
PROBLEMS WITH HOMINID FOSSIL SPECIES TAXA AND THE CONSTRUCTION OF TAXOGRAMS

FREDERICK S. SZALAY

ABSTRACT. A variety of topics which play important roles in the systematics of fossil hominids are discussed. One of the major ontological/theoretical issues that influence the empirical work of species level taxonomy concerns the assumption that fossil hominid samples can be axiomatically considered terminal taxa. Another axiomatized practice is that of employing operational taxonomic units (OTUs) whereby nearly all samples of any level of distinction are considered valid species taxa. These unsubstantiated assumptions, coupled with punctuationist notions of species origin, intertwine to form a practice which results in a taxonomic distortion of what the probable evolutionary realities of evolving lineages were. The selection of extant taxonomic model species for delineating hominid species taxa has been a major issue of contention, and it will continue as long as observed ranges that include all known populations of any one single living hominoid model species continue to be ignored. Paleontological species taxa do not necessarily represent new lineages, but the iconography of taxograms (based on the practices noted) which routinely assume the latter to be phylogenetic trees imply a multitude of closed lineages. Such imagery is probably much more of an artifact than a tested reality of hominid evolutionary history. Examples are discussed.

KEY WORDS. Taxonomic assumptions, phylogenetics, punctuationism, species taxa, lineages, paleoanthropology, stage vs. grade.

If a taxon is defined (as a morphospecies) in such a way that it coincides with the phenon, the taxonomist may facilitate the task of sorting specimens, but this activity will result in species that are biologically, and hence scientifically, meaningless. The objective of a scientifically sound concept of the species category is to facilitate the assembling of phena into biologically meaningful taxa on the species level.

Mayr and Ashlock (1991, p. 24)

INTRODUCTION

Paleoanthropologists are in a unique position, and in terms of fame (or notoriety) researchers who write about any aspect of human evolution

Anthropology, Hunter College, CUNY, and Ecology and Evolutionary Biology, CUNY, New York, NY 10021, USA. / fszalay@hunter.cuny.edu

occasionally attain an exceptionally high profile in the public eye. This is primarily because they are investigating our ancestors and closest relatives, an area that is of justifiably wide public concern. Compared to studies on other fossils (e.g., bony fish, Cretaceous ammonites, various mammals such as rodents or bats,) paleoanthropological research, like the study of dinosaurs, may carry considerable benefits. (Nevertheless I do not subscribe to the recent self serving and somewhat petulant characterization by White, 2000, that the field of paleoanthropology consists of “scientists” vs. “careerists.”) But either actively sought after or unwanted social recognition, and sometimes potential profitability, can result from the study of hominids, because this endeavor is tied to a universal human curiosity about our “roots.” There are also pitfalls that may accrue, which range from an ongoing and constant media-based scrutiny to an occasional discipline-specific myopia. As the adage goes, there are also probably more paleoanthropologists than useful hominid fossils, with a variety of consequences regarding the accessibility of specimens for study and the enormity of literature.

Nevertheless, paleoanthropologists can be one of the standard bearers for an appreciation of scientific evolutionism in the public eye, and also effective advocates for a clearly enunciated theory and practice of phylogeny estimation rooted in all aspects of biology, paleontology, and well-tested Darwinian theory. Because paleoanthropologists, particularly those interested in the taxonomizing of hominid history, scrutinize details of a fossil record of relatively short duration, they are in a potentially excellent position to fully utilize the species-lineage concept of evolutionary theory. Yet this area of systematics is the most contested in all studies related to fossil hominids.

The time span focused on in paleoanthropological inquiries is relatively short, not more than five to six million years. Such a duration is a real chunk of deep time, with its full advantages to be able to track change and diversity in space and time, and it also holds the promise that many of its details will be increasingly recovered. The knowledge of fossil faunas and their increasing fossil hominid content, often well dated even by relative biostratigraphic means, is improving at a rate that no neontological endeavor relevant to the systematics of the family can equal for generating new information, statements regarding molecular phylogeny studies notwithstanding. Yet, as I discuss below, major controversies exist in the evaluation of the diversity of fossil hominids, with the estimation of their phylogeny, and also with the variational taxonomy within other mammalian species in the hominid-bearing faunas (see the seminal study and the goals prescribed by Grubb, 1999, in his review of the distribution of selected African mammals).

But judging from the most recent high profile publications of this popular discipline, an amalgamation of tested evolutionary theory into practice, full use of the paleontological method based on extant species variation, and a taxonomic practice that should derive from these do not often show up in studies. In fact these reflect an ongoing schism in the interpretation of the fossil record. There are, as part of the theoretical orientations, often affiliation- or other loyalty-based partisanships, inter-necine squabbles that reflect views on species/lineage concepts, the species taxon, taxonomic practices, and attitudes regarding the expanding Modern Synthesis. All of these factors are also coupled with punctuationalist assumptions about fossil species taxa using a variety of what I consider questionable applications: the axiomatic use of the "terminal taxon" and OTU perspectives. These factors clearly obfuscate advances in the understanding of hominid evolution.

It is proper to review at the outset of this paper what some of these operational concepts mean as they are fundamental in species level taxonomy of hominids and other groups. Schuh (2000, p. 19), in what I consider a logical positivist (and empiricist) text on cladistics, artfully (and in a revisionist manner) defines the concept of the terminal taxon as "a group of organisms that for the purposes of a given study is assumed to be homogeneous with respect to other such groups." This version of a concept that was originally intended to designate the taxonomic expression of the end of a lineage or clade (e.g., living mammal groups are the terminal taxa of the Mammalia) is no different than the pheneticist operational concept of a sample, the operational taxonomic unit, or OTU. Such units simply signify samples ranging from (often only part of) an individual specimen through samples of demes and populations, all the way to the combined representative samples of well-sampled series of populations of an extant species. The designation "homogeneous" is, unfortunately, plainly vacuous, as it carries no indication that sample variation is in any way tied to that expected for the characters used in well-researched and contextually relevant model species taxa. In a more general and proper way, which is not relevant to this discussion, the OTU concept can also stand (more meaningfully) for supraspecific taxa when higher-level relationships are investigated. But given the elasticity of the basic operational concepts that are used by different researchers in paleoanthropology, even seeming agreements between review papers on the taxonomy of hominids such as those of Howell (1996) and Tattersall (2000), for example, both participants at the Palma conference, have major undercurrents of disagreements.

In this paper I discuss a few basic facts and areas of endeavor, and my own theoretical and empirical interpretations of these, which may have some relevance for hominid history. At the risk of belaboring this point,

this history should be an important intellectual goal for humanity, a central issue on which all participants of this conference agreed. I outline some of the factors that I believe to characterize, and sometimes also set aside, paleoanthropology compared to such related disciplines as, for example, molecular taxonomy. My brief discussions attempt to address only a few general topics in paleoanthropology, problems that are also issues in systematics in general. Yet, as the quote from Mayr and Ashlock above suggests, the “species problem,” and even more so the lineage issue, lie at the very heart of the practice of paleoanthropology (including the idiographic, and decidedly not nomothetic, nature of rates of evolutionary change, White, 2000, p. 289, notwithstanding, to cite merely one paleoanthropologist disciple of punctuationism). In addition to the species-cum-lineage identification and its delineation in the fossil record, analyses using the taxogram approach dealing with designated species taxa of the fossil record are often also issues of contention. A taxogram is a cladogram with a customary representation of the hypothesized splitting relationships of species taxa or higher category taxa in an atemporal “tree.” A taxogram axiomatically bars lineage representation of successive species taxa. It is a fundamentally truncated iconography of phylogeny.

