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The naming of new species in hominin evolution: A radical proposal—A temporary cessation in assigning new names

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Abstract

The species problem is one of the most complex and enduring problems plaguing evolutionary biology in general and human paleontology in particular. In the past 50 years, conceptions of species have diverged and speciated analogous to the present, largely accepted view of the hominin phylogeny. Conventional wisdom supports a ''bushy'' hominin phylogeny. However, chaos reigns because there is no agreed-upon methodology used to delimit species taxa in paleontology. This dispute is complicated by the ever-present intraspecific and interspecific morphological variation, which is itself exacerbated by other types of variation, including behavioral, ecological, geographical and temporal. When two or more of these forms of variation are used to delimit ''new'' extant or fossil species, any decision arrived at might be construed as arbitrary. This paper proposes that temporary cessation in assigning new names should be considered based on several critical problems: (1) the explosion of conceptions of a ''species'' arising from disagreements regarding species definitions, (2) differing interpretations of population variation, which lead to difficulty in interpreting hybridization in nature, leading in turn to the underestimation or overestimation of species, (3) the problem of *modes* of speciation being confounded with criteria used to distinguish among species, e.g., punctuated equilibrium posits high-speciation rates, and (4) the most common of all human traits, vanity.
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Introduction

The species problem is one of the most complex and enduring problems plaguing evolutionary biology in general and human paleontology in particular. In the past 50 years, conceptions of what constitutes ''a species'' have diverged and speciated in tandem with the present, largely ''bushy'' hominin phylogeny championed by most (Cracraft, 1983, 1987; Davis and Nixon, 1992; Donoghue, 1985; Eldredge and Cracraft, 1980; Kingdon, 2003; Mishler and Brandon, 1987; Tattersall, 1986, 2000, 2003; Wiley, 1981; Wood and Collard, 1999a, 1999b). However, there is no standardized list of the traits or characteristics that delimit taxa in hominin paleontology, although some have been proposed (Albrecht and Miller, 1993; Brian et al., 1993; Henneberg and de Miguel, 2004; Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001; Rose and Bown, 1993; Shea et al., 1993). This could be the major reason for the geometric increase in fossil species and species concepts. I do not make this statement lightly or want to give the impression that I have a better solution to this problem. The rules set by the International Commission on Zoological Nomenclature (ICZN) must be modified to deal with the chronic, ''wild west''-style, excessive and arbitrary naming of ''new'' species.

Others have also hinted at this problem. For instance, Kimbel and Rack (1993) have stated that it is not possible to perceive whole species in the fossil record. They go on to say, ''This is why the epistemology of the paleontologist is always a matter of inference; we cannot observe an extinct species, but we can infer its existence and determine its spatiotemporal locale. The proper use of characters is the key to this enterprise'' (p. 470). Henneberg and Thackeray (1995) are more direct. They reiterate what I believe is the most critical point in the species debate: that researchers are not confident about ''whether or not the range of variation observed within a particular assemblage of fossils exceeds that characteristic for a single species…'' (p. 32). Along these same lines, Henneberg (1997) advocates applying ''tools of parsimony and hypothesis testing to the *large sample of hominid fossils*'' (p. 21, italics added). Thousands of hominin fossil bones have been recovered over the years, but only a few individuals have been identified within each putative species. Consequently, any intraspecific range of variation derived from a small sample of individuals would be inaccurate. Plavcan and Cope (2001) use the example of the mixed-macaque distribution and caution that a large number of specimens mask the differences among species. Nonetheless, Rebecca Ackermann et al. (2006) add that comparative patterning of skeletal variation does not exist in the hominin fossil record because only single individuals can be sampled, not biological populations. All of this indicates that the identification of fossil species should be at best difficult and at worst futile.

C. Loring Brace (1964, 1981) has for a long time accused human paleontologists of adopting an outlook rooted in George Cuvier's idea of ''catastrophism,'' where gaps in the fossil record are interpreted as speciation events. Here Brace (1981) emphasizes this point: ''it is interesting to recall that Cuvier himself insisted that 'life was a bush, not a ladder''' (p. 413). Furthermore, Henneberg and Gerry Brush (1994) argue that the concept of species cannot be applied to continuous changes

within lineages. They propose the concept of *similum* and contend that "unlike species *similum* has no holotype, it is defined only by mutual similarities of individuals (similars)" (p. 278). On the other hand, Ian Tattersall (1986) argues that the degree of morphological differences between extant species should be used as a guide to delimit species in the fossil record. Guided by this technique, Tattersall (2000) advocates a "bushy" hominin phylogeny as evidenced in the statement that "…linear thinking still lies heavily on paleoanthropology…" (p. 61).

One might argue that the species problem is as nebulous as Albert Einstein's theory of relativity. In this theory, all uniform motion is relative and there is no absolute or well-defined state of rest; a person on the deck of a ship may be at rest from her or his own perspective, but someone observing from the shore would say that this person was moving (Einstein, 1955). To use this as an analogy in the species problem debate, we can say that some researchers are prone to see within-population variation (Einstein's man on the deck of the ship) and others are prone to see between-population variation (Einstein's man on the shore). Is it all a matter of the researcher's frame of reference or bias due to education and training? Or is this a result of the organisms being studied (see Albrecht and Miller, 1993; Brian et al., 1993; Kelley, 1993; Shea et al., 1993)? For example, is *Cercopithecus* an appropriate comparative analog for hominidae (see the discussion later in the paper)? Others, with some hubris mixed with science, argue that their species concept or their comparative analog is best suited to addressing the taxonomic diversity in nature. This chaos, in addition to the omnipresent variation we witness (i.e., intraspecific, interspecific, morphological, genetic, sexual, asexual, behavioral, ecological, geographical, and temporal) reduces the ability to identify species in the fossil record. It is ironic that the variation that Charles Darwin called 'the spice of life' is responsible for the murkiness that is the species problem. Darwin also doubted the compatibility of the species concept with biological evolution (Henneberg and Keen, 1990; Henneberg, 1997). Presently, some in biology and botany also doubt the reality of species as discrete, objective entities altogether. If these researchers are correct, then there is no reason for writing this paper. However, naturalists manage to label their specimens, systematists reconstruct life histories from species-specific traits, population geneticists measure DNA variation within-species, and ecologists calculate species diversity (Coyne and Orr, 2004). Based on this evidence and the fact that we must investigate the widespread use of taxonomic names in order to find a solution, I will accept the premise that species do exist.

In this paper, I begin by discussing what I call "speciation of the species concepts," because the framework in which many researchers delimit species is built around their respective species concepts. The fact that there are approximately 23 species concepts, and counting, attests to this assessment. I will concentrate on the older and more established species concepts, i.e., the biological, evolutionary, and phylogenetic species concepts. It would be impractical to discuss all 23 species concepts, since this would increase the length of this paper, but Fig. 1 will give the reader a better idea of the speciation of the species concepts than a description in words.

In the second section, I detail the differing interpretations of populational variation that have the effect of overestimating or underestimating species. The
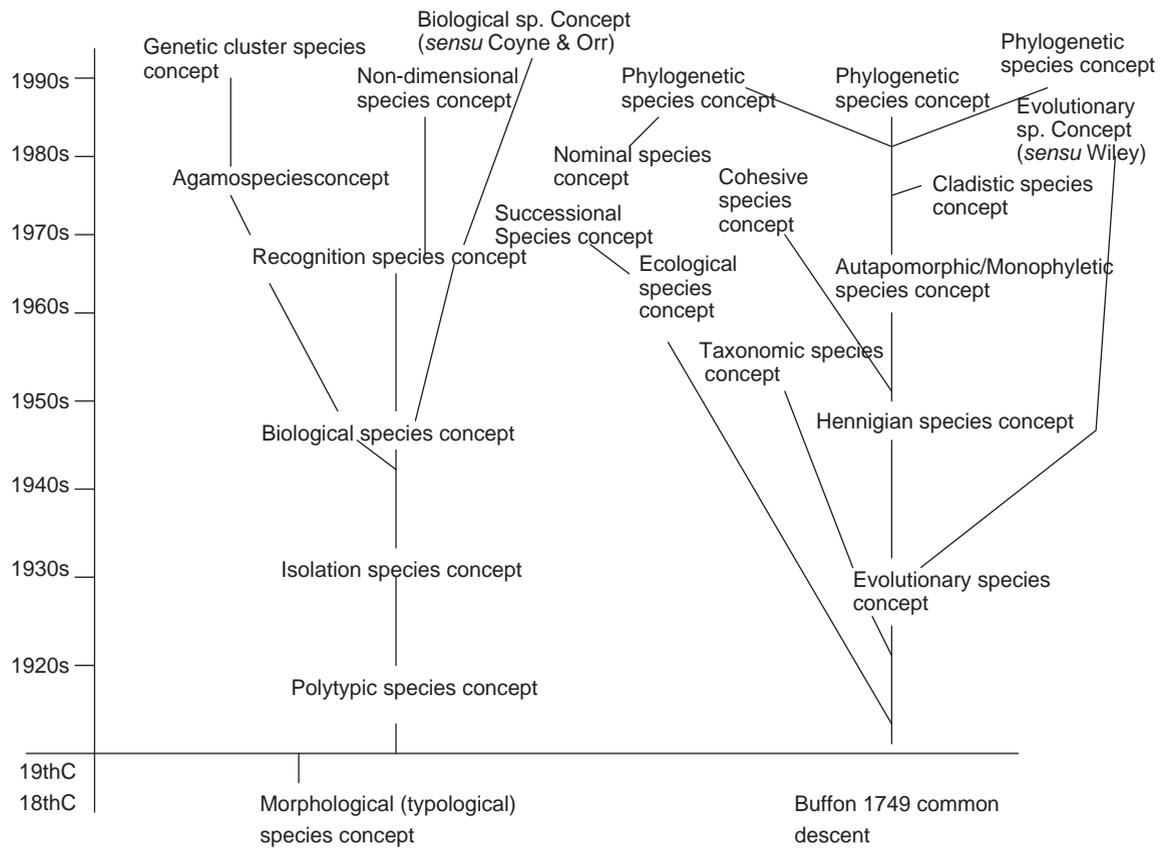
Fig. 1. A "busy" phylogeny of the species concept.

amount of variation in characteristics that must be observed before a population—fossil or extant—is designated a new species is still a matter of contention (Ackermann et al., 2006; Albrecht and Miller, 1993; Brian et al., 1993; Cope and Lacy, 1992, 1996; Henneberg and de Miguel, 2004; Henneberg and Thackeray, 1995; Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001; Rose and Bown, 1993; Shea et al., 1993). Are there specific characteristics, including behaviors, that can be used in the delimitation of species? I believe that those characteristics (in fossils) and behaviors (in extant species) that are important to reproduction (biology and life history) would be appropriate for use in species designation. In the third section, I discuss how the modes of speciation (i.e., punctuated equilibrium or "cladogenesis" and phyletic gradualism or "anagenesis") are the very frameworks that govern researchers' ideas of speciation rates. In the fourth section, I discuss the simple human trait of vanity, which plays a part in the assigning of new names. Finally, I discuss alternatives to taxonomic names proposed by other researchers and offer a tentative working solution to the problem of the excessive naming of new species.

