



FIG. 1. Scaling of postcanine maxillary tooth area (P3-M3) to wild-shot body mass in higher primates (odontometric data from Swindler 1976). The exponent (α) of the power function $y = \beta x^\alpha$ was estimated by least-squares regression upon the assumption of body mass as an independent determinant. Inclusion of P2 of ceboids and major axis fits do not affect our conclusions about *P. paniscus*. Species (male, female) included in the analysis are: *Aotus trivirgatus* (1, 2), *Ateles geoffroyi* (3, 4), *Cebus apella* (5, 6), *Saimiri sciureus* (7, 8), *Alouatta seniculus* (9, 10), *Cercopithecus cephus* (11, 12), *C. nictitans* (13, 14), *C. neglectus* (15, 16), *Cercocebus albigena* (17, 18), *C. galeritus* (19, 20), *Macaca nemestrina* (21, 22), *M. fascicularis* (23, 24), *Papio cynocephalus* (25, 26), *Theropithecus gelada* (27, 28), *Colobus badius* (29, 30), *C. polyomus* (31, 32), *Presbytis aygula* (33, 34), *Hylobates klossi* (35, 36), *H. agilis* (37, 38), *H. moloch* (39, 40), *Pongo pygmaeus* (41, 42), *Gorilla gorilla* (43, 44), *P. troglodytes* (45, 46), and *P. paniscus* (47, 48).

historic times their range may have extended farther, perhaps even into Angola (Reynolds 1967). Furthermore, the eastern limit of the range of *P. paniscus* remains unknown. The best evidence places it at the Lomami River, but some puts it at the Lualaba. Even if the precise range of *P. paniscus* could be identified, another problem confounds ecological speculations such as Johnson's. Chimpanzees occupy a wide range of environments: humid lowland rain forest, savanna, gallery forest, secondary forest of all kinds, and even cultivated areas (Kortlandt 1962, van Lawick-Goodall 1968, Suzuki 1969, Albrecht and Dunnett 1971, Jones and Sabater Pi 1971).¹ It is difficult to base a theory of bonobo evolution on ecological arguments when the isolating mechanism is so tenuous. We do not feel that the island analogy is accurate, especially if the present drainage of the Zaïre Basin and the "island" of rain forest is a phenomenon as recent as the last 500,000 to 1,500,000 years (Cahen 1954 and Mortelmans 1967, cited by Horn 1976).

The evidence does not indicate, as is suggested by Johnson, that *P. paniscus* is a "specialized insular dwarf." Furthermore, no statement about the specialized (derived) or generalized (primitive) nature of a particular trait or complex can be made

¹ Bonobos do not have similar opportunities today, as their range is relatively small and its environment relatively homogeneous. *P. paniscus* does seem to be found in a higher density in disturbed secondary than in primary forest (Kuroda 1979, 1980).

without first establishing the primitive or derived state (i.e., morphocline polarity) of that character for the group in question. We cannot engage in productive discussion on the evolutionary history of *P. paniscus* (such as this one by Johnson and others that have appeared in the last few years) until solid comparative, quantitative morphological data are obtained and we have more accurate estimates of scaling parameters.

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I firmly agree with Johnson's discussion of the bonobo as an unsuitable prototype for the Hominidae. Moreover, there are some persistent problems that make any consistent cladistic interpretation of *Homo* and *Pan* difficult to assess.

From the perspective of the hominids, marked sexual dimorphism and an extremely powerful masticatory apparatus especially suited to maximizing vertical forces were recognized in some of the early hominids (robust australopithecines) by Robinson (1956, 1962) and later predicted as a general ancestral condition by Jolly (1970a). Lovejoy (1974) clearly demonstrated the polished form of bipedal locomotion attained by these hominids. These conditions were then demonstrated in the earlier *A. africanus* sample from Sterkfontein and Maka-

pansgat (Wolpoff 1973, 1976; Lovejoy, Heiple, and Burstein 1973), and their expression in the even earlier *A. afarensis* sample (Johanson and White 1979) clearly points to their importance as ancestral conditions for the hominids.

At the same time, immunodiffusion studies show an especially close relation between *Homo*, *Pan*, and *Gorilla* (Dene, Goodman, and Prychodko 1976, Sarich and Cronin 1976). Indeed, the amount of DNA difference between *Pan* and *Homo* is surprisingly small, approaching the magnitude normal for subspecies differences (King and Wilson 1975). If these data, presumably reflecting genetic divergence, suggest a close relationship (and imply a late divergence) for the hominid and African pongid lineages, the morphology of *A. afarensis* provides additional support.

In this species, polymorphism in P_3 form extends to include a single cusped variant that is sectoral by any definition. Evidence from P_3 wear (Wolpoff 1979, Wolpoff and Russell 1981), as well as the wear on the newly discovered BMNH 18773 lower canine (White 1980), shows that anterior cutting was still a normal variant of *A. afarensis* dental function. Moreover, a number of specific aspects of the cranial base and palate particularly resemble those of *Pan* (Johanson and White 1979). Thus, in sum, the morphology of the earliest recognized hominid species supports the notion of an early appearance of certain unique hominid features (interestingly, some of these are features that are not well expressed in modern populations) while at the same time supporting the biochemical indications of a fairly recent divergence from *Pan* or a *Pan*-like form.

