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BIOSPECIATION VERSUS MORPHOSPECIATION IN THE LATER HUMAN FOSSIL RECORD: LESSONS LEARNED FROM NON-HUMAN PRIMATE SOCIOECOLOGY

ABSTRACT: Speciation is not a monolithic process among primates. I use the concepts of biospeciation and morphospeciation (Godfrey, Marks 1991) to inform my consideration of the patterns of morphological diversification that occurred during the later evolution of genus Homo. Explicit comparisons between the socioecology of lemurs and baboons are used to develop interpretations of likely speciation processes in H. erectus and its descendants. I conclude that we should heed the lessons learned, particularly from baboons, in attempting to reconstruct our species' more recent natural history.

KEYWORDS: Speciation – Lemur – Papio – Homo erectus – Ecological correlates – Evolutionary theory

THE PROBLEM

If there is any point of consensus in the highly contentious field of hominid taxonomy, it is this: there is only one human species inhabiting the world today. This begs the following questions. How recently was this state-of-affairs established? And, how unique is this single-species state in the evolutionary history of our genus? Many paleoanthropologists' answers to these two questions would be "very recently" and "absolutely unique". These scholars perceive our fossil record as documenting a very speciose heritage, full of branching events and extinctions. Our current monospecific genus is a historical aberration, the result of a Later Pleistocene speciation event that produced the qualitatively different modern human species that subsequently replaced its archaic contemporaries throughout the Old World.

This "speciationist" perspective is most eloquently and provocatively championed by Ian Tattersall (1986, 1998, 2000) who claims that paleoanthropologists who do not share his cladogenetic vision of our genus' evolutionary

history are stricken by a "rather fundamentalist adherence ... to the tenets of the Neodarwinian Evolutionary Synthesis" (Tattersall, Schwartz 1998: 113). This has led those scientists to an uncritical acceptance of gradualism and anagenesis in the human fossil record, while Tattersall and his like-minded colleagues alternatively interpret the same fossils as overwhelming evidence of the ubiquity of punctationism and adaptive radiation. In fact, Tattersall often characterizes these scientists as hopelessly outdated since they are "...slow to augment [the] principles [of the Synthesis] with a recognition of the multifarious complexities of the evolutionary process" (Tattersall 2000: 5), and their ideas as orthogenetic: "many paleoanthropologists...view our evolutionary history as a long, single-minded slog from benightedness to enlightenment" (Tattersall 1998: 79). Do the scholars that perceive fewer, rather than more, later human species, operate under a paradigm that "has been willing to declare itself independent from the regularities of nature as expressed in the evolution of non-hominid organisms" (Tattersall 2000: 5)?

I do not think so. In this paper, I will present a synthetic view of previous and ongoing research, which has provided compelling evidence indicating we should expect fewer rather than more hominid species as we approach the origins of modern humans. These studies have employed state-of-the-art evolutionary and ecological theory and are explicitly comparative, focusing upon a number of non-human primate analogues in trying to discern our species' unique natural history.

MY APPROACH

The concepts of biospeciation and morphospeciation, as proposed by Godfrey and Marks (1991), are used to frame the following discussion. Biospeciation results from the cessation of gene flow, while morphospeciation, caused by genetic drift and natural selection, produces phenotypic and/or behavioural differentiation between conspecific populations that may (or may not) eventually become true biospecies. The former process reflects ultimate disjunction in "genetic exchangeability" while an interruption in "demographic exchangeability" characterizes the latter (Templeton 1989).

A presumption of the "speciationists" is that true speciation (biospeciation) must always precede significant morphological divergence (morphospeciation). Therefore the identification of different morphs in the fossil record necessarily reflects the presence of multiple species. Tattersall has consistently defended this perspective for the past two decades: "...where distinct morphs can readily be identified it would seem most productive to assume that they represent species" (Tattersall 1986: 168). He has claimed that this is in fact a conservative line of attack by recognizing "that in some cases real biological species (those distinguished by only minor morphological disparities) will escape recognition under this approach, but erring thus on the side of caution ensures that, while the actual phylogenetic picture will be simplified, it will not be materially distorted" (Tattersall, Schwartz 1998: 114). The implication of this latter statement is that intra-specific morphological variation should rarely, if ever, exceed the amount of anatomical divergence observed between two closely related species.