Speciation of species concepts

The 1990s saw the discoveries of several important hominin fossils from East Africa, including the first early hominin fossil ever to be found in North-Central Africa. With these finds, the number of genera and, particularly, species in hominin evolution has increased. Paleoanthropology can now boast 6 genera and 13 species of australopithecines (all early hominins belonging to the subtribe Australopithecina) and 8 species of hominans (see Tables 1 and 2) (Campbell et al., 2006). Two of the australopithecine taxa are relatively well known. A large percentage of the total cranial and postcranial skeletal elements have been found for *Australopithecus afarensis* and *Paranthropus boisei*, so that much is known about their anatomy. In contrast, only a very small percentage of the skeletal elements for the other East African/Sahel species have been found, making it impossible to provide complete descriptions of their anatomy or propose possible evolutionary relationships to other specimens.

In September 2003, non-fossilized hominin remains were found in Indonesia. These remains have now been identified as belonging to a new species of hominins labeled *Homo floresiensis*—the seventh species of the genus *Homo*. This raises the question: should there be a halt, or at least a tentative moratorium, in assigning new species names until more comparative specimens are found? Indeed, this is a radical suggestion that many human paleontologists would dismiss as impractical. But should we not settle the "species problem" before new specific or generic name designations are made? Or do away with the concept of species and simply identify fossil specimens by numbers as proposed by Henneberg and Keen (1990)?

I have identified at least 23 species concepts within contemporary literature (Fig. 1) and organized them phylogenetically where possible.

The resulting representation is as bushy as the currently accepted bushy models of hominid phylogeny. One might argue that all species concepts are similar in that they

Table 1. Australopithecine species (adapted from Campbell et al., 2006).

Australopith species	Location	Geological age (Ma)	Date of discovery
Sahelanthropus tchadensis	Chad	7–6	2002
Orrorin tugenensis	Kenya	6	2001
Ardipithecus kadabba	Ethiopia	5.8–5.2	2001–2004
Ardipithecus ramidus	Ethiopia	4.4	1994–1995
Kenyanthropus platyops	Kenya	3.5–3.2	2001
Australopithecus anamensis	Kenya	4.2–3.9	1995
Australopithecus afarensis	Ethiopia, Kenya, Tanzania	4.2–2.5	1978
Australopithecus bahrelghazali	Chad	3.5–3.0	1996
Parathropus aethiopicus	Ethiopia, Kenya	2.6–2.3	1968
Australopithecus garhi	Ethiopia	2.5	1999
Parathropus boisei	Ethiopia, Kenya, Tanzania, Malawi	2.4–1.3	1959
Australopithecus africanus[a,b]	South Africa	3.0	1924
Parathropus robustus[a,b]	South Africa	2.5	1938

[a] Not listed in Campbell et al. (2006).
[b] Listed in Conroy (1997).

Table 2. Hominan species (adapted from Campbell et al., 2006).

Taxon Genus	Geological Age (Ma)	First described
Homo, species:		
rudolfensis	2.4–1.6 Ma	1986, 1992
habilis	2.3–1.6 Ma	1964
erectus	1.9 myr–27 (?) ka	1892, 1944, 1964
ergaster	1.7 Ma	1976, 1993
heidelbergensis	850–100 ka	1908
neanderthalensis	350–27 ka	1864
floresiensis	>38–18 ka	2004
sapiens	195 ka-present	1758

are biological, genetic, and composed of diversifying lineages (Cracraft, 2000), and that, in this sense, these species concepts are not significantly different from one another. The late evolutionary biologist Ernst Mayr (2000), however, would strongly disagree. He believed that the various species concepts, be they phylogenetic, evolutionary, or based on other criteria, are not biological because they cannot answer the question, ''Why are there species'' (Mayr, 2000, p. 163). Moreover, there may be some relationship between the characteristics of a particular researcher's subject-organism or the researcher's interpretation of the entity 'species' and the

species concept chosen (Cracraft, 2000, p. 5). For instance, life histories, patterns of variation, extent of diversity, and other factors are different for birds than they are for monkeys. Therefore, a view of a ''species'' as a unit of evolution, as the product of evolution, or as an incipient species will influence the choice of species concepts. This situation, I believe, leads to pluralism or to a type of feedback loop: the increase in the number of species concepts leads to an increase in the number of species, and the increase in the number of species leads to an increase in the number of species concepts. In the first section of this essay, I questioned whether *Cercopithecus* was a good model for hominidae. This statement is related to the fact that the genus *Cercopithecus* is very speciose and is used by some (Cope and Lacy, 1992, 1996; Plavcan, 1993) to falsify the single-species hypothesis for the less speciose hominoids. But the basic question is how we know that two organisms within the same genus are different species. Or how do we identify two species if their skeletal assemblages are mixed together? Plavcan and Cope (2001) emphasize that knowledge about the biology of living species helps us to use correct strategies in interpreting variation in fossil samples. Also, they state that mixed samples (gathered from different time horizons or different geographical regions) can inflate sample variation if the researcher ignores sources of variation—geographic, interspecific, intersexual, and temporal, to name a few. Despite all of this, there is still no standardization in choosing traits or appropriate reference samples to aid in identifying fossil species.

As for extant species, unless one is in the wild 24 hours a day, 7 days a week, the designation of species may be arbitrary. Kimbel and Rak (1993) note that genealogy causes organisms to be members of a species and phenotypically similar to other organisms within this species, but not to be morphologically similar. Others (Lieberman et al., 1996) will agree with this assessment but also add the fact that homoplasy, the presence of a similar character-state in more than one taxon through mechanisms other than direct shared ancestry, is a major problem in the delimitation of species. An example that is often used to demonstrate this is that of Old World monkeys, such like *Papio*, because the genus is speciose and skeletally similar. Splitters emphasize that we would underestimate Old World monkey species numbers if we were to use only skeletons to identify them (Hunt, 2003). Nonetheless, all recognize that in paleontology, one has no choice but to use skeletal morphological characters to distinguish species taxa. This is the vexing problem in paleoanthropology.

At this point, it is apropos that I discuss some of the better known species concepts associated with paleontology and detail how proponents of each of the respective concepts delimit species taxa. This is important because these theoretical frameworks are integral to the species problem and discussions of the nature of taxa cannot take place in a theoretical vacuum (Wiley and Mayden, 2000).

I will begin with the ''biological'' species concept for two reasons: (1) for many decades, paleontologists, ornithologists, mammalogists and researchers from other disciplines have adopted this concept, and (2) whether one agrees with Mayr or not, he poses a critical question: "So we need species concepts that are merely operational prescriptions for the demarcation of species taxa or do we need to first understand the role that species play in processes of the living world, and then formulate species

concepts which can be used as a 'yardstick' in delimiting species?" (Mayr, 2000, p. 161). The role of "species" is to protect (not always successfully) the gene pool from intrusion by non-members. While this idea is generally valid, it is incompatible with evolving lineages over time (Henneberg and Keen, 1990; Henneberg, 1997).

Biological species concept *sensu* Mayr

The biological species concept is defined as "groups of *interbreeding* natural, populations that are *reproductively isolated* from other such groups" (Mayr, 1995, p. 5; italics added). Mayr was confident that this concept answered the "why" of species. However, he insisted that the potential for the interbreeding of isolated allopatric populations must always be inferred because any operational demarcation of species taxa is arbitrary (Mayr, 2000).

As far as reproductive isolation is concerned, Mayr knew that interbreeding between geographically isolated populations could not be observed. Nonetheless, he believed that these isolating mechanisms serve to protect harmonious gene pools (Mayr, 2000).

In paleontology, one often hears that "the biological species concept cannot be applied to fossils because fossils do not mate." In short, the biological species concept is *nondimensional* in that a "the species status of a given population can be tested only where they coexist in space and time" (Mayr, 2000, p.165). For the dimensional context, Mayr believed that a species concept should serve as a yardstick (as in the nondimensional realm). He also believed that Simpson and Hennig failed in their efforts to delimit species taxa in a diachronic context because their proposal to call points above and below budding points on a phyletic lineage as different species was more clerical "bookkeeping" than credible data (Mayr, 2000, p.164). It is interesting to note that Mayr goes on to argue that since the biological species concept works fairly well in *demarcating geographical isolates*, it is much better than any other species concept in subdividing a long, continuous phyletic lineage into species taxa. In other words, the biological species can be applied to fossils because their geographical location is usually fixed. Kimbel and Rak (1993) reject Mayr's argument. They state that species are lineages with a temporal element. Henneberg and Keen (1990) also reject Mayr's argument and offer an alternative solution:

> Unfortunately, the breeding criteria cannot be applied to fossils, or to any individuals separated by more time than the lifespan of two generations. We conclude that the notion of a species is at variance with the logic of the theory of evolution and postulate that the term "species" should be abandoned in evolutionary discussions. Individual fossils should be labeled by nicknames (or numbers), and arranged in lineages. Parts of lineages may be characterized as stages by the fossils commonly found in a corresponding time period (p. 214).

Alan Templeton (1989) also disagrees with Mayr on one of the key tenets of the biological species concept: gene flow and its exclusive role in maintaining species boundaries. I agree with Templeton's suggestion. Both genetic drift and natural

selection (in the case of selection for the heterozygote or selection for a mutation) can increase the variation between populations. In addition, different environments can increase the variation between populations. Templeton also argues that the cohesion of the species concept allows for *interspecific* hybridization, but that the populations maintain their designation as separate species. The biological species concept has been under siege because of this very problem—as Mayr colorfully phrased it, "a leakage of genes" (Mayr, 1996, p. 265). Opponents (Jolly, 1993, 2001; Meier and Willmann, 2000; Mishler and Theriot, 2000; Wiley, 1981; Templeton, 1989) argue that the biological species concept fails because there is ample evidence of gene flow between sympatric species. Mayr responded by stating that the biological species concept is not invalidated by hybridization because it does not allow for intermediate states. In short, Mayr emphasized strongly that the protection of "…well-balanced, harmonious genotypes…" is the insight on which the biological species concept is based.

Biological species concept *sensu* Coyne and Orr

Coyne and Orr (2004), like Mayr, agree that distinct species are characterized by *reproductive isolation*. Unlike Mayr, however, they reject the idea of complete reproductive isolation, allowing limited gene exchange with sympatric relatives. Coyne and Orr (2004) emphasize that understanding the acquisition of reproductive barriers is more important than demarcating species because the *process* of speciation yields intermediate stages, while the species status is irresolvable. We can assume that many paleontologists are not ready to surrender that easily. But there are those (Albrecht and Miller, 1993) who note that if extinct species had the same magnitude of morphometric variation that is found in extant primate species, then assigning taxonomic rank would be difficult, and there are others (Henneberg and Keen, 1990) who propose abandoning taxonomic names altogether.

