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The Savannah Hypotheses: Origin, Reception and Impact on Paleoanthropology

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ABSTRACT - The reconstruction of the human past is a complex task characterized by a high level of interdisciplinarity. How do scientists from different fields reach consensus on crucial aspects of paleoanthropological research? The present paper explores this question through an historical analysis of the origin, development, and reception of the savannah hypotheses (SHs). We show that this model neglected to investigate crucial biological aspects which appeared to be irrelevant in scenarios depicting early hominins evolving in arid or semi-arid open plains. For instance, the exploitation of aquatic food resources and other aspects of hominin interaction with water were largely ignored in classical paleoanthropology. These topics became central to alternative ideas on human evolution known as aquatic hypotheses. Since the aquatic model is commonly regarded as highly controversial, its rejection led to a stigmatization of the whole spectrum of topics around water use in non-human hominoids and hominins. We argue that this bias represents a serious hindrance to a comprehensive reconstruction of the human past. Progress in this field depends on clear differentiation between *hypotheses* proposed to contextualize early hominin evolution in specific environmental settings and *research topics* which demand the investigation of all relevant facets of early hominins' interaction with complex landscapes.

KEYWORDS - Human evolution, history of paleoanthropology, savannah hypothesis, aquatic hypothesis, interdisciplinarity

Introduction

The reconstruction of human evolutionary past is a complex task, characterized by a high level of interdisciplinarity. It includes, among others, the study of fossil material, the analysis of paleoenvironmental and paleoclimatic data, the comparison between humans and their close relatives' anatomy, physiology, behavior and genetics, as well as historical

analyses of paleoanthropological ideas and epistemological discussions. The vast amount of data cannot be processed by single researchers. The integration of paleoanthropological knowledge is only possible through using single topic reviews by specialists in their fields, through synthesis of investigations carried out in several disciplines (which is also dependent on reviews), and through historical research.

These approaches have specific drawbacks. Historical research in paleoanthropology is carried out by historians of science or by practitioners. Historians are sometimes criticized for analyzing topics from fields in which they are not specialized (see Sommer, this issue); practitioners are sometimes criticized by historians of science for not understanding how historical investigations should be performed (see Corbey and Roebroeks 2001; Bowler 2001). Moreover, reviews and syntheses carried out by specialists take place at the expense of depth in knowledge (Geist 1978, x) and rarely can consider the complex influences related to historical developments in the fields they analyze. Besides these drawbacks, students of human evolution with strong faith in modern science's infallibility are tempted to assume that today's debate in paleoanthropology reflects precisely what is needed to reconstruct human evolution. In this line of thought the inclusion and neglect of disciplines, the emphatic refusal or acceptance of ideas and the multiple concurring hypotheses around still unsolved subjects are assumed to reflect the efforts of a reliable scientific process. However, besides its evident tautological reasoning, this judgment reflects a lack of historical awareness. History of science shows that research programs and knowledge once considered as essential, frequently turned out to be irrelevant or vice-versa. On the other hand, the clear distinction between true and false ideas should not provide a definitive criterion for the usefulness of ideas in science, at least not in a historical perspective. As Stephen J. Gould (1941-2002) wrote, "[m]any false ideas have been immensely useful, if only because the process of disproof so often leads to greater knowledge and integration" (Gould 1993, 164).

In the present paper, we show that the process which influences consensus among researchers working in different fields within paleoanthropology is less reliable than commonly believed and in some cases represents a strong bias in contemporary debate. We will demonstrate this through an analysis of the origin, development, and reception of the savannah hypotheses (SHs). We define SHs as ideas suggesting that proto-hominins abandoned forested or wooded habitats and gradually adapted to an open or semi-open environment. The most popular version of the savannah scenario postulated that climatic changes thinned forest areas and caused the appearance and expansion of open plains,

thereby forcing the arboreal primate ancestors of early humans to adapt to the new conditions of life (see for instance Hilzheimer 1921, 189-190; Dart 1925; Wells et al. 1931, 536; Weinert 1932, 339; Robinson 1963). We argue that the SHs reached a high level of consensus in early and modern paleoanthropology not because they arose through an objective interpretation of empirical evidence, as commonly believed, but mainly because they relied on the straightforwardness implied in the open plains ideas and the lack of alternative hypotheses to contextualize human evolution. This concept of organisms evolving in a linear pathway was perfectly compatible with the views defended in the late-eighteenth and early-nineteenth century, when the first savannah models were formulated. This linearity implied in early SHs was intuitively perceived as an expression of "biological parsimony," in which no intermediate stages were needed in the transition of an arboreal ancestor to an early human adapted to an open environment.

