominoids was adapted to an arboreal habitat because australopithecines have an elongated lumbar column. My argument was that the arboreal adaptation of the ancestral form was probably less specialized than in the modern African apes because the six functional lumbar on STS 14 probably reflect the primitive condition (it is more likely to lose lumbar than it is to gain them in an evolutionary sequence). His further statements suggesting that elongated lumbar regions (necessarily?) reflect bipedalism while shortened regions reflect quadrupedal or arboreal adaptations only confuse the issue, since both quadrupedal and bipedal primates have an elongated lumbar column, while a shortened column is associated only with specialized forms of arm swinging.

The focus should really be on the reduced lumbar number in both African and Asian apes (as Fleagle mentions), since this is presumably the derived condition, reflecting a specialized adaptation—mainly to brachiation and associated locomotor activities through trunkal shortening to maximize the linear component of velocity during pendulum-like motions around the wrist.

My argument would necessitate a lumbar shortening parallelism between Asian and African apes. It does imply the potential for more hominid-like locomotor activities in the (hypothesized) ramapithecine common ancestor, but, to clarify comments made by both Walker and Fleagle, I did *not* suggest that this common ancestor was an efficient biped (and I believe that *inefficient* bipedalism is unlikely to be a dominant mode in a species's locomotor range). Actually, I see no contradiction between my suggested locomotor reconstruction (climbing and arm hanging, but without the full suite of brachiation adaptations seen in the African apes) and the suggestions recently made by Fleagle et al. (1981: 360, 372) that "a human ancestor primarily adapted for climbing would show a forelimb morphology comparable to that normally associated with brachiation and a hindlimb morphology pre-adaptive for human bipedalism" and that "our suspensory ancestor was not particularly like any of the extant apes." On the other hand, it

should be admitted that the adding of lumbar vertebrae in the hominid line (making a short lumbar column primitive) is a possibility that cannot be discounted. Selection for such an addition could come from the increased importance of lower back curvature that is integrated into the form of trunkal uprightness characteristic of hominid bipedalism. It seems to me that this is the issue that Walker should have been raising. Its resolution will only come with an expanded Miocene African fossil record.

Fleagle, as mentioned above, raises the question of how hominid-like the ramapithecine common ancestor might have been (i.e., how many hominid characteristics are actually primitive for the African hominoids). Greenfield raises a similar point (from the opposite perspective) in his discussion of possible encephalization in the ramapithecines. Once again, Greenfield seems to have anticipated subsequent discoveries. The most complete ramapithecine discoveries to date have been reported from Lufeng in the People's Republic of China, where one cranium has been attributed to *Sivapithecus* and three to *Ramapithecus* (I believe it likely that these are a male and three females of a single hominoid species). Judging from the published photographs and initial descriptions, this species shows a close relationship to *Pongo*.

Some of the features cited in a preliminary publication on the female crania (Wu et al. 1981) include a vault that is within the pongid size range but more rounded and filled out than modern ape vaults, a weak nuchal crest and smooth nuchal plane, a small canine projecting only slightly below the tooth row, a bicuspid P₃, a short snout, and a foramen magnum "situated in a more forward position than that of the modern ape." Occlusal views of the PA 677 vault (p. 1020) and of male and female mandibles (Xu and Lu 1979) show an extraordinarily *Pongo*-like postcanine dentition.

Such a suite of features found in the *Asian* hominoid clade help confirm, I believe, both my contentions and those added by Greenfield about the ancestral condition for all of the hominoids. Mainly, the ancestral condition is more hominid-like (i.e., *early* hominid-like) than most of us have imagined. An important aspect of the hominoid (basal ramapithecine) radiation was very likely, as Greenfield suggests, a complex behavioral pattern. As they evolved, the ramapithecines became the most intelligent creatures ever seen on this planet and came to occupy the widest range of any primate.

It is time to recognize and reject the essentially anthropocentric view we have had of human evolution, in which humans evolved from apes that remained essentially unchanged while the evolutionary direction of our lineage was altered in a dramatic way. In this context, the fossil and behavioral evidence have converged to indicate an adaptive pattern for the ancestral hominoids (ramapithecines) that includes a number of aspects that have traditionally been regarded as unique to the hominids. As I stated, I believe that there is no living analog to the ramapithecines, that those who argued ramapithecines were hominids because of shared morphological and (inferred) behavioral characteristics were partially correct in their analyses but wrong in their systematics because these turn out to be shared primitive features (plesiomorphies), and that the African apes have diverged from this ancestral condition at least as dramatically as the hominids have (divergence of the *Asian* apes was also in unique directions, only partially parallel to the developments in Africa).

