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Is the “Savanna Hypothesis” a Dead Concept for Explaining the Emergence of the Earliest Hominins?

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similar ecologies of modern chimpanzees and prehistoric hominins but also their phylogenetic proximity. I would never suggest it is useless to investigate the hunting behavior of other mammals in efforts to model that of early hominins, but it is certainly less revealing than focusing on the closest living sister taxon of the hominins. “Taxa that are phylogenetically close and subjected to similar selective forces (e.g., because they reside in similar ecosystems) are predicted to ‘respond’ more similarly morphologically, physiologically, and behaviorally than are more distantly related taxa” (Pickering and Domínguez-Rodrigo 2012:176).

The inferential strength of chimpanzee models of human evolution is that they are based on both homology and homoplasy (Moore 1996)—but only when formulated carefully and with strictly enforced parameters. Indeed, chimpanzees should never be construed simplistically as the singular, all-encompassing surrogate for early hominins. Even cursory familiarity with the fossil record exposes the peril of this stance; a relevant example is *A. ramidus*, whose unique positional and locomotor adaptations would never have been predicted based on study of any extant referent species (White, Asfaw et al. 2009). In fact, we demurred that—beyond their relevance to early hominin hunting—we “hold no illusions that chimpanzees can serve as useful referents for modeling all, most, or perhaps even few other paleoanthropologically salient aspects of early hominin evolution” (Pickering and Domínguez-Rodrigo 2012:174).

We probably overstated our caution. I would bet that chimpanzees are also useful for reconstructing other aspects of early hominin diets. The shared ecological circumstance of savanna chimpanzees and the first hominins predicts similarities in the seasonally fluctuating distributions of their plant foods and seasonally oscillating nutrient load of those resources. More, isotopic data demonstrate that “*Ar. ramidus* had in aggregate a C_3 diet much like that of savanna chimpanzees” (Ungar and Sponheimer 2011:192). Chimpanzee studies also reveal that relationships between foraging and seasonality do not always meet the simple prediction that seasonal decreases in food abundance correlate positively with increased foraging intensity, elaboration (e.g., tool use), or expanded dietary breadth (Hernandez-Aguilar, Moore, and Pickering 2007). So, not only do chimpanzee models have the power to direct our research on hominin behavior, they also provide a delimiting framework to constrain hypotheses of human evolution.

I suspect, however, that the efficacy of chimpanzee referents breaks down for a “second phase” savanna hypothesis (not discussed by Domínguez-Rodrigo), which posits causation between continued expansion of African savannas and hominin cladogenesis ~3.0–2.5 million years ago. Highly derived robust *Australopithecus* appeared during this span, as did plausible immediate ancestors of the genus *Homo*. Fossil, chemical, and archaeological evidence of these hominins probably sets them beyond the credible reach of most chimpanzee behavioral analogies. Their hypermasticatory craniodental anatomies,

occlusal microwear patterns, and isotopic compositions (Ungar and Sponheimer 2011) evoke decidedly nonchimpanzee “adaptive grades.” And, regardless of contrary claims (Mercader, Panger, and Boesch 2002), stone tools of the latest Pliocene hominins were already much more sophisticated than is chimpanzee technology.

As Johnny Cash pledged in much different circumstances, we need to “walk the line”—cognizant that new fossils might force us to reevaluate our notions of human evolution but equally willing to accept that old ideas are not necessarily bad ideas. Applied judiciously, chimpanzee referents continue to serve paleoanthropology admirably. The same goes for the savanna hypothesis.

Savanna Hypothesis, Myth, and Dilemma!

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The general scenario for the late tertiary involves climatic change from the typical tropical (warm and moist) Oligocene forests to the subtropical early to middle Miocene forests and eventually to the more arid and cooler temperate Plio-Pleistocene environments. These climatic changes were critical for the evolution of all mammalian species, with stronger influence, of course, on herbivores. It is recognized for a long time that the general pattern along the tertiary is that forests were reduced and savannas and grasslands developed and expanded (Culver and Rawson 2000; Jacobs et al. 1999; Strömberg et al. 2007).

It is a basic rule of paleoecology and paleoclimatology that evaluation of past ecology and climates is accomplished on the basis of floral and faunal evidences (and other geological/geochemical proxies), with fossil forms compared directly with modern ones considered most similar in morphological respects. It is assumed that the fossil plants or animals being studied lived under ecological and climatological conditions similar to those under which their closest modern counterparts live today. A further step involves the crucial question when from fossil forms we broaden our target trying to study continental fossil ecosystems. The question is, “What was the paleoecology of this studied biome?” Especially during the Neogene, such a question is essential for understanding the morphological changes observed in the continental mammal species.