To corroborate our thesis on the problems related to consensus in paleoanthropological research, we will analyze certain aspects of the SHs' reception. As we will see, this reception was strongly influenced by the aquatic hypotheses (AHs) proposed to contextualize early hominin evolution in a semi-aquatic environment. These ideas were independently proposed by two different scientists outside of the paleoanthropological purview (Westenhöfer 1923; Hardy 1960) and further developed mainly by non-specialists (e.g., Morgan 1972; Verhaegen 1997). We will show that the common categorization of SHs as products of scientific work and AHs as examples of ideas without any relevance to paleoanthropological research is misleading – among others, this categorization ignores several similarities in the argumentation used in both models. Furthermore, we show that crucial topics in the reconstruction of hominin past (e.g., non-human hominoids' and early hominins' interaction with water) are strongly neglected in paleoanthropology, mainly as a consequence of the scientific community's reluctance to get involved with the AHs.

Because of the strong influence of the SHs, it would be expected that the history of this idea is well investigated. To our knowledge, however, there are no published analyses on the origin and development of the open-plains ideas.[1] There are many possible reasons for this gap in the historical research. Previous historical analyses of the hypothetical models of early human evolution have been carried out by a relatively small

[1] Several authors succinctly mentioned early ideas on primeval man abandoning forests and facing the danger of a terrestrial life or more specifically of a life in open places (Bowler 1986, 161-170; Landau 1991, 45-47; Stoczkowski 2002, 55-77) without discussing in detail the SHs' old origins. This topic was investigated in two unpublished theses (Bender 1999a; Bender-Oser 2004).

group of specialists and several basic aspects of the history of hypotheses on human evolution are still understudied (Corbey 1995, 5). In addition to projects conceived for other specific purposes,[2] most of the historical surveys deliver basic overviews of the topic (Eiseley 1961; Bowler 1986; Delisle 2004; 2007; Parker and Jaffe 2008), which do not allow extensive analyses of single evolutionary scenarios. Some excellent reviews of the recent discussion on environmental changes in paleoanthropological hypotheses were published in the last years, without analyzing the paleoanthropological discussion before 1925 (Reed 1997; Potts 1998a; 1998b).

We argue that one of the most important reasons for the absence of historical research on the open-plains ideas is related to the notion that the beginning of the SHs seemed to be clearly identifiable. As we will see, the first description of the famous early hominin known as the child of Taung (*Australopithecus africanus*) by Raymond Dart in 1925 is frequently treated as the beginning of the SHs; the historical events related to this discovery belong to the best-described topics in the history of paleoanthropology (Dart and Craig 1959; Wheelhouse and Smithford 2001; Gundling 2005; Delisle 2007, 222-265).[3] For good reasons, historians of science usually disparage "precursor-hunting" – those attempts to identify precursors for current ideas without paying enough attention to their specific historical context. However, little attention was given to the readiness in accepting the interpretation of fossil evidence as the beginning of a new hypothesis, although this model was widespread in paleoanthropological discussion at the time. We show that the role of Dart as father of the SHs could only become established in paleoanthropology because of a lack of knowledge on the historical context which promoted the crystallization of these ideas in the late-nineteenth and early-twentieth centuries.