Furthermore, Coyne and Orr (2004) argue that during sympatric speciation and reinforcement, "species" designation is arbitrary. If one considers speciation as the conversion of "genotype cluster" species into "biological" species—a process that is continuous, yielding ever-increasing barriers to gene flow—Coyne and Orr believe that their version of the biological species concept is applicable in this case because the entire process of speciation can be viewed as the evolution of reproductive isolation. They state, "arguments about the exact relationship between gene flow and species status have obscured the more important fact that reproductive barriers are essential for producing and maintaining distinct groups in sympatry" (Coyne and Orr, 2004, p. 31). Moreover, they argue with great audacity that reproductive barriers are the "currency" of speciation and studying how these barriers arise is the solution to the species problem.

Generally, the biological species concept as it is defined requires absolute barriers to gene flow between taxa. Historically, Mayr (1963) accepted this view. Later, he modified his view, arguing that as long as populations remain distinct, hybridization should occur between biological species. Coyne and Orr (2004) argue that their version of the biological species concept allows for a low frequency of gene exchange

between groups otherwise considered to be separate species. They state that "hybridization might be a problem for the BSC under two conditions: (1) if one adhered to the strict construction of the BSC in which *no* exchange can occur between species, or (2) if gene exchange were *widespread and substantial* between sympatric taxa" (p. 41). But hybridization may be a very short phase of evolution, according to Coyne and Orr, because reproductive isolation eliminates any trace of intermediates. In other words, hybridizing taxa might be part of the process of becoming a single species. In contrast, others (Templeton, 1989, p. 15; Holliday, 2003, p. 656) would argue that hybridizing populations, despite some gene flow, will remain separate, cohesive species if they are "demographically nonexchangeable."

Coyne and Orr (2004) discuss the biological species concept and its effectiveness in delineating "species" in fossils. They agree with Mayr that applying the biological species concept to the fossil record poses problems. Their approach to the problem of delimitation of species in the fossil record is to use geographical variation in order to study how phenotypic variation in allopatric taxa changes gradually over space (suggesting conspecific status) or if there is an abrupt geographic discontinuity (suggesting two species). If there is no abrupt change in the variation, then the fossil material can be tentatively diagnosed as a single species.

In the early 1990s, Albrecht and Miller (1993) discussed in great detail the importance of geographical variation in living primates and its implications for studying fossils. Consequently, they would agree with Coyne and Orr's (2004) approach. Based on their research, Albrecht and Miller (1993) concluded that living primates from different geographical regions are significantly variable in their skeletal features, and that this variability should be taken into account in distinguishing interspecific and intraspecific variation within fossil assemblages. They use the skulls of extant Hanuman langur, *Presbytis entellus*, to show what geographical variation might resemble in a fossil species.

The Hanuman langur subspecies are distributed across the Indian subcontinent from Sri Lanka in the south to the Himalayas in the north, and the variation among males and females with this geographic range is remarkable (Albrecht and Miller, 1993). For instance, females from the north and south of India could be mistaken for males and females. Specifically, if canine dimorphism is ignored, the female from the north might be mistaken for males from the south. Albrecht and Miller (1993) viewed the langur skull sizes as following a latitudinal clinal distribution—small langurs in the south and large langurs in the north—in a single species. If these skulls were of extinct animals from fossil localities in different parts of India, Albrecht and Miller believe that the "primate paleontologist would assign them to several species" (p. 154). This example has implications for the excessive splitting in hominin evolution, such as among the east and south African Australopithecines or in the creation of three big-brained hominin species: *Homo erectus–Homo ergaster–Homo heidelbergensis*.

Furthermore, Albrecht and Miller (1993) emphasize that the "sampling strategy must be appropriate to the research question being asked" (p. 155). For instance, if the research question involves characterizing sexual dimorphism in a fossil taxon, then one would use fossil samples from a single locality because multiple localities

(or geographical variation) might confound sexual differences. Alternatively, if the research question involves deciding whether fossils found at multiple localities are representatives of a single species, Albrecht and Miller suggest that fossils samples should "represent all levels of variation *in living primate species* from intraspecific through interspecific "(p. 156, italics added).

In summary, what appears to be a "species," a "subspecies," or a hybrid may be only a geographical or local variant in terms of a few otherwise ubiquitous traits. In contrast, others (Wiley and Mayden, 2000) have argued that widespread application of the biological species concept from the 1950s to the 1970s resulted in a considerable underestimation of the actual number of species, for instance in North American freshwater fishes, because the ability to hybridize was mistakenly seen as evidence of there being a single variable species. In paleoanthropology, the argument is similar. If craniodental variability in fossil sample species is greater than that seen in living species, or if novel phenotypes are displayed, then more than one species is *assumed* to be present (Ackermann et al., 2006; Plavcan, 1993; Plavcan and Cope, 2001; Tattersall, 1986).

Evolutionary species concept *sensu* Wiley and Mayden

In the 1950s and 1960s, the evolutionary species concept was competing with Mayr's biological species and Willi Hennig's species concept. According to Meier and Willmann (2000), the evolutionary species concept satisfied the demands of strict phylogenetic systematics because it could be applied to the temporal dimension of species. It incorporated a temporal dimension in order to counter the nondimensional biological species concept. George Gaylord Simpson (1951, 1961), who at this time was the main proponent of the evolutionary species concept, believed that the time element was critical, especially for paleontology. Wiley and Mayden (2000) have argued that Simpson may have abandoned the concept because he (Simpson) believed that evolutionary continuity ruled out the objective delimitation of lineages and therefore evolutionary species. Furthermore, Wiley and Mayden state that their version of the evolutionary species concept is identical to Hennig's (1966) species-as-lineages concept, which is a main part of Hennig's phylogenetic systematics. Hennig wrote that phylogenetic relationships are genealogical relationships that lie between two processes of speciation and arise through the process of species cleavage. Hennig implied that evolutionary lineages—Simpson's "chronospecies"—cannot be arbitrarily divided.

Wiley and Mayden (2000), in my view, are not completely confident that all species can be identified through morphological, behavioral, and ecological studies. They place great value on "tokogenetic" relationships or diachronic, ancestor-descendant relationships (as opposed to synchronic, sister-group relationships) because in their view, the disruption of preexisting tokogenetic systems is the reason for there being few or many species and not morphological change. Hennig proposed that all individuals connected through tokogenetic relationships constitute "a (potential) reproductive community and that such communities should be called species" (Meier and Willmann, 2000, p. 31). This raises three questions: is this reliance on

tokogenetic relationships not similar to some components of the biological species concept? Furthermore, how does one identify tokogenetic relationships in the fossil record? Finally, if only *some* species can be "discovered" through morphological, behavioral, and ecological studies, have we overestimated the number of hominin species? The answer to the first question is no. The criterion for interbreeding can only be applied to the individual reproductive life span and not beyond. While the thought is salacious, there is no way to test whether I could mate and produce a fertile offspring with Cleopatra. To answer the second question, I believe the work of Rose and Bown (1993) is pertinent. They combined stratigraphic data with information on dental variability in Eocene omomyid primates and interpreted the data (plots of tooth-size variation against stratigraphic level) as showing one or more gradual, evolving lineages with normal tooth-size variability comparable to that of living species. For the third question, I must reiterate Albrecht and Miller's (1993) considerations (see previous sub-section). If the research question involves sexual dimorphism, then one must use comparative samples from a single locality and timeframe; samples obtained from multiple localities will overestimate the number of species due to geographical variation and size dimorphism. In contrast, if one is trying to address the single-species question based on fossils from widely spread localities, then one's comparative samples must encompass the intraspecific diversity of living primates. A comparative sample from a single locality would underestimate the number of species.

With hubris equaling Mayr (1969, pp. 181–187) and others (Meier and Willmann, 2000, pp. 167–170; Mishler and Theriot, 2000, pp. 178–184; Wheeler and Platnick, 2000, pp. 185–197), Wiley and Mayden (2000, p. 73) clearly argue that the evolutionary species concept is "the only concept currently capable of recognizing all naturally occurring biological taxonomic entities." They attempt to integrate taxonomy (applying binominal nomenclature to comparable entities), biogeography, phylogenetic systematics, and evolutionary biology to estimate natural diversity. But when it comes to biogeography, allopatry seems to be a confounding problem. For instance, populations of a species may be widespread, i.e., wolves (*Canis lupus*, which are found in North America, the Middle East, the Near East and Eurasia), and have occasional gene flow between them. In other words, they may be temporarily allopatric. Some (Coyne and Orr, 2004; Hennig, 1966; Holliday, 2003; Templeton, 1989; Wiley and Mayden, 2000) might be tempted to call these geographic populations *syngameons* (cohesive units that remain morphologically, genetically, and ecologically distinct) or separate independent lineages. The result may be an overestimation of the number of species [see the Hanuman langur example from Albrecht and Miller (1993) discussed in the previous sub-section].

Taking a cue from Hennig, Wiley and Mayden (2000, p. 76) believe that the goal of phylogenetic systematics is "to discover monophyletic groups at higher levels and lineages at lower levels." Moreover, ancestral species must be separately evolving lineages because synapomorphies diagnose monophyletic groups. In other words, autapomorphies of ancestral species are passed down to become the synapomorphies of monophyletic groups (synchronic descendants of a common ancestor). In essence, Wiley and Mayden (2000) assert that the evolutionary concept and the idea of

monophyly fit well within the phylogenetic system because both are genealogical and nonoperational (as opposed to operational: using characters alone to define taxa).

But there are opponents who see the term *monophyly* as confusing and require ancestral species, or "stem" species, to become extinct at a speciation event. In this modified version of Hennigian's species concept, Meier and Willmann (2000) emphasize isolation and delimiting species in time. They write that after a speciation event, the stem species cease to exist and the new species emerge. They believe that it is the reproductive isolation of members of the same population that is important in delimiting species boundaries. This certainly reduces the complexity of the system and, as Wiley and Mayden (2000) would counter, underestimates the number of species. There is a familiar trend toward the overestimation (geographical population viewed as separate lineages) and underestimation (the requirement that ancestral species become extinct during speciation) of species.

Like others (Cracraft, 2000; Mayr, 2000), I am concerned about the lack of concordance between real characteristics of biological populations and the numerous species concepts. Interestingly, Wiley and Mayden (2000) would admit that the term *monophyly* is problematic because it does not adequately describe individual organisms and/or populations that constitute species. "Better to apply terms and phrases such as *valid, invalid, is a synonym of,* or *cannot be distinguished from,* to denote the relative merits of binomials when applied to nature and leave the adjective *monophyletic* to denote natural higher taxa…" (Wiley and Mayden, 2000, p. 83; italics in the original).

