A Proper Study for Mankind: Analogies From the Papionin Monkeys and Their Implications for Human Evolution

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ABSTRACT This paper’s theme is that analogies drawn from the cercopithecine tribe Papionini, especially the African subtribe Papionina (baboons, mangabeys, and mandrills), can be a valuable source of insights about the evolution of the human tribe, Hominini, to complement homologies found in extant humans and/or African apes. Analogies, involving a “likeness of relations” of the form “A is to B, as X is to Y,” can be usefully derived from nonhomologous (homoplastic) resemblances in morphology, behavior, ecology, or population structure. Pragmatically, the papionins are a fruitful source of analogies for hominins because they are phylogenetically close enough to share many basic attributes by homology, yet far enough that homoplastic modifications of these features are easily recognized as such. In “The Seedeaters,” an analogy between Theropithecus among baboons and Australopithecus africanus among hominines was the source of a widely discussed (and often misrepresented) diet-based scenario of hominin origins that explained previously unassociated hominin apomorphies, interpreted basal hominins as nonhuman rather than prehuman primates, and accommodated a basal hominin adaptive radiation of at least two lines.

Current usage recognizes an even more extensive evolutionary radiation among the basal hominins, originating no earlier than about 7 ma, with multiple lineages documented or inferred by 2.5 ma. Although multilinear clades (especially the Paranthropus clade) within this complex are widely recognized, and emerge from sophisticated, parsimony-based analyses, it is suspected that in many cases, developmental or functional homoplasies are overwhelming the phylogenetic signal in the data. The papionin analogy (specifically the splitting of the traditional, morphology-based genera Cercocebus and Papio mandated by molecular evidence) illustrates the power of these factors to produce erroneous cladograms. Moreover, the rapid deployment of basal hominins across varied African habitats was an ideal scenario for producing morphologically undetectable homoplasies. There seems to be no foolproof way to distinguish, a priori, homologous from homoplastic resemblances in morphology, but one pragmatic strategy is to severely censor the dataset, retaining only resemblances or differences (often apparently trivial ones) that cannot be reasonably explained on the basis of functional resemblance or difference, respectively. This strategy may eliminate most morphological data, and leave many fossil taxa incertae sedis, but this is preferable to unwarranted phylogenetic confidence.

Another source of phylogenetic uncertainty is the possibility of gene-flow by occasional hybridization between hominins belonging to ecologically and adaptively distinct species or even genera. Although the evidence is unsatisfactorily sparse, it suggests that among catarrhines generally, regardless of major chromosomal rearrangements, intersterility is roughly proportional to time since cladogenetic separation. On a papionin analogy, especially the crossability of Papio hamadryas with Macaca mulatta and Theropithecus gelada, crossing between extant hominine genera is unlikely to produce viable and fertile offspring, but any hominine species whose ancestries diverged less than 4 ma previously may well have been able to produce hybrid offspring that could, by backcrossing, introduce alien genes with the potential of spreading if advantageous. Selection against maladaptive traits would maintain adaptive complexes against occasional genetic infiltration, and the latter does not justify reducing the hybridizing forms to a conspecific or congeneric rank. Whether relictual could explain apparent parallels in hominin dentition and brain size is uncertain, pending genetic investigation of these apparently complex traits.

Widespread papionin taxa (such as Papio baboons and species-groups of the genus Macaca), like many such organisms, are distributed as a “patchwork” of nonoverlapping but often parapatric forms (allotaxa). Morphologically diagnosable, yet not reproductively isolated, most alltaxa would be designated species by the phylogenetic species concept, but subspecies by the biological species concept, and use of the term “alltaxa” avoids this inconsistency. A line of contact between alltaxa typically coincides with an ecotone, with neighboring alltaxa occupying similar econiches in slightly different habitats, and often exhibiting subtle, adaptive, morphological differences as well as their defining differences of pelage. “Hybrid zones,” with a wide variety of internal genetic structures and dynamics, typically separate parapatric alltaxa. Current models attribute the formation and maintenance of alltaxa to rapid pulses of population expansion and contraction to and from refugia, driven by late Neogene climatic fluctuations. An overall similarity in depth of genetic diversity suggests that papionin taxa such as Papio baboons, rather than extant humans, may present the better analogy for human population structure of the “prereplacement” era. Neandertals and Afro-Arabian “premodern” populations may have been analogous to extant baboon (and macaque) alltaxa: “phylogenetic” species, but “biological” subspecies. Replacement,” in Europe, probably involved a rapidly sweep-
ing hybrid zone, driven by differential population pressure from the “modern” side. Since the genetic outcome of hybridization at allotaxon boundaries is so variable, the problem of whether any Neandertal genes survived the sweep, and subsequent genetic upheavals, is a purely empirical one; if any genes passed “upstream” across the moving zone, they are likely to be those conferring local adaptive advantage, and markers linked to these.

In general, extant papionin analogies suggest that the dynamics and interrelationships among hominin populations now known only from fossils are likely to have been more complex than we are likely to be able to discern from the evidence available, and also more complex than can be easily expressed in conventional taxonomic terminology. Yrbk Phys Anthropol 44:177–204, 2001.
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To know thyself, look not to apes alone;
A proper study for mankind’s—baboon . . .
Alexander Papyoe (with apologies to Alexander Pope)

This paper is expanded from a luncheon talk presented to the American Association of Physical Anthropologists in San Antonio, April, 2000. Its title and theme recognize the meetings’ host: the Southwest Foundation for Biomedical Research, and the outstanding contribution that the Foundation’s baboons and scientists have made to anthropological, primatological, and medical knowledge for over 30 years. The title of course parodies Alexander Pope’s dictum, and its conceit was that a hitherto unrecognized papionin contemporary—“Alexander Papyoe”—claimed equal relevance for his taxon. It is used here as a peg on which to hang some thoughts about the use of analogies in understanding human evolution.

It was also during the San Antonio meetings that we learned of the death of Professor Sherwood Washburn, who, among many other contributions to our field, was among the first to appreciate the relevance of the large terrestrial monkeys to understanding human evolution’s earlier stages. This paper is therefore dedicated to Sherry Washburn—with respect, affection, and sadness that we cannot enjoy his response to its contents.

Its theme is that the members of the tribe Papionini (baboons, macaques, mangabeys, drills, and their extinct relatives), and particularly its African subtribe, Papionina (all but macaques), can bring fresh insights to the interpretation of the diversity, adaptations, ecology, and population structure of species within our own lineage, the tribe Hominini (= family Hominidae in the older convention). Because a comparable argument presented just over 30 years ago (Jolly, 1970a, 1972a,b) stirred the wrath of some troglodytophiles, it should be emphasized at the outset that nothing in this paper is intended to detract from the unique insights that can be drawn from studies of the living hominoids, and especially the extant nonhuman Homininae (“hominine apes”), Pan and Gorilla. Its thesis is simply that there is information that is distinct from and ancillary to these—insights that arise not from homology but from analogy, using resemblances and differences that have evolved in a different clade, rather than those resulting from common ancestry.

Alexander Papyoe suggests that papionins, especially the African papionins (subtribe Papionina), are likely to be a particularly fruitful source of useful analogies for hominin evolution: not simply hominin origins, but also diversity, paleoecology, and the population structure of all hominins. Unlike the hominine apes, which are just three species of two genera, the African papionins present a complex phylogenetic picture, and include adaptive arrays of widely different ages, so that a variety of evolutionary phenomena is exemplified by extant as well as extinct taxa. Also unlike the African apes, which as far as is known have always been primarily evergreen forest dwellers, baboons of several genera have shared nonrainforest habitats in sub-Saharan Africa with the hominins ever since their respective lineages emerged. Late Neogene climatic and biotic fluctuations that affected hominin distribution, diversity, and adaptations impacted the baboons in parallel ways, rather than inversely, as was presumably the case for forest-dwelling apes. We can therefore expect the papionins to provide bio-historical as well as phylogenetic and functional analogues.

Finally, most extant papionin lineages are now firmly anchored phylogenetically by multiple lines of molecular evidence (Disotell, 2000), and a reasonable, if approximate, timescale for the whole radia-
tion is provided by calibrating molecular divergences (Tosi et al., 2000; Disotell, personal communication) against the paleontologically documented first appearance of Theropithecus apomorphies at about 4.5 ma (Kalb et al., 1982; Delson, 1993; Gundling and Hill, 2000). The overall papionin chronology is comparable to that of the hominines (Pan-Gorilla-Homo), while the African subclade (Papionina) seems to have diversified within much the same time frame as the hominin subclade (Ruvolo et al., 1991; Disotell, personal communication).

After a short examination of the concept of analogy, the paper focuses on four areas of recurrent contention where a papionin analogy may make a contribution: 1) the origins of the hominin ancestral lineage, and specifically, the nature of the first human ancestor not shared with any other living primate; 2) homoplasy and the cladistics of “basal” Plio-Pleistocene hominins; 3) the probability of occasional hybridization and gene flow between basal hominin lineages; and 4) the status of the various populations of “archaic” and “premodern” Homo sapiens, i.e., the Neandertals and their contemporaries. Each of these topics is of course much too extensive to be comprehensively reviewed in a single paper. The most I can hope to do is simply indicate some areas within them where Alexander Papyoe—as spokesmonkey for the baboons—can suggest fresh viewpoint.

**HOMOLOGY, HOMOPLASY, AND ANALOGY**

Although the distinction between homology and analogy is commonly regarded as one of the fundamentals of evolutionary theory, both concepts can be slippery, and have stimulated a considerable body of literature whose analysis is far beyond this essay’s scope. The following brief discussion of usages is scarcely original, but will serve to define this paper’s stance, which reflects a strong nominalist bias and a distrust of reifications.

In an evolutionary context, homology describes an attribute of individuals (either actual individual organisms, or abstracted representations of a taxon). Structures are often described as homologous (as in “the wing of bats is homologous to the human arm,” or “the wing of bees is not homologous to the wing of bats”), but this usage can be confusing (is a bat’s wing homologous to a pterodactyl’s?). Ambiguity is reduced if the term homology is applied not to structures, but to states of a variable character (“possesion of a trunk with fore- and hindlimbs’ is a homologous character-state of chiropterans and humans”). A homologous character-state is one whose shared status derives from inheritance from a common ancestor. (In this context, the distinction between synapomorphies and symplesiomorphies is irrelevant; both are equally homologous, differing only with respect to the ancestor from which the shared state is derived.) This definition of homology, of course, presupposes a known cladogram, and this means that homology cannot be used a priori to sort relevant from irrelevant characters for cladistic analysis, although we can distinguish characters that are likely to be homologous from those that are not. The definition also ignores some fundamental issues, such as the weaselsish attributes of verbal character-state descriptions, and the difficulty of defining “inheritance” in any but a genetic context (and not unambiguous, even there) (Cartmill, 1994).

If “homology” is used in this way, then its antonym is “homoplasy,” a shared character-state that is not derived from common ancestry (Lockwood and Fleagle, 1999). A homologous resemblance results from a common ancestry in which the shared character-state appeared by a single evolutionary transition; in the ancestry of a homoplastic resemblance there are at least two such transitions.

Analogy is not identical to homoplasy, although it also involves nonhomologous resemblances. According to the Oxford English Dictionary, analogy implies an “equivality or likeness of relations,” which is classically stated in the form “A is to B, as X is to Y” (thus, A is the analogue of X). For example, in his discussion of the relationship between “higher mental powers” and cerebral development in human ancestry, Darwin (1871, p. 54) points out that:

“We meet with closely analogous facts in the insects, for in ants the cerebral ganglia are of extraordinary dimensions, and in all the Hymenoptera these ganglia are many times larger than in the less intelligent orders, such as beetles.”

Formally stated, Darwin’s analogy is: “with respect to both central nervous system complexity and intelligence, ants are to insects, as human beings are to primates,” and its implication is that there is a functional relationship between the two attributes. Darwin is not, of course, suggesting that an ant’s cerebral ganglia (“not so large as the quarter of a pin’s head”) resemble a human brain in size, structure, function, or any other respect except their unusual size for an insect. This illustrates the important difference between “analogy” and “resemblance,” concepts that are often confused.

Not all analogical propositions are expressed exactly in the “A is to B . . .” format, but they always include the “likeness of relations.” For example, paleontologists often take dental dimensions from two extant populations (A and B) known to represent good species, and use them as a standard by which to determine whether two species are present in a mixed bag of fossil teeth. If X and Y are heaps of fossils sorted by whatever criteria the paleontologist chooses, he or she is testing a hypothesis in the form of an analogy something like: “when they were alive, the source population of X had the same sort of relation to the source population of Y, as A presently has to B” (e.g., they were reproductively isolated, ecologically distinct, fully diagnosable, or conformed to whatever other species criterion is adopted). Similarly, a paleoecologist might call upon information
about sympatric chimpanzees and gorillas to understand the interactions of large-bodied hominids coexisting at a late Miocene site, proposing an analogy in the form: “N-pithecus related ecologically to M-pithecus, as chimpanzees today relate ecologically to gorillas.” Whereas “homoplasy” annotates any resemblance acquired independently, an analogy, in the sense used here, is a particular kind of logical triangulation that uses significant patterning of independently acquired behavioral, morphological, or physiological traits to help understand and interpret evolutionary events in adaptational and functional terms. Not all such traits may be homologies in the usual sense. In the example of analogous species distinctness, for instance, diagnosticity and/or genetic isolation is a condition shared by the analogues, but it would be stretching the usage to call it a homoplasy. Conversely, many homologies (especially, but not exclusively, in the primary structure of molecules) are certainly the product of pure chance. Lacking any functional significance, such random resemblances are unlikely to be incorporated into a useful analogy.

