From the Editor

ADAPTIVE RADIATIONS, BUSHY EVOLUTIONARY TREES, AND RELICT HOMINOIDS

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Recent developments in paleoanthropology have promoted a shift in attitude toward the question of relict hominoids. Over a half century ago, interpretations of the hominin fossil record were markedly different. Deriving from the influential evolutionary concept of competitive exclusion (Gauss, 1934), as applied to human evolution (Mayr, 1950), it was deemed that only one species could occupy the hominin niche at any given point in time. From this emerged the Single Species Hypothesis (Wolpoff, 1971). This hominin niche was associated with adaptations for habitual bipedalism, reduced canines, tool use, and culture. The latter was thought perhaps most significant, because with culture and the plasticity of learning, a species could conceivably broaden its niche space, further reducing the potential for sharing the landscape with other hominins (but see Winterhalder, 1981).

In 1976, Washburn and Ciochon challenged the reach of the hypothesis and opined that it was not until the emergence of *Homo erectus* that one species became so successful that all others were eliminated. They allowed that the preceding more "ape-like hominins," i.e. the australopithecines, offered a radiation of contemporary coexisting species (see Lewin & Foley, 2004).

Shortly thereafter, the hypothesis further retreated when it was recognized that African *Homo erectus* (now *H. ergaster*), a large-brained human ancestor, had coexisted with *Australopithecus* (*Paranthropus*) *bosei*, a parallel lineage of small-brained facially robust hominins that presumably eventually went extinct (Leakey & Walker, 1976). These species display the expected ecological reaction to a sympatric competitor, i.e. niche partitioning, involving diet, micro-habitat divergence, and possibly also temporal differentiation of resource use (Winterhalder, 1981). Stephen J. Gould (1976) made a prediction in his popular column in *Natural History*, stating: "We know about three coexisting branches of the human bush [*Homo habilis, Homo erectus,* and *Australopithecus bosei*]. I will be surprised if twice as many more are not discovered before the end of the century."

Indeed, mounting discoveries accumulating at a steady pace, reveal dozens of hominin species spanning a seven million year period (see Tattersall, 1996, but see White, 2009). The hominin phylogentic tree becomes increasingly bushy with each additional species. This proliferation of species is not merely an artifact of taxonomic "splitters" vs. "lumpers." Martin (1990) has estimated that a

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mere 3% of past taxonomic diversity in primate paleocommunities has been recognized and documented in the fossil record. Assuming the same holds true for hominins, and taking a conservative tally of a dozen extinct hominin species, according to Martin's estimate there could conceivably be 400 species of hominin as yet unknown. Given the particulars of the inferred natural history of large-bodied primates, and especially the tendencies for generalized behavioral ecology of hominins, such a high figure for hominin diversity seems rather unlikely (Arcadi, 2006). It emphasizes however, that the currently known fossil record likely underestimates past diversity. The perennial discovery of new hominin species attests to that expectation.

In addition to this growing appreciation of the bushiness of the hominin tree, there are revelations of the ever more recent persistence of a number of the branches or lineages within the tree. One of the most surprising discoveries was the enigmatic "Hobbit" or *Homo floresiensis*. This diminutive hominin unearthed on the Indonesian island of Flores has been dated to as recent as a mere 18 ka (Brown et al., 2004). The recognition of this startling species even prompted the editor of *Nature* to point out that since *Homo floresiensis* survived until so very recent, it was now more likely that stories of other so-called mythical, human-like creatures, such as the yeti are founded on grains of truth (Gee, 2004). He went on to acknowledge the possibility that the taxonomic and adaptive diversity of hominins was always high, has remained high until very recently, and might not be entirely extinguished. This was a notable concession reflecting a changing attitude, although one generally not so openly displayed.

The justification of the attribution of the "Hobbit" to the genus *Homo* has been questioned due to its small brain-size and primitive aspects of its skeleton (Meldrum, 2004). Recent studies of wrist and foot bones

reveal primitive anatomies reminiscent of *H. habilis* or *Australopithecus*, again leading some to propose a pre-*erectus* African origin for the species (Tocheri et al., 2007; Jungers et al., 2009; Morwood and Jungers, 2009). This raises even more questions over hypotheses about the origins of *H. floresiensis* and its arrival on the Indonesian island of Flores. Australopithecines are presently only known from Africa. Did a late australopithecine/ early *Homo* disperse across Asia without leaving any record of its passage? This is certainly under serious discussion.