Rose and Bown (1993), as detailed earlier in this sub-section, presented evidence for a gradual (anagenetic) transformation within lineages of Eocene omomyids. They believe that paleontologists should use species concepts that can be applied to fossil samples. As such, they choose Simpson's Evolutionary Species Concept (ESC) rather than a monophyletic species concept (*monophyly*) that would exclude paraphyletic and ancestral species. They argue that Simpson's ESC is a "better reflection of biological reality than the phylogenetic species concept, which is typological and tends to overestimate the actual number of species" (p. 323).

In conclusion, this evolutionary species concept (or largely the evolutionary species concept of Wiley and Mayden, 2000), like the biological species concept, has a difficult time considering *reproductive isolation* and allopatric populations. It is accepted by most that isolated populations will, over time, become new species. But in nature, nothing is so simple. A small amount of gene flow, i.e., "one migrant per 1000" (Lewontin, 1974, p. 213), may prevent speciation. What further complicates this matter is character variation: is this character evidence of a new species, or is it simply geographical variation? Depending on the researcher's philosophical leanings or conventional wisdom, species diversity will be overestimated or underestimated (Ackermann et al., 2006; Albrecht and Miller, 1993; Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001). Nonetheless, lack of gene flow appears to be reasonable evidence of speciation. Still, how can this be reconciled with fossil species? Ackermann et al. (2006) tested nine metric variables (and nonmetric data from crania) collected from known-pedigree yellow, purebred yellow and olive baboons to scrutinize them for morphological distinctiveness—heterosis (larger) or dysgenesis

smaller)—in comparison to their parents. The results, most evident in dentition, showed that primate hybrids were heterotic relative to their parental population. Ackermann et al. (2006) believe that this heterosis "probably indicates the mixing of two separately coadapted genomes…" (p. 632). They believe that their results offer a strategy for, in my words, detecting gene flow and interpreting the hominin fossil record.

Phylogenetic species concepts

Phylogenies are constructed on the assumption that species with many morphological similarities are more closely related than species with fewer morphological similarities. Also, the position of species boundaries depends on the respective characters chosen. However, the choice of characters from one researcher to the next is based on different criteria, which leads to a certain amount of arbitrariness. Phylogeneticists would reject this assessment.

The phylogenetic species concept can be traced to the writings of Hennig (1966). It emerged from the need to add a temporal dimension to the biological species concept. Subsequently, many variations of the phylogenetic species concept (De Queiroz and Donoghue, 1988; Eldredge and Cracraft, 1980; Mishler and Brandon, 1987; Platnick, 1977; Wiley, 1981) appeared on the same theme. There are some (Mishler and Theriot, 2000) who believe that Hennig was wrong when he postulated that there is one single point where reticulating tokogenetic relationships end and divergent phylogenetic relationships begin. Mishler and Theriot do not see a clear cutoff point for the reticulation of lineages. Accordingly, they state that "the point at which the possibility of reticulation goes to zero is well above the level at which cladistic structure can be reconstructed" (p. 44). Others (Eldredge and Cracraft, 1980; Kimbel and Rak, 1993; Nelson and Platnick, 1981; Nixon and Wheeler, 1990) believe in synapomorphies as the criteria for identifying true relationships between species as opposed to reticulate relationships, which are ambiguous in phylogenetic analysis because of homoplasy. The counter-argument is that allowing for reticulation in any cladistic analysis is realistic (Holliday, 2003; Mishler and Theriot, 2000). Finally, Mishler and Donoghue (1982) argue that species should be identified based on monophyly and ecology. In general, these phylogenetic species concepts contain similar components in the sense of their core meaning, which is defined as "the smallest aggregation of populations (sexual) or lineages (asexual) *diagnosable* by a unique combination of *character states* in comparable individuals (semaphoronts)" (Wheeler and Platnick, 2000, p. 56; italics added). Kimbel and Rak (1993) would add that "diagnostic characters are signs of reproductive cohesion that enable the grouping of organisms by virtue of uniquely shared ancestry and descent" (p. 467).

These phylogenetic species concepts come together, so to speak, to challenge the criteria of reproduction used by Mayr and Hennig to group organisms into species. Phylogeneticists claim that the ability to interbreed is pleisomorphic and does not provide new information, unlike synapomorphic traits (Mishler and Theriot, 2000; Rosen, 1978, 1979). This phylogenetic claim is interesting. Nonetheless, I agree with Mayr's suggestion that interbreeding addresses the "why" of species

(Mayr, 2000, p. 163). But the "how" of species delimitation in hominin paleontology, whether using the biological species concept, the evolutionary species concept, or any other classification system, always has qualities of arbitrariness, including phylogenetic trees and grouping based on monophyly or cladistic analysis (cluster links). Wiley (1979) stated that the number of cladograms or phylogenetic trees used depends on many assumptions, *of which some are not biologically meaningful*. For example, the number of cladograms for a given group of biological entities is set by the mathematical possibility of dichotomous and multiple lineage points, and the number of possible phylogenetic trees for the same set of biological entities has been set at between 13 and 22 (Cracraft, 1974; Platnick, 1977). Although proponents of the phylogenetic species concept argue vehemently that lineages can arise nonarbitrarily only through cladogenesis (Kimbel and Rak, 1993; Nixon and Wheeler, 1990; Rosen, 1979; Tattersall, 2000; Wiley, 1981), they do acknowledge the chronic difficulty in assigning individual organisms to particular species. Henneberg and Brush's (1994) solution to this problem, as mentioned earlier, is to abandon the species concept and describe biological diversity in terms of mutual similarities (*simila*) between individuals:

> In the case of fossils the first individual who is clearly dissimilar to others is given a nickname. When other fossils resembling this one are discovered they may be designated similars of this individual if they do not resemble fossils described earlier. A collection of similars (a *similum*) is given a name of the first individual and is a "slice" of a lineage. While species can be created for a single individual by a process of deduction it takes a minimum of two individuals to define a *similum* (p. 278).

Earlier in this section, I stated that the view of the "species" as a unit of evolution, as the product of evolution, or as an incipient species will influence the choice of species concepts and lead to an overestimation of the number of species. Consequently, I believe that all species concepts are problematic. We could take Plavcan's (1993) advice and initially identify "clusters of individuals that are morphologically similar within the bounds of variation of modern species" (p. 261), then assess within and between group relations. Or we could abandon the species concepts all together and replace them with the *similum* concept mentioned in the previous paragraph (Henneberg and Keen, 1990; Henneberg and Brush, 1994). I suggest that we abandon species concepts and find alternative models for use in documenting tempo and mode in evolution, including the concept of *similum*.

Differing interpretation of population variation: overestimation or underestimation of species?

Variation is critical to biological species because it promotes survival and reproduction. But it is also the very problem that makes the delimitation of extant species in general and fossil species in particular extremely difficult. What one

researcher sees as intraspecific variation another sees as interspecific variation. This difference in interpretation correlates with the arbitrariness in choosing traits for species designation. For instance, Randall Skelton and Henry McHenry (1998) looked at trait list bias and early hominin phylogeny, particularly in the relationship of *A. aethiopicus* to the other early hominins. To demonstrate that trait bias can lead to different results, they reanalyzed the data of David Strait et al. (1997), who grouped *A. aethiopicus* with *Australopithecus robustus* and *A. boisei* to obtain a monophyletic clade. Skelton and McHenry repeated the analysis of Strait et al. (1997), but with a twist. First of all, Strait et al. (1997) omitted 30 traits related to mastication because they believed these had an effect on their results. Skelton and McHenry (1998) duplicated the analysis but omitted a different set of masticatory traits, arguing that Strait and colleagues' criteria for selecting traits were too simplistic (Table 3). These 30 traits may have confounded the system because the ontogenetic integration of characters does not imply a unitary functional case, since pleiotropy and linkage disequilibrium can produce a link between morphological characters that have no common functional history (Kimbel and Rak, 1993).

Forty-eight traits were assigned to complexes based on logical functional relationships and then analyzed. Skelton and McHenry (1998) admit, "*This process is partly subjective*, yet we believe that at least most of the 48 traits were assigned to appropriate complexes" (p. 110; italics added). Phylogenetic analysis was performed, generating taxon scores for each complex and several parsimonious trees. According to Skelton and McHenry (1998), their trees or cladograms place *A. aethiopicus* as a sister to a clade including *Australopithecus africanus, A. robustus, A. boisei,* and the *Homo* species. Based on these results, they claim that the robust species do not form a monophyletic group as proposed by Strait et al. (1997). The point of detailing the research data of Skelton and McHenry and Strait and colleagues is to show how different conclusions are reached based on the different methodologies used. Skelton and McHenry's (1998) statement emphasizes this point. They write, "We believe, however, that *trait list bias poses at least as great a problem for the reliability of a phylogenetic analysis as uncertainty of functional relationships, and that an analysis that fails to address this source of error cannot be considered reliable*" (p. 112; italics added).

Table 3. Traits grouped by functional complex (from Skelton and McHenry, 1998).

Functional complex	Strait et al. (1997) Trait number	Number of traits in complex
Heavy chewing	2, 3, 4, 6, 7, 8, 9, 10, 11, 15, 19, 20, 23, 24, 25, 26, 28, 44, 47, 48, 53, 54, 55, 56, 57, 59, 60	27
Anterior dentition	49, 50, 51, 52, 58	5
Basicranial flexion	21, 22, 30, 31, 32, 33, 34, 38, 40, 41, 42	11
Prognathism/ orthognathism	13, 14, 15	3
Encephalization	16, 17	2

Many researchers (Holliday, 2003; Jolly, 1993, 2001; Templeton, 1989) agree that interspecific hybridization was, more than likely, prominent in hominin evolution (extant baboon ecology and population structure may have been similar to those of fossil hominins). But they refuse to raise the specter of "the Single Species Hypothesis." Instead, Trenton Holliday (2003) applies the notion of syngameon (Templeton, 1989)—the maintenance of cohesive units despite gene flow—to hominin evolution. Holliday uses Clifford Jolly's baboon research (1993, 2001) as a model for hominin evolution. The baboon genera *Theropithecus* and *Papio* are widely distributed in East, South, and West Africa. Interestingly, thousands of hominin fossils have been recovered in these same areas. Furthermore, there has been hybridization in the wild between *Theropithecus gelada* and *Papio anubis* and between *T. gelada* and *Papio hamadryas* (Holliday, 2003; Jolly, 1993; Jolly et al., 1997). When the hybrid (F_1) females were mated with a male *P. hamadryas* (backcross), the F_2 female infants (as in the F_1 female) were not sterile. However, the F_1 males seemed to be sterile. Holliday notes Jolly et al.'s (1997) important statement on the above events:

> …these data show that morphological differences sufficient to group taxa into different genera do not necessarily equate with cessation of gene flow between those taxa. Introgression between *Papio* and *Theropithecus*, morphologically identifiable as separate evolutionary lineages for 4.5 million years, may have been an important source of new genetic variability, *a hypothetical possibility with important implications for human evolution* (Holliday, 2003, p. 657; italics added).