In the present paper, we analyze a representative sample of SHs published in the major European languages between 1809 and 1939. This timeframe is determined by two publications which mark relevant aspects in the emergence and consolidation of the SHs: in 1809 Jean Baptiste de Lamarck published the first ideas suggesting a primeval man standing upright in response to an open environment; in 1939 Franz Weidenreich described these ideas as a "widely spread belief" (Weidenreich 1939, 87-88). Our investigation focuses on ideas stressing the influence of climatic and environmental changes and the use of analogies in

[2] For instance, some works describe patterns of narrative in human evolution (Landau 1981; 1991) or identify alleged similarities between ancient and modern paleoanthropological hypotheses (Stoczkowski 2002).

[3] See also the separate contributions of Richmond and Gundling in this issue.

the scenarios depicting the emergence of primeval man in open plains proposed at this time. Additionally, we analyze certain aspects of the debate on the SHs' validity in popular and scientific publications between the 1960s and the 1990s.

Open Plains Ideas by Lamarck and Darwin

It might come as a surprise that ideas about primeval humans emerging in open plains are much older than commonly assumed. These ideas were already outlined in 1809 by the French naturalist Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1744-1829). In his *Philosophie zoologique* (Lamarck 2006 [1809]), he describes in details how an early ancestor of primeval human abandons an arboreal life to adapt itself to open plains.

> As a matter of fact, if some race of quadrumanous animals, especially one of the most perfect of them, were to lose, by force of circumstances or some other cause, the habit of climbing trees and grasping the branches with its feet in the same way as with its hands, in order to hold on to them; and if the individuals of this race were forced for a series of generations to use their feet only for walking, and to give up using their hands like feet; there is no doubt […] that these quadrumanous animals would at length be transformed into bimanous, and that the thumbs of their feet would cease to be separated from the other digits, when they only used their feet for walking. (Lamarck 2006, 170)

Lamarck did not use specifically the expressions "open plains" or "savannah," but, as we can see in the passage below, a "large and distant view" is not to be expected in the context of a forest habitat.[4]

> Furthermore, if the individuals of which I speak were impelled by the desire to command a large and distant view, and hence endeavoured to stand upright, and continually adopted that habit from generation to generation, there is again no doubt that their feet would gradually acquire a shape suitable for supporting them in an erect attitude; that their legs would acquire calves, and that these animals would then not be able to walk on their hands and feet together, except with difficulty. (Lamarck 2006, 170)

[4] We are not alone in our interpretation of Lamarck's ideas. In his paper *Man's posture: its evolution and disorders* the Scottish anatomist and anthropologist Arthur Keith (1866-1955) stated: "From this passage we see that […] Lamarck regarded the erect posture as a result of the chimpanzee-like ancestor having abandoned an arboreal mode of life for one *in the open country*. [...] He was fully alive to the fact that any anthropoid which had acquired the human mode of progression had gained an enormous advantage; it would no longer be confined to tracts of tropical jungle but would have the *whole length and breadth of the earth open* to it" (Keith 1923, 451, our italics).

In Lamarck's view, forests were not adequate to promote the evolution of humankind. Consequently, he believed that the first bipedal ancestor of primeval humans would dominate and banish other primates in localities where he did not occupy; i.e. into forests or other desert places (Lamarck 2006, 170). For him, it was clear that the emergence of bipedalism/freed hands and its consequences for the development of intelligence gave primeval humans a decided advantage in comparison with other animals.[5]

Lamarck's scenario of a bipedal primeval humanity using its free hands for other purposes than climbing trees and grasping branches, an idea that we previously termed "tower hypothesis"[6] (Bender 1999a, 65), was the first hypothesis on human bipedalism embedded within an evolutionary context. Similar models were regularly presented in several publications from the second half of the nineteenth century on (see, e.g., Baer and Hellwald 1874, 526-528; Munro 1897, 90-93; Reinhardt 1906, 6; Knauer 1916; Osborn 1919, 60; Keith 1923; Koch 1929, 54; Suschkin 1933). For instance, Franz Koch (1929, 54), in an early attempt to corroborate his views on the emergence and dissemination of early humans with help from Alfred Wegener's theory of continental drift, wrote about the emergence of an erect posture for purposes of vigilance and defense. "The primeval man, his wife and children probably had to stand up to an incessant search for enemies and prey and frequently betake themselves to flight" (Koch 1929, 54, our translation). Koch gave no specific source to these views, suggesting that this idea already had been defended by other authors. Different versions of the tower hypotheses (today called "vigilance hypothesis") were defended in the three decades subsequent to the Evolutionary Synthesis of the 1930s and 1940s (e.g., Washburn and DeVore 1961; Robinson 1963, 401; Emiliani 1968; Robinson 1972, 257; Heberer 1973, 34; Ravey 1978) and are still stated in paleoanthropological and primatological literature.