Although some useful analogies can be drawn from close phylogenetic relatives, a close relationship of (A + B) to (X + Y) does not necessarily make for a more illuminating comparison. There seems to be little justification, for example, for the practice of unquestioningly using Pan troglodytes and Gorilla gorilla to represent “good species” when attempting to deduce alpha taxonomy from a sample of fossil hominin skulls or teeth. Chimpanzees and gorillas are, of course, good species, but they are not sister-taxa (Ruvolo et al., 1991); the geometry of the hominine cladogram as currently understood means that no pair of hominin species can be as distantly related as are chimpanzees to gorillas. The chimpanzee-gorilla comparison is likely to provide a poor analogy for sorting out hominin lineages, underestimating the number of newly emerged species present in a fossil sample. For hominins, or any case where recent speciation is possible, a more appropriate comparison is with other clusters of good, but minimally differentiated species: lemurs of the genus Eulemur, perhaps, or Cercopithecus monkeys, or dogs of the genus Canis.

Another drawback with drawing analogies from close relatives is that it can be hard to make the important distinction between analogous and homologous resemblances. Chimpanzee carnivory is a case in point. In the early 1960s, Goodall reported the first cases of meat-eating by chimpanzees (Goodall, 1986), at Gombe. Most commentators, noting that Gombe is a “savanna” (actually, woodland-mosaic) habitat, interpreted hunting as an adaptation that appeared separately in early hominins and savanna chimpanzees as each moved “out of the forest.” This made it a homoplastic behavior, suggesting a significant analogy between savanna chimpanzees and supposed savanna-dwelling early hominins, with the strong implication that savanna-dwelling stimulated carnivory. It was quite quickly shown, however, that Pan troglodytes practiced opportunistic carnivory in other (probably all) habitats. This discovery suggested that carnivory, or at least the ability to adopt it when advantageous to do so, was a shared ancestral (homologous) trait of hominins and chimpanzees. It was a component of the behavioral repertoire of the last common ancestor, but no more likely to be significant to hominin divergence than any other such trait (unless, of course, there had been archaeological or anatomical evidence for elaboration of carnivorous behavior in the stem hominin). The two interpretations thus have quite different implications for the context in which simple, chimpanzee-style hunting appeared, and its possible role as a prime mover in hominin evolution, but they are easily confounded, and quite often are. By contrast, when Schaller and Lowther (1969) compared and contrasted the hunting-scavenging strategies of African carnivores with those of early hominins, there was no doubt that they were using an analogy.

Darwin’s ant-brain example is unusual in the great phylogenetic distance between the analogues. Useful analogies, especially for anatomical function, are often more readily found among relatives that are less extremely distant. This fact may bias our search for analogies toward closer relatives, but it is important to note that this bias is purely pragmatic; the logic of analogy does not require that structures whose function is compared should be “homologous” (in any sense). For example, flightlessness has evolved many times on small oceanic islands, among both insects and birds; for the cause to be analogous, the wings of birds and beetles do not have to be homologous structures. One could, in fact, argue that an analogy is all the more powerful if the pairs of analogues are not closely related. As with Darwin’s ants, the more phylogenetically distant the analogues, the more striking the coincidence, and the more obvious the fact that a parallel adaptation has occurred, and demands an explanation.

The papionins are ideally situated, phylogenetically, to provide analogies for hominin evolution. As fellow catarrhines, they share (by homology) many attributes of hominin structure and function. They are basically arboreal (but often secondarily terrestrial) animals that live in permanent, bisexual associations, experience their world predominantly via their sense of vision, and use their hands to feed as well as to locomote. They use 8 incisor teeth for initial food preparation, 20 cheek-teeth for chewing, and 4 canines for agonistic interactions. All these homologies comprise a similar groundplan, liable to be modified in similar ways. Yet the papionins are also far enough removed from the hominins that when analogous forces do modify one of the shared catarrhine attributes, producing a parallelism, it is recognized as such, and is not mistaken for homology. A gelada baboon’s precision-gripping hand, for instance, resembles a human hand in some of its
Australopithecus africanus was still in the terminal Prehennigian). My excuse for summarizing this ancient story here is twofold: first, it illustrates the use of analogy, and, second, it affords an opportunity to correct a few of the misinterpretations that, barnacle-like, encrust its aging hulk. A more complete review of the current status of “Seed-Eaters” will be presented elsewhere.

This analogy was used to construct a novel scenario for the origin of the hominin clade, by explaining, in functional and ecological terms, the fact that a particular suite of new traits had appeared in the earliest undoubted hominin species (at the time, Australopithecus africanus). It is important to note that the analogy, like any such exercise, could not, and did not attempt to, address three other, equally important but quite different questions: “Where does Australopithecus fit within the primate phylogram?”; “What living species most closely resemble Australopithecus?”; and “What anatomical changes separated Australopithecus from its chimpanzee-like ancestor, and what are their functional implications?” These problems require identification and functional analysis of Australopithecus apomorphies in the context of the homologous traits shared with its closest known relatives, i.e., hominine apes and human beings. These are, of course, major, ongoing concerns of paleoanthropology, that continue to produce more refined descriptions and interpretations in response to new fossil discoveries, work on living apes, and the application of more sophisticated comparative and functional anatomical methods. They can be tackled only from a base of knowledge of the behavior, physiology, and anatomy of extant hominine apes and humans, and they fully justify the focus of paleoanthropology upon these species. But the focus of “Seed-Eaters” was on a different problem. At the time, the phyletic position of Australopithecus, and the major features of its anatomy, had been satisfactorily interpreted (e.g., by Le Gros Clark, 1955), to the extent allowed by the current state of knowledge. Australopithecus was indeed a basal hominin. In brain size and overall characteristics, it resembled a hominine ape, but it was a biped (of a sort), with small canine teeth in both sexes, and incisor teeth that were small relative to cheek-teeth. What was not satisfactorily explained was why these apomorphies had appeared.

Contemporary interpretations of the hominin apomorphies, essentially unchanged since Darwin (1871), emphasized not so much their origins as their functional interdependence. Bipedal stance, for example, was favored because it freed the hands for tool-use, tool-use led to reduction in the relative size of the incisor and canine teeth, and to specialization of the hand for tool use and manufacture, which in turn favored more efficient bipedal adaptations, and so on. As Darwin (1871, p. 51) put it:

“Man alone has become a biped; and we can, I think, partly see how he has come to assume his erect attitude... Man could not have attained his present dominant position in the world without the use of his hands, which are so admirably adapted to act in obedience to his Will... But the hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, as long as they were habitually used for locomotion... From these causes alone it would have been an advantage to man to become a biped...”

Darwin’s statement borders on teleology, but it is saved by his cautious insertion of “partly,” and by his passing reference, earlier on the page, to an antecedent cause, a “change in its manner of procuring subsistence, or to some change in the surrounding conditions” (Darwin, 1871, p. 51)—what today we would describe, less elegantly, as an ecological prime mover, responsible for assembling the elements of the positive feedback system.

Paleoanthropologists of the mid-1960s enjoyed a considerable advantage over Darwin in having much more direct evidence about this prime mover: in naturalistic studies of wild great apes, in paleoecological information about the context of hominin origins, and especially in the derived anatomy of hominins very close to the stem itself. Very little attention, however, was directed to stem hominin anatomy itself as evidence for the nature of hominin cladogenesis. If the anatomy of basal hominins was evaluated functionally (as opposed to phylogenetically), it was from the viewpoint of the “path from ape to man,” most commentators apparently assuming that the nature of that path was self-evident, and that a vaguely imagined move from “forest” to “savanna” was sufficient to set the basal hominins on their way along it. Basal hominin features were evaluated according to their resemblance to humans or to apes, and human-like conditions were unquestioningly interpreted as evidence for the beginnings of human-like behavior, e.g., a hand with relatively short phalanges and a long, powerful, and mobile pollex was attributed to tool-making, even in the absence of artifactual evidence.

Besides their tendency to wander into teleology, such explanations suffer from a lack of generality. As a reviewer of this paper’s first draft put it, “All anthropologists are bedeviled by the fact that there is only one living primate (indeed mammal) that is habitually bipedal and that manufactures stone tools regularly.” It is indeed the case that if we insist that the only relevant species are those that share...
both the adaptations we are trying to interpret, and the complete suite of homologous, heritage traits in which they are embedded, the only relevant species for explaining the evolution of hominin traits such as bipedalism are hominins themselves. And since all of them (so far as we know) owe their bipedalism to the same, ancestral event, any explanation for this event, no matter how ingenious, is a “Just So Story,” applicable only to the case from which it is derived. This problem is not anthropology’s alone; every evolutionary transition in any species occurs against the background of a unique heritage resulting from an idiosyncratic evolutionary history.

Analogy offers a way out of the dilemma by allowing, in fact insisting, that the feature to be interpreted (habitual truncal erectness supported from below by the hindlimb, for example) be decoupled from its context of heritage features. The basal hominian transition to bipedalism, for instance, can then be linked to a wider universe of similar events, some of which may prove illuminating. We can ask not only “What caused hominins to become bipeds?” but rather “What common factors, if any, are associated with adoption of hands-free, upright posture or gait in other vertebrates?” Posed this way, the question yields a slew of potentially analogous transitions in the ancestries of clades as varied as theropod dinosaurs, kangaroos, and gerenuks. Not all will prove illuminating, but some may stimulate fresh insights.

“Seed-Eaters” found an explanatory analogy in the many parallels between trends seen in Theropithecus, especially large extinct forms assigned to T. oswaldi (Jolly, 1972b), and canonical descriptions of Australopithecus africanus. Since A. africanus was at the time the earliest and least derived known hominin, its apomorphies were presumed to be adaptive reflections of the origin of the hominin clade itself. Yet the relatively small incisors, especially of the extinct Theropithecus oswaldi, paralleled those of Australopithecus, and artifact-use seemed an unlikely explanation. Moreover, many other distinctive, derived features of Australopithecus jaws and teeth were also paralleled in Theropithecus, especially the large, extinct species. Some of the Theropithecus-Australopithecus parallelisms involved features generally assumed to be functional correlates of tool use or other aspects of culture, while others did not. A reevaluation of the functional implications of all the recognized apomorphies of Australopithecus concluded that few, if any, of these derived traits demanded an explanation as adaptation to culture and tool-using. This was true even of those, like a habitual bipedal stance and long, powerful pollex, that were not paralleled in Theropithecus. Instead, it was suggested that all the dental-gnathic homoplasies comprised a single functional complex related to mastication, summarized as “back-tooth dominance,” and that this, together with lower-crowned canine teeth that permitted molar cusps to wear more evenly, postural changes associated with australopithecine-style bipedalism, and a hand with a precise thumb-index pincer and a palmar pocket, could all be related functionally to “small-hard-object feeding.” Moreover, “small-hard-object feeding” also described the most salient derived feature of the extant Theropithecus gelada’s ecology, though in its case the food objects requiring thorough mastication were grass blades, rhizomes, and corms, rather than seeds, and the gelada is a habitual, upright-trunked squatter, rather than a biped. The stem hominin was presumed to be about as culture-bearing, artifact-using, and carnivorous as extant chimpanzees, but the staple of its mainly vegetarian diet was tough savanna-woodland seeds rather than forest fruits. In the original formulation, grass seeds gathered in edaphic grasslands were imagined to be the staple. Later (Jolly and Plog, 1987), in response to work by Walker (1981) and Peters (1982), as well as my own observations in Ethiopia, I identified the tough but nutritious fruits, seeds, and pods of thornbush shrubs such as acacias and Grewia as a more likely dietary focus than grass seed.

“Seed-Eaters” also pointed out that Theropithecus and Australopithecus each have apomorphies that are not paralleled in the other, and these too are a significant component of the analogy, because they differentiate the respective ecochrones of the analogs. For example, Theropithecus has high-crowned, complex, molar teeth functionally similar to those of other graminivores (grass-eaters). Hominins have low-crowned, thick-enameded molars suitable for milling and crushing. Another contrast in apomorphic traits, not apparent in 1970, also underscores a difference between graminivory and granivory (seed-eating). Theropithecus gelada appears to have a smaller brain than similarly sized Papio baboons (Martin, 1993), while Australopithecus, by some interpretations, may show modest apomorphic brain enlargement. If confirmed, the difference might reflect a nutritional contrast between leguminous seeds eaten by basal hominins (high in calories, protein, lipids, and essential fatty acids) and grassy herbage eaten by geladas (comparatively low in nutrients per unit bulk). It might also reflect a difference in the distribution of the foods: relatively dispersed and patchy in space and time for savanna-woodland seeds, more continuous for grasses and herbs in the gelada’s montane grassland.

I thought that a diet-based explanation for hominin origins was appealingly parsimonious. It ex-

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¹Seed-Eaters”, following the conventional wisdom, assumed that Australopithecus dental proportions differed from those of apes, especially chimpanzees, mainly because incisors had become smaller. In fact, as Wolpoff (1973) soon showed, cheek-tooth enlargement as much as incisal reduction was the cause of the changed proportions, especially in the newly described, and even more basal, A. afarensis. This, of course, fitted the dietary scenario even better, and the artifact-driven model much more poorly.
plained the evolution of the small-hard-object feeding adaptations in hominins, the independent evolution of functionally equivalent features in *Theropithecus*, and the parallelism between them. Compared to previous explanations, it covered a greater variety of derived basal hominid features, and linked features not previously considered part of the same functional complex (e.g., large molars and adept hands). It was also economical in proposing that the initial ape-hominin divergence involved a relatively small and simple change in dietary emphasis: a minimal ecological change of a kind thoroughly familiar from mammalian paleontology, rather than a one-of-a-kind leap into a multifaceted protoculture.