These theoretical expectations apparently derive from two sources – one is methodological and the other biological. The relevant method in this context is the Phylogenetic Species Concept (Cracraft 1983), the preferred species construct employed by the "speciationists". Phylogenetic species are recognized in the fossil record by their possession of diagnostic synapomorphies that distinguish them from other such groups. Therefore, the simple demonstration of a group of fossils that diagnostically share some derived features that are not present in another group is sufficient grounds on which to recognize the presence of two distinct species. The biological source of these expectations apparently derives from the extant primates with whom these researchers

are most familiar. For Tattersall, the genus *Lemur* has been most influential (Tattersall 1993). This primate is characterized by a number of closely related, well-defined biospecies that are functionally indistinguishable from one another osteologically. Therefore, when diagnosable morphs appear in the fossil record, Tattersall and his like-minded colleagues are most comfortable recognizing these differences at the species level.

In fact, Tattersall may be right AND wrong, because "some clades biospeciate before they significantly morphospeciate, while others morphospeciate before they effectively biospeciate" (Godfrey, Marks 1991: 57). The latter portion of this statement suggests that it is possible for significant morphological divergence to occur in the absence of biospeciation. If so, under what ecological conditions can this occur? Are there any non-hominid primates that exist under these conditions? Most relevantly in this context, what does the paleoecology of later human ancestry suggest about the patterning of our species' origins and subsequent divergence? The framework upon which these questions will be addressed is presented in the following section.

THE FRAMEWORK

Godfrey and Marks (1991) summarize the differing ecological correlates of biospeciating versus morphospeciating primate clades (*Table 1*). Primates that tend to biospeciate in the absence of significant osteological differentiation are often characterized by rapid karyological diversification. In these clades, genetic isolation generally does precede morphological divergence, which often is not discernable in skeletal or dental remains. The superficial differences that develop between closely related biospecies (including pelage, vocalizations and olfactory cues) are obvious to a neontologist but invisible to a paleontologist, again lending support to the "speciationist" contention that obvious morphs identifiable in the fossil record should be accorded species status.

The likelihood of chromosomal rearrangements that are adaptively neutral becoming fixed in diverging, nascent biospecies is influenced by a number of social and ecological factors. These include high levels of territoriality, low mobility, discontinuous substrate utilization (e.g. tree canopies), and small effective breeding populations with relatively high levels of inbreeding that are divided into small, structured breeding units (e.g. monogamous pairs). Genetic drift operating on these small, relatively isolated but possibly contiguous, or even sympatric, populations would tend to maximize genetic differences between these groups, increasing the probability of the establishment of reproductive isolation. In addition, gene flow may be restricted and hybrids may be selected against, further increasing the likelihood of biospeciation (Godfrey, Marks 1991).

The lack of mobility, small effective population size, and canopy adaptations in these clades can also illuminate

TABLE 1. Socioecological correlates and evolutionary implications of biospeciating versus morphospeciating primate clades (Godfrey, Marks 1991).

	Socioecological correlates					
	Territoriality	Mobility	Substrate use	Population size	Breeding units	Hybrid viability
Biospeciation	high	low	discontinuous	small	small	low
Morphospeciation	low	high	continuous	large	large	high

	Evolutionary implications				
	Gene flow	Genetic drift	Probability of fixation of karyotypic variants	Differential selection	Morphological divergence
Biospeciation	low	high	high	low	low
Morphospeciation	high	low	low	high	high

TABLE 2. Socioecological correlates and evolutionary implications of *Lemur* species versus baboon subspecies.

	Socioecological correlates					
	Territoriality	Mobility	Substrate use	Population size	Breeding units	Hybrid viability
<i>Lemur</i> sp. ¹	3/7 species are territorial ³	5.4–43.6 ha ⁴	6/7 species are arboreal ⁶	6.6–11.4 individuals per group ⁷	2/7 species are monogamous ⁹	low
<i>Papio hamadryas</i> ²	none	1038–1942 ha ⁵	semi-terrestrial	15.3–94.0 individuals per group ⁸	all are multi-male, multi-female	high

	Evolutionary implications				
	Gene flow	Genetic drift	Karyotypic variants	Differential selection	Morphological divergence
<i>Lemur</i> sp.	low	high	2N=44 to 2N=60 ¹⁰	low	superficial
<i>Papio hamadryas</i>	high	low	2N=42	high	superficial and osteological

Table Footnotes:

¹ Seven *Lemur* species (*L. catta*, *L. fulvus*, *L. coronatus*, *L. macaco*, *L. mongoz*, *L. rubriventer*, *L. variegatus*) identified by Tattersall (1993). Demographic data from Freed (1999), karyotypic data from Tattersall (1993).

