A REVIEW OF THE SYSTEMATICS AND TAXONOMY OF HOMINOIDEA: HISTORY, MORPHOLOGY, MOLECULES, AND FOSSILS

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ABSTRACT. The history of hominoid systematics reveals a general tendency to recognize diversity in the fossil record of "apes" and "basal hominoids," but a view toward taxonomic limitation with regard to hominids, which was exacerbated in the 1980s by the "removal" of fossils such as *Sivapithecus* (=*Ramapithecus*) and their association via morphological synapomorphy with *Pongo*. The latter, in turn, reinforced the increasingly accepted, molecularly based theory of human-African ape relatedness, which was never substantially supported by morphology. Although claims to being cladistic in associating humans with the African apes (or *Pan* alone) abound in the literature, molecularly and morphologically based analyses are, however, not only procedurally different, they identify synapomorphy differently. Continuing confusion of orangutan-like specimens as hominids plus recent re-evaluations of diversity in the human fossil record as well new discoveries of so-called basal fossil hominoids argue for a broadening of hominoid classification until such time as the clades and the relationships between and within them become better understood.

KEY WORDS. Systematics, hominoid, hominid, synapomorphy, orangutan clade, molecules versus morphology, regulatory genes

INTRODUCTION

The questions this conference has raised about the reality and recognition of a "human clade" are numerous, at times hierarchically entwined, and yet also have different implications and consequences for the different approaches that have been brought to bear on what are essentially two different pursuits: systematics and phylogenetic relationships versus classification. The concern of this conference also raises the question of "what

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is Hominoidea and is it a useful construct?" And this in turn derives from a particular history of thought as well as of discovery, of reactions to this history, but never, really, of a sloughing off of the effects of either the real history or a version of it.

Given the breadth of topics and questions the intent of this conference is meant to provoke, where and with which should we begin? I think it should be with history, for it is only from this vantage point that we might begin to see how the issues of today arose and what their relevance may actually be. The history of the questions is interesting but also lopsided because it was at first not concerned with phylogeny, but with taxonomy. It was also a history that was based on morphology and its interpretation primarily of extant, not fossil, taxa. Originally, systematics (the analysis of phylogenetic relationships) and classification had been in the domain of morphological studies, first, of extant and, much later, of fossil taxa. But the playing field was expanded and changed forever in the early 1960s, when Zuckerkandl and Pauling interpreted degrees of hemoglobin similarity in a handful of vertebrates as a reflection of the the pattern of their evolutionary history. True, this pattern was consistent with the scheme of relationships that morphologists had long accepted. However, the implications of their interpretation had far-reaching effects that very quickly came to pit the efforts of the nascent field of "molecularly based systematics" against those of "morphologically based systematics," even though theoretical and methodological concerns should have been a unifying force. But since unity in practice and interpretation does not characterize morphologists—especially with the introduction during the 1960s of cladism and the polarization of neo- and paleomorphologists and factions within each discipline—it would perhaps be too much to expect intellectual camaraderie between what came to be competing and essentially mutually exclusive approaches to phylogenetic reconstruction. The rapid cleavage of molecular from morphological systematists as theoretically and methodologically disparate, and seemingly irreconcilable, endeavors makes the history of "hominoid studies" that much more interesting, but also that much more frustrating.

MAJOR "EVENTS" IN THE HISTORY OF "HOMINOIDEA"

So where to begin? With the Great Chain of Being, of course, since the practice of taxonomy arose as a pursuit motivated by revelation to document the workings of a divine creator. We all know that well before Linnaeus took the bold step in 1735 of classifying humans with other animals, taxonomists had acknowledged that humans were indeed similar—even if this was recognized only at a superficial level—to a small cadre of animals that were themselves clearly different from other organisms. The general concept of "anthropomorphous apes" (the term "apes"

used well into the nineteenth century to include both "tailed apes" or monkeys as well as "tailless apes" or just apes) was widely deployed and commonly understood. Thus even Linnaeus' classifying humans with *Simia*, *Lemuria*, and *Vespertillio* in the order Anthropomorpha (the latter genus would be replaced by *Bradypus* in 1758 when Linnaeus changed the name of the order to Primates) was not so much a matter of providing more information than other taxonomists as it was an intellectually motivated act based on inescapable morphological similarity.

The history of hominoid studies, however, really begins in 1863, with Thomas Huxley's essay "On the relation of man to the lower animals," which was published with two others in *Man's Place in Nature*. In this essay, Huxley predated Haeckel by decades in being the first to attempt to demonstrate through the study of ontogeny that a hierarchy of similarity exists between humans and vertebrates, humans and mammals, and, ultimately, humans and primates. But Huxley was not Haeckelian (or perhaps more precisely, given the historical chronology, a Serresian). His approach relied on the application of von Baerian principles (although he did not cite von Baer), in which the chronology of shared ontogenetic stages is taken as reflecting a common developmental history from which, at some point, an organism deviates as it acquires those characteristics that are specific to its own group and, ultimately, species.

The second part of that essay is largely comparative skeletal anatomy, with a few soft tissue features thrown in. Here, Huxley employs the device of comparing the gorilla with "lower primates" and then humans with the gorilla with the goal of showing that, while there may be real differences between the latter two primates, the gulf between them is nowhere as broad as between the gorilla and the "lower primates." When comparative data was not available for gorillas, Huxley looked to the orangutan and chimpanzee, and sometimes even the gibbon. He argued that, indeed, humans were most similar to the "tailless apes," especially the large-bodied forms, and that not only should humans be grouped with primates among mammals, but, most specifically, with this subgroup of primates. Nevertheless, in spite of his favorable comparisons with the gorilla and other "apes," in the end Huxley concluded that humans were still sufficiently unique and distinct that they should be classified in their own family, with the large-bodied "tailless apes" relegated to a separate family. Thus, in spite of the fact that one could impute to Huxley an evolutionary concern, one cannot cite him as having demonstrated anything more specific than a broad relationship of humans to all apes, gibbons included, and the great apes more specifically. This conclusion, however, has been overlooked by twentieth-century primate systematists who continually misinterpreted one of Huxley's comments—about the African apes most closely approaching humans in aspects of morphology—as

being a conclusion about the closeness of relatedness of these three primates. If Huxley had used overall similarity as a projection of phylogenetic propinquity, no doubt he would have linked humans and gorillas, since he informed his audience early on in the essay that, in his opinion, these two were the most similar of all (see Schwartz, 1986a, 1993, 1999a).

But as Huxley so clearly stated in 1896 in the preface to the second edition of *Man's Place in Nature*, he had not intended to present an argument on the specific evolutionary relationships of "man." As is patently obvious from his essay, he was interested only in providing the first developmental and morphological argument for the taxonomic grouping of humans within Mammalia and within Primates (Schwartz, 1986a, 1993, 1999a). In terms of the details of evolution, Huxley (1896) stated that he would leave that to Darwin (1859), who had referred only obliquely in the *Origin* to his theory shedding light on human evolution. Unfortunately, Darwin's (1871) treatise on human evolution was little more than an invocation of his various evolutionary assumptions (Schwartz, 1993, 1999a). Natural selection could not have molded a species as unique as *Homo sapiens* (which, although puny, had reason, language, bipedalism, tool making) in Southeast Asia (the home of the orangutan), but could have done so in the harsh, predator-filled landscape of Southern Africa. Since there are apes (albeit thousands of kilometers to the north of Southern Africa) and primitive humans in Africa, and since he believed that one should find closely related species living in the same geographic region, Darwin concluded without any attendant morphological criteria that humans and the African apes had to be the most closely related of "tailless apes." Darwin's only attempt to "link" his chosen primitive humans with apes was by citing folklore and myth about the various apelike features and attributes (such as a somewhat divergent hallux and a tendency toward mimicry) these humans supposedly possessed (see review by Schwartz, 1999a). Darwin also thought that one should find the fossil ancestors of closely related species in the same geographic region as the latter, but, unfortunately, in 1871, the only potential fossil apes known were the relatively small *Pliopithecus* (Gervais, 1849; Blainville, 1839) and the larger *Dryopithecus* (Lartet, 1856), both inconveniently from European, not African, deposits. Largely because of size and the robusticity that this confers, the latter fossil made a better ape "ancestor."