Another hominin potentially exhibiting a more recent persistence then previously recognized is Asian *Homo erectus*. Dating of *Homo erectus* sites at the extreme of its range in Southeast Asia has produced ages of 30-50 ka, suggesting possible contemporaneity with modern *H. sapiens* arriving in the region (Swisher et al., 1996). These younger dates were seemingly contradicted by a later study; however the older dates could be attributed to reworked sediments at the site (Indriati et al., 2011). Should the younger dates be substantiated, this would prove a hominin example of relative biogeographic isolation and survival that parallels the persistence of the last Neanderthals.

The discovery of the Denisova hominins added another branch to the bush (Krause et al., 2010). The fragmentary fossils date to only 30 ka and were recovered from a cave site in southern Siberia, in the Altai Mountains near the Mongolian border. The completed sequence of the Denisova hominin genome established this species as distinct from modern humans and Neanderthals (Reich et al., 2010). The remains include remarkably robust teeth and toe bones (Mednikova, 2011; Reich et al., 2010). The tooth, if correctly identified as a third molar, is as large as that of an australopithecine. Green, one of the lead researchers contemplated, "…you have to wonder if there were other populations that remain to be discovered."

That Neanderthals and modern *Homo*

sapiens coexisted on the European continent for tens of thousands of years has long been recognized. During this extensive period of overlap they remained separate and distinct populations. The sequencing of the Neanderthal genome has revealed minimal introgression between the species (Green et al., 2010; Currat and Excoffier, 2011). While much press has been directed to this limited, even trivial, gene flow, of even greater implication is the flip-side to this observation – that such genetically similar species remained almost entirely distinct in spite of millennia of contact.

A new cave site in the Altai Mountains has produced additional Neanderthal fossils, at the most easterly known extent of their range, with preliminary dates of only 10-20 ka (Reich, personal communication). This is less than half the previous latest occurrence for Neanderthals previously documented – 28 ka, possibly as young as 24 ka (Delson and Harvati, 2006). The geographic range for Neanderthals may has increased in another direction as well, with archeological evidence suggesting they occupied the subarctic northern extent of the Ural Mountains in Russia, some 33 ka (Slimak et al., 2011). Only the recovery of skeletal remains will confirm this site as Neanderthal. The possibility of Neanderthal persistence into the present has been examined in the scientific literature by Porshnev (1974), Bayanov and Bourtsev (1976) and Shackley (1982).

Homo heidlebergensis (sometimes referred to as archaic *Homo sapiens*) were large and robust pre-modern hominins considered the common immediate antecedents of modern humans and Neanderthals. Some researchers have portrayed them as "giants" dubbing them "Goliath" in the popular literature (Kappleman, 1997). Lee Berger suggested that *Homo heidlebergensis* populations routinely produced 7 foot tall individuals and reconstructed them accordingly with Steve Churchill for a *National Geographic*

documentary "Searching for the Ultimate Survivor." While middle Pleistocene hominins were large, the Goliath moniker is an exaggeration (see Ruff et al, 1997). Whether *Homo heidlebergensis*' range encompassed eastern Asia is debated (Lu et al., 2011). However, a specimen of pre-modern hominin recovered from the site of Lishu, on display at Peking University, has a preliminary date of 12-20 ka (Lu, personal communication). Therefore, an observer of the Asian landscape of only 20 ka could potentially encounter any of a half dozen hominin species coexisting there.

The implication of the recognized bushy hominin tree was a major theme developed in a *Nova* documentary series "Becoming Human." The final episode, which introduced modern humans, was titled "Last Human Standing: Many human species once shared the globe. Why do we alone remain?" Introductory remarks addressed the singular circumstance of *Homo sapiens'* solitary inheritance of the world. The producers' explanation for this situation echoed the earlier pronouncement of Washburn and Ciochon (1976) on the supremacy of *Homo erectus*, by suggesting that in this case, *Homo sapiens* were so successful that all other hominins were eliminated from the scene. This assertion may prove as unfounded for *Homo sapiens* as it was for *Homo erectus* a quarter century earlier. What was not considered was the implication of the question "Why do we alone remain?" — that is, why would the present be the exception to the rule that has apparently prevailed throughout hominin history?