Holliday (2003) agrees with Jolly (2001) that "much reticulation took place among fossil hominins" (p. 658). Many of the australopiths were contemporaries or lived less than 1 or 2 million years apart. If the hybrid offspring of *Theropithecus* and *Papio* species are viable and fertile, then what does this say about the offspring of *A. boisei* and *A. robustus* or *Homo rudolfensis* and *Homo habilis*? Even more controversially, could one speculate that the hominins mentioned above were two species rather than four? Another key difference between *Theropithecus* and *Papio* that is pertinent to this discussion is the robusticity of the facial features of the gelada baboon, *Theropithecus*, which was in the past argued to be a morphological indicator of reproductive isolation. Geladas have large molars and a large facial skeleton as compared to hamadryas, *Papio* (Hunt, 2003; Jolly, 1970), yet they still hybridize. What does this say about the preoccupation with facial robusticity or facial shape and topography in ranking *A. boisei* as a separate species from *A. robustus* (see Rak, 1983)? Similarly, what does this say about the preoccupation with craniofacial and postcranial robusticity in Neanderthals, used to warrant ranking them as a separate species from *Homo sapiens*? (Franciscus, 1996; Harvati and Weaver, 2006; Stringer, 1994, 1996; Tattersall, 1992; Wood and Collard, 1999a, 1999b; Wood and Richmond, 2000). It seems that different researchers have different ideas about the importance of bone characteristics in indicating reproductive isolation. As a result, we are ignoring information suggesting a simpler hominin phylogeny. Many researchers (Holliday, 2003; Kimbel and Rak, 1993; Kingdon, 2003; Leakey et al., 2001; Tattersall, 1992; Wood and Collard, 1999a, 1999b) would disagree.

Earlier in this paper, I briefly discussed Ackermann et al.'s (2006) research on identifying the morphological signatures of hybridization in known-pedigree, purebred yellow and olive baboons. This research adds to the discussion on hybridization in *Theropithecus* and *Papio* above and might offer strategies "for detecting hybrid zones in the fossil record" (Ackermann et al., 2006, p. 632). Ackermann et al. (2006) support Jolly's (2001) proposition that baboons are valuable analogues for studying issues of hybridization in human evolution because they resemble hominins in ecological and population variation more than they do apes. In addition, living baboons diverged from the most recent common ancestor at approximately the same time *H. erectus* emerged, which is 1.8 Ma. Ackermann et al. (2006) examined the crania of 169 yellow baboons, olive baboons, their first-generation hybrids ($F_1 = olive \times yellow$), and backcrosses formed from the mating of first-generation hybrids with olive baboons ($B_1 = olive \times F_1$) to test whether there were significant qualitative morphological variation or quantitative differences among purebred populations and their hybrids. Hybrids were also analyzed for heterosis or dysgenesis: sizes larger or smaller than expected. The metric data collected by Ackermann and colleagues represented the overall morphology of the cranium, considering 36 unilateral and midline neurocranial and facial landmarks.

Ackermann et al. (2006) used multivariate analysis of variance (MANOVA) and univariate analysis of variance (ANOVA) to analyze the metric data represented by 39 Euclidean distances. Since there were significant morphological differences between the sexes based on MANOVA, all traits were corrected to the female mean to eliminate the potential problem of sexual dimorphism. Following the multivariate and univariate comparisons, they tested each hybrid sample for heterosis measured by the difference between the hybrid and an expected value. Consequently, Ackermann et al. (2006) expected value for the F_1 hybrids was the midparental value (PO) of the means of the pooled-sex olive and yellow purebreds and the expected values for the backcross with the olive baboons (B_1) is half the distance between PO and the olive baboon value. In short, heterosis is present if hybrids are significantly larger than their expected value or absent if the expected values are lower.

In the qualitative trait variation analysis, Ackermann and colleagues found supernumerary teeth, extra sutures in the zygomaxillary region, dental crowding, residual metopic sutures, and large overall size and robustness in hybrids.

Ackermann et al. (2006) reported that purebred olive and yellow baboons were significantly different from each other for 33% of the traits. Both hybrid samples exhibited heterosis: heterosis in the F_1 was found in 28 traits (72%) [basicranium] and significant in three traits (8%) at the $p = 0.05$ level. In the B_1 generation, heterosis was found in 19 traits (49%) [neurocranium/upper face] and significant in seven traits (18%) at the $p = 0.05$ level. Furthermore, the F_1 hybrid values were significantly larger than those in both purebred populations for one trait, larger than those in olive baboons for six traits (smaller for four traits), and larger than those in yellow baboons for three traits. In addition, the B_1 hybrids were significantly larger than both purebred populations for one trait, larger than the olive baboons for four traits (and smaller for six traits), and larger than yellow baboons for four traits.

The results regarding the qualitative differences showed incidence of supernumerary teeth (permanent and bilateral mandibular molars in some hybrids) only in the F_1 generation. Ackermann et al. (2006) note that supernumerary teeth are present in some purebreds, but that their overall incidence is low and that they differ in expression from those of the hybrid in that they are maxillary teeth.

In summary, Ackermann et al. (2006) argue that their strategy of testing for heterosis in metric variables is a good indicator of the presence of hybridization. They caution that hybrids can show a range of morphologies (not a balanced mixture of parental traits), resembling one parent more than the other or displaying intermediate morphology. This knowledge does not make it easier to detect hybridity in the hominin fossil record despite the presence (albeit at a low frequency) of dental crowding in Neanderthals, East African robust australopithecines, and Southern African gracile australopithecines; supernumerary lateral maxillary incisor teeth in a Southern African robust australopithecine; and supernumerary left mandibular molars in an East African gracile australopithecine (Ackermann et al., 2006). Nonetheless, hybridization in human evolution would lead to a higher degree of genetic similarity among populations. Consequently, phylogenetic relationships would be described as reticulate and not branching. However, this evolutionary model conjures up homoplasies and synapomorphies.

Holliday (2003) argues that if two organisms are faced with similar selective pressures, similar adaptations or homoplasies (in cladistic terminology) may emerge. He also argues that homoplasies can occur through reticulation. But chaos reigns because Holliday (2003) admits that "trying to distinguish homoplasies due to reticulation from those due to other processes is likely to be limited" (p. 658). This, in my opinion, means that phylogenetic systematics, its offspring cladistics, and other species concepts are not effective in distinguishing hybrids from non-hybrids in the fossil record. Therefore, we may ask if shared traits or synapomorphies such as large molars, zygomatics, and sagittal crests in *A. boisei* and *A. robustus* represent homoplasies due to reticulation (interspecific hybridization) or synapomorphies due to monophyly. Or, if the papionins model is accepted (in which the hybrid offspring is viable), is it possible that *A. boisei* and *A. robustus* are geographical variants? Is it possible that *H. rudolfensis* and *H. habilis* could be sexual variants of the same species, and that *Homo neanderthalensis* is actually *H. sapiens neanderthalensis*, a population not unlike the Australian aborigines who were "isolated" at the edge of the species range? To answer these questions, we must understand whether variation in the fossil record differs from that of living species. Whatever answers the researcher generates, she must still answer the ultimate question, namely: how much variation is necessary before a new fossil species is recognized? This in turn leads to the overestimation or underestimation of species depending on the researcher's interpretation of variation among fossil and living species (see Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001). In general, the fossil cannot be interpreted only with reference to itself; we must understand the biology (morphology, life history, ontogeny, etc.) of the extant analog in order to interpret variation in the fossil record (Ackermann et al., 2006; Henneberg and de Miguel, 2004; Hunt, 2003; Jolly, 1993; Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001).

Here is a potential scenario. If the archetypal modern Cro-Magnon mated with (for argument's sake I will use *neanderthalensis* as the species designation) a *Homo neanderthalensis*, what would be the result? In the late 1990s in Portugal, a skeleton of a four-year-old was excavated from an upper paleolithic sequence (Lagar Velho 1), dating back 24,500 years (Duarte et al., 1999). This child was said to be a hybrid between a Neanderthal and a modern because it had a "mix" of characters that suggested Neanderthal ancestry, such as a suprainiac fossa, and second lower incisor shoveling (Duarte et al., 1999). Tattersall and Schwartz (1999) argued that if gene flow did occur between a Neanderthal and modern, then Lagar Velho 1 would resemble a Neanderthal or a modern, not a mixture of both. However, we all know that phenotypic expression is complex and that environmental variation is an important component. More specifically, phenotypic expression of all characters, whether affected by one locus or by many loci, will depend at least to some extent on the environment in which the organism develops (Boyd and Silk, 2006). We also know that genes do not blend. Consequently, when there are many loci and each has a small effect on the phenotype, *environmental variation tends to blur or mix together the phenotypes* associated with different genotypes. Therefore, as in the case of Lagar Velho 1, a modern child resulting from mating between a European and an Australian aborigine would have a mixture of Melanesian and European characteristics, i.e., straight hair and dark skin, light skin and curly hair, etc. In short, the Lagar Velho 1 child could have been a viable offspring of a *H. sapiens europeaus* (Cro-Magnon) and *H. sapiens neanderthalensis*. But Ackermann et al. (2006) caution us against the common expectation that hybrids will display the average of their parental phenotypes.

Many (Chamberlain, 1989; Kimbel and Rak, 1993; Lieberman et al., 1988, 1996; Tattersall, 2000; Wood, 1985, 1993; Wood and Utterschaut, 1987) would disagree strongly with some of the arguments in the previous paragraph, particularly on the subject of early *Homo*. Kimbel and Rak (1993) argue that on the basis of cranial characters, a hypothesis of intraspecific variation (due to sexual, geographical, or temporal variation) cannot be supported. They note the evidence showing contemporary geographical and stratigraphic evidence for *H. rudolfensis* and *H. habilis* in East Africa and detail differences in specific cranial characteristics, such as differences in the shape of the frontal squama (which is flat in *H. rudolfensis* and convex in *H. habilis*), differences in superior facial breadth (less than midfacial breadth in *H. rudolfensis* and greater than midfacial breadth in *H. habilis*), differences in the shape of the infraorbital plate (inflated-anterior to the nasal bridge in *H. rudolfensis* and flat and vertical-posterior to the nasal bridge in *H. habilis*), differences in mandibular fourth premolar (molarized in *H. rudolfensis* and not molarized in *H. habilis*), etc. Essentially, according to their data, *H. rudolfensis* has an australopithecine-like face with an expanded brain case, and *H. habilis* has a smaller late *Homo*-like face and an absolutely smaller brain case. This analysis is not without support. Daniel Lieberman et al. (1996, p. 116) used similar craniofacial traits in a cladistic analysis to suggest that "homoplasy is the primary cause of the phylogenetic confusion surrounding the two species subsets of *H. habilis sensu lato*." In other words, any similarities between *H. rudolfensis* and *H. habilis* are more likely

to be homoplasies than homologies. Lieberman et al. (1996) generated several cladograms derived from different subsets of data reflecting different functions or developmental regions (including cranial vault, face and masticatory apparatus, and basicranium) where the cladograms were ranked from most parsimonious to least parsimonious. The variability between cladograms is a running theme in phylogenetic analysis and is probably related to the selection of traits, which may have an arbitrary component to it. To restate another of Skelton and McHenry's (1998) precautions, "trait list bias can affect the results of phylogenetic analysis and different results may be obtained depending upon whether or not an attempt is made to compensate for trait list bias" (p. 112). The results presented by Lieberman et al. (1996) show that *H. habilis* (Lieberman et al.'s "1813 group") and *H. rudolfensis* (the "1470 group") are not sexual variants of the same species. In one instance, they are shown as sister taxa. What is also interesting to note in these cladograms is that *H. habilis* and early African *H. erectus* form a separate clade, while *H. rudolfensis* and the different australopiths form another.