Not all colleagues were convinced. In some cases, the problem seems to have been that the critic misinterpreted “analogy” as “identity,” mentally connected “model” and “baboon,” and jumped to the conclusion that a living baboon was being used as an avatar of an early hominin. (This is equivalent to interpreting Darwin’s analogy to mean that humans have brains like those of ants.) Others seemed to feel, mistakenly, that the importance and relevance of chimpanzees were being slighted. In yet other cases, the objection seems to have been based on a feeling that an event as momentous as the origin of the human lineage must surely have been caused by something more complex and unique than a not-very-profound change of dietary emphasis—a case, I think, of the “humans are special” bias that tends to afflict biological anthropology, and also of confusing a simple prime mover with its multifarious consequences.

Pending the more extensive review, it bears stating, for the record, that “Seed-Eaters” advanced none of the following propositions. Each has been set up as a straw man and gleefully demolished by one colleague or another:

1) that *Australopithecus* (or hominins in general) were more closely related, phylogenetically, to baboons than to chimpanzees.
2) that *Australopithecus* ate grass like a gelada.
3) that *Theropithecus* is a “seed-eating baboon.”
4) that basal hominins inhabited “vast, dry savanna grasslands” (Spenser, 1997, p. 201).
5) that the “Seed-Eater” idea stood or fell with the hominin status of *Ramapithecus*.
6) that *Australopithecus* ate only seeds.
7) that all the derived features of *Australopithecus* were paralleled in *Theropithecus*, or vice versa.
8) that *Theropithecus* resembled early hominins more closely than it did *Papio* baboons or other monkeys.
9) that male *T. gelada* have small canine teeth.
10) that *Australopithecus* (or any other early hominin) resembled a *Theropithecus* baboon more closely overall than it did African apes, specifically, the chimpanzee.

By explicitly decoupling the origins and early evolution of hominins from the concept of an expansive, culture-driven eoniche, and instead invoking dietary and habitat shifts as causal factors, “Seed-Eaters” represented basal hominins not as *prehumans* whose importance was measured purely by how far they had traveled down the road from “ape” to “man,” but as *nonhuman* primates, subject to the same forces of diversification, speciation, and adaptive radiation as other contemporary mammalian taxa. Since all hominins did not have to lie on the same adaptive path, the large-jawed, large-toothed “robust” forms, seen as direct derivatives of the first phase of hominin evolution, were able to live alongside the “human” branch, which by this time had built a new, more carnivorous, artefact-based eoniche on the seed-eater base.

In the last few years, new discoveries have begun to document just how extensive a radiation actually occurred among the basal hominins. Two, possibly three, genera (*Ardipithecus*, *Kenyanthropus*, and the still mysterious *Orrorin*), and three species of *Australopithecus* (*A. bahrelghazali*, *A. anamensis*, and *A. garhi*), have joined the roster of hominins of the 6–1.5-mya period, and the moribund genus *Praeanthropus* has been revived. (Leakey et al., 1995, 2001; Asfaw et al., 1999; White et al., 1994; Haile-Selassie, 2001; Brunet et al., 1995). Some authorities remove one or more lineages of “early *Homo*” from the genus and assign them to distinct ramifications (Wood and Collard, 1999; Wolpoff, 1999). In part, this multiplication of taxa is a product of shifts in evolutionary and taxonomic philosophy and practice. There is less antipathy to proposing new names in cases where the evidence is inconclusive, and wider recognition that the shape of organic evolution in general is “bushier” than previously appreciated. The phylogenetic species concept, and acceptance of clade-based taxonomic usage that abhors paraphyletic and “wastebasket” taxa, have tended to multiply recognized species. As always, some newly named hominin forms may ultimately disappear into synonymy. Nevertheless, even allowing for shifting taxonomic fashion and uncertainties in alpha taxonomy, it is clear that much of the newly described diversity represents biological reality. Moreover, most of this “new” diversity has been recognized in hominins from a single broad eco-geographic zone: the northern savanna-woodland belt, and especially its extension in eastern equatorial Africa. Much of the rich basal hominin material from South Africa, which derives from very different ecological and geographical settings (Bromage and Schrenk, 1999), has yet to be fully described and interpreted within the current, more schizophilic taxonomic climate. It can safely be predicted that even more basal hominin genera and species will ultimately be recognized.

**HOMOPLASY, CRYPTIC SYMPLESIOMORPHY, AND THE DIVERSITY OF EARLY HOMININS**

The recognition of multiple lineages early in hominin history raises the methodological question of
how their cladistic and phylogenetic relationships can be retrieved from the distribution of morphological character-states. The extant papionins, for which we have a reliable molecular phylogeny, provide an informative, if not altogether optimistic, analogy.

Opinions differ as to whether molecular data are best considered independently, or combined with morphology, in phylogenetic reconstruction (Kluge, 1989). As molecular data become more comprehensive, and methods of analysis more sophisticated, the case for building molecular trees independent of other evidence becomes compelling, because they provide a powerful heuristic tool: a map on to which to plot the evolution of morphological character-states (Collard and Wood, 2000). This method assumes that the molecular tree accurately represents phylogeny, an assumption adopted in the following discussion, without implying that present molecular datasets are adequate, or that current analytical methods are infallible.

The accepted molecular phylogeny of the papionin radiation (e.g., Harris and Disotell, 1998; Disotell, 1996; summarized in Disotell, 2000) reproduces many of the features of morphology-based trees (e.g., Strasser and Delson, 1987), but differs in linking *Papio* with *Lophocebus* and *Mandrillus* with *Cercocebus*. This particular discrepancy is especially significant because the molecular phylogeny dismantles two groups traditionally considered single genera: large, long-faced, terrestrial or semiterrestrial “baboons” (*Papio*, s.l., becomes *Papio* + *Mandrillus*), and smaller, short-faced, arboreal “mangabeys” (*Cercocebus*, s.l., becomes *Cercocebus* + *Lophocebus*). We should note in passing that although it is the papionin case, involving higher primates, that has caught the attention of anthropologists, its message—that homoplasies are more frequent, and harder to detect morphologically, than we ever believed—has become almost a cliché in general evolutionary biology. Every issue of the relevant journals seems to include a paper or two (many by morphologists, physiologists, or ecologists) that not only revises a cladogram on the basis of molecular data, but also uses the resulting homoplasies to construct informative analogies based on the homoplastic acquisition of functionally related traits.

As a test case for morphological cladistics, the mangabey-mandrill-baboon case nicely exemplifies two major kinds of misleading, nonapomorphic resemblance. Whether the baboon or the mangabey character-states are considered ancestral, the revised phylogeny implies major homoplasies in both skull form and postcranial features. Some of these were evidently produced by conventional homoplasy: parallel adaptation to similar function. These traits include the degree of posterior angulation of the ulnar olecranon process, which is related to the proportion of climbing and terrestrial locomotion in the animal’s locomotor profile (Jolly, 1967), and unites semiterrestrial mandrills and baboons on the one hand, and the two groups of mangabeys on the other.

Other homoplasies, such as those affecting facial length (and correlated characters) in the African papionins, can be attributed to a less obvious but probably even more powerful phenomenon: ancestral patterns of relative growth that independently produce similar phenotypes in animals of comparable overall size. The relationship between facial and cranial length in Papionini is an extreme case of positive allometric growth, and was one of the earliest to be expressed mathematically (Huxley, 1932). In overall skull proportions, the adults of small papionin species resemble the juveniles of larger ones, while the adults of large-skulled forms (mandrills, geladas, and *Papio* baboons) all have relatively long faces. If the developmental relationship itself (rather than its size-determined phenotypic expression in adult skulls) is considered the character-state, it is a plesiomorphy of papionins, and the homoplasy that links baboons and mandrills is not facial length but absolute skull (and body) size. Whether long faces are labeled a phenotypic homoplasy, or a developmental plesiomorphy, the trait is equally misleading and phylogenetically uninformative. It is interesting to note that a truly derived state of the morphogenetic character can be recognized among papionins, but not in the long-faced baboons. It occurs in some Sulawesi macaques (*Macaca nigra* and close relatives). Their relative facial length is baboon-like, but because it is combined with a much smaller, macaque-sized skull, it implies that a shift in relative growth trajectory occurred in the ancestry of this particular subscale of macaques (Jolly, 1965; Albrecht, 1977).

Another lesson to be drawn from the papionins is how completely the combined effects of true homoplasy and unrecognized morphogenetic symplesiomorphy can obscure real phylogenetic relationships, and powerfully support false ones. We sometimes tend to assume, I think, that detailed resemblance in complex anatomical features is sufficient evidence for true synapomorphy, because such complexity is unlikely to be duplicated in evolution. The papionin case illustrates this argument’s flaw: as morphological genetic work is documenting more and more clearly, structural and genetic complexity are not closely correlated. Though changes in shape may be complex in the sense that many structures (and an almost infinite number of possible metrics) are affected, they nevertheless can be duplicated in parallel evolution, presumably because their genetic basis is comparatively simple. In fact, it is not hard to envision an array of related forms in which great diversity in phenotypic characters is determined by the differential expression of a few simple developmental symplesiomorphies. Here, the real apomorphies would be the factors underlying the differential expression of the developmental patterns; they themselves would be excellent candi-
dates for cladistic analysis, but their detection is still in its infancy.

As Collard and Wood (2000) recently demonstrated, the formal, computer-aided application of cladistic logic to large suites of morphological characters is no more likely to give the correct (i.e., molecule-concordant) answer than is the kind of intuitive, seat-of-the-pants analysis favored by many paleontologists and morphologists. Like some traditional, premolecular classifications, the PAUP analyses of Collard and Wood (2000) suggest that mandrills and Papio baboos are sister taxa, and unite the great apes to the exclusion of Homo. Both morphologists and tree-building computer programs are misled because the basic logic of parsimony cannot detect cases where an erroneous tree is overwhelmingly supported by suites of unrecognized, correlated homoplasies, and by developmental sympleiomorphies concealed by allometry. Parsimony-based systems are designed to recognize clades by concordant, shared, derived character-states. Suites of phenotypic similarities resulting from functional homoplasy and cryptic sympleiomorphy are not synapomorphic, but they are both derived and shared, and they are often distributed concordantly, as “bundles” or complexes.

Having shown convincingly that PAUP produces statistically robust but spectacularly inaccurate trees when applied to an extensive set of standard craniodental measures, Collard and Wood (2000) suggested that craniodental data may be intrinsically inadequate: a gloomy prospect for the paleontologists who must rely on such data for phylogenetic reconstruction. Collard and Wood (2000) do not sort their characters by utility (as measured by concordance with the molecular phylogeny), but it seems likely those (such as facial length) that are affected by cryptic sympleiomorphy were highly influential. (It should be noted that the analytic method of Collard and Wood (2000) for eliminating the influence of overall size as a factor in the analysis also effectively concealed size-related effects.)

The situation may, however, be less hopeless than Collard and Wood (2000) imply. We know, after all, that the morphological data do contain the necessary information, because an informed eye can discern the correct story. Primed by strong molecular hints of the Cercocebus-Lophocebus dichotomy (Croinin and Sarich, 1976; Hewitt-Emmett et al., 1976), Groves (1978) was able to find cranial, dental, and soft-part characters that supported it. Similarly, dental and postcranial character states linking Cercocebus with Mandrillus, and Papio with Lophocebus, could be discerned (Fleagle and McGraw, 1999), once morphologists knew to look for them. Moreover, once identified, the phylogeny-concordant traits could then be plausibly interpreted in terms of ecology and behavior.

If, as this suggests, phylogenetically meaningful morphological traits are concealed in a mass of uninformative or misleading information, simply adding characters uncritically to a mechanical cladistic analysis is not the solution. The new characters are unlikely to be functionally and developmentally independent of the existing list, resulting in still larger bundles of covariant homoplasies, and even stronger statistical support for spurious phylogenies. The problem is not too little information, but too much that is misleading, so pruning the dataset may be as productive as augmenting it.

Is it even possible to identify the informative traits and cut away the misleading ones, without a molecular crib-sheet? In the mandrill-mangabey case, “good” characters were comparatively few, subtle, and not concentrated in any one tissue or structure. Apart from the dental features noted by Fleagle and McGraw (1999), many of them were irrelevant with respect to function. Obviously, a more accurate tree would result if homoplasies were excluded at the outset, but there is no foolproof way of doing this. The correct cladogram can be built (even by PAUP) only if homoplasies are identified and excluded, but homoplasies are defined by their discordance with the correct cladogram.

While we cannot reliably identify homoplasies by the definitional criterion, we can spot and exclude data that are most likely to be affected by homoplasy (Haszprunar, 1998). Such data-pruning has become unfashionable with the ascendency of parsimony-based computerized methods, but is implicit in much intuitive phylogeny building. One strategy devalues characters that are likely to covary because they are components of a single functional system, identifying them intuitively (Skelton and McHenry, 1992), or by using statistical measures of association (Strait, 2001), and collapsing them into a single variable to be entered into the analysis. The whole “small-hard-object-feeding” complex might, for example, be collapsed to a single entity. This will not remove all homoplasies, but it will ensure that each functionally or morphogenetically determined homoplastic “bundle” that is identified contributes no more than one data point to the analysis. (It will, of course, also limit the contribution of true synapomorphies, such as those identified by Fleagle and McGraw (1999), that comprise, or might comprise, functional complexes.)

A complementary, somewhat more radical procedure is to produce a matrix of intertaxon concordances, using all available data without regard to descriptive level, from the physiological to the gross morphological, splitting and rewording comparisons to make the analysis as comprehensive as possible. This dataset can then be rigorously censored, excluding any resemblances or differences that can be plausibly explained in terms of documented resemblances or differences in behavior, natural history, or morphogenetic processes (Jolly, 1970b). For example, geladas are close to humans in their “opposability index,” an expression of the relative lengths of thumb and index finger, presumably related functionally to an efficient precision grip (Napier, 1980).
As a trait, the simple resemblance in proportions obviously tells the wrong phylogenetic story (geladas and humans are not sister-taxa), but would be excluded because it is easily explained by functional parallelism (parallel adaptation to a particular kind of manipulation). It can, however, be broken down by considering the relative lengths of the digits as separate characters. The gelada achieves its efficient opposability by shortening its index finger, while humans have a relatively long thumb. This difference does carry phylogenetic weight (in this case, against relationship), because the function of the two mechanisms is closer than their structural resemblance. It therefore points to two separate pathways for achieving the same functional end, and, hence, to separate ancestries: one knuckle-walking, the other digitigrade quadrupedal.