² Data provided represents up to 10 populations of three baboon subspecies (*P. h. anubis*, *P. h. cynocephalus*, *P. h. ursinus*) from Melnick and Pearl (1987).

³ *L. mongoz*, *L. rubriventer* and *L. variegatus*.

⁴ Seven species' average ranges of minimum and maximum home range in hectares.

⁵ Ten populations of three subspecies' average ranges of minimum and maximum home range in hectares.

⁶ Only *L. catta* is semi-terrestrial.

⁷ Seven species' average ranges of minimum and maximum group sizes.

⁸ Eight populations of three subspecies' average ranges of minimum and maximum group sizes.

⁹ *L. mongoz* and *L. rubriventer*.

¹⁰ *L. macaco* (2N=44), *L. variegatus* (2N=46), *L. rubriventer* (2N=50), *L. catta* (2N=56), *L. fulvus* and *L. mongoz* (2N=60).

potential reasons why morphological divergence between these biospecies is often superficial or absent. Small, overlapping home-ranges constrained by reliance on tree-top resources will rarely cross-cut significantly different habitats. Therefore, there would be minimal selection among these species for the development of adaptive morphological differentiation. Instead, obvious visual, olfactory and auditory distinctions would be favoured since these animals will often be within one another's range of sight, smell or hearing.

In contrast, clades that tend to morphologically diverge without necessarily establishing full reproductive discontinuity (i.e. morphospeciation) exhibit a markedly different set of ecological and behavioural characteristics when compared to their biospeciating cousins. In these organisms, karyotypic differentiation rarely occurs because of the lack of territoriality, high mobility, adaptation to continuous substrates (e.g. terrestriality), and their large effective breeding populations. Under these ecological conditions, gene flow minimizes between-group

heterogeneity and the frequency of occurrence of natural hybrids is increased (Godfrey, Marks 1991).

Large home-ranges and population sizes, in association with highly mobile terrestrial travel, translates into an increased likelihood of these nascent morphospecies encountering differing environmental regimes across their geographic ranges. This in turn would expose these clades to natural selection operating differentially on populations occupying varying habitats. Therefore, significant morphological (including osteological) divergence could be established while (bio)species integrity is maintained by minimal levels of recurrent gene flow. Free interbreeding, in association with low levels of genetic drift (because of relatively large breeding populations), would maximize within-group heterogeneity and minimize the genetic differences between these populations. Although "morphs" are likely to be identifiable throughout these species, their presence does not have to signify the cessation of "intermorph" reproductive compatibility.

As Godfrey and Marks (1991: 56) summarize, "clade-specific patterns of morphological, behavioural and chromosomal divergence exist among primates. Primatologists (and paleoanthropologists) need to quantify these patterns, as well as possible explanatory variables, in order to understand the plurality of processes of speciation that affect primates." In the following sections, specific examples will be presented to illustrate patterns of biospeciation and morphospeciation among non-human primates. These examples will finally be utilized to examine expectations of the speciation process within our own species.

BIOSPECIATORS – TATTERSALL'S (1993) LEMURS

The extant species of the genus *Lemur* described in Tattersall (1993) appear to be excellent representatives of closely-related biospecies. These species differ in superficial characteristics such as pelage, facial markings and ear tufts, but there is a marked "absence of sexual dimorphism either in body size or in the morphology of the hard tissues" (Tattersall 1993: 165). Remarkable karyotypic variability is displayed among these lemurids with chromosomal complements ranging from $2N=44$ (*L. macaco*) to $2N=60$ (*L. fulvus* and *L. mongoz*). Among the forms recognized as different species by Tattersall, none of the sympatric taxa have been observed to hybridise in the wild and experimentally produced hybrids generally display reduced-fertility or sterility (Table 2).