Similar to Lamarck, the British naturalist Charles Darwin (1809-1882) envisioned primeval humanity leaving the forest and adapting to open plains. In his *Descent of Man* he wrote:

[5] Ideas on the role of freed hands for human beings can be found in the text *Memorabilia* by the Greek historian, philosopher, and soldier Xenophon (ca. 431-355 BC) (1994,1, 4, § 11). The concept of primeval humans having "freed hands" to use weapons or tools also belongs to the topics discussed by philosophers of the Enlightenment in the seventeenth and eighteenth centuries, often tied to antique theories on the origin and development of culture (see Müller 1968; Stoczkowski 2002, 124-126).

[6] Modern versions of this idea are usually called "vigilance hypothesis." Although modern models abdicated completely statements suggesting "a trend to evolve" in early hominin evolution, they show a remarkable similarity with Lamarck's tower hypothesis, often mentioning the aspect of vigilance against predators.

> As soon as some ancient member in the great series of the Primates came, owing to a change in its manner of procuring subsistence, or to a change in the conditions of its native country, to live somewhat less on trees and more on the ground, its manner of progression would have been modified; and in this case it would have had to become either more strictly quadrupedal or bipedal. (Darwin 1871, vol. 1, 140-141)

The similarity between Lamarck's and Darwin's ideas relies not only on the same overall adaptive scenario exposed by both authors (an arboreal primate abandoning the forest, occupying an open landscape and developing habitual bipedalism in response to the new environment), but also on the identification of two alternative causes for the evolutionary phenomenon. Lamarck's picture of a primate abandoning the forests "by force of circumstances or some other cause" (Lamarck 2006, 170) correlates with Darwin's scenario fully quoted above of a primate adapting to a more terrestrial life "owing to a change in its manner of procuring subsistence, or to a change in the conditions of its native country" (Darwin 1871, vol. 1, 140). It is therefore not surprising that at least one early historian pointed to the strong coincidences in the open plains scenarios of both authors.[7] A further indication for the relationship between these ideas is supplied by the succinct remarks on the astonishing modernity of these early models by contemporary authors. For instance, Ernst Mayr pointed out that Lamarck's hypothesis "is startlingly modern" (Mayr 1982, 352) and Richard G. Delisle came to a similar conclusion when he stated, "Lamarck's view is modern in that it is fairly close to what we believe today to be true" (Delisle 2007, 43). It did not escape the attention of modern paleoanthropologists that "Darwin's view of the origin of bipedalism remains useful" (McHenry 1982, 156), and that some open plains ideas expressed in 1925 by Raymond Dart (see below) are similar to Darwin's views on the emergence of humankind (Tobias 2004, 388). These indications cannot be interpreted as definitive evidence that Darwin's SH was directly inspired by Lamarck's open plains scenario. Given the concise nature of Darwin's statements on this topic, it is beyond the scope of this discussion to further explore this issue. More relevant for the present investigation is the influence of Lamarck on modern-sounding open plains ideas expressed in early-twentieth century, which is discussed in the next chapter.

[7] When commenting on Lamarck's open plains ideas, the American entomologist and paleontologist Alpheus Packard (1839-1905) succinctly stated: "This is certainly, for the time it was written, an original, comprehensive, and bold attempt at explaining […] the probable origin of man from some arboreal creature allied to the apes. It is as regards the actual evolutional steps supposed to have been taken by the simian ancestors of man, a more detailed and comprehensive hypothesis than that offered by Darwin in his *Descent of Man*, which Lamarck has anticipated" (Packard 1901, 371).