The fossil record of apes has likewise grown into a very bushy tree. A remarkable taxonomic and adaptive diversity of ape species is unfolding, with nearly 100 extinct species throughout the Miocene and Pliocene (Begun, 2003; Cameron, 2004). We find apes associated not only with evergreen tropical forests but also with swamps, grassland

savannas, seasonal woodlands, and subtropical to even temperate habitats not usually considered associated with preconceptions of ape lifeways. We find a diversity of dietary and correlated dental adaptations, with Eurasian hominids displaying enamel molar thickness and canine reduction rivaling even the most extreme morphologies of later African hominins, such as the robust australopithecines. We learn that the derived ape form of locomotion, i.e., forelimb suspension, must have evolved independently in the Dryopithecinae, the modern African apes, and a third time in *Pongo* — a powerful example of parallelism to consider when contemplating the multiple evolutions and derivations of bipedalism. And yet even this broadened perspective is inherently biased, since representation in the fossil record is skewed toward those habitats most conducive to fossilization and those strata subsequently uplifted and exposed to funded explorations.

There is a notable gap in the fossil record of apes for the past 5 million years. The extant great apes are themselves merely relict species in tropical forest refugia, poised on the brink of extinction. Virtually no immediate fossil antecedents of the African apes are known, with the exception of three isolated teeth of a fossil chimpanzee 500 ka (McBrearty and Jablonski, 2005). Sparse dental remains of orangutan-like species are found throughout the Pleistocene of mainland southeast Asia (Zhao et al., 2009). The extant orangutan is now restricted to the islands of Borneo and Sumatra.

Few additional species emerge from the gap. An Asian "mystery ape" has been suggested as a newly recognized member of the mid-Pleistocene Stegedon-Ailuropoda fauna (Ciochon, 2009). However this may be less mysterious than proposed and instead be a late survival of *Lufengpithecus,* or a closely related descendant form (Etler et al., 2001; Etler, 2009).

The only other ape currently recognized in the Asian Stegedon-Ailuropoda fauna is

Gigantopithecus. This massive ape has been referred to as the "fifth great ape" because it had been the only species, other than those now extant, recognized to have persisted well into the Pleistocene, until 250-300 ka (Cameron, 2004; Rink et al., 2008). The very real potential for the persistence of *Gigantopithecus* into the recent has been acknowledged by past researchers such as John Napier (1973), who observed, "It is possible that these creatures, thought by anthropologists to be long extinct, survived in refuge areas such as some of the deep forested river gorges of the Himalayan range until relatively recent times. The absence of a fossil record is not necessarily evidence of extinction."

As recently as 1998, Chris Stringer acknowledged that the yeti legend might not be so far-fetched as often presumed, and may indeed have been inspired by surviving populations of *Gigantopithecus*. He allows that the giant ape may survive today in the dense forests of Southeast Asia. Stringer recognized that it would be wrong to assume that *Gigantopithecus*-like creatures could not survive to the present day without being discovered. "It could have survived until the appearance of modern humans 50,000 years ago, and it is at least possible that it is still living as a very rare creature in remote forest areas," Stringer contemplated. On this matter, David Begun noted, "There is no reason that such a beast could not persist today. After all we know from the sub-fossil record that gorilla-size lemurs lived on the island of Madagascar until they were driven to extinction by humans only 1,000 years ago" (Begun, 2003).

There are numerous isolated specimens that are suggestive of as yet unrecognized species. We have likely only begun to scratch the surface. Is the five million year gap in the ape record actually the demise of this radiation? Obviously the progenitors of the extant great apes bridge the gap, although we have very little to show for it. As for extant species —

the Bili (or Bondo) ape is remindful that the discovery of the mountain gorilla in 1902 could well be repeated. In this instance, genetic testing determined that the Bili ape is a known subspecies of chimpanzee, *Pan troglodytes schweinfurthii*, although a population that is exceptionally large and displays a unique culture with many habits similar to those of gorillas (Hicks, in press).

Certainly it is possible that *Homo sapiens* is indeed the last hominin standing; likewise, that gorillas, chimps, bonobos and orangutans are the last apes standing, or hanging as the case may be. Extinction happens. But if we are to learn from history, and recognize the implications of the growing bushiness of the hominoid tree, combined with the recent persistence of several of its branches, then the possibility of relict hominoids should not be dismissed out-of-hand, particularly when evidence – suggestive at least, if not yet definitive – accumulates to that end.

Could a relict pre-modern hominin, e.g. *Homo neandertalensis*, or *Homo denisova*, be the explanation for the Russian almas? Could a relict ape, e.g. *Lufungpithecus*, be the explanation for the yeti of the subtropical forests of the Himalayas? Could a relict australopithecine be the explanation for the orang pendek in southeast Asia? Could *Gigantopithecus*, or some hominin, e.g. *Paranthropus*, be the explanation for the Chinese yeren, or the North American sasquatch? In the context described above, these are legitimate and timely questions worthy of the serious consideration of the anthropological community. Thus the birth of the RHI.

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