Although the genera and species designations of *H. habilis* and *H. rudolfensis* have tentatively been accepted (see Leakey et al., 2001) by the field, questions about intraspecific sexual variation or sexual dimorphism continue to emerge. Kelley's (1993) analysis of postcanine variability in *Lufengpithecus* may have implications for the *H. habilis–H. rudolfensis* species argument. Initially, Kelley (1993) used canine shape to sort Lufeng upper and lower canines by sex. In previous research (Kelley and Etler, 1989), Kelley and his colleague found that canine shape differs between males and females in extant ape species. The canines were used to sex the lower premolars, and indices of sexual dimorphism were then calculated for the sexed postcanine dentitions of *Lufengpithecus lufengensis* and compared to the same indices for the orangutan, *Pongo pygmaeus*.

With life history, morphological patterns, and body size in mind, Kelley (1993) initially hypothesized that *Lufengpithecus lufengensis* was no more dimorphic than *Pongo pygmaeus*, since *Lufengpithecus* may belong in the orangutan lineage. For *Pongo pygmaeus*, Kelley created a probability distribution of values for the index of dimorphism for each tooth position, selecting sample sizes similar to those of the Lufeng samples. Based on the results, Kelley concluded that *Lufengpithecus lufengensis* exceeded the orangutan in postcanine sexual dimorphism and, more importantly, therefore supports a single-species hypothesis for *Lufengpithecus*.

As far as body-size dimorphism is concerned in *Lufengpithecus lufengensis*, which has far-reaching implications for competition in ecology, Kelley argues that the extreme dental dimorphism is a result of a high degree of body-size dimorphism. Plavcan (1993) disagreed with this conclusion. He states the following:

> …dimorphic teeth such as P3 or canines should not be used to test a multiple species hypothesis, since sample variation due to dimorphism is often as great as that due to interspecific differences in tooth size…If tooth-size variation in a fossil sample exceeds that in all living species, we have little choice but to infer that the sample is composed of more than one species, rather than two sexes, unless there is other strong evidence to support the dimorphism hypothesis (pp. 255, 259).

Despite this early disagreement, Plavcan would eventually support the single-species status for *Lufengpithecus* (Kelley and Plavcan, 1998). In summary, species competition prevents two large-bodied extant hominoids (and we can extend this to hominins) from existing in sympatry. Consequently, *H. habilis* and *H. rudolfensis* could be a single species. Nonetheless, I believe that the same rigor applied to the Lufeng dental samples in Plavcan (1993), Kelley (1993), and Kelley and Plavcan's (1998) analyses should be used to address the *H. habilis–H. rudolfensis* species problem and similar arguments in hominin evolution.

However, the chaos continues in the form of a new call (Leakey et al., 2001; Tattersall, 2003; Wood and Collard, 1999a, 1999b) to place early *Homo* in the genus *Australopithecus*. Wood and Collard (1999b) made a detailed study of *H. habilis* and *H. rudolfensis*, comparing them against known australopiths and several hominans. Based on functional analyses of six global traits (body size, body shape, locomotion, jaw and tooth development, and brain size), they concluded that *H. habilis* was australopith-like and not human-like or intermediate for all six measures. *H. rudolfensis* was also australopith-like, despite the fact that only jaw and tooth development and brain size could be measured due to a lack of fossils. As a result, Wood and Collard (1999b, p. 70) suggested that "both *H. habilis* and *H. rudolfensis* should be transferred to the genus *Australopithecus*." Subsequently, Meave Leakey et al. (2001) saw such strong craniofacial similarities between the *H. rudolfensis* and the genus *Kenyanthropus* that they were ready to create a new taxon: *Kenyanthropus rudolfensis*. As a matter of fact, some paleoanthropologists (Kingdon, 2003; Tattersall, 2003) have already included *Kenyanthropus rudolfensis* in their hominin phylogenies. It is interesting that based on some of these global traits, in addition to body weight, geographical latitude and geological time (before 1.8 Ma and after 1.8 Ma), the single-species hypothesis could not be falsified (Henneberg, 1989, 1997; Henneberg and de Miguel, 2004; Henneberg and Thackeray, 1995) This analysis will be addressed in greater detail later in the paper.

The confusion continues as a recent study (Spoor et al., 2007) uses new evidence to show that *H. habilis* and *H. erectus* were not time-successive segments of a single anagenetic evolutionary lineage as is generally interpreted. The evidence consisted of a small calvaria catalogued as KNM-ER 42700 and a right maxilla catalogued as KNM-ER 42703, with estimated geological ages of 1.55 and 1.44 Ma respectively, found during fieldwork in 2000 at Ileret, Kenya. KNM-ER 42700 was assigned to *H. erectus* because the researchers believed that it had the general characteristics of that species, such as frontal and parietal keeling, mediolaterally narrow temporomandibular joints, distinct coronal and sagittal orientation of the tympanic and petrous elements, a posterior mid-sagittal profile with low occipital upper scale, and opisthocranion positioned close to the lambda. Yet, Spoor et al. (2007) admit that

> …*endocranial capacity, measured from computed tomography (CT) scans is estimated at 691cm³…A multivariate analysis of calvarial dimensions confirms the affinities of KNM-ER 42700 with* H. erectus. *Some characters often considered diagnostic of the species (for example, a thick cranial vault and supraorbital torus, and strong occipital angulation) are lacking in KNM-ER 42700"* (p. 688; italics added).

Knowing the range of variation in cranial capacity is critical to preventing the underestimation and overestimation of fossil species (see Fitzpatrick et al., 2008; Henneberg, 1997; Martin et al., 2006). Unfortunately, there are not enough individuals within a respected fossil hominin species to obtain accurate ranges of variation.

As noted above, KNM-ER 42700 has a cranial capacity of 691 cm^3, which is within the *H. habilis* range. Consequently, why 'force' this specimen into the *H. erectus* taxon? Furthermore, Spoor et al. (2007) have placed KNM-ER 42703 into the *H. habilis* taxon based on dental analysis. In short, what we probably have here are two *H. habilis* species, with KNM-ER 42700 representing a transitional point between them. If one accepts Wolpoff and Caspari's (1997) views on the evolution of the genus *Homo*, no speciation occurred in this lineage. Wolpoff and Caspari (1997) argue that from the end of the Pliocene until ancient and modern *H. sapiens*, it remained a single variable species.

In hominin paleontology, there seems to be disagreement regarding the choice of characteristics and the biology behind this choice. In other words, there is some confusion regarding characteristics that are mainly functional, ontogenetic, epigenetic, or heritable. This lack of understanding has probably lead to either the "lumping" or the "splitting" of fossils in paleoanthropology (Albrecht and Miller, 1993; Henneberg, 1997; Henneberg and de Miguel, 2004; Kelley, 1993; Plavcan, 1993; Plavcan and Cope, 2001). It might be prudent for us to learn more about characteristics that are important in behaviors that prevent gene flow. For instance, if we study the divergent toe of the "Little Foot" *A. africanus* compared to the non-divergent toe of *A. robustus*, there may be a strong argument for species separation. This specific trait tentatively indicates a drastic behavioral difference. In addition, one might offer the same argument for separate species designation for OH 9, *H. habilis* (divergent big toe) and *H. rudolfensis* (non-divergent big toe). The difference in brain cases between *H. habilis* and *H. rudolfensis,* when body size and range of variation is accounted for, could indicate separate species. These traits, in my opinion, suggest critical behavioral differences (i.e., survival and reproduction) that are substantial/substantive reasons for species designation as opposed to arbitrary bony structures.

Other researchers (Gingerich, 1985; Kelley, 1993; Kelley and Plavcan, 1998; Plavcan, 1993) have used tooth-size variability to help discriminate between species in the fossil record. Plavcan (1993) argued that dental variability within and between fossil species is similar to that between closely allied extant species. In other words, if dental variability in fossil sample species is greater than that seen in living species, more than one species is assumed to be present. While this supposition is still debated, measures of relative variation in fossils and how they should be interpreted in living analogs are continually being refined (see Plavcan and Cope, 2001). Nonetheless, Plavcan (1993) tested the multiple species hypothesis by focusing on variation in upper and lower P4-M2 of 34 cercopithecoid primates (although he was severely criticized by Kelley (1993) for using cercopithecoidea as an analog for fossil hominoids) whose geographic ranges overlap in the wild. The length and breadth dimensions of fossil sample P4-M2 were compared to similar dimensions from living

species and from single and mixed species; a computer program was used to generate coefficients of variation (CV) for all dental dimensions.

Plavcan (1993) found that within single-species samples, CVs of P4-M2 are consistently low. In fact, when species differed greatly in terms of tooth size, CVs of postcanine tooth dimensions were consistently higher than those generated from any single-species sample, and that when species had identical tooth dimensions, single and mixed-species CVs were similar. In Plavcan's analysis, for example, a mixture of *Macaca fascicularis* and *Macaca nemestrina* generated higher CVs than in single-species samples. Furthermore, mixtures of *Cercopithecus pogonias*, *Cercopithecus nictitans*, and *Cercopithecus cephus* (single and mixed species) inflated the CVs, but not above the range of a single species. For geography, mixtures of *P. entellus thersites* from Sri Lanka and *P. entellus ajax* from Kashmir generated CV well above that of single species samples. It is interesting that Henneberg and Thackeray's (1995) analysis of the mixed *Australopithecines* and early *Homo* molar tooth crown areas generated CVs that were insignificantly different from those of a single modern human species. Kathleen Fuller (1996) and Cope and Lacy (1996), using the same genera, could not find multiple species.

Plavcan concluded that CVs should be used with caution; they cannot identify mixed fossil species, but high postcanine CVs suggest the presence of multiple species. Also, the effect of sexual dimorphism (particularly in *Lufengpithecus*) and tooth-size seemed to underestimate species in the fossil record. Five years later, computer modeling experiments would convince Plavcan that the single-species hypothesis for the Lufeng sample could not be rejected (Kelley and Plavcan, 1998).