In a previous study, Tattersall and Schwartz (1991) identified 37 craniodental characters that varied within and between the seven species of *Lemur*. The authors' expectations were to discover patterns of apomorphies among these characters that would consistently demarcate the neontological species boundaries of these lemurs. However, upon analysis, these data proved to be unexpectedly

"messy" – nearly half of the characters' consistency indices were less than 0.6, meaning that homoplasy was almost as good an explanation for these traits' distributions as was apomorphy. This prevented the osteological and dental morphs identified among the skeletal samples to be reliably correlated with the living lemur species that are traditionally distinguished from one another on the basis of karyological and superficial anatomical differences.

Based on these data, Tattersall (1993) arrived at the following conclusions: 1) very closely related species are unlikely to be morphologically differentiated more than a single, geographically differentiating species, 2) homoplasy is extensive among closely related species, and 3) craniodental variation within *Lemur* underestimates the number of species involved and misidentifies species boundaries. In fact, these three conclusions are logically predictable given what is known about biospeciating clades and lemur socioecology. Most of these lemur species have small home ranges, are primarily arboreal and have relatively small group sizes (two are monogamous). Three of these species are at least somewhat territorial and up to three of these species can be found sympatrically in large Malagasy forests (Freed 1999). The shared habitats and lifeways of these species are unlikely to select for adaptive morphological differentiation within *Lemur* and would be more apt to allow for stochastic (with respect to the environment) homoplastic developments in each clade that do not correlate with biospecies boundaries. Nevertheless, Tattersall amply demonstrated his major point: fossil species that evolved under ecological conditions similar to those experienced by *Lemur* would be very difficult to identify accurately and the number of biospecies represented in such fossil samples would likely be underestimated.

MORPHOSPECIATORS – JOLLY'S (1993, 2001) BABOONS

Although Tattersall's conclusions regarding speciation and the lack of correlated morphological diversification within *Lemur* are well-founded, there is less than universal support to be found among other primates for his extrapolation that when morphs can be identified, biospeciation has already occurred. Specifically, the baboons of Africa supply a compelling counterpoint to the expectations provided by *Lemur*. Jolly (1993, 2001) has used the terms "zygostructure" and "phenostructure" in his treatments of baboon systematics over the years. These concepts are analogous to Godfrey and Marks' (1991) biospecies and morphospecies, respectively. As Tattersall observed with the primates he studied, Jolly too has demonstrated a disconnect between zygostructure and phenostructure among his species of interest. Unlike Tattersall's lemurs, however, Jolly's baboons display significant osteological differentiation (phenodiversification or morphospeciation) in the absence of the establishment of full reproductive discontinuity (zygodiversification or biospeciation).

Jolly (1993) cites the example of the Kinda baboon (*Papio hamadryas kindae*) to illustrate the discordance between phenostructure and zygostructure mentioned above. Imagine a future paleontologist, muses Jolly, having access to only the skeletal remains of extant baboons. This scientist would surely divide the cranio-dental remains into two, non-overlapping samples: one would include the small Kinda skulls, while the other would include the balance of the (larger) savanna baboon subspecies. However, because there are no impermeable barriers to gene flow between Kinda and other savannah baboons, the identification of two morphospecies among these samples would overestimate the number of true biospecies present.

The ecology and adaptations of savannah baboons provide explanations for their discordant patterns of phenostructure and zygostructure. Baboons are not territorial, have relatively large group sizes and range widely across terrestrial substrates. These parameters foster gene flow and dampen the effect of genetic drift, thereby increasing genetic variation within baboon troops and lessening that found between groups. These ecological factors may also be responsible for the remarkable conservatism of baboon karyotypes which are invariably $2N = 42$ (Jolly 1993). Thus, well-defined genetic and karyologic (zygostructural) divisions among baboon groups have not been readily established. In contrast, owing to their broad geographic distribution cross-cutting many habitats, selection has produced baboon subspecies that are not only superficially distinct but in some cases (as in the Kinda baboons) osteologically differentiated as well (Table 2). Although Jolly (1993: 79) makes it clear that each major form "lives in a variety of habitats...the boundary between forms tends to lie at the junction between distinct ecovegetational zones" implying that adaptive patterning of anatomical differences evolved between baboon subspecies who nevertheless remained fully interfertile.