I am not a specialist in paleoanthropology, and in spite of my broad acquaintance with some of the record and a modicum of research in that area, and the publication of a few papers on hominid evolution, I would never claim that I know better than the colleagues I disagree with in this paper. But I do believe that I know differently some of the pivotal issues, and perhaps that gives some level of legitimacy to my discussions that follow. Also, as a final preamble, I would like to state that there are no zoological priority rules which dictate that the family Hominidae must include other than living humans and their bipedal relatives, no matter how closely related we are to the great apes (*contra* Howell, 1996, p. 5). The level of investigation, focused on a morphologically only modestly diverse mammalian family (the conventional notion of Hominidae that I would diagnose by the origins of bipedality, an attribute testable by fossil evidence), also requires the collection of important contextual data about paleoenvironments, faunal and floral information, biogeography, and sundry aspects of taphonomic factors. These are critical components that are essential to an understanding of hominid evolutionary history (e.g., see contributions in Bromage and Schrenk, 1999).

MOLECULAR SYSTEMATICS AND BEHAVIORAL FIELD STUDIES

For vast numbers of species and groups without a fossil record, or for morphologically similar species groups, molecular approaches have been indispensable and continue to clarify a universe of relationships and

population dynamics often unattainable morphologically. The importance of these endeavors for understanding extant biological diversity cannot be overstated. Molecular taxonomists, however, are axiomatically (and often, in an outright manner, arrogantly) blind to the temporal and, therefore lineage-related, aspects of paleontological data. There are some rare exceptions to this generality from the part of molecular phylogenetics, but one time-related issue that continues to challenge the value of some molecular studies is the often highly contested (fossil-based) molecular clock calibration of phylogenetic events. Paleoanthropologists, like other paleontologists, however, have available a rapidly increasing record with specific time values, coupled with a diversity and geographic context not available to neontologists. Such factors as unique population and quasi-species level morphological units and their time and place contexts are not merely equivalent to the data extracted from living representatives in testing hypotheses of phylogeny. Such factors are often far more relevant for explanations of the phenotypically detailed and causal aspects of evolutionary history than neontological data. This is so in spite of the conformist denial of the uniqueness of the fossil evidence by some atemporally disposed cladistic systematists (many paleontologists as well) who work on fossil material.

A recent, and high profile, example of this time-blindness phenomenon is the book by the science writer and editor of *Nature* magazine, H. Gee (1999). Gee's bizarre, but nevertheless "proper" notions (within the present atemporal zeitgeist of parsimony-based cladistic systematics) reflect his nomothetic fervor when he simply denies not only the ontological importance and epistemic usefulness of any concept of ancestry, let alone specific ancestral species taxa, but also the scientific value of historical-narrative explanations. Gee's popular book echoes, with variation, the early and trend setting prescriptions of Eldredge and Cracraft (1980) for an alleged scientific propriety in the practice of phylogenetics. The latter book established a strong link between punctuationism and the taxonomic practice of current parsimony-cladism (see Schuh, 2000). This perspective (studiedly substituting "subjective" for individual contributions which are objective and scientifically testable) became connected and reinforced by views that have come to reject analysis of characters independent of parsimony procedures.

While molecular phylogenetics has been exceptionally helpful in delineating relationships of closely related extant primate and other taxa where morphology has failed, it is a general canard perpetuated in the literature that, for example, primate family relationships have been also "decisively" determined by various molecular studies. Comparative anatomy and fossils have been far ahead in such areas of endeavor by many decades, and this continues with advances in the paleontology of that

order. The achievements of molecular phylogenetics in mammalian higher taxon studies, for example, cover a huge and confusing spectrum with some astonishing claims that have grown out of some perplexing methodological manipulations of raw data (see reviews in Szalay and Schrenk, 1998; Szalay and Sargis, 2001).

Whereas the data of molecular systematics point specifically to the closest affinities of humans with African apes, more particularly with chimpanzees (after much debate in that field), one should not forget that by 1871 Darwin (even without a fossil record) surmised almost that much about the African roots of humankind. Increasing understanding of field observations of behavioral strategies of gorillas and chimps also give unequivocal support for a chimp-hominid clade, independently from other subdisciplines. This has enormous significance for the behavioral and paleobiological reconstruction of early hominids, and, as I suggest below, for choosing the great range of cranial diversity in that species as part of the taxonomic model for delineating hominid fossil species taxa. As I note in more detail later, it should also be considered that early hominids (e.g., *Australopithecus afarensis*) were probably more dimorphic in size than chimpanzees are today. The record of hominids also seems to be approaching the details of chimpanzee's osteology as one samples increasingly older fossils. Yet, the lack of a significant fossil record of the African great apes leaves morphology lagging beyond both molecular inference and explanations of behavioral strategies in regards to our specific ties to chimpanzees.

ONTOLOGICAL AND EPISTEMOLOGICAL PROBLEMS IN TAXONOMY

Conceptualization and attendant language that is involved in the description and analysis of fossils is usually taxonomic, but not evolutionary in a strict sense. Much of the communication about such issues is conducted through an increasingly, and sometimes unavoidably, jargon-ridden taxonomic vocabulary, with the dual danger of both a) a vague reification of obscure method-based concepts as evolutionary realities, and b) the taxonomic entities themselves becoming surrogates for process, i.e., real evolutionary events and dynamics. Such issues are particularly acute on the species and lineage level because there is no meaningful ontological difference between a biological species and its antecedent history (its lineage; see Szalay, 1999, 2000, for discussions). Nevertheless, in addition to distinct species in their "realtime" (i.e., their duration when delimited as a specific dimensional taxon), the conventions of taxonomic species designations (the multidimensional concept of Mayr, the lineage segment of Simpson, and the fuzzy set of Van Valen) are needed for purposes of communication (classification), particularly for well-tested lineages with

changing morphological patterns. A major confounding historical factor in this communicative labyrinth is the Linnaean heritage, which was never meant to deal with the classification of the seamless continua of stages of lineages that are occasionally recovered in the fossil record.

But from a theoretical perspective, as I explore below, all taxonomic species are in one form or another delineated segments of lineages, given the vertical continuum of descent. Consequently the artifices of classification of a continuum do not in any theoretical sense precede the evolutionary process itself, the latter being the combination of the mechanisms, their rate of effecting populations, and the generation of novelties through time and a highly specific spatial context that are expressed as the broad spectrum of anagenetic, cladogenetic, and intercalating (hybridizing) events. These factors alone require careful interpretation of issues when dealing with the morphological evidence of the fossil record. In turn, this renders paleotaxonomy secondary to an understanding of the evolutionary processes themselves, even if we phrase the events in terms of taxonomic language. The delineation of paleotaxonomy without theoretically steeped interpretations in this process is only mythically objective. Post-Darwinian taxonomic practice has always required the drawing of an artificial boundary vertically. Such actions were and are based on various scientific considerations, all of which reside in the availability of fossils and the interpretation of the lineage specific dynamics of the samples and their mostly adaptive (Darwinian) evolutionary dynamics.

THE NATURE OF KNOWLEDGE CLAIMS

Whenever knowledge claims are made regarding paleophena and their *process-based interpretation* such as “adaptive radiation, diversification, divergence, stasis, endemism, extinction, dispersal, and range extensions” (Howell, 1996, p. 10; and one should add rate of change of characters), it is important to be specific regarding the relationship of the phenomenon and the specifics of the type of samples assessed. Adaptive radiation is a concept usually restricted to lineages of full species, not to allopatric differentiation of populations of a species, or their larger cousins the subspecies. Diversification is a general term; it applies to the whole continuum from demes to populations, as well as to full lineages. Stasis in some hard parts (e.g., molar teeth, other skeletal elements, tissue characteristics, etc.) certainly does not mean that for the rest of the skeleton or for all soft anatomy. Mosaic evolution clearly addresses such problems (see later). Endemism, dispersal (geographical range extension is the same as the latter) on any level is difficult to gauge in the fossil record because stratigraphic evidence is often geographically restricted. Furthermore, statements such as “Evolutionary theory has now abandoned presumed

gradualism" (White, 200, p. 289) display not only ignorance of large segments of evolutionary studies, but show a studied disregard for Chamberlain's advice about the need for multiple working hypotheses, particularly in geology and paleontology. Multiple hypotheses are good empirics for all historical problems in science.