Not surprisingly, especially in the broader context of Darwin's theories of gradual evolution and natural selection being soundly rejected by the leading comparative anatomists (who were saltationists [e.g., Huxley, 1863, 1869; Mivart, 1870]) as well as paleontologists of his day (e.g., Owen), Darwin's plea for an African origin of *Homo sapiens* and for this species' relatedness to the African apes largely fell on deaf ears. Comparative

anatomists and taxonomists, such as Flower (1883), formally represented the primate subgroup Hominoidea as Huxley had basically conceived it, with gibbons apart from a great ape group from which humans were clearly separated. Although, in the decades that followed, there were occasional suggestions that humans might be closely related either to the African apes together, or to either the chimp or the gorilla alone, Huxley's "Hominoidea" was the dominant taxonomic opinion and the one that Adolph Schultz defended against all others throughout his long career (see reviews by Fleagle and Jungers, 1982, and Schwartz, 1986a).

It is thus of note that, as might be expected in the middle decades of the nineteenth century, the original concept of Hominoidea derived from studies (or at least perceptions) that were based solely on extant taxa. In addition to *Pliopithecus* and *Dryopithecus*, on the hominid side of paleontology, the only fossils then known publicly were the Feldhofer Grotto Neanderthal bones and the juvenile partial cranium from Engis, which Huxley (1863) argued represented normal and expected variants of human morphology. When, in the late 1870s and then in the late 1880s, respectively, more fossil "apes" and hominids began to surface, their "place in nature" was predetermined by a taxonomic structure and bias of interpretation that was predicated on extant taxa. As for the fossil hominids, and despite King's (1864) case for recognizing the species *Homo neanderthalensis* (and for rejecting Huxley's scenario of how the Feldhofer Grotto Neanderthal calotte was nothing more than an extension of primitive human cranial morphology as supposedly evidenced in Australian Aborigine and occasional early Danish skulls), Neanderthals continued to be thought of as being merely earlier and more primitive versions of modern *H. sapiens* (e.g., Fraipont and Lohest, 1886). Dubois' (1892, 1894) *Pithecanthropus erectus* was acceptable as a bridge between the "acknowledged" most primitive of humans and apes because, when the Great Chain of Being drove the efforts of taxonomists, links were sought between the lowest of humans and the highest of the brutes (see reviews by Schwartz, 1986a, 1999a). Later on, the great anatomist and evolutionist Ernst Haeckel (e.g., 1874) predicted the existence of a speechless "ape-man" stage in the course of human evolution and, in anticipation of finding evidence of this in the fossil record, had coined the genus *Pithecanthropus* for it. But Dubois' claim of having found the "missing link" between humans and apes was contested early in the twentieth century as a result of the discovery of the Mauer mandible, which its discoverer, Schoetensack (1910), dubbed *Homo heidelbergensis*. Schoetensack asserted that, with its supposedly apelike jaw but humanlike teeth (especially the non-projecting lower canines), this specimen shed light on the conformation of the common ancestor of humans and apes.

As for fossil apes, their existence had also been foreshadowed by the Great Chain of Being. Since, in this context, fossils of nonhuman animals were allowed by church doctrine to be antediluvian (see review by Schwartz, 1999a), a window on extinct ape species had been opened with the discovery of *Pliopithecus* and *Dryopithecus*. With the recognition of evolution, late nineteenth-century paleontologists could seek the remains of extinct faunas with an eye toward filling in the gaps in the picture of life's evolutionary history, and fossil apes were part of this endeavor. In 1878, in the Siwalik Hills of Indo-Pakistan, Lydekker found the first of an eventual array of "apelike" fossils: a partial left upper jaw he allocated to *Paleopithecus sivalensis* [which Lewis (1937) would later refer to the genus *Sivapithecus*]. Subsequently, Pilgrim (1910, 1915) suggested that some of the Siwalik fossils he had found were reminiscent of *Dryopithecus* and referred them to the species *D. punjabicus* and *D. giganteus*. He also allocated an upper molar, which he thought was very orangutan-like, to *Paleosimia rugosidens* and a lower jaw to *Sivapithecus indicus*, which he believed had been ancestral to humans. Gregory (1915), however, rejected the latter proposal on the grounds that the teeth of *S. indicus* were more similar to orangutans than to humans.

By 1927, when Pilgrim added yet another species to *Sivapithecus*, the picture of human evolution had not increased substantially. Besides the discovery of additional specimens of Neanderthal and a few teeth from Zhoukoudian, which Black (1927) referred to *Sinanthropus pekinensis*, there was the child's partial skull and endocast from Taung, which Dart (1925) thought was intermediate between apes and humans. To embody this belief, Dart created for it the genus *Australopithecus* (meaning "man-ape") and the cumbersome and nomenclaturally incorrect family, Homo-Simiadae. Dart also sought support for this transitional form and its presence in Southern Africa in Darwin, who, of course, had "predicted" its existence. Unfortunately, paleoanthropology was not yet ready to consider seriously human origins in Africa, as is attested to by the tirades of the leaders in the field, including and most notably Sir Arthur Keith (e.g., 1931), who argued that the Taung specimen was merely a fossil African ape.

With regard to more plausible fossil apes, Lewis' (1937) review of the Siwalik specimens led him to name two new genera, *Bramapithecus* and *Ramapithecus*, both of which he believed held a central position in ancestry of humans: *Bramapithecus* was linked via its supposed similarity to *Dryopithecus* and *Ramapithecus* via its presumably short face. But the potential relationship of these fossils to humans was seriously muddied when, in 1938, Gregory, Hellman, and Lewis' study of additional Siwalik fossil "ape" material resulted in allocating a more ape- than hominid-like specimen to *Ramapithecus*. With Miocene ancestry for humans essentially

ruled out until the 1960s, when Simons (1964) revived and added to Lewis' arguments for *Ramapithecus* in this role, the general picture of hominoid phylogeny mirrored that of the preceding century: There were early apelike fossils and much later more humanlike fossils, with varying degrees of "pithecoidlike" morphology. Thus in 1933, and for the first time in East African deposits, Hopwood identified a new genus and species of fossil "ape," *Proconsul africanus* (to which Le Gros Clark and Leakey's [1951] added two more species). And from Sterkfontein in South Africa, Broom (1936) described a new species of Dart's *Australopithecus*, *A. transvaalensis*, which he believed compared most favorably in dental morphology with *Dryopithecus* from Europe.