IMPLICATIONS

Primate biospeciators and morphospeciators are, of course, not limited to the lemurs and baboons discussed above. Other clades that reflect the biospeciating pattern observed in lemurs would include species of the genera *Cercopithecus* (Cope 1993) and *Hyllobates* (Groves 1993), while primates displaying morphospeciating tendencies similar to *Papio hamadryas* include the Hanuman langur, *Presbytis entellus* (Albrecht, Miller 1993) and the crab-eating macaque, *Macaca fascicularis* (Fooden 1991). Notice that although the cited morphospeciators are all cercopithecoids, the biospeciators include a prosimian, an Old World monkey and an ape. Therefore, it is difficult to argue that these patterns reflect shared phylogeny, rather than the more reasonable explanation of similar socioecologies.

So now the central issue of this essay can be addressed: are hominids biospeciators or morphospeciators? Evidence from our clade's natural history suggests that BOTH

processes have produced our ancestors: biospeciation appears to have dominated our earliest evolution while there was an apparent shift to morphospeciation during the development of our genus. Hominidae's earliest representatives (e.g. *Orrorin*, *Ardipithecus ramidus*, *Australopithecus anamensis*, *A. afarensis*, *A. africanus*) were likely still semi-arboreal and inhabited relatively constricted geographic ranges, in comparison to modern baboons and humans. These paleoecological parameters may have fostered genetic and karyotypic diversification among these forms. Humans are karyotypically distinct from the African great apes, our closest living relatives ($2N=46$ in us, $2N=48$ in chimpanzees and gorillas). It is possible that earliest hominid diversification was in part maintained by karyological speciation among populations inhabiting sub-divided forest-fringe habitats that were not grossly dissimilar from one another. Therefore, as Tattersall (1986) suggests, it may be quite reasonable in interpretations of our earliest fossil record to identify distinct hominid morphs as biospecies.

But with the advent of early *Homo erectus* ("*H. ergaster*" to some) circa 1.8 Ma, this biospeciating pattern among hominids may have shifted to one more characteristic of morphospeciating clades. Early *H. erectus* is the first hominid to manifest modern human-like limb proportions (Ruff, Walker 1993), suggesting that in this species obligate terrestriality was first mandated among hominids. It is also in this time range and presumably with this species that there is a marked geographic expansion out of the continent of hominid origins. This was likely facilitated by the dramatic increase in body size and bipedal locomotor effectiveness provided by relatively longer legs first seen in early *H. erectus*, as represented by specimens such as KNM-ER 15000 (Walker 1993). *Homo erectus*' initial diaspora from Africa not only demonstrates an increase in range but also suggests that population pressure, owing to larger population sizes, may have contributed to these migratory tendencies. Levels of craniofacial and postcranial sexual dimorphism in *H. erectus* are at least as great as those seen in modern humans (McHenry 1994), indicating that monogamous mating patterns were unlikely to characterize this species' breeding structure.

In all of the above socioecological parameters, *H. erectus* mirrors patterns seen in baboons rather than in lemurs. As in baboons, *H. erectus*' wide-ranging, terrestrial adaptation would have exposed this species to a broad spectrum of selective regimes across its spatial distribution. This has produced differing geographic morphs that are often identified as distinct paleospecies (e.g. *H. ergaster* in Africa and *H. erectus* in Asia). The baboon model, however, suggests that increases in population size and breeding unit complexity (e.g. multi-male, multi-female vs. monogamous mating patterns) in association with reduced territoriality, would enhance free interbreeding across the species' range. This in turn would render less likely the establishment of reproductive isolating mechanisms between widely dispersed *H. erectus* populations whose species' identity

was maintained by low levels of recurrent gene flow (Templeton 2002). The genetic inter-connectedness between adjacent populations would also dampen any tendencies towards karyotypic differentiation, thus it is probable that the human karyotype of $2N=46$ has been conserved since the origins of *H. erectus*.

Coincident with *H. erectus*' range expansion out of Africa, was a likely shift in dietary adaptation towards carnivory (Shipman, Walker 1989; Antón *et al.* 2002). This is relevant because carnivores having large ranges are relatively less speciose than herbivorous mammals (Foley 1991). In addition, Foley (1991) demonstrated a tendency for speciation rates to reduce as clades expand into higher latitudes. Therefore, *H. erectus*' broadened dietary adaptation, emphasizing animal protein, in association with this species' spatial expansion into Europe and temperate Asia added two additional socioecological factors that would predict dampening of speciation tendencies, in comparison to earlier primarily herbivorous hominids restricted to tropical and sub-tropical Africa.