One would hope that the issue of progress (a much debated area of knowledge claim in the past, with different meanings to different contestants) has been put aside in paleoanthropological arguments by this time. The clear (albeit sometimes studiously contested) meaning of that concept in modern evolutionary theory goes back beyond the Synthesis to Darwin himself. Darwinian, contextual, progress of selectionally favored attributes (hence the organisms) is real (from lengthening the trunk of elephants to the displays of male peacocks, or to even seemingly "random" fluctuations of certain parameters plotted through time, but for which environmental context is missing), in spite of Gould's (1988, 318) eloquent, but highly agenda-driven polemics regarding the nature of evolutionary trends (but see Howell's, 1996, p. 10, endorsement). For Gould, linearity of lineages where stages can be designated as paleospecies (chronospecies) is anathema because it goes against one of his pivotal macroevolutionary views, namely that most evolutionary trends are statistical shifts in variance of punctuated species taxa (Szalay, 1999, and references therein).

Accusations leveled against "gradism," "stagism," or "transitionalism" (whatever these notions may mean) belie a perspective where the notion of knowledge is restricted to "factual" patterns, without regard to the dynamic relationship between objective evidence and their most probable (and theoretically meaningful) interpretations, depending on the nature of evidence and context, either inductively- or deductively-assessed.

Attainment of taxonomic and phylogenetic knowledge is a major area within which knowledge claims widely differ. As adherence to one or another form of logic of inference underlying knowledge claims is critical in the study of both species delineation and evolutionary history (phylogeny), this suffuses all aspects of systematics. One approach I subscribe to is a pursuit of truth content through probability-based analysis of biological and biostratigraphic factors of specific aspects of available extant species and fossil samples, all within the context of tested evolutionary theory. This is necessary in order to estimate species and their lineages, or reconstruct phylogenetic history, and subsequently to order supraspecific taxonomy accordingly (e.g., Szalay and Bock, 1991).

A different approach to phylogeny is to search for consistency and resolution strictly within a framework of one or another nomothetic system that orders the specific (idiographic) data through parsimony algorithms with the minimum assumption, namely that there was de-

scent. I believe that the pivotal notion of numerical cladistics, that a basically Darwinian (= adaptive) evolutionary transformation of variously designated morphological attributes can be validly tested through parsimony *at any level of the categorical hierarchies*, is fundamentally flawed (Szalay, 1994; 2000). The confounding issue is that parsimony analysis appears to give answers to problems for which valid answers often cannot be attained without independent character analysis. The choice for systematists is, therefore, whether historical-narrative accounts of contingent information (based on nomological-deductive foundations), or inductophobic, and solely deductive, approaches based on algorithm-mediated decision making about the relevance of data for analysis, should be the methods for revealing the connections between evolutionary units. The logical outcome of this latter Popperian proposition is to ultimately adhere to the consequence of algorithm-based analysis, which is that truth content as such is unattainable, and therefore irrelevant (e.g., Norell, 1996). I reject, along with Cartmill (1999), this Kuhnian approach to "truth-cum-nihilism."

As a relevant aside here, on the other hand, I categorically reject the general arguments by Cartmill (1994, p. 115), those reflecting his conversion to the taxic and circular view, that "homology is an essentialist concept; two things are homologous only if they are in some essential sense the 'same' thing and properly called by the same word" and that "[the] concept can be made intelligible in an evolutionary context only by giving it a cladistic interpretation that makes homology judgments dependent on the outcome of a phylogenetic analysis." Cartmill's surprising logical positivist stand of 1994 on cladism wedded to algorithms, one that posits access to a "falsifiable" cladogeny without the independent phyletic analysis of attributes, results in the rejection of what descent (usually) with adaptive modification means. (In fact there is an inconsistency in his response to Chamberlain and Hartwig noted above and his cladistic notions of "homology.") Given adaptive evolution, the fundamentally Darwinian analysis of the adaptive biology of organisms permits probabilistic assessment of homology vs. convergence. It is through such complex character analysis, and the fossil record when available, that particular states of attributes can be chosen or rejected for phylogenetic estimation (Szalay, 2000).

SPECIES AND SPECIES TAXA

The species concept is primarily of the domain of evolutionary theory, and not of systematics (Szalay and Bock, 1991). Demes, populations, or species (all evolutionary units) have the property of the frequencies and observable ranges of traits (alleles, morphological attributes, etc.). Individual specimens, therefore, cannot, and should not, set the limits for a

realistic estimation of fossil species taxa. Equally, for sound taxonomy, poor, often glaringly inadequate, samples of fossils should not set limits either. Ignoring this obvious factor, and presenting the complexity of alpha taxonomy in the often simplistic manner of identifying restricted OTUs and matching statistical aspects of these with, again, restricted extant species samples, results not only in an inaccurate estimation of species taxa or lineage diversity. It can also seriously distort the view of macro-evolutionary dynamics that the fossil record offers, i.e., what are the lineages and the real terminal taxa of a given fossil record, in this case of the Hominidae.

It is also widely accepted that delineation of a species taxon does not, in some ontologically meaningful way, sever it from its antecedents. This perspective is neither "stagism" nor "transitionalism." Species taxa are static and artificially (and properly) delineated empirical units (the multidimensional of segments of lineages), not indicators of either a continuity or its lack in a particular evolutionary process. Exceptions to this ontological perspective are the stand of punctuationism, and the complexly argued for thesis of the individuality of taxonomic units by Ghiselin (1997), often embraced by taxonomists. The taxon individuality thesis is sharply critiqued (as bionominalism) by Mahner and Bunge (1997). Ghiselin's position is based on an essentialistic ancient Greek metaphysics that has become inadequate for considering living organisms after 1859 (see also Bock, in press). The Darwin-Wallace discovery of variational evolution ushered in a need for a scientific metaphysics that was never within the reach of essentialist Greek philosophers. In such a metaphysics where individual organisms are indivisible although have *parts*, and are recognized as *members* of groups, should replace an "individual vs. essentialistic classes" dichotomy (Bock, in press).

It is also often completely overlooked that biological species taxa in their realtime diachronic frame are based on different criteria than paleospecies taxa, and therefore they are different kinds of entities. At best, the paleospecies taxa completely depend on the transfer of some measure or estimation of properties from extant species taxa that may help deduce reproductive, genetic, and ecological attributes for the fossil samples. Paleospecies, out of obvious necessity, are morphologically delineated units that should be based on some chosen model of a modern species within which the known extremes somehow set the boundaries of variation acceptable in the fossil species taxa (and on these points Howell, 1996, and I are certainly in agreement). It is of help that the clinal and regional patterns exhibited in the morphology of polytypic extant model species taxa can be often applied to a specific temporal, stratigraphic, framework. Such ranges of variation are critical yardsticks for gauging reproductive continuity within multidimensional fossil species taxa. How

well this inferential work is carried out, even though morphology is essentially the core data, becomes a measure of the (validity) reliability on any one fossil species taxon. This work becomes an indication whether the investigator is closer to delineating analogues of the relevant extant species, or even superspecies, encountered today, or prefers the archaic practice of a morphological species concept that has been so prevalent in the past in both mammalian and hominid paleontology. Robinson's (1956) classic study on australopith teeth and Miller's (2000) analysis of cranial variation in *Homo habilis* are exemplar studies in this difficult area of paleoanthropology.