In offering the latter opinion, not only did Broom formally recognize a fossil link between humans (now including a fossil record of some taxic as well as time dimension) on the one hand, and apes on the other, via their presumed ultimate common ancestor, *Dryopithecus*; he also reinforced Huxley's legacy of a divide of some significance between humans and living great apes. Thus, even though the 1930s and decades thereafter witnessed a proliferation of discoveries that added to the picture of diversity in the fossil records of both apes and humans, consideration of specific and detailed phylogenetic relationships between any members of the two "groups" was sorely lacking, in spite of the fact that, collectively, all were regarded as being "hominoid." In truth, however, the hominoid status of fossil "apes" was accepted not so much because of specific morphology as for the fact that there were no apparent alternatives to considering them being related to anything else. For virtually one hundred years, general similarities between these Miocene fossils and living apes in dental morphology (e.g., upper and lower molar cusp disposition, anterior lower premolar orientation and elongation, and upper and lower canine stoutness) and mandibular depth and robusticity sufficed to unite them. Since Old World monkeys, the other major catarrhine group, could easily be distinguished on the basis of distinctive upper and lower molar bilophodonty alone, it seemed that hominoids could be identified through their lack of bilophodonty: in other words, on the basis of their generalized molar cusp patterns. And, indeed, it was this presumed dichotomy that served as a guide to various interpretations of Fayum primates: e.g., *Propliopithecus* as an ancestral hominid (Schlosser, 1911), *Parapithecus* as an ancestral Old World monkey (Simons, 1962), and *Aegyptopthecus* as ancestral to all later hominoids (Simons, 1965).

[Even the more recently discovered early Miocene *Otavipithecus* (Conroy *et al.*, 1992) has been analyzed in terms of its being a hominoid largely, it would seem, because it does not blatantly present features of another group. However, the alignment of the basally melded protoconids and metaconids opposite one another on P_2 as well as M_{1-3}, the small size of

M_1, the miniscule hypoconulid on and straightened up distal side of M_{1-2}, the heel on the distally tapering M_3, and the oblique orientation of the very mesiodistally compressed and buccolingually quite elongate P_1 would certainly seem to be broad synapomorphies with cercopithecoids (see review by Schwartz, 1986b).]

These points aside for the moment, the 1940s and '50s that witnessed the continued recognition of taxic diversity in the Miocene fossil record—regardless of the veracity of assigning fossils to Hominoidea—also saw the deliberate truncation of diversity in the human fossil record, primarily through the arguments of Dobzhansky (1944, 1955) and Mayr (1950). Dobzhansky asserted that, since humans had culture, which could act as both modifier and natural selector, all culture-bearing hominids controlled their own evolution and were, therefore, exempt from the forces that affected creatures in the wild. The ability to control what would be naturally occurring circumstances would preclude opportunities for speciation that would otherwise exist in nature. Mayr proclaimed that, as there is an incredible amount of variation among living humans, so there also was among fossil hominids. It was, therefore, this extreme in variation that allowed hominids to invade all available econiches. Thus, with the possible exception of two or three species during the Plio-Pleistocene, there could have been only one hominid species at any given point in time because, in order to speciate, a subspecies needs a vacant econiche into which it can spread. Consequently, after lumping *Paranthropus* and its species into *Australopithecus*, Mayr arranged hominids chronologically, from *Homo erectus* directly into *H. sapiens*; he (1963) later interposed the newly described *H. habilis* between the australopiths and *H. erectus*. The legacies of Mayr and especially Dobzhansky dominated the interpretation of human fossils thereafter.

It was not long, however, before the "ape" fossil record, for different reasons, underwent a similar taxonomic truncation. Although Simons (1964) had resurrected Lewis' *Ramapithecus* both in name and as a potential hominid ancestor, he and Pilbeam (1965) reviewed the entire (non-*Australopithecus/Homo*) large-bodied hominoid fossil record and concluded that, with the exception of *Ramapithecus* and *Gigantopithecus*, all other large-bodied forms could reasonably be accommodated in the genus *Dryopithecus*. The European, African, and Asian forms were relegated to the subgenera *Dryopithecus*, *Proconsul*, and *Sivapithecus*. It is important to point out that Simons and Pilbeam's reconstituted subfamily Dryopithecinae (basically for *Dryopithecus* and *Gigantopithecus*) was still considered ape-related, and consequently classified with the extant forms in the commonly used family grouping, Pongidae. In 1969, Simons objected to Leakey's (1962) identification of *Kenyapithecus wickeri* as the East African counterpart of *Ramapithecus* and sank the former into the latter genus.

Perhaps the unrealized impetus for Simons and Pilbeam's (1965) submerging a plethora of potential species, and even genera, into a handful of taxa, with most being subsumed in the mega-genus *Dryopithecus*, derived in part from the earlier act of restricting hominids to a single evolving lineage. Together, these taxonomic decisions had the effect of continuing the perception based on extant taxa that, in contrast to virtually all other groups of primates (the tarsier, for one, being an outright exception—but one that was probably not well known to paleoanthropologists), hominoids must have had a unique evolutionary history because there are, and were, so few of them. The taxonomic surgery on the Miocene forms that reduced their numbers so drastically also made it easier to claim their direct descent from the Oligocene *Aegyptopithecus* and, in turn, specific, direct ancestor-descendant relationships between some of them and extant taxa (Pilbeam, 1969, 1970): *D. major→Gorilla*, *D. africanus→Pan*, *Sivapithecus→Pongo* as well as *→Gigantopithecus*. With most Miocene hominoids being relegated either indirectly or directly to a relationship with extant apes, the apparent hominid-like features of *Ramapithecus* stood out even more. If *Ramapithecus* had been the ancestor of hominids and it had descended from an even more distant *Dryopithecus*-like ancestor, then the evolutionary history of humans had indeed been long-separated from that of other hominoids.

The taxonomic myopia regarding Miocene hominoids was, however, relatively short-lived. With new discoveries or re-assessments of previously known specimens of small- and large-bodied apes in, for example, China (Li, 1978; Wu *et al.*, 1981), Greece (de Bonis and Melentis, 1977), France (Ginsburg and Mein, 1980), Hungary (Kretzoi, 1975), and East Africa (Andrews, 1978), it became impossible to deny a sweep of taxic diversity that went well beyond the taxonomic limits that had been imposed. And with this expanded sense of the potential enormity of taxic diversity during the Miocene came a return to the recognition of many of the "original" Miocene genera, especially of *Proconsul* and *Sivapithecus*. Most of the smaller bodied hominoids, some of which had been thought to be specifically related to gibbons, were now interpreted (often via cladistic analysis) as having phylogenetic relationships that lay not only outside the traditionally recognized group, Hominoidea, but also outside the larger group, Catarrhini (Harrison, 1982, 1987; Schwartz, 1986a). Even *Proconsul*, at one time proposed as a possible direct ancestor of the chimpanzee, emerged from various cladistic analyses as being a sister taxon either of all hominoids, gibbons included, or at least of all large-bodied hominoids (cf. Andrews, 1992; Harrison, 1982, 1987; Schwartz, 1986). As for the presumed ancestor of all hominoids, *Aegyptopithecus*, it shared, along with others of its (propliopithecid) group, few synapomorphies with catarrhines as a whole (Harrison, 1982, 1987; Schwartz, 1986).