Climatic and Environmental Changes: Incipient Interdisciplinarity Surround Open Plains Ideas

After 1859, naturalists began to envision evolutionary scenarios in which organisms were strongly influenced by climatic and environmental changes, an effort that is also clearly visible in early anthropological texts. Primeval humanity began to be depicted as a miniature piece on a giant chess board, subordinate to the inexorable forces exerted by geological and climatic events. It is highly instructive to analyze how early authors tried to corroborate models on human evolution using this new paradigm. The German geologist and paleontologist Gustav Steinmann (1856-1929) is a good example of an author using this line of argument in the early-twentieth century. In his book, *Die geologischen Grundlagen der Abstammungslehre* (Steinmann 1908), he considered the causes driving the ancestors of humans to abandon the primordial quadrupedal locomotion. He envisaged a pithecoid creature, with a similar quadruped locomotion as today's apes living in forests; climatic changes had gradually thinned the forests and transformed them into savannah regions. According to him, the arboreal ancestors of humans were then forced to adapt to the modified conditions and occasionally adopt an upright or semi-upright posture, similar to today's apes. Few modifications of these intermediate stages, affirmed Steinmann, would be necessary for the adoption of a permanent bipedalism (Steinmann 1908, 266). With some irrelevant adaptations in the vocabulary, Steinmann's open plains ideas would fit perfectly into a paleoanthropological work of the late 1990s.

Steinmann saw all further modifications as a consequence of this crucial phase in early human evolution, especially the increased development of the senses, the evolution of hands to a versatile organ, and (as a result of both modifications) the increased mental faculties and brain mass. He had also an explanation for the alleged fact that a decrease in forest area was beneficial for the evolution of human beings, but not for apes.

> We can imagine the geographic area of such pithecoids being occupied by different closely related species, which we might fuse in a systematic sense into a "genus", and that this area would be affected by a climatic change in the sense described above. In that case, some species living close to river plains or in very humid areas would retreat into their original environment, keeping their previous habits; in contrast, other species living close to the timber line would adopt a bipedal locomotion and so gradually be able to occupy the newly formed and already present savannah and brushwood areas. (Steinmann 1908, 266; our translation)

Despite the inclusion of climatic and environmental changes as crucial

factors in early human evolution, several arguments proposed by Steinmann are quite similar to Lamarck's ideas. Steinmann's general scenario of primeval humans abandoning the forest and adapting to open plains is basically the same as those proposed by Lamarck. For instance, Steinmann's explicit statement on other primate species forced to retreat into their original environment, keeping their previous habits (Steinmann 1908, 266), is coincident with Lamarck's view of a primeval humanity banishing other primates "into forests or other desert places" (Lamarck 2006, 170). Perhaps more revealing than mere coincidence in evolutionary scenarios of early humans are Steinmann's speculations on vertebrates' evolution. He argued that giraffes are descendant from aquatic dinosaurs and dolphins are descendant from *Ichthyosaurus* (Steinmann 1908, 278-279). Although Steinmann was not the only scholar in the early-twentieth century who went beyond the pale with speculations on evolution, his interpretation of vertebrate's phylogeny was an incredible *faux pas* for a professional paleontologist in this time. (The negative remarks should not revile Steinmann's whole scientific career; he was seen at that time as a hardworking and competent geologist [Pfannenstiel 1957].) If we consider that Steinmann's ideas were the product of an uncritical assimilation of Lamarck's views, his error is understandable. In his *Philosophie zoologique*, Lamarck erroneously suggested that birds descended from turtles, amphibian mammals from crocodiles, monotremes from penguins, and ruminants and pachyderms from animals living close to the shore (like walruses and manatees; Lamarck 1994, 646-647). All indications are that Steinmann could not resist attempting to enlarge Lamarck's original list with further aquatic counterparts to terrestrial vertebrates. He did it without considering the accumulated evidence showing that several aquatic animals are not primarily aquatic, but descend from terrestrial animals and therefore are secondarily aquatic. The strong similarities between Steinmann's and Lamarck's views can barely be regarded as coincident, since Steinmann was an ardent proponent of neo-Lamarckism, often quoted Lamarck and even dedicated his *Grundlagen* to him.