SOME NECESSARY ASSUMPTIONS FOR DELINEATING HOMINID SPECIES TAXA

It has been stated recently in preambles and/or homilies dealing with taxonomic contributions in paleoanthropology that the hominid fossil patterns (i.e., species taxa) should be based on "biological processes" rather than some artificial perceptions. Biological processes, of course, produce individual differences, as well as deme, population, and species level differences in any one moment in time. Add to this the time successive complexities of populations of individual organisms that make up a lineage, or the regionally variable and temporally zigzagging various evolutionary units, and we have considerable complexities masked by "biological processes." Furthermore, in spite of the evocation of such proprieties, it is the right comparisons and acting on specific assumptions (either subconscious, unquestioned, or theoretically examined, and subsequently either discarded or accepted) that will, or will not, result in a meaningful delineation of a fossil species taxon (Szalay, 1993).

Taxonomists give species nomina to samples of fossil mammals (hominids included) based on what they consider an appropriate level of difference from other samples. As Howell (1996) reiterated recently, based on Simpson's (1963) schema of the structure (or "hierarchy") of the various levels, taxonomic assessment involves all levels such as individuals, demes, or increasingly more inclusive but reproductively connected populations, although not all of these are given formal taxonomic recognition in practice. Thus, the meaning of taxonomic statements, to use Simpson's phrase, is critical in describing the patterns of fossil samples and their *interpretation* in terms of specific taxonomy. The results of ignoring the different levels of taxonomic assessment and thus biology (as Mayr and Ashlock noted) would be not only taxonomic mayhem, but it would distort the evolutionary process that can be recovered from the record, the proponents of OTU philosophy notwithstanding. Pattern clearly needs interpretation! But criteria in delineation obviously vary based on underlying assumptions, and such assessments are theory-laden (in fact

they are drenched in theory). These criteria, therefore, are not only "factual," as some plaeosystematists would like to think of their enterprise. The biological significance (hence species level validity) of these operational taxonomic units (OTUs), beyond customary statistics, depends on the type of model chosen from among living species, and, particularly for fossils, also on both the stratigraphic record and the characters that are preserved and analyzed. In addition to the documentation and understanding of ontogenetic, individual, interdemic, interpopulational ("sub-specific") differences and the sexual dimorphism encountered in the polytypic extant models, the application of this knowledge to the fossil samples is critical in evaluating proposed species level nomina.

What does remain in common to the testing of validity of the two kinds of species taxa, the extant and extinct, however, is the need for sympatry. For extant species this is straightforward, and for proposed fossil taxa there is the conceptually almost equivalent requirement of lithosympatry. Broad stratigraphic synchronicity that usually involves distance and differences in realtime as well, however, are neither theoretical nor operational equivalents to the extant conditions of sympatry. Such scrutiny of criteria are obviously not particularly relevant to morphologically unquestioned units such as the fossils of a big cat and a hyena, to cite outlandish examples which occur in "roughly" equivalent beds. But the issue regarding species identification of close relatives based on pieces of the skeleton becomes a complex one, as the "obvious" is a slippery concept. Note, for example, the increasing range of differences between the morphological attributes of cranial ontogenetic polymorphism and sexual dimorphism in various specimens of Hanuman langurs, or between the crania of a small female gorilla and a large male one from either the same or different subspecies, or opposite sex cranial specimens of a drill and a mandrill, or of a mangabey and a female baboon, or the size incremental dental remains of an impala, wildebeest, and eland (see especially Albrecht and Miller, 1993, fig. 14).

It is only lithosympatrically clustered and adequate samples of specimens that can provide rigorously tested reliable answers for various quandaries in hominid systematics. To ignore this is to turn a blind eye to the fact that hominid species taxa of time successive periods usually differ in frequencies of incremental features only (or the reverse), various statistical assumptions and manipulations notwithstanding. As noted, the highly inferential issue of synchronicity of geographically and stratigraphically distinct provenance of specimens from different localities that may span up to hundreds of thousands of years without means to detect this difference does not suffice as a surrogate for lithosympatry. One of several such quandaries of hominid taxonomy, for example, is the assertion that a species level distinction is reflected in the specimen-specific

(preservational) and size-related (and probably sex-related) differences of the famous specimens 1470 ("*Homo rudolphensis*") and 1813 (*Homo habilis*), that I briefly discuss later (see also Miller, 2000).

The morphological attributes of hominids (within the complex context of often imperfect preservation) such as polymorphism, and functionally-modeled dimorphism (coupled with such unique manifestations of these organisms as tools, probably low population densities, and scattered distribution, judged by their fossil samples) render hominid taxonomy far more complex than the cook book methods culled from cladistic manuals. The hominid record allows glimpses at taxonomic species through time but, at the same time, also raises questions about restrictive OTU practices employed in hominid taxonomy that do not pay attention to these factors. Oddly enough, use of single specimens of all kinds of taxa when subjected to either taxonomic or phylogenetic analysis based on morphological generalities at a certain comparative level (genera, families, and even above) rest on far more secure theoretical and empirical grounds than what these same individual specimens or small fragmentary samples can offer for species level taxonomy.

Taxonomic species are often necessary artifices in a lineage context, as particularly well demonstrated by students of various fossil mammals where stratigraphic succession and the fossil record is carefully controlled and individual strata yielded large samples (see Rose and Bown, 1993, Redline, 1997, and references therein). Unlike neontologists, limited in their conceptualization of diversity of species taxa and expressed through Linnean taxonomy, paleontologists work with not only tested (sympatric) species and a variety of potentially untestable allotaxa, but also with stages (not grades) of the phylogeny of lineages. Paleontology, in spite of the nonsense rhetoric that is the ultimate logical exegesis of atemporal cladistic assumptions (e.g. Gee, 1999), can provide epistemological means to access a real history in the closest possible way adhering to evolutionary theory. This obviously does not mean a return to the notion that all hominid fossil taxa are merely "pseudoextinct" segments of a single hominid lineage (early, and effectively, rejected by Robinson, 1956). It does mean, however, that fossil species taxa should have *at least morphological equivalence to what are well-delineated species limits in extant biological species. It should not mean the shoehorning of coefficient of variation values of poor fossil samples into those of local population samples of today (see later)*. Still, there is often no real equivalence between fossil species taxa and modern ones tested by sympatry.

Populations or even demes can be loosely conceived as lineage segments because they are results of (incomplete) cladogenesis along a diachronic continuum of this phenomenon (see discussion of issues of anagenesis and cladogenesis in Grubb, 1999; Szalay, 1999). But to overlook

(and to fail to apply) the morphological limits exhibited by geographically widely separated samples of extant model species is a particularly confounding aspect of the practice of taxonomy in paleoanthropology. Modern species offer solid empirical information which demonstrates that most geographically widespread extant species are not only composed of polymorphic populations but are also polytypic, without deserving species level recognition.

It is now a well-established general observation that the early fossil hominids, both the gracile and robust lineages, display exceptional sexual dimorphism in their cranial size and morphology. Whether or not this phenomenon is due to a probably diet-driven alteration of the anterior (incisor-canine) dentition which had the consequence of obliterating ancient display differences in the relative size of the canines (and consequently augmenting the display features anew with size differences) is a moot point at present (e.g., Szalay, 1975). Nevertheless, the significance of such dimorphism in size probably also affected the range of morphological diversity in cranial structure, perhaps well beyond the living chimpanzees that are distinctly canine dimorphic. But such contextual aspects of morphology are not often considered in the paleotaxonomy of the Pliocene samples of gracile hominids.

When perusing the systematic literature of hominid alpha taxonomy of the past several decades one is struck how little specific character-oriented reference is made to the cranial polymorphism and polytypy of the combined known population samples of either *Gorilla gorilla*, or particularly that of *Pan troglodytes*. At the same time such unfortunate canards that "new techniques at classification" allowed us to recognize many new species of hominids is unwittingly perpetuated in deference to the activities of hominid taxonomists. Such notions presumably mean a combination of statistics and highly restricted OTU practices, and which, as noted already, morph into the "terminal taxa," the end of the lineage variety. What is fundamentally missing from such views, sounded by non-taxonomists regarding the business of species delineation of hominids, is an understanding that the fossil species taxa are based on choices of living models and specific theoretical evolutionary models of process.