This period of taxonomic proliferation of fossil hominoids was marked as well by, first, the discovery that taxa other than *Ramapithecus (Sivapithecus, Kenyapithecus, Ouranopithecus [= Graecopithecus], Gigantopithecus)* also possessed the few synapomorphies that linked the former Miocene taxon with hominids (namely, thick molar enamel and low-cusped cheekteeth) (see review by Kelley and Pilbeam, 1986) and then by the interpretation not only that the distinction at the genus level between *Ramapithecus* and *Sivapithecus* was apparently unwarranted, but also that the newly realized facial anatomy of *Sivapithecus* was synapomorphically similar to the orangutan (Andrews and Tekkaya, 1980). The conclusion from the latter interpretation was that *Sivapithecus* was actually closely related to *Pongo* and, by implication, that at least some of the thick-enameled Miocene forms also belonged to that clade (e.g., Kelley and Pilbeam, 1986). The consequences of this were enormous.

Without a fossil record earlier than the Plio-Pleistocene, the time scale of human evolution became severely truncated. In turn, this validated the molecularly derived dates for the divergence of humans from apes, which some (e.g., Sarich and Wilson, 1967) had estimated to be between 4-6 Mya. It seemed also to validate the relationships among extant hominoids that most molecular studies were generating: gibbons had diverged first, orangutans next, and then humans and the common ancestor of the African apes (see review by Schwartz, 1986a). This rearrangement of ordering within Hominoidea did nothing to affect the ongoing belief that hominids had evolved in an essentially linear fashion from one species to the next, but it did produce another scenario about hominoid evolution in general. Namely, since orangutan molars were hominid-like and the thin-enameled African apes were now considered to be the living hominoids most closely related to humans, thick molar enamel—which had earlier convincingly united *"Ramapithecus"* with hominids (australopiths and *Homo*)—was now interpreted as an apomorphy that had characterized the last common ancestor of all large-bodied hominoids (Martin, 1985). Consequently, the possession of thin molar enamel in the African apes had to be secondarily derived. But what is the justification of a human-African ape clade?

ON HUMANS AND THE AFRICAN APES

Even in the context of Huxley's great ape group, the African apes were thought of as being more closely related to each other than to the orangutan. Given the various morphological features the African apes share that exclude other primates (e.g., Schultz, 1936), this seems to be a reasonable hypothesis. As can be gleaned from Schultz's works, morphological evidence of a close relationship between humans and the African apes was

slim at best (see review by Schwartz, 1984). Perhaps the most potentially significant feature shared by humans and African apes—a feature to which Gregory (1922) had also pointed—was their common development of frontal sinuses.

But more than from morphology, the hypothesis of relatedness of humans and the African apes derived support from studies in molecular biology, first in the form of tests of immunological reactivity. As initially conceived by Nuttall (1904: 137), the premise was simple: "the degree of blood reaction [is] an index of the degree of blood-relationship." From this, Nuttall (ibid) concluded that his study of blood antiserum/serum reactivity indicated that "within Anthropoidea we find that the Old World apes are more closely allied to man than are the New World apes, and this is exactly in accordance with the opinion expressed by Darwin."

A more formal explication of the rationale for using "degree of blood reaction as an index of degree of blood-relationship" was offered almost six decades later by Zuckerkandl and Pauling (1962: 198-9) in their discussion of hemoglobin:

> The foregoing observations can be understood at once if it is *assumed* [emphasis mine] that in the course of time the hemoglobin-chain genes duplicate, that the descendants of the duplicate genes 'mutate away' from each other, and that the duplicates eventually become distributed through translocations over different parts of the genome As species gradually get to be more different from each other, so presumably do the genes at the homologous loci.
> The over-all similarity must be an expression of evolutionary history. This is indicated by the gradually increased amount of differences found when human hemoglobin is compared with hemoglobin from progressively more distant species.

Based on these assumptions, Zuckerkandl and Pauling (p. 201) proceeded to calibrate the average rate of hemoglobin change by taking from paleontology an assumed age of "between 100 and 160 millions of years ago" for the common ancestor of human and horse (two of the seven mammals in their sample). Clearly, the extremely early date of this presumed mammalian ancestor aside, the calculation of rates of molecular change involves a separate set of assumptions (derived from paleontology, geology, and a comparative morphology-derived phylogeny) that is predicated on the assumptions that initially generated the phylogeny. As Nuttall had sought validation of his arrangement of primates in Darwin, the assumed mechanism of molecular change was also Darwinian. That is, change is ongoing and therefore accumulated during the existence of a species until it gives rise to daughter species, which, in turn, continue to accrue their own specific sets of changes. Thus, overall similarity can be a mirror of the history of species divergence and relatedness because the

more recent the split between taxa, the greater will be the sum of the change that accumulated prior to the split.

It would be unnecessarily repetitive to review the history of molecular studies that subsequently built upon the basic assumptions articulated by Zuckerkandl and Pauling (for a review of the salient points see Schwartz, 1984, 1986a, 1993). Suffice it to say that we must certainly take note of the impact on the field, especially on primate systematics, that Goodman (1962), and Sarich and Wilson (1966) had with their early efforts using various blood serum proteins. But it must also be pointed out that the validation of their work, as with Zuckerkandl and Pauling's, came from their theories of phylogenetic relationships being consistent with a generally accepted arrangement of relationships of taxa that had been achieved from study of comparative morphology. Since during the 1960s (and even at this late date) the number of taxa sampled for molecular analysis was far fewer than the number actually known, most potential inconsistencies between molecularly and morphologically derived phylogenies were not detected—except for the break up of the great ape group and the sometime aligning of humans with the African apes. But although Goodman's (1962) studies were not at the time unequivocal in this conclusion. Thus, at this general level of interpretation, there seemed to be reasonable validation of the assumed properties of molecular change, even, as between Sarich and Wilson and Goodman, the calculations of how rapidly or slowly these changes accrue differed. This difference aside, however, it was clear from the beginning that, as long as relatedness was based on the notion of overall similarity, humans and the African apes would be grouped together to the exclusion of the orangutan. What had not come into question was, however, whether the basic assumptions of molecular change were appropriate. The problem was that the model was so internally consistent that it could not be falsified by other molecular data since all other phylogenies, although generated from analysis of other molecules and even sequence data, were interpreted within the same framework of how molecular change is supposed to occur.

By the 1970s and early '80s, antigenetic studies of blood serum proteins had been joined by those based on DNA-DNA hybridization as well as the sequencing of proteins and even of DNA. While the technology required to obtain these data had progressed significantly, the interpretation of the data had remained essentially the same. Disagreements between molecular laboratories were often the result of differences in the algorithms they worked out for linking or clustering taxa (e.g., Czelusniak *et al.*, 1990; Felsenstein, 1988; Goodman, 1988; Hasegawa and Yano, 1984; Marshall, 1991). As molecular sequencing became more feasible, various criticisms arose about its employment, particularly with regard to the accuracy and correctness of aligning sequences from different taxa (Lake, 1991). But at

the same time there was also a heightened emphasis confered to the reliability of resolution of molecular data, especially the increasingly popular subject of study, mtDNA. The result was that, where previous molecular studies had only been able to generate an unresolved trichotomy between humans, chimpanzees, and gorillas, the claim now was that the chimpanzee was most closely related to *Homo sapiens,* not, as morphology would indicate, the gorilla (e.g., Horai *et al.,* 1985; Ruvolo *et al.,* 1991).