Continuing, Henneberg (1997) has proposed using chemical analysis as a new source of measurable data: concentrations of chemical elements and isotopes (strontium/calcium) rather than sizes of morphological structures. Henneberg's contention is that since the strontium/calcium (Sr/Ca) ratio is indicative of the amount of meat in the diet, it should differ between herbivorous *Australopithecines* and carnivorous *Homo*. However, the isotopes are identical for both genera, indicating similar diets. Henneberg's analysis is incompatible with the scenario of two or more sympatric species adapted to similar diets because the competitive exclusion principle does not allow it (Harding, 1960). I believe that Sr/Ca ratio certainly reduces some of the complexity of tooth dimension variability.

Furthermore, Holliday (2003) uses Templeton's "cohesion" species concept to explore the possibility of interspecific hybridization in hominin evolution. He also used baboon systematics, based on the work of Jolly (1993, 2001), as a model. Despite the fact that Holliday and particularly Jolly emphasize the evidence of interspecific hybridization between *Theropithecus* and *Papio* or *Macaca* and *Papio* and the birth of interfertile offspring, they stop short of reviving the single-species hypothesis. For instance, Holliday (2003) states that the suggestions of possible reticulation discussed above may strike some as "a revival of the 'single species hypothesis' of Brace (1967), Wolpoff (1971), or Henneberg and Thackeray (1995). This is not the case" (p. 660). The field of human paleontology is absolutely convinced that the single-species hypothesis is dead and buried. But Kevin Hunt (2003) questions this in the colorful title of his paper, "The Single Species

Hypothesis: Truly Dead and Pushing Up Bushes, or Still Twitching and Ripe for Resuscitation?'' Hunt writes, "I, for one, believe that the single species hypothesis' death has been greatly exaggerated" (p. 485). There are others who might agree.

While accepting simple branching patterns, such as that between *Homo* specimens and Australopithicine specimens, Brace (1967, 1981, 1995) has for many years complained about the excessive naming of species in human paleontology. Yet, he has not totally abandoned the single-species hypothesis. While the current fad is excessive "splitting" because some (Lieberman et al., 1996, p. 99) believe that "lower taxonomic units can, if necessary, be recombined to make higher ones after resolving their phylogeny," Brace (1981) was quite prescient in his statement with regard to phylogenetics and cladistics: "There are still major questions in regard to the cladistic affinities of more than a few important early hominids" (p. 421). In other words, Brace implies that cladistics cannot handle mosaic evolution or the distinction between evolutionary parallelism and evolutionary convergence. By default, differing rates and times of change for different traits within a single lineage or between lineages are interpreted as speciation by the cladist. Lieberman et al. (1996), in attempting to assess homology and homoplasy, admit the difficulty: "even more problematic is attempting to evaluate which characters are homoplasies and which are homologies" (p. 116).

Hunt (2003) attempts to "resuscitate" the single-species concept by looking at extant primate species and several important morphological and ecological behavioral factors (including the tendency to hybridize, body size, level of sexual selection, brain size, daily travel distance, home range size, habitat type, canopy use, species range, population density, and diet) in choosing an analog for hominin speciosity. Hunt readily admits that some of these variables cannot be applied to fossils. Yet, he believes that they can be productive. The tendency to hybridize is one of those behavioral characteristics that most (Holliday, 2003; Kimbel and Rak, 1993; Wiley and Mayden, 2000) would agree cannot be assessed in fossils. But Hunt notes that larger home ranges increase the chance of encountering semispecies (interbreeding between genera), with the potential of reducing the rate of speciation. In particular, Hunt notes that analogies between hominins and smaller primates, i.e., the genus *Cercopithecus*, will lead to splitting. His argument is based on the fact that *Cercopithecus* has a home range of 29 hectares consisting of forest, it is the most speciose genus in the Order *Primates*, and it does not have a hominin-sized brain. Hunt believes that a cautious approach for a primate model would be to select a primate with a hominin-sized brain, a large home range (i.e., 2150 hectares of forest/woodland), and low speciosity. In other words, the genus *Pan*, containing only two species, fits this expectation very well.

Modes of speciation and the number of species

Charles Darwin advocated anagenesis or straight-line evolution. However, this mode of species change has been accused of being too arbitrary. Under the

phylogenetic species concept, speciation can only occur through cladogenesis (Cracraft, 1974, 2000; Eldredge and Cracraft, 1980; Kimbel and Rak, 1993; Mishler and Donoghue, 1982; Platnick, 1977; Wheeler and Platnick, 2000; Wiley, 1979, 1981; Wiley and Mayden, 2000). By default, ''gaps in the fossil record'' are interpreted as a nonarbitrary way to delimit species. There are many gaps in the fossil record, the logic goes; therefore, there must be many species. This logic is at the root of the ''bushy'' hominin phylogeny advocated by modern paleoanthropologists. This high-speciation perspective uses extant nonhuman primate genera, i.e., *Macaca* and *Cercopithecus*, as models (Hunt, 2003). It is interesting to note that Henneberg and de Miguel's (2004) analysis of average body weights of various species of *Macaca* correlate with latitude ($R = 0.58$), indicating that latitude is an important factor in their speciation rates (unlike with hominins). Continuing, this high-speciation model is embodied in the punctuated equilibrium hypothesis (Eldredge and Gould, 1972). Punctuated equilibrium suggests that once a species has been established, it changes little through time. Also, Eldredge and Gould view speciation as a rapid event occurring within small, isolated populations on the periphery of a species range, so that they will appear rather quickly without evidence of a transitional state—Simpson's quantum evolution (1953). But Brace (1981) argues to the contrary: ''The preceding expansion in brain size took place gradually over a suitably long period of evolutionary time and evidently shared by the entire hominid population'' (p. 422). Henneberg and Keen (1990) also reject Simpson's quantum evolution. They contend that rigid species definitions used to describe evolution lead to explanations such as that of punctuated equilibria and cladistic branching; ''Both of these imagine new species emerging quickly (by processes usually not detailed)'' (p. 214). Moreover, Henneberg's research (Henneberg, 1989, 1997; Henneberg and de Miguel, 2004) shows similar trends (as Brace) in that all hominins appear to form a single gradually evolving lineage. For instance, Henneberg and de Miguel (2004) analyzed the cranial capacities of 207 adult hominins, including 107 *Homo*, and the body weights of 285 hominins, including 184 *Homo* dated between 5.1 Ma and 10 ka, in a ''taxonomically blind'' study (meaning that taxonomic groupings were used after the fact). Henneberg and de Miguel included latitude in their analysis to test the widely held belief regarding species formation in new latitudes. Initially, they found that cranial capacity and body weight correlated with geological dates and with geographical latitude. Then, when the effects of date were removed, cranial capacity showed a significant partial correlation with latitude ($R = 0.27$, $p < 0.0001$), while weight did not correlate with latitude. Furthermore, they found a gradual relationship of brain size and body size to geological dates, even when the effects of Bergmann's rule (latitude) were removed ($R = 0.88$ for cranial capacity and $R = 0.39$ for weight; $p < 0.0001$ for both). Finally, keeping the date constant for two chronological subsamples, before 1.8 Ma and after 1.8 Ma, Henneberg and Miguel calculated partial correlations between cranial capacity and latitude. They found no significant correlation between cranial capacity and latitude. Also, residuals around regressions of cranial capacity and weight on date did not correlate with latitude. They concluded that ''were there a speciation resulting from dispersal of populations into new latitudes, residuals around regression on date should correlate with latitude''

(p. 28). These results confirm Henneberg and Thackeray's (1995) Single Hominid Lineage Hypothesis (SHLH), which states the following:

> During the last 5 Ma there was no more than one species at any one time in the hominid family, thus there was a single lineage leading, without branching, from a hypothetical ancestral ape to modern humans. The term "species" is used here in its evolutionary sense (as a sequence of populations evolving separately from others, Simpson ,1961, p. 33).

Using cranial capacity and body size reconstructed for fossil specimens covering 3 million years (Table 4), Henneberg and Thackeray (1995) generated CVs.

Based on their data, the temporal and geographical variation of a sample of hominins appears to be similar to that of modern humans (CV around 11.6%). Interestingly, they found that *A. robustus* had a CV of 3.5%, significantly lower than that of any species of ape or human. Furthermore, all hominids from Olduvai dated at approximately 1.8 million years had a cranial capacity CV of 10.4%. Body size and height estimates, when plotted, form a smooth exponential line. According to Henneberg and Thackeray (1995), "this indicates a continuous, gradual nature of the evolutionary change of body size, devoid of punctuated events and cladogenesis" (p. 35). But Cope and Lacy (1992) argue that CVs are not robust enough to test the single-species hypothesis because fossil samples are usually small and confidence limits of CV are therefore large. Simulated sampling distributions of single species and pooled CVs were generated based on four dental characteristics of three extant sympatric *Cercopithecus* species. Cope and Lacy found that their methodology had greater power in detecting multiple species. Based on their results, they feel confident that the single-species hypothesis can be rejected. However, is *Cercopithecus* an ideal model to use for hominidae (see Hunt, 2003)? Kelley (1993) argues that

Table 4. Characters of cranial capacity (in mililitres) of variously grouped specimens (from Henneberg and Thackeray, 1995).

Group	N	Avg	Std	CV
Australopithecus africanus	10	462.5	35.6	7.7
Gracile australopithecines (*A. africanus* + *A. afarensis*)	12	468.4	38.7	8.4
Early *Homo*, excluding *H. erectus*	8	666.0	106.4	16.0
Early *Homo plus* robust australopithecines	13	611.4	75.8	12.4
Robust australopithecines	5	524.0	17.4	3.3
Only East African robust australopithecines	4	522.5	19.2	3.7
African *Homo erectus*	3	881.3	140.6	15.9
All Olduvai hominids dated at approximately 1.8 ma	5	629.0	65.4	10.4
All Javanese hominids dated at more than 300 ka BP	8	939.1	81.4	8.7
Zhoukudian *H. erectus*	5	1043.0	100.6	9.6
All australopithecines	19	489.2	56.9	11.6
All *Homo erectus*	18	946.2	119.0	12.6
All hominids dated between 1.0 myr and 0.5 ma	10	886.6	95.0	10.7
Modern humans worldwide	Approx. 1000	1349.3	157.0	11.6

cercopithecoids are biologically different from hominoids, which means that a cercopithecoid model cannot be applied to the hominoid fossil record. This, alternatively, puts the multiple species hypothesis in jeopardy because two large body size hominin species cannot exist in sympatry based on the competitive exclusion hypothesis (Harding, 1960).

Vanity: fame and notoriety that comes with the naming of new fossil species

When a hominin fossil is found, there is wide media attention associated with the discovery. There is even more media attention if this respective fossil is described (in a few weeks for some researchers and later for others) as a ''new'' species of hominin by its discoverer(s). The discoverer(s) secure for themselves a place in hominin paleontological history, not only for discovering a ''new'' hominin species but also for singlehandedly changing the present, accepted view of hominin phylogeny. What hubris. What vanity. This unrestricted power (with no strong regulation by ICZN of assignments of new species names) is too seductive to relinquish, with the result that the assigning of new names will continue in zoology and paleontology.