I am particularly struck by the assumptions used in delineating fossil taxa based on a few cranial specimens. Such specimens are often distorted through plastic flow or need to be reconstructed from fragments, or are mandibular fragments that are frequently altered due to sundry diagenetic factors. For example, Wood (1993) in his detailed treatment of early *Homo* (*H. habilis* and "*H. rudolphensis*") has taken considerable pains to gather coefficient of variation statistics (CVs) for cranial samples of gorillas, chimps, and humans. He then compared these values with those obtained for the entire sample of the few specimens of early *Homo* and

concluded that, because the range of these values for a few attributes of the fossil sample exceeded those of the extant samples, this difference warranted two valid species taxa. (I am here discounting the postcranial evidence, which is not only scarce, but also highly variable ontogenetically and regionally in all known hominoid species known by fossils.) But what statistics and samples are compared do influence, and in my view either invalidate or justify, the process of statistical evaluation of samples for taxonomic purposes.

Wood (1993) compared large, local (meaning geographically relatively restricted), undistorted, morphologically and numerically internally well-graded (given the number of specimens) samples of one instant in time (Recent) that yielded the usual, relatively low, CVs in many instances. He then assumed that these values should hold for the heterogeneous fossil sample (an almost certainly deep one temporally) that is made up of a few cranial specimens, as if that was a "species level" (i.e., a particular sample level) entity comparable with his extant samples. But because the CV values were exceeded by some aspects of the fossil samples, the null hypothesis of co-specificity of the fossil samples was overturned, according to him.

The combined hypodigm of the null hypothesis taxon (i.e., of *Homo habilis*), however, was very unlikely a representative population sample, primarily because of paucity of cranial specimens, and because of the time and geographic differences between the specimens of the sample. Consequently if the criteria of comparison are not met, then there is no validity to the application of local CV values from extant samples (see especially Miller's, 2000, detailed analysis that contradicts Wood's conclusions from another perspective). As Redline (1997), Rose and Bown, (1993), and others have shown unequivocally, zigzagging of (at least mammalian) lineages is the rule rather than the exception. Given the context of paleontological considerations, the complex nature of morphological variation in species noted above (undoubtedly also in fossil hominids), the use of CV values (which are not size-independent; Polly, 1998) derived from local samples of extant populations is highly questionable.

The usage of CV values of *restricted extant samples* as models for gauging the validity of fossil species taxa is a modern quasi-equivalent of morphospecies typology. It is basically saying that certain morphs, translated into a tight range of values, are the measure of what one is likely to encounter if a species was sampled (with the geographic and time dimensions of fossil species taxa). This practice simply sets aside not only the polytypic nature of species taxa but makes no allowances for the temporal vagaries exhibited by virtually all lineages that have been studied to any degree in mammals. This is not a perspective unique to my critique. Major contributions on the nature of variation in geographically widespread

living species (e.g., baboons) by Jolly (1993), and particularly the manifestations of morphological variation in a sample of extant primate species carefully presented by Albrecht and Miller (1993), corroborate my stance both theoretically and empirically. Commenting in general on the misrepresentation of variation in the taxonomy of primates, Albrecht and Miller (1993, p. 147-148), in their seminal and data rich contribution on the geographical variation of skeletal (particularly cranial) features in primates note the following (with its full paleontological implications): “[these] results refute the assertions of those who claim ‘cranioskeletal differences between primate subspecies of the same species tend to be tiny, if observable at all’ and ‘sister-species within modern primate genera usually differ little in their skeletal and dental anatomies’.”

For assessing the taxonomic significance of the cranial evidence for early *Homo*, a measure (and qualitative depiction, when appropriate) of the extreme variants in proportions, general size, or brain size of *sample specimens representative of the entire extant model species (and not only samples of their selected local populations)* would represent a far more meaningful measure of species taxonomy than the CV statistics, such as those published by Wood (1993). Observed ranges and qualitative accounts come nearer to giving some biological significance than do other statistics to the temporally and geographically complexly sampled fossils that make up fossil species taxa. I emphasize again that fossil species taxa are not equivalent to samples drawn from recent local populations of polytypic species. Wood (1993, p. 494) makes the statement (puzzling, because as an anatomist he must be well aware of brain size variation in living humans) that: “[the] cranial capacity of early *Homo* is more variable (CV = 13.1) than one would expect for a single hominid species.” But what human sample, even a geographically restricted one, would lack the *relatively equivalent range* of the absolute values of 610 c.c. for *H. habilis* versus 737 c.c. of the “*H. rudolphensis*” sample (figures from Wood), even without recourse to regional, sex, and otherwise variously correlated, variation that undisputedly existed even in the late Pliocene?

PALEONTOLOGICAL SPECIES TAXA
ARE NOT AXIOMATICALLY NEW LINEAGES

Tying together “paleospecies” level cladistics, lineage choreography, with uncritical assessments of models constructed from samples of extant species taxa is a flawed practice in spite of the aura of “objectivity” that can cloak such efforts (see strong warnings raised by Albrecht and Miller, 1993; Jolly, 1993; Szalay, 1993). Yet such a *modus operandi* is often prominent and often endorsed in all of the literature that relies on the latest taxic views that advocate a plethora of species-lineage multiplicity in hominid evolution (e.g., Howell, 1996; Tattersall, 2000). Bushy hominid phylogeny

is likely to have existed on the population and demic levels, not on a level of fully evolved species lineages. In my view, perhaps the most fundamental issues surrounding hominid taxonomy are whether the observed range of morphological expression of relevant attributes within the combined known samples of either baboons (see Jolly, 1993), Hanuman langurs (see Albrecht and Miller, 1993), the still inadequately studied cranial and postcranial variational taxonomy of the chimpanzee (*Pan troglodytes*), or the single species of gorilla, are more appropriate models to judge hominid OTU variation in sample-defined usable traits, then the use of restricted local samples. Using restricted samples of humans as "models" is a taxonomic practice that appears wholly inadequate to me. Furthermore, the use of *Homo sapiens* as a model is meaningful only if the total current and at least past variation, down to at least 50 000-100 000 years, is well sampled and considered as representing the observed range (OR) limits in the morphological latitude of certain attributes. But to repeat, the ultimate test for sympatric lineage validity in paleontology remains the lithosympatry of two well delineated fossil samples as fossil species taxa. This assures that we do not name every sample of a polytypic lineage that is an expression of local geography and the zigzags of an evolving lineage.

Somewhere between untenable extremes of recognizing either "one lineage" or "up to twenty lineages and beyond" of fossil hominids in the last six million years, there is the need for some reasoned scientific judgment beyond statistics. In the non-monotonic logic of Darwinian systematics it does not follow that if some species show no morphologically meaningful differences (as, for example, in many regionally restricted sibling species), then slight differences within morphological samples in the fossil record justify species taxon level designations for these differences. Similarly, the extreme nineteenth century notion that every time one found a specimen, given the rarity of the fossil record, it was likely to represent a new species, is equally absurd. Yet, with the aid of punctuationist iconography, this old practice has its modern resurrection in the notion, and practice, that because one cannot appreciate deep time (it is so vast) and because fossils are so rare, any "homogeneous sample" (with its cloak of statistics chosen with disputable assumptions) is likely to be not only a new species but also a real terminal taxon.

Morphological polymorphism and polytypy in populations are widespread, even in our time slice, in primate and other mammalian species (see especially Albrecht and Miller, 1993). Judgment calls that minor morphological differences represent species level distinctions should be backed by not only selected statistics and uninterpreted details of fossils. A taxonomic position should be accompanied by the careful biological analysis of the details in the context of their place and time, with a full perspective on the nature and duration of the times sampled, the size of

the samples, the missing gaps, and most of all, a far fuller understanding of the morphological and biological intricacies of skeletal variation in the extant model species chosen. Even the gorilla and the common chimpanzee today display a largely relict distribution, and an undoubtedly diminished morphological variation within these two lineages. (In spite of some increasingly popular molecular assertions, I do not believe that populations of *Pan troglodytes* represent more than a single species.)