By this time, an interesting element of many studies was that the claim of close relationship between humans and chimpanzees was often generated from a very limited sampling of taxa in which the orangutan and/or the gibbon were not necessarily included (see criticism by Marks, 1993). Although unstated, the license for being able to generate a theory of relatedness on the basis of a very small set of taxa came from the assumptions of how molecular change is supposed to occur and accrue. That is, if a greater degree of molecular similarity does indeed reflect recency of common ancestry, then it is unnecessary to include all potentially related as well as outgroup taxa because of the assumed nature of molecular change: If one thinks that overall molecular similarity reflects closeness of relatedness, then, in order to resolve a presumed human-*Pan-Gorilla* trichotomy, it is only necessary to sample these three taxa and perhaps one other (any other, monkey or hominoid) that would serve as the primitive outgroup in which to root the computer-generated dendrogram. This taxon would be primitive by definition because it is assumed from the start that, up to the point of the ancestor of the human-*Pan-Gorilla* trichotomy, molecular divergence had occurred in the expected manner. In addition, the presumptions about the process of molecular change allow for the assumption that, since the general arrangement of taxa is sufficiently corroborated by previous molecular studies, one need focus only on the details of the relatedness of enigmatic taxa and have a ready-made primitive outgroup in which to root the analysis. Thus, for instance, in their study of the Y-linked RPS4Y locus, Samollow *et al.* (1996) contested the sister relationship of *Homo-Pan* offered by various other molecular analyses (e.g., see Horai *et al.,* 1995) on the grounds that, because their data linked humans (albeit weakly) with gorilla, a trichotomous branching pattern between *Homo, Pan,* and *Gorilla* was really the best available solution to the problem. In manipulating their data on these three hominoids, Samollow *et al.* rooted their tree in the orangutan, which they took without question as the primitive outgroup in their analysis. No other taxa were included in the study.

A similar approach has been applied to speculating where and when modern humans arose. Using mtDNA, various researchers (e.g., Hedges *et al.,* 1992; Vigilant *et al.,* 1991), have argued that there was a branching pattern to the emergence of major human groups, with Africans diverging

first, perhaps 300-500 Ka, followed sometime later by the split between the European and Asian groups. In order to evaluate degrees of overall similarity, the chimpanzee alone was used as the primitive outgroup because this hominoid is supposed to be our closest living relative. Of course, the justification for the latter hypothesis also derived largely from study of mtDNA. Although this general procedure follows from the underlying premises, a morphological study that used so few taxa to assess character polarity would be considered sorely inadequate.

Along with the acceptance of these procedures in what was being called "molecular systematics" is another interesting aspect of this history: cladistic terminology crept into the molecular literature (e.g., Ruvolo *et al.*, 1997; Samollow *et al.*, 1996). Thus the concept of synapomorphy, by which morphological systematists designate specific features hypothesized as being shared derived among taxa, came to refer to the sharing of the most similar molecular elements (whether sequence, hybridization, or immunologic data). As such, molecular synapomorphy is identified *a posteriori*, after the phylogeny is generated, rather than as a result of broad outgroup comparisons that yield hypotheses of character polarity, some of which (as any morphological cladist has certainly discovered) may be in conflict. Molecular synapomorphies, however, can take the form of either entire sequences or specific sites in sequences that are identified only as a consequence of the clustering analysis used. Thus, there never is any character conflict within a particular molecular study, only trees of differing lengths. Whereas hypotheses of morphological synapomorphy can be used in attempts to falsify other hypotheses of synapomorphy, no such methodological procedure can be applied to phylogenies generated from molecular data, because the guiding principle in the latter endeavor is one of a "minimum number of steps" needed to achieve the most parsimonious theory of relatedness. As a result, it is common practice to embrace the molecular tree that involves the fewest steps, even though the difference between itself and its closest competitor or competitors may be trivial, being a matter of only a few base pairs or one or two cleavage sites in a field of thousands.

In a morphological cladistic analysis, the issues of determining character polarity are dealt with first, and then competing theories of relationship are generated from the alternative combinations of character states. Basically, features are investigated prior to the phylogenetic assessment of taxa. In molecular analysis, polarity is determined by specifying a particular taxon (and thus its molecular attributes) as primitive relative to the taxa of interest, and then generating a tree based on nested sets of increasing overall similarity among the non-rooted taxa. Molecular synapomorphy is subsequently defined in the context of the already-determined branching sequence. Clearly, the application of similar-sound-

ing cladistic terminology in morphological and molecular analyses does not, in any way, reflect similarity of theoretical concern or methodological practice. One would have reason to think that a competing morphologically based theory of relatedness would serve as potential falsification of an alternative phylogenetic scheme based on molecular data, especially since the initial validation of the molecular approach was the arrangement of tax based on morphology. But to do so would demand facing the possibility that the fundamental assumptions of molecular "systematics" would have to be rethought.

There are, however, lessons to be learned along the way that should at least result in formulating important questions as to how molecular as well as chromosomal data have been interpreted. For instance, there is a concern to identify whether the data have been either used to generate a theory of relatedness (by whatever means), or interpreted in the context of a presumed theory of relationship. Although, for example, Yunis and Prakash's (1982) chromosome study is cited (e.g., Ruvolo *et al.*, 1997) as having demonstrated synapomorphy between *Homo* and *Pan*, scrutiny of their report reveals that, rather than generating this theory of relationship, the data were interpreted in the context of a scheme of relatedness that portrayed a branching pattern from *Pongo*, to *Gorilla*, to *Pan* and *Homo* (Schwartz, 1984). In arguing from other chromosomal data that *Pan* and *Gorilla* were sister taxa, Marks (1993) actually did the same as Yunis and Prakash.

[This is not to suggest that morphologists do not also succumb to this avenue of interpretation. Martin's (1985) claim that thick molar enamel is primitive for large-bodied hominoids and that thin molar enamel is thus synapomorphically secondarily derived for the African apes, was based on the application of his data to an arrangement of taxa wherein humans and the African apes constituted a clade to which the orangutan was more distantly related. Most recently, G. Schwartz (2000), although presenting detailed data on enamel deposition and thickness within the crown and between different teeth, did the same as Martin: interpret the phylogenetic "history" of hominoid enamel thickness in the context of an assumed closer relationship between humans and the African apes than between *Homo* and *Pongo*. His claim that thick molar enamel is intrinsically different in the latter hominoids is further confounded by incorporating theories of function and adaptation first into his phylogenetic assessment, rather than, more neutrally, the other way around. On the basis of his data, humans and the orangutan are delineated by thicker molar enamel than the African apes, and humans are distinguished from the orangutan in having even thicker enamel in some regions of the crown. The phylogenetic conclusion from the data would be that *Homo* and *Pongo* are

synapomorphic for thick molar enamel, and *Homo* autapomorphic in its differences.]

Perhaps the most important lesson—one that pertains to all systematic investigations, whether morphological or molecular—is the need to have one's assumptions and reasons for making certain decisions clearly stated and accessible for testing and potential falsification. The recent re-discovery that sperm may contribute mtDNA to offspring (Awadella *et al.*, 1999) certainly demonstrates that not all the "kinks" have yet been worked out with regard to molecular systematics. In this study, the mtDNA of humans and chimpanzees were analyzed with the obvious conclusion that statements about a close evolutionary relationship between these two hominoids "will now have to be reconsidered" (ibid: 2525). This in no way implies that one should not incorporate molecular data into systematics analyses. Rather, that it might be fruitful to deal with molecular data in the same way morphological cladists confront theirs: with an eye toward falsification. Indeed, even if recombination is not a full-time factor in mtDNA transmission, the increasing disagreement among studies on modern human origins that have also used Y chromosome or PDHA1 gene data (see review by Pennisi, 1999) point out that, when sufficiently differing data sets are available, molecular data (even if interpreted differently from morphological data) can yield differing theories of relatedness (as morphological data sets do). As such, they should both be subject to similar constraints of corroboration and falsification.