The evolutionary direction of *each* surviving hominoid lineage has been unique, although all begin with adaptive potentials found in the ramapithecines. Differing adaptive patterns emerged, based on differing combinations of commonalities resulting from a ramapithecine heritage. Frayer finds the question of why a *Eurasian* ramapithecine did *not* evolve into a hominid fundamental. One might as well ask why *Gigantopithecus* didn't evolve into *Gorilla* or *Pan* into *Pongo*. We are

a long way from understanding the specific evolutionary history of any of the surviving hominoids except ourselves, but surely this understanding must entail the combination of common inheritance, expressed in progressively differing biomechanical patterns, and unique histories of ecological adaptation and competition. Before asking why one hominoid pattern did not evolve into another, we have a long way to go in our understanding of why each hominoid pattern evolved the way it did.

Curiously, the only substantial hostility comes from the place one might least expect it: the group that has consistently maintained that divergence is late (Sarich, Zihlman and Lowenstein). I can sympathize with their tone, since it appears as though I have taken their conclusions (although see below) without accepting a shred of their supporting arguments or evidence. My sympathy, however, does not extend to the persistent misreading of the last decade's literature or, for that matter, of the paper being discussed.

Sarich claims that I discard comparative anatomy and biochemistry—99% of the data base, in his words—in my discussion. Of course he is not specific, since I do in fact discuss the morphological studies showing a particularly close relation between *Homo*, *Pan*, and *Gorilla*, as well as the increasing behavioral evidence for this close association which he should have but has not included in his 99%. Indeed, it is the behavioral evidence involving cognition, language ability, and tool making that leads me to suggest a model of a more hominid-like last common ancestor than many find acceptable. I suspect, however, that the real bone of contention is a biochemical one, involving the fact that I insist on separating the genetic and biochemical evidence for closeness (or distance) of relationship from the use of this evidence for calibrating a time scale for divergence—the Sarich and Wilson contribution. To use this evidence to help determine closeness of relationship, and therefore *sequence* of divergence, is to treat these data in parallel to morphological data, assuming in both cases that some changes are directed under the action of natural selection while others are random and involve neutral or close-to-neutral changes established by drift. The evidence for this treatment is substantial, and I note that the most recent publication of chromosomal data (Yunis and Prakash 1982) strongly supports the divergence sequence discussed here. However, to use these data for calibrating the *times* of divergence requires the assumption that *all* changes are neutral (or close to it) and random. This assumption cannot be made for morphological changes, and I am in agreement with a substantial body of literature that suggests it also cannot be made for the chromosomal and biochemical ones. Sarich is critical of my not giving any indication that the objections raised by this body of literature have been answered. I have referenced the objecting literature, and presumably Sarich has referenced the "answers," so I can leave it to the interested reader to determine whether any of the numerous objections to the "molecular clock" have been met. I will stand on my "remarkable" statement.

I *do* agree with Sarich that evolution is concerned with "the whole organism," although I would substitute "population" for "organism." Once again we part company, however, for he seems to feel that the fossil record contributes only 1% of the evidence for evolutionary relationships, while I do not believe that evolutionary questions can be answered by weighing lines of evidence from different sources in this way. I believe that Sarich's comments reflect a fundamental misunderstanding of how to deal with evolutionary problems. The fact is that *any valid* source of evidence has the potential of 100% weight (in his terms) through its potential for refutation. For an evolutionary hypothesis to be acceptable, all valid lines of evidence must tell the same story, and none can stand in refutation of it. In my view, it has only been in the last few years that we

have approached these conditions in hypothesizing about the phyletic position of the ramapithecines.

In the end, Sarich was right in insisting on a late divergence time, but this was based on an analysis that many thought (and still believe) was invalid and therefore was not widely accepted. Moreover, the time of divergence may determine what the ramapithecines were *not* (i.e., hominids), but it provides no information about how ramapithecines relate to hominids or other hominoids. Finally, divergence time may delimit the possible models of hominid origins, but it does not provide one. Thus, while he can claim credit for getting part of the story right, there has turned out to be much more to it than that.

Also reflecting this tone are the remarks by Zihlman and Lowenstein. I am accused of "joining the growing troop of paleoanthropologists shifting from the long-held belief in an early divergence of apes and hominids." I was quite surprised by this statement; while I have been accused of *being* a troop at various times, this is the first time, I believe, that I have been accused of joining one! Therefore, it was with some interest that I reviewed my earlier writings to determine whether the comment was justified. Actually, I have written very little on this topic, since for most of the last decade I have been unable to make up my mind about likely divergence times on the basis of the scanty evidence available. In fact, the only statement I could find was published in 1971, from my dissertation, written in 1968. It may surprise Zihlman and Lowenstein that I wrote "even if 'Ramapithecus' is ancestral to hominids, it cannot itself be considered a hominid" (1971a:22).

It has been my own consistent attitude of skepticism that has underlain the (perhaps more courageous) attempts of my students (Greenfield, Frayer, Yulish) to debunk the hominid status of *Ramapithecus*. If this makes us all look like "heroes," in Tattersall's words, so be it. However, I don't believe that this story has either heroes or villains. I have tried to show that the interpretation of the ramapithecine remains has developed pretty much in accordance with the model of paradigm change outlined by Kuhn, a model which, *contra* both Tattersall and Jacobs, I consider to be very Popperian and explicitly optimistic. If there are grounds for pessimism, they might better be sought in the attitudes of a discipline that responds with disdain when a researcher appears to be wrong and with sarcasm when a researcher appears to be right.