I will pose the following rhetorical questions (certain to be unpopular) regarding the species level taxonomic aspect of hominid phylogeny. Is it possible that many (not all) paleoanthropologists specializing in the taxonomic delineation of samples have a subconsciously vested interest in having their field to be as "speciose" (bushy in the full lineage sense) as the most extreme interpretation of the scattered and incomplete fossil record allows? In the early days of postwar (WWII) paleoanthropology, with its roots firmly entangled in cultural anthropology (in the United States at least), the single species lineage notion of hominid evolution (untenable from its very inception) lumped gracile and robust australopiths, and seemed to provide for many anthropologists a special importance to our "humanity." In contrast, the postmodern public transformation in our awareness about nature and ecology, namely that we are merely a part of a complex history of lineages, may be unwittingly facilitating another perspective. A view that we are a mere "twig" surviving numerous other "species" of hominids (axiomatically assumed to be independent lineages) may fuel efforts in the paleotaxonomic arena where the discovery of not only fossil samples, but the "revelation," due to "discovery operations" inherent in a strict empiricist and operational tradition, of new species-lineages is of special significance.

This approach to hominid fossils is also reinforced lately by the special agenda-laden taxonomic splitting that often happens in the service of conservation biology. While species discovery and delineation are fundamental in systematics, not all allopatric populations of a species represent what can be justifiably considered genetically closed separate lineages. Such populations, even when sampled and shown to have differences with new molecular techniques, or shown to have differing aspects of their behavioral repertoires, cannot be realistically considered distinct lineages, as would be two sympatric species.

THE INAPPROPRIATENESS OF GRADE, AND THE APPROPRIATENESS OF STAGE FOR TAXONOMY

The concept of 'grade', much in vogue during the first sixty years of the twentieth century systematics and evolutionary conceptualization, has come to be misused with the rise of cladistics in the partisan rhetoric of "classification wars" where it was constantly leveled against the "evolu-

tionists," the "gradists." It has also become so thoroughly conflated with the distinct concept of stage of evolution that even in paleoanthropology with its few lineages, grades instead of stages are discussed (e.g., Collard and Wood, 1999), or both grades and stages are considered inappropriate concepts (e.g., Howell, 1996). The concept of 'grade' is a useful *descriptive concept* used to refer to biological attributes of organisms that have been attained independently (with nothing "natural" about it in any phylogenetic sense). Its use for hominid taxonomy is perhaps well beyond its intended creation for discussing macroevolution of higher taxa, let alone species taxa. Simpson used it to describe a "mammalian grade" for various poorly understood lineages that may have crossed what he considered then as a threshold. Similarly, endothermy is often described as a grade obtained independently by various vertebrate lineages. Today we know that the mammals (wherever we draw the line with as strict a phylogenetic control as we can) are a clade, as are euprimates, anthropoids (there is no taxon "monkey"), or hominids, but that endothermy is probably independently attained. In fact the concept of "adaptive zones" (a descriptive conglomeration of "niches" of species, without any ontological substance of its own) has had some vague relationship to grades. At any rate, at least in the paleontological literature, grade has always referred to attributes of distinct lineages attained convergently (or in parallel).

The 'stage', however, is a theoretically concrete concept, meaning a particular stage of evolution of a particular lineage (which is not simply a clade that has taken on taxonomic significance). The stage concept simply refers to a segment of a lineage at a particular moment in time. In fact, all species are stages at any moment in time in their respective lineages. Recent species are truly terminal (as of now) stages of their lineages, and lineages (but not a species taxon) extend back into deep time either to the period of their furcation or beyond, depending how they are delineated—always artificially—because they are an unbroken continuum. By calling a group of fossil 'samples' (with a proper vernacular taxonomic designation) as representing a stage in the specific temporal span of a lineage (or even of a species taxon) is just as valid a time-specific descriptor as designating a species taxon nomen for these specimens. In contrast to the 'stage' concept, the 'grade' notion, while useful for a variety of discussions in comparative biology, is largely devoid of lineage specific, and therefore systematic significance. It is certainly difficult to see how it is useful in paleoanthropology unless we wish to return to Coon's taxonomic notion of *Homo sapiens*.

While strategies related to survival and reproduction can and did undoubtedly change within lineages (which evolved their attributes with varying rates, and subsequently displayed mosaic patterns), and the recognition of a certain magnitude of these can properly result in taxo-

nomonic species delineation (chronospecies), *there is no axiomatic connection between a change in adaptive and reproductive strategies that are fundamentally anagenetic on the one hand, and between the origin of new lineages on the other hand*, punctuationist assertions notwithstanding. To repeat, regional and expectedly polytypic (and often clinal) expressions of minor shifts in "strategies" (expressed morphological differences) within extant species are not acceptable criteria for taxonomic species boundaries. Nevertheless, distinct shifts in morphological expressions of such strategies (*judged to be sufficiently great*) are the most common, widely employed, and reliable hallmarks of supraspecific (genus, family, etc.) taxa in systematics, *especially in paleontology*. Thus, attainment of bipedality and the undoubted cascade effects of such altered biomechanics (see Szalay and Costello, 1991), unless shown to be a grade and not an apomorphy of the ancestor, is still the most widely useful and phylogenetically meaningful delineation of the stem of the hominid clade. This ancestral taxon was a stage in the unbroken lineage from a probably chimp-like ancestor to the Pliocene hominids.

ICONOGRAPHY OF PHYLOGENETIC HISTORY AND TAXIC DELINEATION

While the iconography of phylogenetic trees axiomatically depicts history with a time dimension, cladograms (as they have come to be defined in cladogeny analysis of taxa; taxograms) have the function to depict taxonomic units in an atemporal manner as noted before. Both these diagrams serve useful purposes in communicating hypotheses, when tested to various degrees and discussed in a text. The furcation sequence of cladograms-cum-taxograms is based on either putative or tested synapomorphies, although the nodes do not represent an antecedent segment of a lineage, which would be an ancestral taxon (either concretely suggested or hypothetical) on a tree. As a result of an atemporal (usually algorithm-based) sorting, the ancestral segments of a lineage on such a species-level taxogram may be somewhere next to (or in between) its descendants.

The temporally and morphologically combined analysis of species taxa, unlike taxogram approaches, express a far more precise (hence vulnerable) hypothesis in trees which can be based on the full Darwinian theory of descent. Phylogeny without time values, relative or absolute, and without ancestors and descendants, is an oxymoron. Furthermore, lines on taxograms, which represent no evolutionary process, are, to say the least, constantly confusing for either students or the intelligent lay public who are not part of the systematist guild.

The ancestral points of the lineages/taxa depicted on our trees would be, axiomatically, paraphyletic species taxa, were we to recover them in

the appropriate temporal position, corroborated by their morphological attributes. Subsequently any holophyletic classification on the species level in a family group (or within anywhere in the taxon "Life" itself) is patently impossible; it is another oxymoron as far as the theory of descent is concerned. For example, while delineating lineages such as the robust australopiths as *Paranthropus*, the consideration of a gracile australopith-*Homo* lineage as *Homo* might be reasonable. But a stage antecedent to such clades (other descendants of which may also appear collateral to these without any change), if recovered and named, must be truncated and thus this ancestral taxon is necessarily rendered paraphyletic. Because artificial cuts are obviously necessary in any taxonomy (except in the illusory practices advocated by cladistic classifications), delineating *Homo* (providing it is demonstrably a single stem-based concept) from *Australopithecus* is perhaps another not unreasonable solution based on some highly finessed adaptive considerations, if such is possible. Such a taxonomic action obviously retains *Australopithecus* in a somewhat modernized but traditional sense as a useful paraphyletic genus, a source for both *Paranthropus* and *Homo*. And on we go backwards in time rendering one taxon holophyletic at the expense of its paraphyletic roots. There is no escaping from paraphyly.