Phylogenetically weighty differences and resemblances are also exemplified by the very close and detailed similarity in shape of female sexual swelling that unites Cercocebus with Mandrillus, and Lophocebus with Papio (Hill, 1970). Ressemblances based on the character “sexual swelling occurs/is absent” are of low phyletic weight, because the feature is related functionally to social structure and mating strategy. But, absent evidence to the contrary, we can presume that any of the swelling shapes seen among African papionin species would perform as signals. To the extent that the resemblance of Cercocebus to Mandrillus, and Papio to Lophocebus, is closer than function demands, the shape and position of sexual swellings may be phylogenetically significant. By similar logic, the gelada’s pectoral sexual skin, though a radical departure from the papionin norm, loses its phyletic weight when it is interpreted as a functional correlate of squat-feeding.

Yet another example is provided by cercopithecoid bilophodonty (as opposed to “hominoid” molar structure) (Jolly, 1970b). Suppose that all we knew of the anatomy of (say) Hylobates lar, Cercocebus ascanius, and Nasalis larvatus was their dentition. Assuming that character-states could be unambiguously defined, a matrix of resemblances would produce some (Hylobates + Cercocebus) character-states, others uniting Cercocebus and Nasalis, and possibly some (Nasalis + Hylobates). Rather than proceeding directly to cladistic analysis, the “pruning” method would then evaluate each resemblance or difference against resemblances or differences in natural history. We would ask, for instance, whether documented dietary differences between Hylobates and Cercocebus are sufficient to explain the four-cusp/five-cusp contrast in lower molars. Having decided that they are not, we deduce that this character-state difference probably has phylogenetic weight: it reflects “ancient” evolutionary events. The same conclusion would be drawn by comparing cusp number and diet in Cercocebus and Nasalis: in this character, their molars are more similar than their contemporary diets demand; there is a component in their degree of resemblance that is “nonadaptive.” In fact, across all extant catarrhines, no dietary variable explains the dichotomous distribution of the two molar types, so its relevance must be “historical”—it can be presumed to date to the initial divergence of hominoid and cercopithecoid stocks. There is nothing original about this way of looking at morphology: it is what Darwin implied when he wrote (1871, p. 153):

“it appears more correct to pay great attention to the many small resemblances, in giving a truly natural [i.e., phylogeny-based, in current usage] classification.”

Unfortunately, Darwin’s insight in this respect has tended to be overshadowed, for morphologists in general, and physical anthropologists in particular, by an equally important, but quite distinct, evolutionary generalization: that major adaptive radiations have often been founded on major, functionally important changes, the transition from a “monkey-like” to an “apelike” forelimb morphology being a frequently cited example.

The same process (of attempting to spot the “non-adaptive,” and therefore phylogenetically weighty, aspects of resemblance and difference) should also be applied to the analysis of fossil forms, but here the logic is necessarily even less direct. We cannot evaluate structural resemblance directly against functional similarity, so we have once again to call upon analogy to ask whether, from our knowledge of extant cases, such structural resemblances and differences seem to arise frequently, in similar ecological circumstances, and in comparable combinations.

All this is obviously tortuous, subjective, and plausibility-based; but it is surely a process that any experienced evolutionary morphologist routinely applies to judgments about what an organism “really is,” usually without making it explicit. No contemporary paleontologist, given only a posterior mandibular fragment and an auditory bulla, would interpret Archaeolemur as a monkey with a lemuroid auditory region, rather than a lemur with cercopithecoid-like molars. Some such mental process as I have described must underlie this interpretation, unless we resort to pre-Darwinian notions of “archetype,” or the idea that some structures or features are in some way more “fundamental” than others, and therefore more reliable indicators of phylogeny.

The logic of pruning or censoring the data in this way is similar to that of molecular systematists when they collect their data base by base, and then narrow their analysis to third bases and introns, but there is an important methodological difference. The molecular biologist excludes or devalues first and second nucleotides, or whole coding regions of genes, generically, and can justify this procedure both empirically (it gives results that are internally consistent) and theoretically (introns and third bases have fewer epigenetic effects, and their variation is there-
fore less likely to be driven by natural selection). Precensoring morphological data, on the other hand, cannot, in the present state of knowledge, be similarly generic. A moment’s reflection tells us that it will not work if we try to generalize about the phylogenetic information content of structures (“teeth are better indicators of phylogeny than postcrania”), of characters (“molar cusp number is a good phylogenetic indicator”), or even of character-states (“bilocodonty reliably identifies primate clades”). The evaluation has to be applied to particular concordances and discordances in character-states (the shared bilocodonty of Nasalis and Cercopithecus is a good indicator that they are more closely related to each other than either is to Hylobates).

This “pruning” of the data matrix does not replace cladistic analysis. Phylogenetically weighty resemblances and differences can be either apomorphic (bilocodont molars shared by cercopithecoids) or plesiomorphic (“hominoid” molars among eucatarrhines) and require the usual Hennigian analysis, by whatever logical scheme is preferred: either brute-force, parsimony-based methods (where the data are numerous, as in molecular phylogenies), or methods that use inferred character-state polarity (preferred by many morphologists).

The process of identifying and eliminating potentially misleading characters, and identifying useful ones, is the mirror-image of the analogy-building process discussed above. To discern functional complexes, analogues are analyzed by subtracting their respective heritages, leaving the informative parallels. To obtain phylogenetic information, the common features that might have functional significance are subtracted, hopefully leaving a residue of informative heritage characters. Because the basis of censoring is the functional and developmental interpretation of characters, judgments may be changed radically by new information on behavior, function, and morphogenesis. For example, before naturalistic studies of gelada baboons (Crook and Aldrich-Blake, 1968) showed them to be specialist, bottom-shuffling grazers, their many anatomical peculiarities seemed to betoken a long, independent evolutionary history and great phylogenetic distance from other baboons (Leakey and Whitworth, 1958; Jolly, 1966), but this interpretation was immediately invalidated when it was shown that most, and perhaps all, gelada autapomorphies formed a functional complex that could be related to unique features of present-day gelada ecology (Jolly, 1970b).

As a formal procedure, however, precensoring faces some formidable difficulties. It depends entirely on reliable information about functional anatomy and morphogenetic patterns in the group concerned, which are then used to make ad hoc, qualitative estimates of phylogenetic information content. Functional and morphogenetic interpretations are generally supported by arguments from plausibility rather than statistics, and will probably be debated (Strait et al., 1997). In the present state of knowledge, these judgments can only be made individually, case by case. We can only hope that, as morphological datasets are tested against molecular phylogenies in more vertebrate taxa, and functional complexes are identified by the recognition of significant homoplasies, and as the genetics of morphogenesis become better understood, regularities will emerge that will make the weighting process less haphazard.

As the gelada example shows, censoring will frequently remove many hard-won morphological data from the analysis as phylogenetically uninformative. Worse yet, some real synapomorphies will be discarded, because they are function-based. For example, the dental features (e.g., large, broad, P3) linking Cercocebus and Mandrillus are actually concordant with molecular phylogeny, and are probably synapomorphies, but they would be explicable because they are plausibly explicable as dietary specializations (Fleagle and McGraw, 1999), and thus could have arisen independently. Losing the “real” phylogeny by excluding some true synapomorphies is, I think, preferable to supporting an erroneous one by including homoplasies. Uncertainty, which stimulates further investigation, is always preferable to unwarranted confidence.

This uncertainty will be greatest for fossil taxa, especially those known only from fragmentary remains. It must be recognized that many such taxa will inevitably be left in a cladistic limbo, because all their scorables characters have been rejected. Some may consider this a weakness; others will prefer it to cladograms that are statistically well-supported by problematic data.

In fact, it seems realistic to suppose that there will be frequent cases in nature where internodal distances are so short, and adaptive radiation so fast and frequent, that homoplasy in adaptive features is virtually complete, leaving little or no morphological information to indicate the true phylogeny. While the “real” clades in such groups might be revealed by analysis of fast-evolving, selectively neutral molecular markers, recognizably nonhomoplastic, morphological indications of the correct relationships may be so few, obscure, and trivial, that they will stand little chance of being found, especially in fossil material.\textsuperscript{2}

The basal hominin radiation as a whole may be just such a “difficult” group. Internode intervals must be relatively short, because successiveclado-

\textsuperscript{2}Note that this scenario does not imply that speciation in these cases is caused by the accumulation of the trivial, nonadaptive morphological features whose distribution would be good phylogenetic evidence. Reproductive isolation presumably would have resulted from any combination of the usually postulated factors: differential ecological adaptation, chance or adaptive fixation of behavioral, physiological, or genetic barriers, and so on. Of these, the first would be discounted because of possible homoplasy, and the others would be invisible in fossil evidence.
genetic events are constrained to a total of only about 3–4 mya between the well-established Pan-Hominini divergence at 6–8 mya, which must antedate any intra-Hominini divergence, as well as the paleontologically documented time (say, 3.5 ma) at which multiple hominin lineages are documented or inferred. Though a “young” radiation, basal hominins were geographically widespread, with ranges eventually extending across much of tropical and subtropical Africa. Since each new, clade-founding species presumably originated in a limited homeland, rapid population expansion across suitable habitats and resultant genetic structuring of the expanding population (Templeton, 1998) must have been influential. Furthermore, judging by the distribution of contemporary African mammals (Kingdon, 1997), suitable hominin habitats were discontinuously distributed, with the edaphic flood-plains and other broad, habitable, nonrainforest areas connected by narrow corridors through less hospitable forests and highlands. The East African transequatorial savanna-woodland zone was surely a critical pathway between northern and southern hominin habitats (Bromage and Schrenk, 1999), but as Kingdon (personal communication) has pointed out, major rivers flowing from forested highlands eastwards to the Indian Ocean presented hurdles for expanding hominin populations. The first population to reach a pristine, extensive, and ecologically varied stretch of nonforest habitat (such as the southern African temperate and subtropical grasslands) would undergo population expansion, and would also be faced with varied ecological opportunities. Adaptive radiation might well occur within each area, with different morphs in the array duplicating those that had appeared in other regions. This is a phenomenon that is well-documented among extant organisms, with most cases being unsuspected until documented by molecular phylogeny (Schluter and Nagel, 1995; Schluter, 2001; Taylor and McPhail, 1999). The resultant patterning of morphological traits is the least propitious for reconstructing phylogeny, because internodes representing common ancestry, during which informative, synapomorphic trivia can accumulate, are relatively short, and adaptive radiations, which spawn homoplasies, are frequent.

Among basal hominins, the problem is most clearly exemplified by the taxa usually assigned to Paranthropus (the South African P. robustus, including P. crassident); and the East African P. boisei and P. aethiopicus). They share relatively large molars, relatively small incisors, very large masticatory muscles, a deep mandibular ramus, and a strongly buttressed facial structure. The generic grouping, implying a shared and exclusive ancestry, is regarded as one of the most firmly established among Hominini (Grine, 1988), and was supported consistently in an exhaustive, PAUP-driven cladistic analysis of hominin phylogeny (Strait et al., 1997). In fact, the Paranthropus clade was supported even by an analytic run (Strait et al., 1997) explicitly omitting characters considered (Skelton and McHenry, 1992) to be related to the “heavy-chewing” complex. Yet in spite of this impressive support, the evidence for Paranthropus monophyly has been cogently challenged (McCollum, 1999), on the grounds that all the cranial resemblances, some of which are only indirectly related to the large-back-tooth, heavy-chewing complex, boil down to a single functional package with a relatively simple morphogenetic base. If this interpretation is correct, the shared features in Paranthropus species might be true synapomorphies, but because they can also be explained by a combination of functional parallelism and allomorphosis, they carry little or no phylogenetic weight. It remains to be seen how Paranthropus monophyly will fare against the alternative hypothesis (parallel derivation of “robust” morphs from separate “nonrobust” ancestries) if all morphogenetically related characters as well as functional complexes are rigorously excluded from the analysis. The work of McCollum (1999) hints that a few nonfunctionally correlated dental traits might remain to tell the true story.

The papionin analogy, then, suggests the general principle that we should not rely too heavily on even the most formally rigorous and apparently well-supported early hominin cladograms (Strait et al., 1997), since, unless the data are prescreened and censored, much of the apparent cladistic structure may be an artifact of functional and developmental homoplasy. But there is yet another source of phylogenetic noise to be considered.

RHEBOONS, GEBOONS, AND EARLY HOMININ RETICULATIONS

A major assumption of most studies of the hominin fossil evidence is that relationships among diagnosable species- or genus-level taxa are accurately represented by dendrograms rather than reticulations. Cladogenesis is a clean break, in which complete genetic isolation between sister lineages is established either before paleontologically recognizable ecological and phenotypic divergence, or so soon afterwards that the interval between is inconsequential on a geological timescale. This assumption is almost essential for conventional cladistic analysis, which cannot easily accommodate reticulation.

Various lines of evidence, however, suggest that this assumption may not be altogether valid for the papionins, and perhaps by implication, in hominins also. Papionins show a remarkable ability to hybridize (“crossability”). Hybridization, in this context, is defined as the production of offspring by interbreeding of members of genetically differentiated populations (Barton and Hewitt, 1985). The definition deliberately does not specify the level of taxonomic separation of the interbreeding populations. Among papionins, as in many extant taxa, hybridization occurs across a wide spectrum of taxonomic levels.
At one extreme, we have rare, unusually artificial, inter-subtribe crossing, and at the other extreme, the formation of natural hybrid zones between differentiated, parapatric populations of the same, or very closely related, species. Although we might be tempted to divide this spectrum at the conventional “species level” (assuming, of course, that we could agree upon what that is), this would be an artificial and unhelpful division of a continuum. The present discussion concerns crossing between taxa at the upper end of the continuum, between taxa that are normally allocated to different subtribes, genera, subgenera, or species-groups.