The negative effects of this tradition are troubling. In recent years, species names have been auctioned off or sold to donors to support research programs in need of funding (Chang, 2008). It seems that the rarer and more evolved the organism, the more money its species name is worth. The ICZN (with no strong regulation capacity) does not have a position on this matter (Chang, 2008). This might certainly increase the already present proliferation of new species names. These events speak to the trivial nature of taxonomic names. Specifically, if they can be assigned arbitrarily, or bought or sold so easily, then we might as well replace them, abandon them and use numbers as suggested by Henneberg and Keen (1990), Henneberg and Brush (1994) and Henneberg (1997). We would be eliminating two problems at once: taxonomy and vanity in hominin paleontology.

Conclusion: alternatives to taxonomic names and a tentative working solution to the problem

The speed with which hominin fossils are given a species designation is alarming. For instance, the skeletal materials recovered from the Indonesian Island of Flores in September 2003 were described and given a new hominin taxon name, *H. floresiensis*, in 2004 based largely on a single nearly complete adult skeleton, Liang Bua 1 (Brown et al., 2004). This single individual's traits, the defining one being an "endocranial volume equal to the smallest-known australopithecines" (Brown et al., 2004, p. 1055), came to characterize a new species. This is similar to my Australian Aborigine example, detailed earlier in this paper. If one were to study the traits of a modern Australian aborigine skull, one would be tempted to establish it as a new species.

Even more troublesome is the misunderstanding surrounding the range of variation within a single species, to the extent that one might be tempted to put, for example, the Cro-Magnons of Europe and the Mungo of Australia into two separate species because the Mungo does not have universal, prototypically modern characteristics such as a high forehead, a small brow, small jaws and teeth, and little facial prognathism. In contrast, Robert Martin et al. (2006) argue that Liang Bua 1 (LB1) may be a microcephalic *H. sapiens* and not a new species. Their comparison of the skull of LB1 (estimated to $400\,cm^3$ (Brown et al., 2004; Falk et al., 2005)) to other microcephalic adult human skulls and endocasts shows similarities in terms of overall size and proportions, such as the receding forehead. One of the endocasts, with a volume of $340\,cm^3$, was derived from the skull of a 32-year-old woman from Lesotho who had the body size of a 12-year-old child (Martin et al., 2006).

Along similar lines, Jacob et al.'s (2006) analysis of Liang Bua 1 (LB1) suggests that dramatic skeletal characteristics are indicative of pathological abnormalities rather than interspecific variation. Specifically, Jacob et al. (2006) state that "LB1 is drawn from an earlier pygmy *H. sapiens* population but individually shows signs of a developmental abnormality, including microcephaly" (p. 13421). Furthermore, they found that cranial characteristics placed LB1 within the modern range of human variation, resembling Australomelanesian populations. Fitzpatrick et al.'s (2008) close examination of human burials at the early (3000 BP) and stratified site of Chelechol ra Orrak in Palau (western Micronesia) supports this conclusion. Specifically, their analysis of cranial, postcranial, and tooth elements of the Chelechol ra Orrak hominin sample indicated that they were normal-sized Oceanic individuals as opposed to the "pygmoid" or dwarfed populations proposed by Lee Berger et al. (2008). Berger et al. (2008) claim that small-bodied hominin fossils (2890–940 BP) from the Ucheliungs and Omedokel caves (also in Palau) represent cases of insular dwarfing well below that expected for normally sized modern humans, as indicated by small frontal dimensions, distinct supraorbital tori, weakly developed mental eminence, relatively large dental dimensions, and small body size. Fitzpatrick et al. (2008) argue that when the small frontal (small minimum frontal breadth) dimension of specimen Orrak D is compared to that of a large sample of other early Palauans, it is not found to be as aberrant as indicated by Berger and colleagues. Fitzpatrick et al. (2008) note that the small minimum frontal breadths of 90–96 mm (based on 14 adult male crania) were likely common among early Palauans. Specimen Orrak D has a minimum frontal breadth of 90.5 mm, maximum cranial length of 187 mm, maximum cranial breadth of 143 mm, and basion-bregma height of 148 mm.

Within the Berger et al. (2008) and Fitzpatrick et al. (2008) papers, I recognize two critical themes important to the problem of delineating species. First, these researchers never gave their prehistoric Palauan discoveries new species designations, despite the suite of "unique" traits visible in these fossils. In fact, Berger et al. (2008) note in the Palauan sample patterns of reduction in the craniofacial and postcranial traits similar to those of LB1. The wide media attention associated with the discovery of "new" species might have tempted some researchers to designate a new species taxon. Fortunately, that did not happen with these researchers. Second, the emphasis on the range of variation by Fitzpatrick et al. (2008) is instructive. In one of their

more pointed criticisms of Berger et al.'s (2008) work, Fitzpatrick et al. (2008) stated that they (Berger et al.) had reached their conclusions without comparing their data to Micronesian skeletal and dental samples that were readily available, missing the opportunity to learn that body size in early Palauans was actually ''well within the range of variation for early Oceanic populations of Homo sapiens'' (p. 2).

In another study, wrist bones attributed to LB1 were examined to test the competing hypotheses of their representing a new species versus a pathological modern human (Tocheri et al., 2007). We agree with these researchers' statement regarding the modern human trapezoid, which is shaped like a boot, as opposed to the palmar half of the bone, which is radio-ulnarly and proximo-distally wide. Furthermore, they state that Upper Paleolithic H. sapiens and Neanderthals both share these derived morphological features with modern humans, suggesting that they are most likely inherited from a common ancestor. In contrast, other primates have a trapezoid that is more wedged—shaped with narrow palmar tip and wide dorsal base. When three carpal bones—trapezoid, scaphoid, and capitate—were analyzed, multivariate statistics of 3D shape differences distinguished modern humans and Neanderthals from LB1. Tocheri et al. (2007) note that the three carpals—a trapezoid, scaphoid, and capitate—all of which are from the left wrist, display none of the shared, derived features of modern human and Neanderthal carpals. Instead, they show the general sympleisiomorphic pattern exhibited by all extant African apes, as well as fossil hominins that preserve comparable wrist morphology and date before 1.7 Ma. Are differences in wrist morphology enough to support species distinction, particularly in bipedal hominins? Or, more to the point, would LB1's primitive wrist morphology prevent mating with a modern human (i.e., Mungo) from the same time period? I am skeptical. Tocheri et al. (2007) include archaeology to bolster their argument that primitive stone tools correlate with primitive wrist morphology. Apparently, LB1 was found in association with stone tools comparable to those of the Oldowan and other Lower Paleolithic sites throughout the Old World. In addition, there were tool types associated with H. sapiens (and have not previously linked with other hominids) (Martin et al., 2006). Nonetheless, this indirect evidence for species separation is weak; it is dangerous to link biology and technology because there is not always a strong correlation.

The H. floresiensis disagreement is another of the many examples where competent human paleontologists are interpreting skeletal characters differently (see Berger et al., 2008; Fitzpatrick et al., 2008). This means that there is no standardization in the choice of traits to delimit species, and that there is trait bias and continuing difficulty in deciding between epigenetic and functional characters. But it is not all the researcher's fault. The difficulty in differentiating homoplasy from homology and reticulation increases the complexity. Kimbel and Rak (1993) compare identifying species in paleontology to diagnosing an illness in medicine. The patient can have all of the symptoms and not have the disease, or the patient can have none of the symptoms yet still have the disease. This is the problem as I see it.

Until we are able to understand the biology behind characters in terms of ontogenetic, epigenetic, functional, life history, morphological, and behavioral elements in order to interpret variation in the fossil record; temporal variation;

geographical variation; appropriate comparative analogs; and appropriate methods of statistical comparison for variation between samples, a temporary cessation in assigning new fossil species names should be considered. This list of requirements is a "tall" order, but it would have the effect of slowing down the assignment of new taxonomic names every time a fossil is found, by encouraging researchers to be rigorous. Also, these requirements could be melded with the existing rules of the ICZN in order to give them legitimacy (see sub-section on tentative solution for details on how a new name could be assigned).

Alternatives to taxonomic names proposed by other researchers: numbers or nicknames?

In 1990, the abandonment of the species concept was proposed by Henneberg and Keen (1990) based on the idea that species concepts, whether biological or typological, either cannot be applied to fossils or lead to the overestimation of species (see the first section of paper). In 1994, Henneberg and Brush (1994) proposed the concept of *similum*. Their contention is that fossil hominins should be described in terms of simila (as opposed to species) for the purpose of describing synchronic diversity and variability (see the introduction and first section of this paper). Furthermore, *similum* has no rigid holotypes or taxonomic definitions based on a suite of characteristics. Additionally, *similum* can be organized into lineages. In short, individual fossils would be labeled using nicknames or numbers and arranged in lineages, stages, and corresponding time periods (Henneberg and Keen, 1990; Henneberg and Brush, 1994; Henneberg, 1997).

A tentative solution: a temporary cessation in assigning new names

My tentative solution involves working with the ICZN to enhance the existing rules, where the first published name of an organism or group (in this case, hominin fossils) takes priority; later names for the same organism or group are *junior* synonyms and are not considered valid (ICZN, 2000). Listed below is my five-point plan to halt the proliferation of species names:

(1) The discoverer of the hominin fossil must provide supporting data (see last paragraph of the conclusion section) to justify the addition/application of a "new" *species* name. Initially, the fossil in question should be labeled using a number (Henneberg and Keen, 1990; Henneberg and Brush, 1994).
(2) A tribunal should be called by the ICZN, consisting of experts (a specific number to be determined by the ICZN) chosen based on their education, training, and research. At that time, all data pertinent to the case (the fossil itself and any artifacts) must be released to the tribunal for its own analysis.
(3) The tribunal, using as much time as it needs, will study the evidence and conduct its own analysis, taking into account existing fossils materials.
(4) After the tribunal's analysis, all data analyses must be released to a different tribunal consisting of paleontologists who specialize in skeletal species other than

hominoidea. They should be given a detailed description and explanation of hominin phylogeny and terms specific to hominin paleontology in order to evaluate the information. The rationale here is that these particular paleontologists should be more objective, since they are less sensitive to (have less stake in) the arguments regarding hominin evolution.

(5) After this new tribunal's evaluation of the evidence, a decision based on a majority vote of both tribunals combined can be taken to determine whether or not the "new" *species* designation is warranted. If there is no resolution, then the initial designated number will be the identifier.

Of course, there should be deadlines for the completion of the analyses corresponding to each stage of the process. This is not a perfect solution; it is a tedious working solution. Others can build on it or refine it in order to enhance the rules of ICZN. Nonetheless, taking this first step, in conjunction with understanding the biology behind characters, how to choose appropriate fossil samples and comparative reference analogs, the nature of variation in living species, and how to interpret variation in fossil samples, will stop the arbitrary naming of "new" fossil species.

Acknowledgements

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