Curiously, in their general statements on the evolutionary path of living organisms, Lamarck and Steinmann were much closer to the views proposed by the French diplomat Benoît De Maillet (1656-1738) in the manuscript *Telliamed* (an anagram of De Maillet's name). *Telliamed* was first circulated as manuscripts, written between 1722 and 1725 (see Neubert 1920; Carozzi in De Maillet 1968, vii-x) and posthumously published with several editorial changes (De Maillet 1748). Although the idea of aquatic counterparts was sometimes expressed by eighteenth-century naturalists (Bender 1999b, 50-53), De Maillet was the first au-

thor who tried to identify such counterparts in the framework of a detailed evolutionary concept. The biologist and historian Sinai Tschulok (1875-1945), a specialist on Lamarck's work, pointed out that some of Lamarck's statements on abiogenesis and propagation are almost word-for-word reproductions of De Maillet's ideas (Tschulok 1938, 336).

"Biological Parsimony" in Early Savannah Hypotheses

Climatic and environmental changes are obviously not restricted to single regions of the planet. Consequently, there were few places on Earth that were not considered suitable for the emergence of primeval humanity. Contrary to Darwin's views, which suggested Africa as the most probable cradle of humankind (Darwin 1871, vol. 1, 199), East and Central Asia with the impressive Tibetan highlands and vast open plains became a popular place to contextualize the evolution of early humans in the early-twentieth century (Bowler 1986, 173-185; Dennell 2001). It is difficult to assess to what extent various factors influenced views on Asia as the location of human evolution, at that time. With the growing number of fossil discoveries in the last quarter of a century, it is tempting for modern paleoanthropologists to regard this evidence as the main factor in establishing this idea.[8] However, this view is problematic when confronted with historical facts. Above all, it ignores the wide spectrum of influential discussions in the eighteenth and early-nineteenth centuries in which Asia was seen as the place where certain races (Poliakov 1977, 205ff; Banton 1987; Graves Jr. 2008), certain languages (Borst 1995), or the whole of humankind originated. The German prefix "Ur-" reflects the vivid early interest on the origin (*Ursprung*) of language (*Ursprache*), primordial people (*Urvolk*), primeval humans (*Urmensch*) or an early form of civilization (*Urzivilisation*). These discussions were of course carried out in the complete absence of hominin fossil material. In German-speaking countries, Immanuel Kant (1982 [1775], 23) and especially Johann Gottfried von Herder (1852 [1784-1791], vol. 28, 393-414) defended eloquently a positioning of humankind's childhood in Asia. Early concepts of Tibet as the cradle of humans were also influential in the development of racist "evolutionary" ideas from theosophists, which were adopted among others by sympathisers of Nazi ideology and are

[8] The most relevant of these discoveries was *Pithecanthropus erectus* (today *Homo erectus*) by the paleoanthropologist Eugène Dubois (1858-1940) in 1891 and 1982 at Trinil, in central Java and the subsequent research by the paleontologist and geologist Gustav H.R. von Koenigswald (1902-1982) from 1931 to 1941 (see Tobias 1984). See also the contribution of Caspari and Wolpoff in this issue.

still present in neo-Nazi discourses today (Brauen 2000, 36-93).

In the early-twentieth century, scientists increasingly used arguments on climatic and environmental changes to corroborate their views on Asia as the location of human evolution. For instance, the paleogeographer Theodor Arldt (1878-1960) provided explanations based on geological causes for the cooling of climates in the Pliocene – the massive rise of the Tibetan highlands (Arldt 1907a; 1907b). Very similar views were expressed in 1944 by the German-American paleontologist Amadeus W. Grabau (1870-1946) in a manuscript published posthumously in 1961. He also regarded Tibet as the cradle of humankind and the emergence of early humans as strongly influenced by geological events with subsequent environmental changes. Especially interesting for the present discussion is his opinion on the causes of the split between apes and primeval humans.