The most phylogenetically distant pair of papionins to have produced a well-attested, viable offspring are rhesus monkey (Macaca mulatta) and baboon (Papio) (phylogenetic separation ± 10 ma). Twenty-six offspring (“rheboons”) were produced at the Southwest Foundation, of which one male, when adult, was subjected to detailed karyotypic and reproductive evaluation (Moore et al., 1999). This animal was considered behaviorally abnormal (J. Rogers, personal communication), and histological examination showed him to be sterile, although, significantly, no mismatching of his parental haploid chromosome sets could be detected. We can presume that if rhesus monkeys (or other macaques) and Papio baboons were sympatric in the wild, most if not all hybrids produced are most unlikely to breed, and probably would not survive.

The best-documented recent case of hybridization between papionin genera is that between Papio and Theropithecus (Jolly et al., 1997) (phylogenetic separation, ± 5 ma). When caged together, they readily hybridize (Markarjan et al., 1974; Jolly et al., 1997; J. Rogers and T. Newman, personal communication), producing F1 offspring, i.e., “geboons.” In captivity, female F1 geboons are certainly able to function socially, and to attract Papio males, are both viable and fertile, and produce viable backcross offspring with Papio males. In fact, an F1 female was mated by a hamadryas male who also had access to hamadryas (and anubis and hybrid) females in the cage. The resulting female backcross (3/4 Papio grandparents) (Jolly et al., 1997), when last observed, was still alive and healthy at age 5, but there was no indication that she had bred. The fertility of F1 males is also unproven. In parts of Ethiopia, geladas coexist with anubis or hamadryas baboons (Papio anubis and Papio hamadryas), and occasional natural hybridization is suspected (Dunbar and Dunbar, 1974). The case reported by Dunbar and Dunbar (1974) occurred in an area that supported balanced populations of both species, and human disturbance was no more severe than in most of the gelada’s range. Here, “bachelor” males of T. gelada, a harem-holding species, were seen mating with young female Papio anubis, a species in which females are philopatric and polyandrous, and fully adult males are only weakly attracted to subadult females. The probable hybrids belonged, however, to the gelada herd, which suggests that they may have been backcrosses to this species (Jolly et al., 1997).

The genus Macaca is commonly divided into species-groups, which are sometimes given subgeneric rank (Fooden, 1976). These groups appear to be phylogenetically valid, and are ecologically distinct to the extent that species of different groups often have overlapping ranges, while species of the same group do not. The time of divergence between macaque species-groups is not well-documented paleontologically, but from molecular evidence (Tosi et al., 2000), is probably in the 3–4 ma range. Bernstein (1966, 1968) documented natural hybrids between members of sympatic species belonging to two different, well-defined species groups, Macaca fascicularis (mulatta-group) and M. nemestrina (silenus-group). It was suggested that interbreeding occurred because female M. nemestrina joined a M. fascicularis troop after local extermination of male M. nemestrina (Bernstein, 1966). The hybrids apparently functioned well as normal, long-term members of a M. fascicularis social group (Bernstein, 1968).

Assuming that in these cases some interspecies-group or intergeneric hybridization, with survival and backcrossing by at least some of the hybrids, occurs in the wild, what evolutionary impact can it have? Can significant effects be ruled out, given that the two parental populations overlap widely in range, remain completely distinct phenotypically and ecologically, and, in the case of Papio and Theropithecus, are known to have done so for several million years?

Presuming that some of the hybrids produced are at least partially viable and fertile, the effect of sporadic hybridization is to introduce a trickle of genes from one population to the other, the direction of flow guided largely by sex-specific, inter-species interactions. In the Papio × Theropithecus gelada case, for example, F1 females would probably remain in the baboon troop where they were born, and presumably would then mate with resident male Papio baboons to produce backcross offspring. Male F2s would presumably emigrate, and females would remain in their mothers’ group. With each generation of backcrossing, the admixture would become less phenotypically visible. The backcross Papio × (Theropithecus × Papio) female produced in Bihere Tsige Zoo in Addis Ababa, when observed as a young adult, was phenotypically very close to a normal hamadryas female. Her 0.25 gelada inheritance would not be readily apparent in a wild hamadryas group. Similarly, in the Macaca nemestrina × M. fascicularis case, hybrid females would presumably remain in their mothers’ troop, while males would disperse to spread their “foreign” genes to other groups.

All this is, of course, quite speculative. The critical field genetic studies to detect introgression in the sympatric populations of baboons and geladas in Ethiopia, and macaques of different species-groups...
in overlap areas of east Asia, have yet to be carried out. Parallel cases in other vertebrates, however (e.g., Goodman et al., 1999; Lehman et al., 1991; Arntzen and Wallis, 1991), suggest that cryptic introgression of genetic markers is likely to be much more widespread than suggested by the rate of primary hybridization, or observable phenotypic hybridity. For example, where native red deer (Cervus elaphus) are sympatric with introduced sika (Cervus nippon) in Britain, only 0.1–0.2% of matings were cross-specific, yet 66% of phenotypic sika, and 33% of phenotypic red deer, carried allelic evidence of mixed ancestry (Goodman et al., 1999). Presumably, this indicates that prezygotic barriers become less effective as backcrossing progresses, and maladaptive genetic combinations are weeded out by selection.

As a source of new variation for the recipient population, genes entering by hybridization are somewhat comparable to mutations. Unlike mutations, however, immigrant genes have been tested in a donor population. They may be disadvantageous in their new genetic and ecological setting, but are unlikely to be lethal, and in general the chance of their being advantageous must be better than for random mutations. Moreover, whereas advantageous, random mutations are most unlikely to recur in the same population and the same form, hybridization will present a steady, even if slow, supply of identical “immigrant” alleles for selection in the recipient population.

Most immigrant genes that are neutral in effect will disappear by drift in a few generations, though a random minority will persist or even increase. Natural selection will presumably remove genes determining species-specific adaptive characteristics of the donor species, those that are directly related to mate preference, and any that are functionally incompatible with the host’s genome at a molecular level, together with neutral markers closely linked to any of these. Any alleles that are universally advantageous (and hitch-hiking markers genetically linked to these) could become rapidly established by positive selection in the recipient species. In evolutionary perspective, the effect would be homoplas, with similar adaptive features appearing in separate species lineages.

Is hybridization of this kind (minimal but possibly influential gene flow between fully differentiated taxa, i.e., entities that any paleontologist would be happy to call different species, if not genera) likely to have occurred among basal hominins? We cannot hope to answer this question directly, since even if a steady trickle of genes passed between populations, the chances of finding a recognizable hybrid individual as a fossil (a true morphological intermediate like the F1 geboons; Jolly et al., 1997) must be vanishingly small. Testing the proposition that basal hominins were “crossable” thus depends on the analogy of the papionins and other vertebrates, especially mammals (e.g., cervids, camelids, bovines, equids, or canids), among which hybrids are commonly produced between parental species of equivalent degrees of evolutionary divergence.

One potential objection is that some of these cases of hybridization, especially those between relatively distant parental species (Gee, 1999), occurred in situations that were entirely artificial (such as in a cage), or where human influence was strongly suspected. As has been noted for many other taxa (e.g., Carr et al., 1986; Lehman et al., 1991; Struhsaker et al., 1988), interspecific hybridization is most likely when sex ratios in one or both species are locally biased. This situation may be an effect of human disturbance or hunting, but it can also occur naturally, especially on the edge of the range of one species. In most papionin societies, wandering bachelor males are a perennial feature. An emigrant male in a marginal population might find few conspecific mates, and would therefore try to mate with any sympatric females with which he shared enough of his mate-recognition system. Cross-taxon mating is presumably rare even when conditions favor it, and favorable conditions are themselves relatively unusual. Nevertheless, they are not unrealistic, and can be expected to occur even without human intervention, especially when environments are unstable. Even situations mimicking the extreme situation of a zoo colony, bringing together a few individuals of species that can interbreed, but rarely or never meet in the wild, are quite conceivable where species ranges are fragmenting or adjusting rapidly to climatically or tectonically driven environmental shifts. If it were not for the barriers created by people, for example, a relatively slight climatic-vegetational shift in the Arabian peninsula could allow hamadryas baboons to spread from their present range in the southwest to the Persian Gulf coast, and hence into Iraq, Iran, and the Indian subcontinent, and eventually “bachelor” hamadryas would meet a similarly expanding population of rhesus monkeys. While most of the resultant rhebons would undoubtedly perish without issue, repeated natural expemtation might produce a few fertile survivors.

It might also be objected that papionin hybridization is a poor analogy for hominins, first because such hybridization has never been demonstrated among extant hominines, and second because the propensity to hybridize successfully across wide taxonomic gulfs is probably a papionin peculiarity, dependent on their unusual karyotypic uniformity (not to mention their notorious sexual promiscuity). This argument is worth examining more closely. It is the case that gorillas, chimpanzees, and bonobos have never been reliably shown to hybridize in the wild or in captivity. Rumored wild chimpanzee-gorilla hybrids have so far always turned out to be one or the other, and extreme differences in genital anatomy, at least, might be expected to limit the possibilities of unaided cross-fertilization. Chimpanzee-human hybrids are occasionally rumored, but the one sup-
posed hybrid individual I have seen (“Oliver”) was certainly a mutilated Pan troglodytes. Pan troglodytes and P. paniscus do not presently meet in the wild, and if opposite-sexed adults of the two forms have been housed together in captivity, the fact, and its outcome, have not been reported as far as I know. In general, successful captive breeding of hominine apes postdates the era in which primates were housed haphazardly in mixed-species groups, when most reported monkey hybrids were produced (e.g., Gray, 1954).

Assuming, however, that papionins are indeed much more crossable than extant hominine apes, can the difference be attributed to gross karyotypic factors? The papionins share a 2N = 42 karyotype that is very similar in overall morphology, though the Cercocebus-Mandrillus clade appears to carry a minor chromosomal rearrangement as an autapomorphy (Dutrillaux et al., 1982), and Macaca fascicularis may also have its own minor rearrangement. The papionin karyotype has also retained a high level of structural homology, even in the most distantly related branches (Papio vs. Macaca, Moore et al., 1999). By contrast, the extant hominines are karyotypically diverse, with humans (2N = 46) differing from both Pan and Gorilla (2N = 48) (Nickerson and Nelson, 1998; Jauch et al., 1992).

The role of gross chromosomal rearrangements in the evolution of reproductive isolation, especially in animals, is debatable, however. A recent review concluded that while speciation driven by gross karyotypic rearrangement may occur, the “more widely held view is that the accumulation of chromosomal differences between populations is largely incidental to speciation” (Rieseberg, 2001, p. 351). Even if chromosomal rearrangements are implicated in the evolution of hybrid sterility or inviability, changes large enough to be seen in a metaphase karyotype may not be more influential than minor changes invisible at that scale. The better-supported alternative view is that genetic changes, both small and large, and including a few large enough to be visible as karyotypic mutations, accumulate stochastically, as a side effect of overall divergence. Some of these changes may increase genetic isolation, at times dramatically (O’Neill et al., 2001), by introducing prezygotic barriers to hybrid formation, by reducing hybrid fitness, or by decreasing recombination rates (Searle, 1998), but such effects are as likely to follow from physically small chromosomal rearrangements as large ones. This incremental model seems to account better for the facts of hybridization among the catarrhine primates, both hominoid and cercopithecoïd. Thus, successful hybridization can occur between some species within Cercocebus (Dutrillaux et al., 1982) and Hylobates (Van Tuinen et al., 1999) that differ in gross chromosomal morphology and number, as well as karyotypically uniform papionins, while karyotypically similar chimpanzees and gorillas do not interbreed. Among the papionins, with their highly conserved, 42-chromosome karyotype, hybrid viability and fertility range from the sterile and dysfunctional rhebon, to geboons, in which F1s function and breed, at least in captivity, and Macaca fascicularis/nemestrina hybrids, which were functional and probably fertile in the wild. Although the sample of papionin cases is small, and the data are incomplete, they do not support the notion that members of this tribe are exceptional in their ability to form viable and fertile hybrids. They are, however, consistent with the hypothesis that in all catarrhines, hybrid fitness is more or less inversely proportional to the time since divergence of the parental species. Chimpanzee and gorilla stocks separated shortly after rhesus and baboons, twice as early as baboons and geladas, and about three times as long ago as macaque species-groups. If we assume a common catarrhine scale of stochastic divergence leading to reproductive isolation, their lack of natural hybridization is not unexpected.

Of course, we have no idea when in the course of hominin evolution the gross karyotypic autapomorphies of the human species were acquired, how they were distributed across basal hominin lineages, and what, if any, effect they had on the ability to hybridize. If the present interpretation is correct, however, we do not need to reconstruct the karyotypes of hominin lineages coexisting 3–4 million years ago to predict that most of them retained an ability to exchange genes occasionally. Such lineages cannot have been separate from each other for more than 3 ma, and from the common chimpanzee stem perhaps 1 ma more. The vicariance events, population splits, and genetic divergences that resulted in hominin cladogenesis were, at the time, much more recent than the Papio-Theropithecus split is today. If we assume a common catarrhine scale of crossability, basal hominins were, on average, somewhere between macaque species-groups and baboon-gelada in their ability to hybridize. This suggests that whenever extrinsic, premating barriers were lowered (e.g., if colonizing individuals of opposite sex and different species entered a habitat isolate simultaneously), the basal hominins could have produced viable and fertile hybrids, both among themselves and perhaps also with species of the chimpanzee clade. Such hybrids could serve as a conduit for the flow of advantageous genes between the parental populations, or could even be, themselves, the founders of new species.