Like past lineage segments, or ancestors surviving contemporaneously with their descendants, most speciose genera are also paraphyletic; they will remain so, and would be so for the sheer practicality they provide, even if we knew the whole history of their evolution. In fact, the extant *Pan troglodytes* may be paraphyletic (if it were morphologically indistinguishable from its 5-6 million years old antecedent), and perhaps gave rise not only to *Pan paniscus* 1-3 million years ago, but to the first hominid as well, somewhere in the early Pliocene. The endless rhetoric about only holophyletic monophyla qualifying as "natural groups," and the consequent futile attempts to banish paraphyletic monophyla, is an ultimate expression of taxonomic sterility, and a sure sign that taxonomy without the infusion of evolutionary theory is disconnected from the reality of the evolutionary process. Some taxonomists, however, do not seem to mind a search for the nonexistent Holy Grail.

The known and well documented sequences of several fossil lineages (ranging from various planktonic foraminifera to ammonites, to various lineages of mammals such as fossil rodents, primates, horses, etc.) and the deductive consequences of tested Darwinian theory strongly suggest that successive chronospecies (fossil species taxa) must involve the phenomenon of overlapping frequencies of traits. Furthermore, modern developmental biology instructs us with increasing force that mosaic evolution, a long recognized objective pattern of macroevolution (and not a hoary old canard) results from differential evolutionary rates of character com-

plexes within single lineages. It is validated by the modularity of areas in complex organisms that are the results of instructions from independent homeobox-genes (Raff, 1996). Yet, largely to aid the proselytizing of the underlying monotonic logic of cladistics, but mainly because it causes discomfort to the “logical” sorting of characters, the concept of mosaic evolution is artfully redefined and explained away in the most recent textbook treatment of cladistics (e.g., Schuh, 2000, p. 69-70).

PHYLOGENETICS AND PALEOANTHROPOLOGY

I note here what I consider a major inadequacy in many recent papers dealing with the “phylogeny” of hominid “terminal taxa,” and some major flaws in both the methodology and the reliability of the products of various conceptual method-driven techniques. While the uncovering of patterns is of fundamental importance in any taxonomic endeavor, the justification of units depicted on a cladogram or tree (in particular regarding species taxa) should conform to some theoretically valid guidelines. But it is precisely where the now largely axiomatized cladistics applied to OTUs (of species and lower units) comes into an irreconcilable conflict with paleontology, in spite of various explicit or implicit efforts to hide this. The rhetoric surrounding the concept of “synapomorphy” also continues unabated in paleoanthropology as if all shared unique similarities (often minutiae) were automatically homologous in their origin. But the less complex the shared similarities are, the more probable it is that they are just as likely to be convergent as homologous.

There is no conflict with the application of cladistic analysis to most (but certainly not all) genus or family level taxa (providing the data is carefully selected, and the ordering and polarization of characters are based on valid character analysis rather than algorithms). But this cannot be meaningfully done with the demes, populations, and species that have a good fossil record without a major distortion of what the probable course of events was. Attempting a level of precision that these studies hope to reflect results in not only nonsense phylogenies, but it goes so far beyond the data as to distort the framework that is supposed to be the very bases for evolutionary history. Yet many paleoanthropologists continue this adherence to the doctrinal prescription of the various cookbook approaches that have sworn off the bad habits of time and ancestry, and are subject to parsimony decisions. Such practices (compounded by an occasional misuse of statistics regarding the nature of morphological variation) undeniably have a certain appeal. They are founded on the attractive pure vision of a monotonic logic-based nomothetic science that ignores the complex four-dimensional realities of the evolutionary process. However, as often stated before, this methodology only creates an artificial and deceptive pattern of the evolutionary process. In reality, the

latter is usually the story of polymorphic and polytypic evolutionary units changing or becoming extinct locally, intercalating, or just zigzagging through time. To add insult to injury, dichotomous cladistic classifications generated from taxograms, using the Linnean system that is incapable of expressing hierarchically the ties of taxa based on stages of lineages, results in a considerable obfuscation of evolutionary dynamics and the specific processes of evolving lineages. Some textbooks further this perspective in their depiction of hominid evolution where they simply turn such taxograms into mythical trees.

CODA

A number of powerful perspectives, namely punctuationism, parsimony cladistics, and a strict OTU approach, have created, reinforcing one another in a Kuhnian fashion, a formidable operational concoction, a pure empiricism that many in paleoanthropology have begun not only to practice, but to profess as the only avenue to understand evolutionary history. Added to this is a whole list of proscriptions by those who bemoan what they consider the remnants of the theoretical backwardness in the discipline of paleoanthropology. The evolutionary "orthodoxy" of the Synthesis is often the target of such attacks (e.g., Tattersall, 2000; and to a lesser degree Howell, 1996). Discontinuities of the fossil record have been fingered as proof for the punctuated appearance of fossil species taxa, following Eldredge and Gould, and such assertions also continue to parade the straw bogeyman of alleged rate-dependent Darwinian gradualism. Evocations of the punctuationist version of "gradualism," in spite of numerous rebuttals that have shown Darwinian gradualism to be rate-independent, continues to serve this rhetoric (e.g., White, 2000). The adaptive nature of speciation (the latter categorically, and wrongly, equated with morphological differences of varying magnitudes of phenon) is routinely questioned, and the Darwinian and (an expanding) Modern Synthesis-based perspectives are accused of being concerned only with linearity and ancestors. The concept of lineage diversity has been certainly given a new meaning when individual or population level differences have come to be called as evidence for successive and intensive adaptive radiations of lineages within the Hominidae. Anyhow, the most unfair of accusations has been that the Modern Synthesis somehow fostered a perception of human evolution where the direction of linear change is a long trudge towards some state of perfection. No one who read Simpson's (1949) *The Meaning of Evolution* could possibly level such charges against a then admittedly incomplete, but currently vastly expanding, Synthesis. Simpson, one of the architects of the much maligned Modern Synthesis, who reasserted what *Darwinian progress* really meant (independent of the various baggage tied to that word in the humanities and social

sciences), championed the notion of bush-like phylogenies, even if he did not consider every identifiable population sample a distinct and closed lineage.

The “minimalist” OTU practice, wedded to the axiomatic “terminal taxon” designation of samples, helps to generate complex hominid taxograms. But such topologies provide neither a framework for the pejorative “scenario” (i.e., history estimation in the parlance of taxogram practice that is relegated to the role of “story telling”), nor is it in any sense history. This practice on “species and lineage” level taxonomy is an expression of a full logical positivist (and empiricist) practice. A fossil OTU without the stringent biological consideration of researched variation in an entire and relevant model species is merely an axiomatized pattern, driven by its epistemic assumptions, but without the ontological roots supplied by relevant biological species. The taxogram based on such OTUs is a product justifiably called a “pretheoretical classification” by Mahner and Bunge (1997).

As one of the several antidotes to the analysis of atemporal perspectives of species taxa in the fossil record in the less high profile paleontological literature on fossil mammals, Redline’s (1997) detailed treatment of the conflict between cladistic analysis of species taxa vs. stratigraphically controlled reconstruction of phylogeny should be consulted. This revision of the North American Wasatchian early Eocene small condylarth mammal *Hyopsodus* deals with the record of thousands of specimens during a span of approximately six million years, a temporal equivalent of hominid evolution.