Where the picture becomes unfocused is over the problem of divergence itself and the question of what, if any, morphological changes are associated with it in the two diverging lineages. While the evidence just discussed indicates that some of the hominid characteristics we can deal with directly (powerful masticatory apparatus, marked sexual dimorphism, bipedal locomotion) can probably be traced back to the time of divergence (especially if it is recent), the question is whether any or all of these may precede divergence. If so, we would be forced to consider a number of characteristics found in *Pan* as the derived condition (in spite of similarities between *Pan* and *Proconsul* in many of these), and our attention would be directed to the unique features of *Pan* in the all-important consideration of why the divergence occurred.

What helps bring this possibility to the forefront is the question of a ramapithecine ancestry for hominids. The ramapithecine adaptive radiation is characterized by two of the three hominid features just discussed—a powerful masticatory apparatus especially suited to vertical loading and marked sexual dimorphism (Greenfield 1979, Wolpoff 1980). (None of the known postcranial remains [from Hungary and Pakistan] indicate an adaptation to bipedal locomotion.) Several recent analyses have suggested an especially close relation between one of the ramapithecine species and *Pongo* (Greenfield 1980, Wolpoff 1980). The problem is that both morphological and biochemical evidence suggests an earlier divergence for *Pongo*. This would indicate that at least some of the ramapithecine species diverged from the lineage leading to hominids before the hominid and African pongid lineages diverged and thus that the ramapithecine features represent the ancestral condition for all three of these lineages.

Should this be the case, it might be more productive to consider *A. afarensis* as simulating a possible prototype for the ancestors of the bonobos than vice versa. Of course, this need not be the case. The alternative possibility is that none of the ramapithecines are on the lineage leading to the hominids and African pongids. This notion is also not without support. Certainly, the fact that only one of the ramapithecine forms is African (represented by less than a handful of specimens) may not be wholly irrelevant. This possibility would allow the hypothesis that the hominid features discussed above are associated with the divergence event or its adaptive conse-

quences. One could then turn to a *Pan*-like (although, for the reasons Johnson discusses, clearly not a particularly bonobo-like) model for the predivergence hominoid form.

I don't believe this issue can be settled at present. However, consideration of the boundary conditions helps delimit the form that a solution must take. In particular, it seems increasingly unlikely that these ancestral models can be combined. Any form of a ramapithecine ancestry for hominids draws our attention to certain (therefore) derived features in *Pan* as an important consequence of divergence, while only the complete elimination of the ramapithecines from hominid ancestry allows us to consider some of the important features of the early hominids as uniquely hominid and to hypothesize a role for them in the process of divergence or its immediate consequences.

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Johnson has set up a straw ape which bears little resemblance to the prototype for the common ancestor of chimpanzees/humans/gorillas that I proposed, and he has proceeded to knock it down with conceptual cannonballs like "synapomorphies," "neontology" and "insular dwarfism." He also misattributes to me the phrase "ideal prototype," which I have never used: I have merely suggested that, of all living hominoids, the pygmy chimpanzee, or bonobo, is most like the probable common ancestor (Zihlman et al. 1978).

This conclusion is based on three lines of evidence: biochemistry, comparative anatomy, and the fossil record. Comparisons of DNA and numerous proteins indicate that humans, chimpanzees, and gorillas diverged from a common ancestor about 5,000,000 years ago, that orangutan and gibbon are about twice as distant from these three as the three are from each other, and that Old World monkeys are about four times as distant. Assuming that the common ancestor was an ape, we then have a choice between a chimpanzee and a gorilla. Even before the early African hominids were discovered, comparative anatomists implied that the common ancestor of humans and African apes must have been something like a small chimpanzee (Gregory 1930, Coolidge 1933). As there is no fossil record of chimpanzees, we must choose between the two living species or imagine a composite of both.

Granted that chimpanzees are more generalized than gorillas (Simpson 1963), my choice of *P. paniscus* in preference to *P. troglodytes* is based on a number of anatomical and behavioral characteristics. Though smaller on average than *troglodytes*, *paniscus* overlaps it considerably in body weight and differs from it mainly in its proportions: a narrower chest, shorter upper limbs, lighter trunk, and heavier lower limbs, all differences that tend in the "human" direction and add up to a lower center of gravity (Zihlman and Cramer 1978, Zihlman 1979b). Behaviorally, this results in the bonobo's being oriented bipedally more than the common chimpanzee and being, in this respect, a more apt precursor to fully bipedal hominids (Zihlman 1980).

Going to the fossil record, we find that the earliest known African hominids, *A. afarensis* from East Africa and *A. africanus* from South Africa, are strikingly similar to *P. paniscus* in several ways: mean femur length, as well as hip, knee, and ankle size, are within a standard deviation of each other. "Lucy's" (AL 288) humerus is shorter than that of *paniscus*, and the fossil's humerus/femur ratio of 84 is intermediate between that of *paniscus* at 98 and that of modern man at 76 (Zihlman 1979a). And Lucy's pelvis is that of a habitual biped. Because the brain size of *A. afarensis* lies within the chim-

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A series of national summaries of research on the Mesolithic will appear on an annual basis beginning in 1982. The newsletter is intended to be an informal communication among researchers interested in the European Mesolithic and will only be successful if all subscribers regularly contribute new information. Interested participants should write the editor: T. Douglas Price, Department of Anthropology, 5240 Social Sciences Building, University of Wisconsin, Madison, Wis. 53706, U.S.A.

Institutions

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