Finally, one more line of evidence may be brought to bear on the issue of later hominid speciation patterns. Jolly (2001) cites mtDNA, nuclear genetic, and phenotypic data that support initial diversification of extant savannah baboon subspecies from a last common ancestor dating to approximately 1.7 Ma. Since these living subspecies are all interfertile, Jolly proposes "a common timescale of average, intrinsic reproductive isolation for all catarrhines" (Jolly 2001: 196). He further suggests that since *H. erectus* (including "*H. ergaster*") evolved from habiline ancestors circa 1.7 Ma, "all human lineages stemming from the *H. ergaster* stock were probably as fully interfertile as are extant *Papio* lineages" (Jolly 2001: 196). The capability of post-*H. erectus* hominid morphospecies to hybridise can be potentially tested by the fossil record. Evidence of long-term hybridisation between Neanderthal and early modern human populations in Europe has been suggested by the Lagar Velho child from Portugal (Duarte *et al.* 1999, but see Tattersall, Schwartz 1999, for a vigorous rebuttal) and the Oase 1 mandible from Romania (Trinkaus *et al.* 2003). In the Near East, the only region in which there may have been significant temporal and spatial overlap between "*H. neanderthalensis*" and "anatomically modern" *H. sapiens*, metric (Corruccini 1992; Kidder *et al.* 1992) and cladistically-informed studies (Kramer *et al.* 2001) have mutually demonstrated evidence in support of hybridisation between these oft-cited biospecies.

CONCLUSIONS

An understanding of non-human primate socioecological parameters relevant to the processes of speciation now allow a reconsideration of the questions posed at the beginning of this paper: "When was humanity's monospecific status established and how unique has this situation been during our family's natural history?" In comparisons with

biospeciating lemurs and morphospeciating baboons, the genus *Homo* shares demonstrably more similarities with the latter, rather than with the former. This has not always been the case, however, since the earliest hominids may have exhibited a more lemur-like pattern of speciation. But with the expansion of *H. erectus* from Africa and the subsequent diversification of its descendants, the later evolution of Hominidae is likely to have been typified by time-successive morphospecies evolving in a reticulate fashion across the Pleistocene Old World. Therefore, our current single biospecies state may be relatively ancient and was likely typical of hominid species status for the last 1.8 million years.

However, this does not deny the very real likelihood that hominid extinctions and originations continued to occur during this time period, albeit at a reduced rate in comparison to the Plio-Pleistocene. Before the very recent human population explosions, Pleistocene population densities must have been significantly less than today. The maintenance of pan-Old World species integrity by adequate levels of recurrent gene flow may have been periodically challenged by climatically-forced allopatry. The possibility of long-term isolation, particularly in peripheral and ephemeral island situations, would have been likely given the dramatic climatic and sea-level fluctuations over the last two million years (Foley 1991). Fossil evidence in support of this comes from the Indonesian archipelago where the Ngandong hominids may have represented a late-surviving relict population of *H. erectus* on Java (Swisher *et al.* 1996) and from the startling discoveries of the miniature hominid species of *H. floresiensis* that survived as recently as 18,000 years ago on the island of Flores (Brown *et al.* 2004).

Nevertheless, the natural history of *Papio* suggests that the later evolution of *Homo* was primarily characterized by continuity across time maintained by interfertility between populations across space. Although different morphs can readily be identified throughout our genus' chronological and temporal distribution, the paleoecology of morphospeciating clades imply that viable hybrids may have been produced by potential matings between *H. erectus*/*H. ergaster*," "*H. heidelbergensis*"/*H. rhodesiensis*," and "*H. neanderthalensis*"/*H. sapiens*. Although most of these names serve as convenient labels, I believe that their continued use obscures the real biological nature of our evolution. Ideally, paleospecies should be analogous to neontological species with their identification in the fossil record implying a lack of reproductive compatibility with their contemporaries (contra Bräuer, Stringer 1997: 193). The number of hominid taxa presumed by speciationist scholars to have existed during the Middle-Late Pleistocene is very likely an overestimate of hominid biodiversity when the appropriate primate analogues are utilized. As paleoanthropologists trying to understand the origins of our species, we would be well-served to heed the lessons taught by lemurs and baboons regarding the multiplicity of processes that affect speciation in primates.

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