HOMINOID EVOLUTION AND THE TRAIL OF FALSIFICATION

If we return to a question I raised earlier—in essence, if the assumptions about molecular change were validated by apparent congruence with a commonly accepted morphological theory of relatedness, why can't morphological hypotheses test and perhaps also falsify molecular ones—how might we go about assessing the interpretation of molecular data? Let us begin with a quick review of the morphological data in support of various theories of hominoid relationships.

As long-standing as Huxley and then Schultz's pet theory of hominoid relationships was—that the great apes constituted a group (which came to be regarded as the family Pongidae) to which humans (Hominidae) were related, but distantly so—there was very little morphology that could be mustered to support this theory (e.g., see Schwartz, 1984, 1986b, 1988). Schultz was impressed by the three great apes having proportionately long arms and cervical spines, but even an independent scrutiny of Schultz's life-long collection of data and that of others can add little to suggest that these hominoid constitute a clade (e.g., Andrews, 1987; Groves, 1986; Schwartz, 1984, 1988). As for what might unite humans and

the great apes—the four extant large-bodied hominoids—Schultz and others were rather vague about that, too. But, in addition to large size, there do appear to be a suite of apomorphies uniting these hominoids (cf. Andrews, 1987; Groves, 1986; Schwartz, 1984, 1988), such as thickening of the palate with concomitant elongation of incisive canals, reduction in number of lumbar vertebrae, truncation of palatine ridges, delay in onset of ossification of the distal ulna and metacarpals, excretion of estriol, prolonged gestation periods, notable cerebral and Sylvian sulcus asymmetries.

Although morphological synapomorphy does unite the African apes as sister taxa, the delineation of features uniting them with humans has been fraught with difficulty. Groves (1986) concluded that, from a list of 200 characters, the two most strongly supported theories of relationship were human-African ape and human-*Pan*. Andrews (1987, personal communication) and I (1988) reviewed Groves' characters and could delineate at most fourteen potential synapomorphies uniting humans and the African apes and only five uniting humans and *Pan* (see tables in Schwartz, 1988). The other features Groves cited in support of these two competing theories of relatedness were shared more broadly, by other anthropoid taxa, and thus were symplesiomorphies. Groves and Paterson (1991) responded by running the data set of 200 characters through the phylogenetic program PHYLIP and arrived at Groves's (1986) earlier conclusion. This result is not surprising, however, since Groves and Paterson used Groves' (1986) assessment of character polarity, which combined plesiomorphic with apomorphic features. Conroy's (1994) computer analysis delineated only the possession of ethmoidally derived frontal sinuses as being potentially synpomorphic of humans and the African apes.

Recently, Begun (1992; also Begun *et al.,* 1997) has argued that *Dryopithecus* and hominids via *Australopithecus* are synapomorphic in having a swollen glabellar region and continuous, barlike supraorbital tori. Andrews *et al.,* (1996) expanded this potential clade to include the African apes as well as *Ouranopithecus* (= *Graecopithecus*) (see also Dean and Delson, 1992). It is, however, the case that neither *Australopithecus* nor any other hominid can be described as having a barlike supraorbital torus (*Homo sapiens* typically has no supraorbital distension of note) (see review by Schwartz, 1997; also Kimbel, 1986). Indeed, the configuration of the supraorbital region of *Australopithecus* and *Paranthropus* is unique among hominoids and anthropoids in general (Clarke, 1977; Kimbel, 1986; Schwartz, 1997). In addition, barlike supraorbital regions are more accurately described for many cercopithecid taxa, both fossil and extant (Schwartz, 1997). The supraorbital tori of *Pan* and *Gorilla* tend to be more undulating, often dipping down slightly in the region of glabella and

curving gently over the orbits and down the side (ibid.). As for the fossils, the Rudabányan *Dryopithecus* frontal (RUD 44) may have low but well-defined temporal lines that course up from behind the lateral orbital margins and converge slightly toward the midline—a configuration that also describes the orangutan, *Sivapithecus, Ankarapithecus, Lufengpithecus,* and various other taxa, including australopiths (cf. Clarke, 1977; Kimbel, 1986; Schwartz, 1990, 1997)—but this does not mean that it had a torus of any sort. Indeed, the profile of this specimen, as is evident in Begun's (1992) illustration, clearly demonstrates the absence of surpaorbital adornment. RUD 77, a more gracile specimen, is even less convincing in these purported synapomorphies.

With regard to the presence of a swollen glabellar region, this is a feature that emerges during growth and is seen more broadly among extant (as well as extant-like fossil) anthropoid primates than just the African apes, and is also common among Plio-Pleistocene and various later hominids (with the notable exception of *Homo sapiens*) (Schwartz, 1997). A swollen glabellar region can be found among fossil anthropoids, including, for example, *Ouranopithecus, Afropithecus, Proconsul, Aegyptopithecus, Laccopithecus, Pliopithecus, Oreopithecus,* and *Victoriapithecus.* The widespread development of this feature among anthropoids emphasizes the symplesiomorphic nature of this feature. In his reanalysis of Begun's data, Conroy (1994) pointed out that Begun had actually based his assessment of character polarity on the assumption that *Pan* and australopiths were sister taxa.

The suggestion that *Ouranopithecus* (= *Graecopithecus*) can be linked to a presumed African ape-hominid clade is based on the interpretation of synapomorphy not only in glabellar and supraorbital, but also in subnasal region morphology (Andrews *et al.,* 1996; Dean and Delson, 1992). Although Dean and Delson argued that this fossil hominoid shared with an African ape-hominid clade the apomorphy of a distended supraorbital torus with a posttoral sulcus behind, this configuration does not describe the australopiths, most other fossil hominids, or even *Ouranopithecus,* because a posttoral sulcus can only exist when the supraorbital region is distended superiorly (cf. Clarke, 1977; Kimbel, 1986; Schwartz, 1997). As discussed above, the swollen glabellar region of *Ouranopithecus* would be a plesiomorphic feature. The suggestion that the subnasal region of *Ouranopithecus* is African ape-and hominid-like (and thus synapomorphic of them all) is an extrapolation to the development of klinorhynchy that is supposed to be reflected in the possession of "a prominent surpaorbital torus, prominent glabella, shallow supraorbital sulcus, and the development of frontal sinuses" (Andrews *et al.,* 1996: 180; also see Shea, 1985). Clearly, these features do not describe the many non-hominoid anthropoids, as well as of the prosimian *Daubentonia,* which Shea (1985, 1988)

also depicted as being klinorhynchous. Since the presence of a sinus in the frontal region does not de facto signify that it is ethmoidally derived (see Schwartz, 1997), and it does seem that, as in *Sivapithecus* and *Pongo*, the "frontal" sinus of *Ouranopithecus* as well as *Dryopithecus* derives from expansion superiorly of the maxillary sinuses (see Schwartz, 1997 for review; also Brown and Ward, 1988), the latter configuration may indeed by synapomorphic for these hominoids, which we might, therefore, refer to as an orangutan clade.