It should be emphasized that such shenanigans in no way represent an argument for reducing the hybridizing forms to congeneric status, let alone con-specificity. Occasional, opportunistic hybridization is consistent with separate species status under any current definition. It is also completely compatible with maintenance, and even reinforcement, of divergent adaptive trends in the parental species. Papio and Theropithecus populations, for instance, have probably been sympatric, and occasionally exchanging genes, for several million years, but have remained separate entities with their own distinct and
diverging evolutionary trajectories, and have also themselves speciated internally (Delson, 1993; Jablonski, 1993), attributes that systematists generally recognize by separation at the genus or subgenus level.

The analogy of hybridizing papionins does not, of course, prove that hominins did hybridize, but it does suggest that crossing might have been possible, even between forms as distinct morphologically (and presumably ecologically) as Paranthropus boisei and Homo (now Kenyanthropus) rudolfensis, or Australopithecus afarensis and K. platyops, or Ardi pithecus ramidus kadabba and the proto-chimpanzee. As long as they remained ecologically distinct, occasional gene flow would not necessarily undermine their distinct adaptations, because selection among backcrosses would effectively prevent maladaptive genes moving between them. But by the same token, advantageous genes could be rapidly incorporated, without disrupting the balanced, divergently adaptive genotypes of the parental species. Contrary to the standard model, the fuzzy zone in which evolution is somewhat reticulate as well as divergent can be prolonged well beyond the point of adaptive, and paleontologically documented, morphological divergence.

But could limited gene-flow of this kind cause paleontologically recognizable anomalies in the distribution of morphological character states? To answer this question, we need to know much more about the genetic basis for such traits (Weiss, 1994; Weiss and Buchanan, 2000). Those dependent on an integrated complex of genes at unlinked loci may not survive the recombination inherent in backcrossing long enough to be selected, whereas traits with a simple genetic base should be more visible, both paleontologically and to natural selection. The possibility of significant intertaxon gene-flow should certainly be entertained. Increase in relative brain size, highly homoplastic in hominins by any cladistic permutation (Strait et al., 1997), would be an obvious candidate.

From the cladist’s perspective, opportunistic interlineage gene-flow represents yet another way that species might acquire similarities that do not reflect their phylogeny, at least as that term is generally used. If the assumption of speciation by clean breaks without subsequent reticulation is relaxed to allow some hybridization-driven reticulation, one can often reduce significantly the number of steps in the most parsimonious cladogram (Haszprunar, 1998), but presumably the probability of the hybridization itself should be factored into any parsimony comparison, and it is difficult to see how this might be done.

Considering the possibility of occasional reticulation, along with the adaptive homoplasy and cryptic symplesiomorphy that were probably rife in basal hominin evolution, Alexander Papyoe feels compelled to ask whether a reliable cladogram of the group may be a practical impossibility. And, if so, does this fact significantly affect our understanding of early hominin evolution? Certainly, as Tattersall and Eldredge (1977) have long argued, establishing the cladistic relationships among a cluster of related taxa is a logical and highly desirable first step towards understanding their evolutionary history: not only their phylogeny, but also causal factors such as dispersal, vicariance, and adaptation. The preceding discussion, for example, includes several interpretations that would not have suggested themselves before ((Homo, Pan) Gorilla) Pongo replaced ((Homo (Pan, Gorilla)) Pongo) or even (Homo, ((Pan, Gorilla) Pongo)) as the accepted cladogram of extant Hominidae. However, it could also be argued that the importance of determining the correct cladogram, as well as the practical possibility of doing so, decreases in proportion to the lengths of its internodes. For example, two “robust” hominin species derived in quick succession from the same, or closely similar, “gracile” stocks might well have been very similar as living animals, as well as unrecognizable as separate clades by any methods we can bring to bear on their fossil remains. Moreover, for a considerable time after they acquired their distinctive, derived, adaptive traits, they would probably have been interfertile both with each other and with their respective “gracile” sister taxa. While a reliable cladogram of early hominins remains a worthwhile goal, some of its details may be inherently insoluble. (This doubt seems to be increasingly shared; recent commentaries (Wood and Brooks, 1999; Collard and Aiello, 2000) tend to omit lines of descent from their depictions of hominin phylogeny).

Fortunately, the early hominins present plenty of other important questions: numerous problems of alpha taxonomy, for example, and paleobiology at the local deme level (e.g., Lee-Thorp and van de Merwe, 1993; Teaford and Ungar, 2000; Grine and Kay, 1988). which (again on a papionin analogy; Benefit, 2000) was probably more diverse than we presently perceive.

The papionin analogy (supported, in this case, by analogies from other, similarly divergent mammalian clades) suggests that the hominin “morphs” that we recognize as synchronous, often sympatric, and ecologically distinct species and genera, were probably capable of limited interbreeding, even after several million years of divergent adaptation.

By extension, the papionins suggest that hominin lineages were even more capable of interbreeding at an earlier stage of differentiation, after newly emergent stocks had become widespread, and when populations were diverging by drift, adaptation to local conditions, and econiche specialization. At this stage, gene flow between them would depend less on their inherent reproductive and genetic compatibility (their “crossability”) than on extrinsic factors: accidents of biogeography that created or removed physical barriers to contact between them, and the intensity of disruptive selection that maintained the distinctness of their gene-pools.
Several papionin taxa (especially species within the genus *Papio* and within *Macaca* species-groups) have presently attained this stage of differentiation and exemplify in their contemporary population structure the complexities that occur among partial isolates (e.g., Hoelzer et al., 1994). There seems no reason to doubt that the history of hominins from the late Miocene onwards was at least as complex, and equally intractable to adequate description in terms of a simple, ramifying phylogeny and taxonomy. We can hope that the paleogeographic picture will eventually become sufficiently continuous and fine-grained in time and space to allow some specific comparisons and predictions. This remains a distant goal for early hominin history, and meanwhile, Alexander Papyoe suggests that early hominin phylogenies and taxonomies should be regarded as disposable approximations.

The same principle applies to the most recent radiations within *Homo* and *Papio*, but here the level of documentation has reached the point where the complexity of the problems, if not their solution, can be discerned.

### HYBRID ZONES AND POPULATION REPLACEMENTS IN BABOONS AND HUMANS

The “Neandertal problem” has had different connotations for every generation of human evolutionists. One constant theme, however, has been the degree of distinctness between Neandertals and anatomically modern people. In contemporary discussions, this question tends to be couched in taxonomic terms: whether or not the Neandertals should be classified within *Homo sapiens*, or, more generally, how many species of the genus *Homo* existed contemporaneously during the later Pleistocene, say, from ca. 150–30 ka. Answers to the second question from contemporary paleoanthropologists range from a firm “one” to an equally positive “unknown, but certainly several.” Even a cursory review of the “Neandertal problem,” which has produced several large volumes and innumerable papers over the past few years, is far beyond the present scope. However, Alexander Papyoe suggests that a new angle or two may emerge by comparing it to an analogous problem in Papionini: the question of how many species should be recognized among contemporary forms of the genus *Papio*, or at a more particular level, whether the olive baboon, or for example, should be considered a different species from the hamadryas, or the yellow baboon, or both.

In both cases, real biological issues are often obscured by the perennial but inevitably unproductive discussions about what a species “really is.” A recent review (Hey, 2001) counted 24 active species definitions. Those seemingly most widely used among zoologists and paleontologists (the “biological” and the “phylogenetic” species concepts; BSC and PSC, respectively) are both population-based. The disagreement between them seems to hinge on how much emphasis to put on the distribution of probabilities of zygote formation (“zygostructure”; Jolly, 1993), or the distribution of traits within and among populations (“phenostructure”). The BSC emphasizes zygostructure (species as reproductive isolates), while the PSC emphasizes phenostructure (species as consistently diagnosable clades). Justification for the BSC tends to look forward in time, emphasizing that if genes can flow across populational boundaries, all populations so linked can at least in theory evolve as a single unit, and that gene-flow might even homogenize them in the future. Adherents of the PSC tend to look backwards in time, emphasizing species as terminal taxa in a cladogram defined by their historical relationships. The PSC and the BSC are equally valid descriptions of aspects of population structure resulting from evolutionary processes. Both are compatible with the traditional, ontologically appealing but epistemologically weak concept of a species as a cluster of populations with a common and distinct evolutionary trajectory. Neither kind of species is more “real” than the other; both are abstractions from the observable attributes of organisms. My nominalist bias suggests that, since both species definitions use the same basic attributes of populations (pheno- and zygostructure), merely differing in how to weight them, we should focus on describing these attributes, and shelve indefinitely the largely bogus “species problem” (Jolly, 1993).

In taxonomic practice, the BSC-PSC distinction is most significant where phenotypically distinct, parapatric populations interbreed at their boundaries. The PSC calls such populations “species” (in spite of the fact that hybrid individuals can be assigned only arbitrarily, and thus all individuals will not be strictly assignable). The BSC calls them semi-species of a superspecies, or subspecies of a Rassenkreis or polytypic species, since they are potentially linked by gene-flow (even though in most cases no gene-flow has been demonstrated). Because such situations are very common in nature, the seemingly minor difference in species definitions greatly affects the number, and size, of recognized species. Moreover, within the BSC, many closely related “species” are very similar in diversity and scale to “subspecies,” differing from the latter only in that marginal gene-flow has not been shown to occur. If such gene-flow is later demonstrated, the discovery mandates a wholesale taxonomic revision (for the baboon case, cf.Thorington and Groves, 1970; Groves 2001).

The population structure and dynamics of taxa at this level exemplify crucial evolutionary processes gathered under the rubric of “speciation” (Barton, 2001; Turelli et al., 2001): the evolution of phenotypic distinctiveness or reproductive isolation, or both. Investigation of these processes is too biologically important to be sidetracked by the empty semantics of the “species question,” and to avoid this pitfall, Grubb (1999) introduced the concept of the *allotaxon*. Allotaxa are phylogenetically close, but
well-differentiated and diagnosable, geographically replacing forms whose ranges do not overlap, but are either disjunct, adjoining, or separated by comparatively narrow zones in which characters are clinally distributed. Related allotaxa typically exhibit distinct adaptations to their respective habitats, but their defining allo- or parapary suggests that they are close enough ecologically and behaviorally to preclude actual coexistence within the same ecosystem. Where the ranges of allotaxa meet, often at an ecotone, a zone of intermediate phenotypes (a “hybrid zone”) frequently occurs. Such zones have been aptly called “natural laboratories of the evolutionary process” (Harrison, 1993), and a lively biological specialty has grown up around their theoretical and empirical study (Barton and Hewitt, 1985, 1989; Harrison, 1993), the latter greatly facilitated by the growing availability of genetic markers (serological, allozymic, and most recently genomic). The use of genetic markers, combined with advances in paleoclimatology, has added a fourth dimension to the picture by documenting genetic patterns that can be related to the late Neogene genealogy of repeat, often very rapid, environmental change. The dynamics of such processes have been most thoroughly investigated in Europe (Hewitt, 1996, 2001) and North America (Avise, 1994), but there is ample evidence that environmental fluctuations were equally influential in the tropics and subtropics, and in the southern hemisphere, though the nature and distribution of barrier zones in these areas is less obvious.

The model developed by Hewitt (1996, 1999, 2001) describes a plausible process by which late Neogene paleoclimatic oscillations converted local populations within species into fully diagnosable allotaxa. Responding to rapid habitat shifts, the ranges of geographical populations would have expanded and contracted, repeatedly dividing and reuniting, forcing equally rapid fluctuations in population size. The core area of each population, habitable during adverse climatic periods, tends to preserve ancient genetic variation, both adaptive and random. Colonizing subpopulations at the fringes individually lose variation, but local adaptation, drift, and founder-flush effects may cause them to become diverse and genetically idiosyncratic. The descendants of “colonists” dominate numerically during expansions, and as populations expand it is the demes at their fringes, which are the most genetically derived, that meet their neighbors. Repeated contraction and expansion from separate refugia thus tend to generate and accentuate the kind of genetic differences that define adjacent allotaxa, and sometimes push the process to the point of partial or complete reproductive incompatibility (Hewitt, 2001).

When such differentiated allotaxa make secondary contact, initially at a sharp boundary, interactions between them may fall anywhere between complete interfertility and total reproductive isolation. Secondary hybrid zones generated by marginal interbreeding are often quite restricted in breadth. This spatial restriction may indicate that contact is too recent for the interpopulational clines to have reached equilibrium, or that habitat-specific or intrinsic hybrid disadvantage is balancing outward and inward gene-flow. Field studies of particular hybrid zones have revealed a great variety of structures and dynamics (Barton and Hewitt, 1985; Harrison et al., 1987).

Like many other terrestrial organisms, extant *Papio* baboons (and *Macaca* species-groups) show a typical “patchwork quilt” internal phenostructure of geographically replacing, parapatric allotaxa (Fig. 1). Though many details and some crucial areas remain to be investigated, the distribution of baboon allotaxa (Jolly, 1993; Groves, 2001) is better known than implied by their chronically confused formal taxonomy. Five “forms” are customarily recognized, either as PSC species (Groves, 2001) or BSC subspecies (Williams-Blangero et al., 1990; Jolly, 1993), or as a species of a “superspecies.” At least 2 of the 5 include two or more allotaxa, which, strictly, should disqualify them as single PSC species. The geographically circumscribed allotaxa are distinguished most readily by characters of pelage texture and color. Dental and cranial features also differ among allotaxa (Jolly, 1965, 1970b; Phillips-Conroy, 1978), but are less diagnostic. The precise number of allotaxa that can usefully be recognized is still uncertain; some “forms” that have been described and named, especially in the east African corridor from Tanzania to Sudan, may turn out to be hybrids or segments of a continuously varying cline (Groves, 2001). The number of allotaxa recognized also depends upon how broad an intergradation zone the systematist is prepared to tolerate between them. For example, the small yellow baboon (*Papio kindae* or *P. cynocephalus kindae*) has a wide range that stretches from Angola to the Luangwa Valley in Zambia. It is quite distinct from the large, “typical” yellow baboon of Tanzania and Malawi (*P. cynocephalus*, sensu stricto), but the clade that links them is relatively broad. Conservatively, 8 or 9 allotaxa are recognized here.