A suite of recent papers (Deng 2006; Solounias, Rivals, and Semperebon 2010; Solounias et al. 1999) offer results on ongoing research on the so-called Pikermian biome, addressing the core of the research issue as the “savanna myth” (Solounias et al. 1999). The Pikermian biome is presented as a case study, given that it has been identified since early studies (“Hipparion faunas”; Kurtén 1952) and usually is assumed

to represent savannas similar to the savannas of Africa. As a matter of fact, the majority of Pliocene fauna appear to be made up of mixed feeders, associated with minor occurrences of browsers and some grazers. Thus more than savanna-like, the Pliocene biome instead would better represent a sclerophyllous evergreen woodland and was in part a precursor of the modern African woodlands. Some of the Pliocene species extended their range into Africa and ultimately evolved into the Pleistocene and recent savanna and woodland biomes of east Africa (Solounias et al. 1999).

The matter of Pliocene fauna and the savanna myth relates to the question discussed in the Domínguez-Rodrigo paper—the savanna hypothesis and the dilemma: did savannas play a significant role in the emergence of human evolutionary processes or not? It relates since one of the debated issues in hominin evolution is the ancestry of the African ape/human clade (Begun, Nargolwalla, and Kordos 2012; Rook and Bernor 2004) and—as new analytical tools or different approaches to understanding the fossil record or the palaeoecological proxies are available—changing interpretation of the Pliocene biome offers different support for opposite scenarios.

Back to Africa savannas and human evolution: I think that in his 1925 paper, Raymond Dart (1925:198; see also n. 3), far in advance of the times when ecological approaches to the study of human evolution were expanding (from 1960s onward), emphasized the savanna hypothesis: in my opinion, southern Africa, by providing a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution. We do not need to reject the savanna hypothesis in human evolution. What we need more would be tuning, among paleontologists, of the use of the term “savanna,” with the necessary understanding of transition from wooded to more open areas within different habitats of the same ecosystem.

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Without original research or new data, Domínguez-Rodrigo attempts to resurrect “the spirit of the old savanna hypothesis” via word games and revisionist history. He admits that this was never a scientific hypothesis but rather an “exercise of creative imagination” or “philosophy.” He superficially traces the myth’s seventeenth-century intellectual roots but fails to cite Bender, Tobias, and Bender’s more nuanced and scholarly assessment of the mind-set’s history (2012).

Domínguez-Rodrigo relies on isotope geochemists who

parsed *Ardipithecus* habitat as grassland (Cerling et al. 2010; Cerling, Wynn et al. 2011) rather than a mosaic spanning grassy woodlands to wooded grassland. But their meta-analysis of our data was flawed by biased standards.⁶ Worse, the attempt to rehabilitate the seventeenth-century savanna mind-set into something relevant to the hominid clade’s *origins* ignores a broad set of paleobiological fundamentals.⁷

Evidence now shows that mosaic landscapes with open grassland components were available much earlier than previously thought (Bonnefille 2010; Feakins 2013; Feakins et al. 2013; Kingston 2007), predating the chimpanzee/hominid divergence (estimated between 10 Ma and 7 Ma; e.g., by Langergraber et al. 2012). Moreover, Late Pliocene and Pleistocene hominid lineages evolved within broadly defined savanna biomes that featured a variety of available ecological habitats, from forest to open grasslands (Bonnefille 2010; deMenocal 2004, 2011; Feakins 2013; Feakins et al. 2013; Kingston 2007; Reed 2008; White et al. 2006). These mosaics of habitats changed through time, patterned by climate, steep altitudinal gradients, and complex watersheds (Reynolds, Bailey, and King 2011).

Consequently, the simplistic narrative that hominid origins were initiated in open savannas created by climate change stands largely abandoned. Which available ecological habitat(s) among Africa’s diverse landscapes was favored by the earliest hominids (*Ardipithecus* subsumes *Orrorin* and *Sahelanthropus*; Haile-Selassie, Suwa, and White 2009)? Multiple, independent, and mutually consistent lines of geological and biological evidence bear on that question (see White, Asfaw et al. 2009, and therein):

- **Taphonomy.** Sedimentology, bone modification, element representation, and taxa all indicate a habitat time-averaged assemblage for Aramis at 4.4 Ma, where mixing by pre- and postmortem agencies was minimal.
- **Paleontology.** Aramis features the largest recovered African Pliocene fauna bearing a clear woodland stamp. Plentiful and diverse fossil land snails, birds, small mammals, and larger mammals taxa are closely associated with *Ardipithecus*. The most sensitive and abundant species indicate a closed environment via ecomorphology and enamel isotopics.

6. The assertion that Aramis paleosol carbonates indicate only 5%–25% woody cover (Cerling et al. 2010; Cerling, Wynn et al. 2011) is invalid because their regression was anchored by non-African forest endpoints, biasing their woody-cover estimates significantly toward the open side. An alternative application of the same method and comparative data (Cerling, Wynn et al. 2011) using only their “East African” data set produces an Aramis range of 9%–78% cover. Furthermore, isotope values among the Aramis colobine specimens analyzed show the presence of closed canopy forest patches in the vicinity at 4.4 Ma. Combined with the Gona carbonate data (which range from 25% to 86% cover), all isotopic data are consistent with our published interpretation of the preferred habitat for *A. ramidus* (White et al. 2010).

7. Hominidae (“hominids”) per traditional use circumscribes all taxa in the human clade after the separation of chimpanzee and human species lineages.