This last point leads to the consideration of another, albeit typically disregarded (e.g., Andrews, 1982; Andrews *et al.*, 1996; Begun, 1992; Groves, 1986; Kelley and Pilbeam, 1986), theory of relationship among hominoids: namely, that hominid (= australopith and *Homo*) and orangutan clades are sister taxa (e.g., Schwartz, 1984, 1986a, 1988). With regard to the extant taxa, a survey of Schultz's (e.g., 1936) and Groves' (1986) data yield a plethora of potential synapomorphies that far exceed those that might suggest the relatedness of humans with the African apes collectively or with either *Pan* or *Gorilla* alone (Schwartz, op. cit.). More recently, Thiranagama *et al.*, (1991), who demonstrated that humans and orangutans uniquely share a particular pattern of superficial veins of the forelimb, had to admit that, even if Groves and Andrews had correctly rejected some of the more than three dozen potential synapomorphies between *Homo* and *Pongo*, there were still minimally twelve that resisted falsification (thirteen including their own discovery). Thus, of the competing theories of possible relationships among the large-bodied hominoids, that of *Homo* and *Pongo* as sister taxa emerges as the most robust (i.e., supported by the most synapomorphies). Even Beynon's *et al.*, (1991) assessment of molar enamel thickness delineates humans and orangutans as distinctive in their development of this feature (in contrast to the primitively thin-enameled *Pan* and *Gorilla*). And if distinctiveness leads to recognition of synapomorphy, then this dental similarity between humans and orangutans is potentially phylogenetically significant.

Without reviewing here all of the historical background to, or morphological evidence for this latter theory of relationship, it should be pointed out that the consequences of accepting it are less profound than accepting any alternative. For example, even if the ethmoidally derived frontal sinuses of African apes and humans are homologous (but see discussion in Schwartz, 1984), the multifocular ethmoidal sinuses of these three hominoids, as well as the various other features that would support specific combinations of these taxa would, of course, have to be interpreted as either primitive retentions or homoplasies. But the same logic would demand that the far greater number of potential synapomorphies of *Homo* and *Pongo* would also have to be taken as either primitive retentions or homoplasies. Clearly, the latter proposition has not been

seen among paleoanthropologists as a major obstacle, largely because of the supposed historical demonstration by Huxley and Darwin of a relationship between humans and the African apes, as well as because of the weight of the molecular studies of more recent vintage—in spite of the fact that the morphologists who embrace a human-African relationship of sorts acknowledge that the anatomical basis for any version of their relationships is scanty at best (e.g., Andrews, 1987, 1992; also see discussion in Conroy, 1994).

The reluctance even to consider that the orangutan might be the sister taxon of *Homo* is, however, deeply rooted. An interesting historical note to this effect is that when paleontologists were considering that there had been a thick molar-enameled group of Miocene forms from which the proper thick-enameled hominids evolved, the orangutan also emerged as having thick molar enamel (e.g., Kelley and Pilbeam, 1986; Martin, 1985). But since, first, the great apes were thought to constitute a clade and, then, the African apes were seen as most closely related to humans, the potential synapomorphy of thick-enameled molars that would group *Pongo* with the hypothesized extended hominid clade was rejected as a parallelism (i.e., homoplasy) between these hominoids. When it became apparent that *Sivapithecus* (including the subsumed *Ramapithecus)* was the possible sister taxon of *Pongo*, thick molar enamel was then claimed to have been present in the last common ancestor of large-bodied hominoids. Thus the possession of thick molar enamel became plesiomorphic within this group, and thin molar enamel secondarily derived and synapomorphic for the Africa apes. Since, however, one systematist's primitive retentions or homoplasies are another's potential synapomorphies, a working hypothesis that could have been considered is that all thick-enameled hominoids constitute a clade (see discussion of Beynon *et al.*, 1991)—which, would, of course, exclude the African apes from any particularly close relationship with humans. Clearly, as history reveals, this would not do.

As has been known for some time now, hominids, *Pongo, Sivapithecus, Gigantopithecus, Ouranopithecus,* and even some *Dryopithecus* (e.g., "Rudapithecus," "Hispanopithecus") have thick molar enamel (the latter point further emphasizing the possibility that *Dryopthecus* is a paraphyletic assemblage). If we take this as a potential synapomorphy, which from comparison with other primates seems reasonable, then the features that are shared uniquely by humans and orangutans also make sense in terms of synapomorphy. Within this clade, the fossils mentioned appear to share a hierarchy of synapomorphies with the orangutan (see reviews by Schwartz, 1984, 1988, 1990, 1997). Excluded from this larger orangutan-hominid clade are the African apes and all other Miocene large-bodied fossil hominoids, none of the latter of which present evidence of special relatedness to either *Pan* or *Gorilla*.

Taken from the perspective of the hominid clade, these proposed relationships are not terribly outrageous, especially when dental, particularly molar, morphology is considered. Historically, specimens that have been regarded as being hominid, upon close scrutiny, have been found to have extraordinarily orangutan-like dental morphology. In the case of isolated, low-cusped and thick-enameled teeth from middle-to-late Pleistocene deposits in Vietnam that had been allocated to *Homo erectus*, most could not be confirmed as being "hominid" in the traditional sense (Schwartz *et al.*, 1995). Rather, as in the analogous situation with the isolated, supposed *Homo erectus* teeth from Sangiran (Grine and Franzen, 1994), but more in the extreme, most of the Vietnamese "hominid" teeth emerged as being extinct species or subspecies of *Pongo*. In addition, a large number of these Vietnamese "*H. erectus*" teeth were referable to a new genus and species of hominoid that can be characterized, of course, by its simultaneously orangutan- and human-like molars. A similar situation applies to the Longgupo specimens—a mandible and two preserved teeth—which had been equivocally attributed to either *H. habilis* or *H. ergaster* (Wanpo *et al.*, 1995). However, aside from the molar being low cusped and apparently thick enameled (although it was originally described as being thin enameled), there is nothing specifically hominid about it (Schwartz and Tattersall, 1996, and recent observations). In addition, if the teeth (especially the cheekteeth and canines) of South African species of *Australopithecus* and *Paranthropus* as well as of East African *A. afarensis, A. anamensis, P. boisei, P. aethiopicus,* and even *H. habilis,* are appreciated on their own terms and not in the context of a presumed theory of hominoid relationships, it becomes patently obvious that, beyond being generically hominoid in dental morphology, they are essentially orangutan-like in specific morphology; that is, the comparisons are not unfavorable with *Sivapithecus, Gigantopithecus, Lufengpithecus, Ouranopithecus,* various extinct species and subspecies of *Pongo,* and even specimens of extant *Pongo* (Schwartz, 1990, 1997; Schwartz and Tattersall, in preparation). StW 252 stands out as a good example of a hominid that is particularly orangutan-like in dental and even somewhat in facial morphology (Schwartz and Tattersall, in preparation), and the newly discovered StW 573 is also significantly orangutan-like in major aspects of its postcranial skeleton (R. Clarke, personal communication). Interestingly, these observations, although updated with newly discovered fossil specimens, are strikingly reminiscent of past arguments that sought to link, for example, Indo-Pakistani "*Ramapithecus*" (Lewis, 1937; Simons, 1964) and *Sivapithecus* (Pilgrim, 1915), *Gigantopithecus* (Pilbeam, 1970), some Rudabányan *Dryopithecus* (Kretzoi, 1975), and Lufeng "*Ramapithecus*" (Wu *et al.*, 1981) with hominids. The case is further highlighted by the debate between Pilgrim (1915)

and Gregory (1915) over whether *Sivapithecus* was more human- or orangutan-like in dental morphology.