In the cohesion species concept of Templeton (1989), a crucial criterion of conspecificity is that conspecific organisms should be ecologically interchangeable. Like other species criteria, this one situates the allotaxa of *Papio* on the cusp of species status. On the one hand, the ranges of some *Papio* allotaxa roughly correspond to broad vegetational zones, and the lines of contact of parapatric allotaxa often fall close to an ecotone (Jolly, 1993; Kingdon, 1997). In at least one case (the hamadryas), we can demonstrate a pervasive pattern of subtle, physiological (Kaplan et al., 1999), behavioral (Kummer, 1968), and anatomical (Jolly and Phillips-Conroy, 2001 and unpublished data) adaptations to the semidesert habitat in which most populations are found. Other habitat-specific adaptations (e.g., yellow baboons to the woodland vegetation of the Afri-
can southern seasonal tropics) have been suggested (Kingdon, 1997), but have yet to be demonstrated.

On the other hand, ecological similarity is indicated by the fact that Papio allotaxa are parapatric, with ranges that meet but do not overlap, presumably because groups from either side of the allotaxon boundary interact ecologically and socially as competitors when they meet. At allotaxon interfaces, individuals are in fact literally interchangeable, because they migrate across allotaxon lines and successfully take up residence in a “foreign” group (Alberts and Altmann, 2001; Samuels and Altmann, 1986; Phillips-Conroy et al., 1992), where their ecological behavior and preferences are indistinguishable from those of their hosts (Nystrom, 1992). Moreover, a closer examination of the range of the various allotaxa reveals many exceptions to the broad ecological associations. For example, hamadryas baboons in Eritrea occupy comparatively moist montane habitats that immediately to the south, in the Ethiopian highlands, are occupied by anubis baboons (Zinner and Hapke, 2001). Conversely, it is anubis, not hamadryas, that occur in the semidesert Saharan massifs of Tibesti and Air (Jolly, 1965). All Papio baboons are ecological generalists, a trait that perhaps makes them especially relevant to human evolution. Their modest, habitat-specific ecological adaptations have not become specializations precluding expansion into neighboring habitats. Consequently, the distribution of each allotaxon seems to result not so much from ecological determinants or preferences, as from population history, some of it quite recent. For instance, the ecologically anomalous distribution of anubis and hamadryas in Eritrea may be due to the fact that hamadryas reached and colonized the moist highlands first, and have yet to be displaced by anubis, which are still confined, in low numbers, to the western savanna lowlands (Zinner and Hapke, 2001). This hypothetical scenario is supported by observations from western Tanzania.

Fig. 1. Geographical distribution of some of the recognizable allotaxa of Papio baboons.
partly by displacement, and partly by genetic introgression (J. Moore, personal communication), Ethiopia (Phillips-Conroy et al., 1992), and southeastern Kenya (Maples and McKern, 1967; Alberts and Altman, 2001). In each of these areas, anubis baboons seem to be expanding their range, at the expense of neighboring yellow baboon and hamadryas populations, partly by displacement, and partly by genetic introgression.

In captivity, all allotaxa appear to hybridize indiscriminately (Jolly, unpublished data), and there is no evidence for hybrid breakdown, behavioral incompatibility, or intrinsic sterility. Similarly, there is no evidence that *Papio* baboon allotaxa ever avoid interbreeding when they meet in the wild, though many boundary areas have yet to be investigated. The fact that documented baboon hybrid zones are narrow, in spite of the lack of obvious, intrinsic barriers to gene-flow, strongly suggests that they are the result of secondary contact following range oscillations (Barton and Hewitt, 1985; Hewitt, 2001; Harrison, 1993).

In East Africa, where genetic sampling has been more dense than elsewhere, the distribution of mtDNA haplotypes across baboon allotaxa strongly hints at previous cycles of hybridization. In particular, all haplotypes so far found in anubis baboons in Ethiopia form a clade that is distinct from, but related to, haplotypes of Ethiopian hamadryas baboons, while haplotypes of anubis baboons from Kenya are closer to those of Kenyan and north Tanzanian yellow baboons (Wildman, 2000 and personal communication; Newman et al., 2001). In external phenotype, all anubis baboons are (by definition) quite different from either yellow or hamadryas, and moreover, Kenyan and Ethiopian anubis baboons are externally indistinguishable. This combination of phenotypes and haplotypes is difficult to explain except by a scenario involving a cycle of hybridization previous to the present one, with sex-specific introgression, and probably also radical fluctuations in allotaxon ranges (Wildman, 2000 and personal communication; Newman et al., 2001). With benefit of hindsight, we can see vestiges of this earlier hybridization cycle in the skull structure of Ethiopian and Kenyan anubis baboons, which in some aspects of size and shape resemble those of neighboring hamadryas and yellow baboons, respectively (Jolly, 1965 and unpublished data). If this scenario is approximately correct (and much more genetic work is needed to test it fully), it suggests that the pelage phenotype defining anubis baboons, which is very stable not only in Ethiopia and Kenya but across the whole northern savanna belt as far as Sierra Leone, was already characteristic of the baboons contributing the anubis genes to the mix in Kenya and Ethiopia. If this is so, it must have originated well before this round of hybridization.

The anubis phenotype itself may have originated in a still earlier round of hybridization. MtDNA (Wildman, 2000; Newman et al., 2001), nuclear genetic (Williams-Blangero et al., 1990), and phenotypic (Jolly, 1965, 1993) evidence all suggests that the primary division among stocks leading to extant *Papio* was between a “southern” branch, ancestral to extant chacma baboons, and a “northern” one, ancestral to all the others, and that this split occurred about 1.7 ma. Genetically and phenotypically (as well as geographically), anubis baboons are “northern,” but have some “southern” traits such as tail shape (Jolly, 1965). As Kingdon (1997) suggested, the anubis phenotype may have originated as a stabilized hybrid, in a small, isolated “northern” population, resembling Guinea baboons, that received and incorporated “southern” immigrants, resembling chacmas, via a glacial-period corridor through the central African rainforest. This scenario will require testing against extensive genetic information from anubis baboons of west-central Africa, which at present are totally unknown.3

The complex populational history of *Papio* is not unique, or probably even unusual, among taxa of comparable time-depth. Among the papionin monkeys, observational and genetic investigation of species-groups of macaques has revealed a phylogeography that is at least equally complex, involving all degrees of hybridization, sex-specific gene-flow, and secondary fusion between differentiated taxa (Fooden, 1963; Bynum et al., 1997; Tosi et al., 2000; Hoelzer et al., 1993; Melnick and Hoelzer, 1992; Evans et al., 1999).

How can these speculative scenarios about populational structure and phylogeographic history in *Papio* baboons be translated into useful analogies for understanding evolution within the genus Homo? A comparison of chronologies indicates that the initial diversification of stocks leading to extant *Papio* forms (Wildman, 2000; Newman et al., 2001) is comparable in age (at about 1.7 ma) to the origin and rapid deployment of *Homo*, sensu strico (i.e., the clade stemming from African *Homo erectus* a.k.a. *H. ergaster*, but excluding “H.” *habilis* and “H.” *rudolensis*) (Wood and Collard, 1999). If we can indeed assume a common timescale of average, intrinsic reproductive isolation for all catarrhines, as argued above, this suggests that all human lineages stemming from the *H. ergaster* stock were probably as fully interfertile as are extant *Papio* populations. On these grounds, they could be regarded as members of a single, polytypic (BSC) species (cf. Wolpoff et al., 1993; Hawks et al., 2000). Several caveats should be observed, however.

First, the postulated “common catarrhine crossability scale” is at best a stochastically driven approximation that is necessarily less predictive for particular cases and over shorter timescales. Mutations contributing to reproductive isolation, perhaps

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3The phyletic position of yellow baboons is ambiguous. Their genetics seem to ally them closely with anubis baboons (Newman et al., 2001; Williams-Blangero et al., 1990), but they have been sampled only from East Africa, close to a zone of hybridization with anubis. Morphologically they are certainly “southern.”
initiating a rapid “cascade” to full intersterility with neighboring populations (Barton, 2001; Rieseberg, 2001), could arise at any time in any geographically isolated lineage. Such an event in a human lineage would be difficult, if not impossible, to detect from fossil evidence.

Second, it is important to stress that if we reduce recognizable “forms” of Homo (currently, often named as PSC species such as H. neanderthalensis and H. erectus) to (BSC) subspecific status because of the possibility of some marginal gene flow between them, this would not imply that they were “ephemeral” or “evolutionarily unimportant,” any more than these terms could be applied to, say, anubis baboons. This point is worth emphasizing, because a suggestion to the contrary seems to have crept into the debate over the implications of the Lagar Velho “hybrid child” (Duarte et al., 1999). It seems to represent a semantic confusion. If indeed the Lagar Velho child was the result of marginal gene-flow between Neandertals and “moderns,” it would prove them to be conspecific by the BSC, but not by the PSC. But it is only PSC taxa that are defined so closely that intraspecific variation is, almost by definition, unimportant. Large, polytypic BSC species can and often do include persistent, diagnosable, “important” allotaxa, named as subspecies.

Nor would the assumption of universal interfertility within the genus Homo (strictu senso) conflict with evidence pointing to long-term, consistently diagnosable human lineages, such as a pre-Neandertal-to-Neandertal lineage persisting for ~300,000 years in Europe (Trinkaus, 1991, 1993; Rosas, 2001), or Homo erectus populations locally surviving the origins and spread of “modern” humans (Swisher et al., 1996). Even if they were not surrounded by intrinsic barriers to interbreeding with their neighbors, the genetic integrity of such populations could be effectively maintained by a combination of periodic geographical barriers, selection for habitat-specific ecological adaptations, behavioral differences (which themselves could have a combined genetic and environmental basis), and simple, outward population-pressure. A PSC advocate could happily name each one a full species, while a BSC enthusiast could describe the same phenomenon as polytypy and regional continuity within a single species. From the point of view of hybrid-zone theory, such cases just represent some of the many possible interactions between neighboring allotaxa.

As for the “Neandertal question,” it is a reasonable working hypothesis that, like baboons today, the genus Homo by the beginning of the Late Pleistocene presented a patchwork of allotaxa, each with its own history of successive glacial (cold-dry period) retreats and interglacial (warm-humid period) expansions. As with the baboons, we can assume that all human allotaxa alive at that time were not equally related to each other: that if a time-traveling geneticist could sample them in depth, genetic markers would reveal a comparable, underlying cladistic history, probably greatly complicated by successive events of marginal gene-flow and hybridization. Some human allotaxa (e.g., the one represented by the Ngandong specimens), analogous to Guinea or chacma baboons, might have been more-or-less isolated and little changed since the initial deployment of the genus Homo (strictu senso). Others, analogous to contemporary hamadryas, anubis, and yellow baboons of the East African corridor, probably had a more recent and complex history of intermittent genetic interaction.

We can also assume that where they met, the boundaries between human allotaxa showed the kind of complex dynamics seen in other vertebrate and invertebrate contact zones. Unfortunately, in most cases the meager fossil evidence limits us to observing that there was appreciable regional variation in cranial form among humans of this period (Wolff, 1999). The analogy of Papio (and other catarrhines) suggests that early human allotaxa were probably much more distinct in the flesh than from the kind of evidence available in the fossil record. There are significant average skeletal and dental distinctions among the baboon allotaxa, but they are not easily seen without large samples and prior allotaxon assignment, based on soft-part (pelage) characteristics. On the other hand, Papio does not altogether fit the predictions of “Tattersall’s law” (Tattersall, 1993), which suggests that any taxon diagnosable on hard-part criteria can be assumed to be even more distinct in the flesh. For example, the “kindae” and “typical” yellow baboon allotaxa have very similar coloration (and are classified together in 1 of the traditional 5 species), but are easily distinguishable on cranial and dental size, and are connected by a phenocline in the wild. The only generalization that we can make on the analogy of the baboons is that we should expect our diagnosis of individual fossil human specimens to be unreliable, even if the existence of significant phenostructuring can be inferred from divergent central tendencies in geographically defined clusters of specimens. At best, a much denser record will be required to discern what the human allotaxa were, where their geographical limits lay, and how they interacted with each other.

In fact, in the densest fossil record that we have (of the Neandertals and their neighbors to the south), the pattern on one corner of the Late Pleistocene human patchwork is dimly discernible. Leaving aside the largely semantic question of Neandertal species status, and the issue of their genetic contribution to later human populations, we find substantial agreement. It is generally accepted that Neandertals were a localized, recognizable human population of Europe and southwestern Asia, comprising an allotaxon distinct from pene-contemporary Afro-Arabian populations. The latter are represented by specimens such as Skhul V, Kafzeh, and Omo II, which are widely believed either to repre-
sent the ancestral modern human stock itself, or at least to be more closely related to it than the Neandertals were. If Neandertals and Africans came into periodic contact, this probably occurred at an ecotone in the eastern Mediterranean, where an alternation of faunas and human allotaxa seems to have occurred in synchrony with glacial-driven oscillations (Tchernov, 1989). This extended, marginal interaction between Neandertal and Afro-Arabian allotaxa, apparently similar in culture, technology, and ecological role in their respective habitats, would have been quite distinct from subsequent “replacement” events.