Through their comments about my alleged earlier viewpoint, Zihlman and Lowenstein contribute to a growing tendency to develop a revisionist history of prehistory. While this is perhaps less serious when limited to popularizations, we will probably all be better off not rewriting our own history in academic journals. It is a broad brush indeed that can tar all of the unnamed "they" who are said to "deduce a recent divergence from the same morphological evidence of teeth and bones that formerly was seen as proof of an early divergence." These authors are not unique in their rewriting; for instance, both de Bonis and evidently Schwartz have me following Pilbeam (1982) in the contention of a ramapithecine ancestry for *Pongo* when I actually suggested this somewhat earlier (1980) and Greenfield (unmentioned by both) suggested it at the same time (1980). However, much more than any of the others, this commentary is peppered with misunderstandings and/or misquotations. For instance, "those who (like himself) held that *Ramapithecus* was a hominid were wrong for the right reasons—namely, the shape and size of the teeth," or "denying the validity of the molecules" when all I denied is that they can be used to determine divergence dates. Similarly, I cannot account for the rendition of ramapithecines' "giving birth" to *Pongo* in Asia 10,000,000 years ago and then moving to Africa to originate the African apes and hominids. Rather than discuss these points again, I refer the reader to the relevant parts of the paper.

It is reasonable to question the validity of the "*deus ex machina*" comparison with Piltdown. There are obvious analogies with the ramapithecine issue, as Zihlman and Lowenstein contend. There is the use of fossil evidence to refute a major hypothesis (Darwin's, especially as expressed by Dart) and the presence of only a few doubters (Weidenreich, Weinert, Gorjanović-Kramberger) while most of the field accepted the consequences of the fossil. These analogies, however, are surely more apparent than real. Piltdown was a fraud, while the ramapithecines are the remains of real populations that once lived and that have discernible relationships to other hominoids. The Piltdown remains were not made available for many potential studies (a behavior which most paleoanthropologists would now consider unethical), while progress in understanding the ramapithecine remains has been stimulated by the original specimens by all observers and the wide dissemination of casts and data. Most important, however, is the fact that in the resolution of the Piltdown issue a large number of people were proven wrong and a few were proven correct for exactly the right reasons. It was a proper victory of right over wrong, complete with villains and heroes. Resolution of the *Ramapithecus* issue, in contrast, has not taken on the character of a morality play. Zihlman and Lowenstein ridicule the contention that most workers have grasped important elements of truth in their understanding of the ramapithecine remains, even from before the time that *Ramapithecus* was created as a taxon. This is probably because the emerging picture of hominid and African ape origins developed here leaves absolutely no place for a last common ancestor that in any specific way resembles a pygmy chimpanzee (Latimer et al. 1981), with its weak masticatory apparatus, thin enamel, specialized adaptations for brachiation, and low magnitude of sexual dimorphism. Like so many others, Zihlman and Lowenstein correctly interpreted an important element of the story, for them, in their insistence on a late divergence time, but then incorporated it into what now appears to be an inappropriate model.

Of course this is 20/20 hindsight. If the picture had been this clear before, someone would have proposed this model earlier. But I find nothing to ridicule in the idea that a model of the relation of the ramapithecines to hominid origins could involve "something old, something new, something borrowed, something blue," since this reflects the fact that most workers have been competent and insightful but limited by the frameworks they brought to their studies, which dictated the questions they asked of their data, just as Zihlman and Lowenstein have been and, I would assume, I have been.

There *is*, I believe, a satisfying contrast to the Piltdown situation in the intertwined development of ramapithecine interpretations and hominid-origin theories. In the case of Piltdown virtually everyone was fooled by a fraud for almost half a century, reflecting on the people, the power they gave the hypotheses they held, and the inability to accumulate data to refute these. It was truly information from outside this system (the fluorine test) that convincingly discredited the fossil, and this was hardly a new technique, since Gorjanović-Kramberger used it at Krapina in 1890. None of us, I believe, can be pleased with this history. In the case of the ramapithecines and hominid origins, a mere 20 years has seen the development of two paradigm changes, with roles for changing interpretations and accumulating discoveries in the evolution of what I hope will be a widely acceptable model precisely because it draws on the insights so many workers have had in their interpretations of the relevant data. If this is not scientific progress in Kuhn's sense, I fail to understand what *will* pass for progress in our field. With Fleagle, I believe that if the more journalistically oriented of our colleagues can truly

overturn all current views of evolution every few years, we have been wasting our time in trying to understand the accumulating data from fossils, biochemistry, genetics, functional and comparative morphology, comparative behavioral studies, paleodemography, and evolutionary ecology.

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