The discussion of the relatedness of the orangutan clade to hominids aside for the moment, it is worth noting that, of the large-bodied apes, *Pongo* is the only one with a fossil record. Although the maxillary fragment from the Samburu Hills, dubbed *Samburupithecus* (Ishida and Pickford, 1997) has been cited as being related to the African apes because of its elongate upper molars, this description only pertains to *Gorilla*. This general similarity notwithstanding, there is nothing compelling about this latter possible relationship (personal observations). At the other end of the spectrum of large-bodied hominoids, the fossil record of potential sister taxa of this clade, or even of the clade of all extant hominoids, is continuing to be expanded. For example, the newly named genus *Equatorius* (the type of which had originally been part of the hypodigm of a species of *Kenyapithecus*, but which is now represented by many dental, gnathic, and postcranial specimens) has been described as one of a number of somewhat enigmatic, "basal" hominoids (Ward *et al.*, 1999). So also, for example, have *Gryphopithecus, Otavipithecus* (but see earlier discussion), and the unnamed taxon from Pasalar. Clearly, this attribution does nothing to clarify hominoid relationships. But if, as Ward *et al.*, (1999) suggest, *Equatorius* is related to *Afropithecus* (to which the formerly *Proconsul*-identified Moroto palate, sometimes referred to the genus *Mabokopithecus*, may be allocated), then this group may be the sister taxon of the clade that includes all extant large-bodied hominoids (cf. Schwartz, 1997).

The present situation, with the proliferation in recent years of recognized Miocene taxa, surely reflects a state of taxonomic diversity that would not necessarily lead to the prediction that hominoids all but went extinct by the end of this epoch. This, however, is precisely the scenario that has dominated paleoanthropology and hominoid studies in general: after the Miocene, most hominoids died out, leaving only the living forms and a restricted succession of fossils hominids. Even Dobzhansky and Mayr's stranglehold on the study of hominid evolution can no longer be sustained. Wood and Collard's (1999a, b) argument for recognizing not only many species within the genus *Homo*, but also the inconsistency of referring all of these taxa to this genus, highlights problems inherent in treating hominids as if they were exempt from both nature and rigorous systematic scrutiny. This point is further emphasized by a review of the African *H. ergaster* and Asian *H. erectus:* not all specimens typically relegated to each species can be accommodated cladistically therein (Schwartz and Tattersall, 1999a, b). Indeed, it appears that KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000 represent separate taxa, as also do the specimens from Trinil and Sangiran, Zhoukoudian, and Ngandong (ibid.). Equally obvious, even given non-cladistic approaches to sorting

out relationships and assuming that the species are viable as currently designated, is that the taxon *Australopithecus* is not monophyletic (e.g., see Lockwood and Fleagle, 1999).

CONCLUSION

So, where does this leave us? In terms of the overall concerns of this conference, which are embodied in the title "Taxonomy and Systematics of the Human Clade," I would suggest that an attempt to solidify a classification of Hominoidea would be premature for the very obvious reason that the potential clades and the relationships of taxa within clades need to be more clearly delineated on the basis of potential synapomorphy. With an interest in minimizing miscommunication, the simplest approach would be to continue to use the taxon Hominoidea and subgroups with the broadest meaning and even, perhaps, with more historically traditional usage. I suggest this in order to expand what has become commonplace: i.e., the inclusion of the African apes and some number of Miocene taxa in the family Hominidae to the exclusion of the orangutan and its clade, which is often identified as Pongidae. But the continued use of a classification that emphasizes one scheme of relationship over alternatives can only and negatively restrict fresh and perhaps even unconventional reconsiderations of the systematics and phylogeny of the group and its presumed members. As so often happens, once one particular arrangement of taxa becomes immortalized in a classification, the classification wrongly takes on the aura of a phylogeny. The rest is obvious: any future work will be constrained by these historically but not necessarily phylogenetically predicated biases.

In spite of a reasonably long history of attention given to hominoid systematics, it is obvious that only now, and in very fundamental ways, are questions being asked of both the specimens and the data. New analyses that apply cladistic methodology to the recognition and systematic and phylogenetic assessment of hominoid and specifically hominid relationships are showing more convincingly than ever that the unnatural taxonomic truncation of hominoid diversity that occurred from the 1940s through '60s was certainly the "dark ages" of primate systematics. However, we still have a long way to go in reconciling approaches to analyzing morphological and molecular data. For one thing, it would seem that the current state of affairs—especially with the diametrically opposed "methods" for delineating synapomorphy in morphological and molecular studies—is counterproductive. Theoretically, one would think that the same methodological procedures should be applicable regardless of the source or type of data. And, if there is anything worthwhile about a cladistic approach, it is in recognizing that overall similarity is not, certainly not a priori, a reflection of closeness of relatedness.

Before we become too complacent about our sources of comparative molecular or morphological data, we should be aware of advances in the fields of developmental biology and genetics that will forever impact the ways in which we think about these data and even the processes of evolution. At base is the fact that the morphologies we analyze are the products of cascades of protein communications that begin with regulatory genes and end with structural genes. For the study of morphological "morphology," this presents an interesting analytical situation, but at least we can predict that the similarities and differences we see between taxa are the result of gene regulation. A taxon—for example, the orangutan—can be different from others—say, humans and the African apes—for various reasons: it is either more primitive or autapomorphic in the feature being compared. In the case of the former possibility, a regulatory change would have "made" the hypothesized common ancestor of humans and African apes different. In the case of autapomorphy, a regulatory change "made" the orangutan different. Without knowing the details of the mutations that have affected regulatory genes (e.g., mutation being broadly defined as effecting, for example, promoter or enhancer genes, transcription factors, or regulatory genes themselves, or even being the effects of such elements as retrotransposons), one can still sort out character polarity and generate alternative theories of relatedness using a cladistic approach (Schwartz, 1999b). What becomes even more interesting is considering that homoplasies could very well be caused by the same, fortuitous combination of regulatory interactions (Schwartz, 1999c).

For the study of molecular "morphology," recognizing a hierarchy of genetic levels of significance poses a different and potentially troublesome problem. At present, molecular data are typically obtained through the delineation of gene products (proteins), structural genes, non-coding regions (introns), or larger essentially undefined "units" (e.g., on chromosomes). Theoretically, one should be able to apply a cladistic analysis to any kind of data that can be concretely compared between taxa. But until the comparative database is representative of a broad suite of low-level taxa, the assessment of character polarity will be compromised. Another issue to consider, however, is that since noncoding regions, by default, tell us nothing about the working biology of a eukaryotic organism (the assumptions of being invisible to selection and thus revealing true phylogenetic relationships set aside for the moment), and gene products tell us only which underlying controlling genes may be active at a given point in development (which, if studied in the adult, do not reflect any development that went before), it might be more productive to investigate at the regulatory level. This course of action would require sampling at different ontogenetic stages in order to identify those genes (as well as their timing and interaction) that actually contribute to the formation of a

feature, and it would be at least a start in trying to determine at the molecular level whether differences between taxa are the result of primitive retention, synapomorphy, or autapomorphy. One has to study different ontogenetic stages because certain genes will only be active during the formation of a structure, not necessarily in its maintenance thereafter. And, of course, in order to pursue a cladistic analysis, one would still need a broad comparative base in order to determine character polarity.

Perhaps the protocol I have sketched out will seem too difficult to enact or even unnecessary. The former reaction is not relevant if the goal is to understand evolutionary processes and the pattern of evolutionary history. The latter sentiment could only reflect the need to do that which seems "unnecessary." For when we begin to think that we know the general picture and that we need only sort out the finishing touches, we are surely far from actually doing so.

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