In a recent and equally relevant study on ancestry and species definitions in paleontology, Polly (1997, p.1) noted the following:

The ability to distinguish between terminal taxa and those that form a continuous lineage is important for most paleobiological enterprises, including documentation of pattern diversity, extinction, and morphological change through time. Especially in cases with a dense fossil record containing closely related species, conventional cladistic analysis is not adequate for this task because a priori judgments about the monophyly [i.e., holophyly] or paraphyly of operational taxonomic units are impossible. Even when a fossil taxon contains an autapomorphy, it is impossible to test its monophyly [i.e., holophyly] using cladistic analysis without resorting to assumptions about the irreversibility of evolution. (Contents in brackets added.)

Finally, in regards to paleoanthropology, where is the paleosystematics of hominids taking the field of human evolutionary studies? Are paleoanthropologists to be experts working on either: a) a few but highly polytypic lineages of hominids with local variants arising, intercalating, and becoming extinct in an ongoing bushy succession, with a remarkable history of some (maybe even one) of these lineages spreading throughout the world,

or, b) will they increasingly place primary emphasis on OTU taxonomy and be occupied largely with naming the spectacularly scattered and numerous samples that, when given epithets and treated cladistically, give the widely perceived impression that they were fully evolved and closed species-cum-lineages?

The second option axiomatically reifies largely taxonomic, not evolutionary concepts that cannot be adequately tested except through sympatry of these samples. Have these numerous taxonomic species recognized under the second approach pursued vastly different ways of life through the Plio-Pleistocene? I certainly do not know the answer, but the eventual, and theoretically rigorous and audience-independent, evaluation of the fossils and the resulting taxonomy, should help us choose between these alternative approaches to the hominid fossil record.

ACKNOWLEDGMENTS

This paper was supported by funds obtained from a PSC-CUNY doctoral research grant. I am grateful to Justine Salton for her careful reading of the manuscript.

REFERENCES

- Albrecht, G. H. and Miller, J. M. A. (1993, "Geographic variation in primates: A review with implications for interpreting fossils," in Kimbel W. H., and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp. 123-161.
- Bock, W. J. (in press), "Towards a new metaphysics: the need for an enlarged philosophy of science," *Biology and Philosophy*.
- Bromage, T. G. and Schrenk, F. (1999), *African Biogeography, Climate Change, and Human Evolution*. New York: Oxford University Press.
- Cartmill, M. (1994), "A critique of homology as a morphological concept," *American Journal of Physical Anthropology* 94: 115-123.
- Cartmill, M. (1999), "Revolution, evolution, and Kuhn: a response to Chamberlain and Hartwig," *Evolutionary Anthropology* 8(2): 45-47.
- Collard, M. and Wood, B. (1999), "Grades among the African early hominids," in Bromage, T. G. and F. Schrenk (eds.), *African Biogeography, Climate Change, and Human Evolution*. New York: Oxford University Press, pp. 316-327.
- Eldredge, N. and Cracraft, J. (1980), *Phylogenetic Patterns and the Evolutionary Process*. New York: Columbia University Press.
- Gee, H. (1999), *In Search of Deep Time: Beyond the Fossil Record to a New History of Life*. New York: The Free Press.
- Ghiselin, M. T. (1997), *Metaphysics and the Origin of Species*. Albany: State University of New York Press.
- Grubb, P. (1999), "Evolutionary processes implicit in the distribution patterns of modern African mammals," in Bromage, T. G. and F. Schrenk (eds.), *African Biogeography, Climate Change, and Human Evolution*. New York: Oxford University Press, pp. 150-164.
- Howell, F. C. (1996), "Thoughts on the study and interpretation of the human fossil record," in Meikle, W. E., F. C. Howell and N. G. Jablonsky (eds.), *Contemporary Issues in Human Evolution*. California Academy of Sciences, Memoir 21, pp. 1-45.
- Jolly, C. F. (1993), "Species, subspecies, and baboon systematics," in Kimbel W. H., and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp. 67-107.
- Mayr, E., and Ashlock, (1991), *Principles of Systematic Zoology*, 2 ed. NY: McGraw.
- Mahner, M. and Bunge, M. (1997). *Foundations of Biophilosophy*. New York: Springer-Verlag.
- Miller, J. M. A. (2000), "Craniofacial variation in *Homo habilis*: an analysis of the evidence for multiple species," *Am. Journal of Phys. Anth.* 112: 103-128.
- Norell, M. A. (1996), Ghost taxa, ancestors, and assumptions: a comment on Wagner. *Paleobiology*, 22(3): 453-455.
- Polly, P. D. (1997), "Ancestry and species definition in paleontology: a stratocladistic analysis of Paleocene-Eocene Viverravidae (Mammalia, Carnivora) from Wyoming," *Contributions from the Museum of Paleontology, the University of Michigan* 30(1): 1-53.
- Polly, P. D. (1998), "Variability in mammalian dentitions: size-related bias in the coefficient of variation," *Biological Journal of the Linnean Society* 64: 83-99.
- Raff, R. A. (1996), *The Shape of Life*. Chicago: University of Chicago Press.
- Redline, A. D. (1997), Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 13. Systematics and phylogenetic pattern of early Eocene *Hyopsodus* (Mammalia: Condylarthra). *Annals of Carnegie Museum* 66: 1-81.

- Robinson, J. T. (1956), "The dentition of the Australopithecinae". *Transvaal Museum Memoirs* 9: 1-179.
- Rose, K. D. and Bown, T. (1993), Species concepts and species recognition in Eocene primates. In Kimbel W. H., and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp. 299-330.
- Schuh, R. T. (2000), *Biological Systematics—Principles and Applications*. Ithaca and London: Cornell University Press.
- Simpson, G. G. (1949), *The Meaning of Evolution*. New Haven: Yale University Press.
- Simpson, G. G. (1963), "The meaning of taxonomic statements," in Washburn, S. L. (ed.), *Classification and Human Evolution*. Chicago: Aldine, pp. 1-31.
- Szalay, F. S. (1975), "Hunting-scamenging protohominids: a model for hominid origins," *Man* 10: 420-429.
- Szalay, F. S. (1993), "Species concepts: The tested, the untestable, and the redundant," in Kimbel W. H., and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp.21-41.
- Szalay, F. S. (1994), *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. New York: Cambridge University Press.
- Szalay, F. S. (1999), "Paleontology and macroevolution: On the theoretical conflict between an expanded Synthesis and hierarchic Punctuationism," in Bromage, T. G. and F. Schrenk (eds.), *African Biogeography, Climate Change, and Human Evolution*. New York: Oxford University Press, pp. 35-56.
- Szalay, F. S. (2000), "Function and adaptation in paleontology and phylogenetics: why do we omit Darwin?" *Paleontologia Electronica* 3(2) 25p, 366 KB; <http://palaeo-electronica.org/pleo/2000-2/darwin/issue2-00.htm>
- Szalay, F. S. and Bock, W. J. (1991), "Evolutionary theory and systematics: Relationships between process and patterns," *Zeitschrift Zoologische Systematic und Evolutions-Forschung* 29: 1-39.
- Szalay, F. S. and Costello, R. K. (1991), "Evolution of permanent estrus displays in hominids," *Journal of Human Evolution* 20: 439-464.
- Szalay, F. S. and Schrenk, F. (1998), "The middle Eocene *Eurotamandua* and a Darwinian phylogenetic analysis of "edentates," *Kaupia-Darmstädter Beiträge zur Naturgeschichte* 7: 97-186.
- Szalay, F. S. and Sargis, E. J. (2001), "Model-based analysis of postcranial osteology of marsupials from the Paleocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria," *Geodiversitas* 23 (2): 1-166.
- Tattersall, I. (2000), "Paleoanthropology: the last half-century," *Evolutionary Anthropology* 4(1): 2-16.
- White, T. D. (2000), "A view on the science: Physical Anthropology at the Millenium," *American Journal of Physical Anthropology* 113: 287-292.
- Wood, B. (1993), "Early *Homo*: How many species?" in Kimbel W. H., and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp. 485-522.