During a period that was recently narrowed to 36–30 ka, Neandertal morphology was replaced in Europe by a more “modern” type of human (Churchill and Smith, 2001), a local manifestation of the general replacement of “archaic” by “modern” humans that had begun some time before in the tropics. The interface between them is believed to have moved quite rapidly from the southeast westwards, reaching northwest Europe and Iberia last. The disagreement concerns dynamics at the interface.

When considering Neandertals’ interactions with neighboring populations, most paleoanthropologists have drawn analogies from the behavior of extant Homo sapiens, assuming for instance that cultural factors such as language (rather than “hard-wired” differences in mate recognition systems, believed to be characteristic of other mammals) were the major determinant. An early, extreme form of the multiregional hypothesis saw only cultural elements flowing between populations, and physical changes as indigenous adaptations to the resultant technological shifts. Certainly, only modern humans approach the cultural sophistication inferred for both Neandertals and their contemporaries, but they present a poor analogy in that no two modern human populations are as distantly related as were Neandertals and the precursors of modern humans, or have had as long a period of separation in which to acquire distinct mate-recognition systems. Whatever the reason, it is now clear that the genetic structure of the extant human species is very unusual among widespread primate taxa. It is distinguished by a paucity of ancient genetic lineages, except in loci where diversity is likely to be maintained by selection (Disotell, 1999), and in general is dominated by the effects of massive population expansions, most of which occurred in the past 20 ka (e.g., Harpending et al., 1998). At the very least, this suggests that additional analogies should be sought outside the genus Homo. Another reason for doing this is that the uniquely human, culture-driven, in situ conversion of Neandertals to “moderns” (Hawks and Wolpoff, 2001) without any appreciable population movement or “gene-flow” is now hard to reconcile with the rather short timescale of replacement (Churchill and Smith, 2001), and has been abandoned by its original formulators. As a result, discussion now focuses on whether replacement was a matter of gene-flow between static populations, or an expanding population replacing a shrinking one, or something in between. The problem is thus brought into the realm of general hybrid-zone theory, in which news (Arntzen and Wallis, 1991), crows (Saino et al., 1992), and baboons are at least as relevant as human beings.

The fragments of Neandertal mtDNA sequence (Krings et al., 1997; Hoss, 2000; Ovchinnikov et al., 2000) suggest the point at which the Neandertal story can be linked to the analogous history of baboons. Discussion of the Neandertal mtDNA sequence has focused mainly on its relatively ancient separation from the root of all extant human sequences, and its implications for a Neandertal genetic contribution to modern human populations. From the baboon (or chimpanzee, or gorilla) perspective, however, the separation is not very ancient. It is comparable to ~600 ka divergences between olive and hamadryas baboon mtDNA haplotypes, and much more recent than, e.g., the Guinea-hamadryas split. Mitochondrial diversity in Papio may be analogous to the condition in Homo before the “event” (generally interpreted as an “out-of-Africa” expansion of a relatively small subpopulation) that eliminated most of the diversity from its collective mitochondrial (and Y-linked, and autosomal) gene-pool. Unfortunately, investigation of continent-wide genetic phenostructure in Papio is still in its earliest stages, so we cannot pursue the analogy further in this direction. We can, however, make some suggestions based on work in contemporary zones of hybridization, especially the Awash anubis-hamadryas hybrid zone. For example, we can conclude that unless an undocumented, radical genetic event occurred in the 600 ka since they shared mtDNA ancestry with the Neandertals, premodern humans were certainly able to interbreed with them and produce viable, fertile, offspring, as hamadryas and anubis baboons do.

The baboon analogy does not, however, inspire confidence that the detailed dynamics of “archaic”–“modern” interactions will ever be determined. Certainly, finding any fossil documentation is quite unlikely, as obvious evidence of intergradation (or its absence) is likely to be seen only in a spatially (or, with a moving zone, chronologically) very restricted zone at the allotaxon interface. In Ethiopian and Kenyan baboon hybrid zones, as in many zones involving other taxa, there is a very narrow region in which most individuals are phenotypically obvious hybrids, yet such hybrids are found only within one or two dispersal distance units (about 30 km) of the zone’s center, although genetic evidence of hybridization is much more widespread. For the human case, this has an important implication: demonstrating phenotypic distinctness (lack of overlap) of Neandertal and “modern” samples drawn from areas remote in time and space from the zone of contact does not disprove the occurrence of interbreeding at
the interface. It also means that the Lagar Velho child, if indeed it is a hybrid, is a rare and valuable find, even though it is irrelevant to the Neandertal “species question,” and does not tell us whether Neandertals (or other “archaic” humans) contributed genes to the Upper Paleolithic, or the extant, human gene-pool. Not that these are equivalent, as is often implied; there was ample opportunity for the loss of a few stray Neandertal genes from European Upper Paleolithic populations when the latter shrank and were replaced by food-producing peoples.

If interbreeding did occur at the Neandertal-modern interface, the number of different possible scenarios of hybrid zone dynamics is enormous. Any number of factors besides intrinsic hybrid disadvantage could have restricted gene-flow out of the contact zone, or filtered it, or directed it asymmetrically toward one population or the other. Only one such zone in primates (between anubis and hamadryas baboons in the Awash National Park, Ethiopia) has been the subject of both detailed behavioral and genetic work, and this has revealed a complex situation in which gene-flow into and out of the hybrid zone is directed and limited largely by idiosyncratic patterns of social behavior distinctive of the two parental taxa and their hybrids (Sugawara, 1979; Nystrom, 1992; Bergman, 2000; Beyene, 1998).

In the Neandertal case, the fact that the interface moved historically from east to west indicates that the pressure of gene-flow was greater in that direction; if a hybrid zone existed, the genes in it were contributed disproportionately by “moderns.” “Neandertal morphological genes” may have been removed by natural selection from a narrow zone of hybridization, or been swamped by differential genetic inflow, or perhaps they simply died out with their carriers without any hybridization at all. Any combination of these factors could have contributed to their disappearance. A much more fine-grained temporal record of the transition would be necessary to decide between these alternatives, and the precise scenario is immaterial both for the eventual outcome, and for the so-called “species question.”

What is important, and hotly contested, is whether Neandertals (and other archaics) contributed any genes to the gene-pool of the human population who succeeded them. This would imply a flow of genes from the marginal hybrid zone into the expanding modern population: swimming, as it were, against the tide. The important question is not whether Neandertals could have passed some genes by hybridization to incoming Afro-Arabsians; they almost certainly could. It is certainly not the neoes- sentialist (Cartmill, personal communication) red herring of whether or not they were “really” different species. The important questions are purely empirical: first, whether they actually did contribute any distinctive alleles to the incoming population, and second, whether any of these have survived post-Pleistocene upheavals in the human gene-pool. The first question can only be answered by genetic investigation of the DNA of post-Neandertal fossil humans (cf. Hawks and Wolpoff, 2001); the second by trawling the extant human gene-pool itself.

So far, almost all genetic systems investigated in extant humans show no signs of a Neandertal inheritance, but perhaps we need to be more selective in our search. A moving hybrid zone may leave in its wake a few neutral markers derived from the retreating population (Arntzen and Wallis, 1991), but these are likely later to be eliminated by drift. Most likely to survive and be incorporated are genes for traits strongly favored by local conditions (and “hitch-hiking” markers linked to these). Some years ago, a popular work (Kurtén, 1971) plausibly suggested that Neandertals were blond and blue-eyed in adaptation to cloudy, periglacial Europe, while incoming “moderns” had the darker pigmentation of a subtropical people. Perhaps we should survey nordic Europeans for unusually “deep” diversity in non-coding genetic elements closely linked to loci determining pigmentation. Less fancifully, Parham et al. (1994; and Parham, personal communication) speculatively identified a possible Neandertal legacy: an allele of the human MHC system that is found at low frequency in the old Neandertal range. It is remarkable for its inferred ancient separation from other alleles, which themselves form a tight, young clade. MHC alleles are among the likeliest genes to pass through a semipermeable hybrid zone, since selection favors immunological diversity per se, so if the interpretation is confirmed it would set a likely upper limit on the Neandertal genetic contribution to extant Europeans.

The message from A. Papyoe is, once again, to concentrate on biology, avoid semantic traps, and realize that any species-level taxonomy based on fossil material is going to be only an approximate reflection of real-world complexities. With extant taxa such as Papio baboons, we can document soft-part as well as dental and skeletal anatomy, and sample enough individuals to document inter- and intrapopulational diversity (Fig. 2). Even then, we cannot reach a consensus about the “number of baboon species.” At a less global level, our research group has studied gene-flow on the ground in the best-known of the intergrade zones, and has typed mitochondrial haplotypes and 10 microsatellite loci in nearly 1,000 individuals, as well as examining their external phenotype and features of their dentition, and observing and quantifying mating preferences, social barriers to interbreeding, and the behavior of hybrids. Yet we still have only a very general notion of the amount of gene-flow between these populations, the breadth of the genetic hybrid zone, and the factors that determine its structure. This suggests that it is hardly worth getting too exercised about similar problems with fossil Homo, or with any other fossil taxon for that matter. We can, of course, define convenient paleospecies by carving the continuum of spatial and temporal variation into chunks that roughly match the diversity...
of whatever living taxa one considers to provide the best analogy. There is no harm in this, provided that we recognize that we have not thereby answered many biological questions (about degree of phentetic overlap or separation; about the position, breadth, and permeability of hybrid zones; and about the existence of population structure defined by mating preferences and probabilities) that complicate the definition and diagnosis of extant species.

**DISCUSSION AND CONCLUSIONS**

I have argued that paleoanthropology could take greater advantage of analogies drawn from across biological science, to supplement the insights that it has always drawn from the anthropocentric sciences. I have also tried to illustrate with a few examples that the papionin monkeys (especially the baboons) are an unusually valuable source of such analogies, especially for the earlier, less “human” periods in hominin evolution. Apart from particular analogies, the major lesson to be drawn from the papionins (in fact, much of it could be derived from any widespread, diverse group of actively speciating, terrestrial vertebrates) is that some areas of inquiry are likely to be difficult to resolve for hominins, simply because most hominin lineages have no living representative. The areas that will challenge paleontologists most severely include the detailed cladistics of closely related extinct forms, the population structure of the genus *Homo* for much of its history, the dynamics of most interpopulational hybrid zones and replacement scenarios, and, of course, to the extent that it depends on such information, the species-level taxonomy of the hominins.

The use of analogy in the ways suggested here is routine in zoology. The value of phylogenetically distant analogues seems to be much less appreciated by paleoanthropologists working on early hominins, who seem to reach almost reflexively for the nearest collection of *Pan* and *Gorilla* material, often without considering whether alternative analogues might be more appropriate. If they justify the ape analogue, it is usually in terms of phylogenetic proximity: a sure sign, as I have attempted to show, that the true value of analogy has been misunderstood.

The practice of drawing analogies from wherever they can be found in nature is an application of a very broad scientific principle, that particular cases are to be explained wherever possible in terms of general “laws,” and that such explanations are to be

![Fig. 2. Distribution of ecologically related and presumably adaptive traits in neighboring baboon allotaxa, chosen to be analogous to cranial and postcranial features believed to be diagnostic of Neandertal and “modern” *Homo sapiens*. The pattern common to both is the highly significant difference between mean values for comparable age and sex categories in the two allotaxa, but overlapping ranges of variation in which bimodality is hardly observable, and where individuals would not be readily assigned to the correct taxon. All data are from Awash National Park.](image-url)

- **A:** Relative toe length in male hamadryas and anubis baboons. Mean and 95% confidence intervals for age categories. Within each taxon cluster, age categories are (left to right): young juveniles, older juveniles and subadults, and adults. Note that there are clearly significant age and intertaxon differences, concordant with the ecology of the two forms: anubis, more arboreal, hamadryas, more of a rock-climber.
- **B:** Same variables as a bivariate plot of individuals. The mean difference is apparent, but only when individuals are identified by taxon.
- **C:** Relative molar row length in adult anubis and hamadryas baboons, both sexes. The index is an approximation of the relative importance of molars in the dentition.
- **D:** Same variables as a bivariate plot; sex-associated size clusters are apparent, but taxon clusters are not separate.
preferred over particularistic, ad hoc explanations. It is not surprising, then, that analogies and comparative studies that range widely across taxa, searching for broadly applicable generalizations, are commonplace in vertebrate socioecology and paleontology, as in biological science in general. What is surprising is that many paleoanthropologists, especially those whose subjects are human and prehuman hominins, seem suspicious of them. Perhaps the reason is historical rather than scientific or rational. Paleoanthropology, whose major roots lie in the anthropocentric disciplines of anthropology, archaeology, medicine, and human anatomy, rather than in general biology (Spencer, 1982), sometimes seems to treat human (and by extension, prehuman) biological evolution as a phenomenon to which other organisms have relevance only in proportion to their phylogenetic proximity to humans. Chimpanzees and gorillas are not human, but they are the next best thing, and other primates come a distant third.

Using more analogies drawn from nonhuman sources would, I believe, open up the anthropological imagination, suggesting new and alternative directions to take, and new hypothetical scenarios and explanations to test. But analogies are not themselves hypotheses; they are not “refuted” by showing that the correspondence between analogues is not exact—which, of course, it can never be. In fact, divergences between analogues may be as informative as resemblances, especially when viewed against the backdrop of the parallel resemblances: the molar crowns and brain size of geladas are a case in point. One of the most difficult aspects of the study of human evolution has always been to reconcile the fact that early hominins were more like living humans than are any living species, with the concept that they were not themselves human. Moreover, the “mix” of human and nonhuman itself evolved in the lineage from which H. sapiens is derived: by the beginning of the late Pleistocene, humans can be considered mentally “like us,” yet closer to many nonhuman species in terms of population structure and diversity. Though no living species can provide an exact analogy for these intermediate stages, the baboons can, I think, often provide insights into the nonhuman element.

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