> The only conceivable change that would bring about this new condition is the disappearance of the forests themselves. Instead of the apes leaving the trees, the trees left the apes. Then, when the trees were gone and no escape from the tree-less area was possible, it became a struggle to continue under such new conditions, a struggle for existence, where survivors would be few, while those that were doomed to extinction, because they were incapable of adaptation, formed the majority. (Grabau 1961, 158)

The idea of "the trees leaving the apes" was a groundbreaking element in the anthropological discussion and became the foundation of the SHs defended in the last 100 years. In the attempts to justify why the occupation of open plains should promote primeval man's evolution, some authors began to defend a very peculiar view of the role of environment on the emergence of the first upright ancestors of humans: the contrasting representation of forests as a place of stagnation on one hand and open plains as a place of development on the other hand. This idea was repeatedly propagated by the influential German anthropologist, Hans Weinert (1887-1967), in several scientific and popular works in the 1930s and 1940s. The ancestor of early humans, according to him, did not come down from the trees; instead, "the trees went out from under the ape, thus putting him on the ground whether he wanted it or not" (Weinert 1932, 339, our translation). Weinert frequently stressed the alleged difference between a paradisiacal life in the forest and the hard conditions on the open plains, for instance in 1940: "[…] the *dolce far niente* of a tropic or subtropic forest life with abundant food did not exist anymore" (Weinert 1940, 72, our translation). One year later, he stated that "[t]he forest was in any case not a place appropriate for the emergence of man. Then man emerged not in a paradise; he appears

because the paradise disappeared" (Weinert 1941, 48, our translation). The integration of specific geologic and climatic events in paleoanthropological research allowed scholars to consider a vast body of empirical evidence to corroborate their own evolutionary scenarios.

Although the terms "open plains" or "open glades" in connection with human evolution was sporadically used in the nineteenth century (Wallace 1889, 459) and early-twentieth century (Keith 1923; Wells et al. 1931, 536; Weinert 1932, 209), the primary adaptation of early humans to the savannah was normally not specifically termed as "hypothesis" until the 1980s (see below). The primary early human adaptation to the savannah was usually regarded as a fact, and open plains and forest margins as the only conceivable environment in which primeval humanity could evolve. This hegemony of the SHs is all the more surprising if we consider that paleoanthropology is characterized by strong controversies and multiple hypotheses regarding almost every aspect of early hominin evolution (Lewin 1989, 20; Delisle 2012). The reasoning behind the identification of open plains as the only conceivable environment for human evolution was clearly expressed by the British naturalist and evolutionist Alfred Russel Wallace (1823-1913).

> It has usually been considered that the ancestral form of man originated in the tropics, where vegetation is most abundant and the climate most equable. But there are some important objections to this view. The anthropoid apes, as well as most of the monkey tribe, are essentially arboreal in their structure, whereas the great distinctive character of man is his special adaptation to terrestrial locomotion. We can hardly suppose, therefore, that he originated in a forest region, where fruits to be obtained by climbing are the chief vegetable food. It is more probable that he began his existence on the open plains or high plateaux of the temperate or sub-tropical zone […]. (Wallace 1889, 459)

Wallace's statement implies a popular use of a specific principle of parsimony in the interpretation of early human evolution which can be summarized as follows. The ancestral form of humankind could not evolve in a forest environment since humans (and consequently his early bipedal ancestors) do not show the same adaptive features to an arboreal life as other primates. Therefore, the only conceivable environment to contextualize the evolution of early humans was "on the ground" and "outside of the forest." This conviction supplied the rationale to formulate several concurring hypotheses addressing the exact way in which early hominins interacted with this new environment. When focusing on the multiple ideas proposed within the SHs' framework, early scientists did not challenge the general scenario of a primeval man adapting to the open plains; they rather accepted it as a fact.

Kangaroos, Horses, First Terrestrial Vertebrates: The Role of Analogies in Early Savannah Hypotheses

An interesting aspect of the incipient interdisciplinarity in paleoanthropology in the early-twentieth century was the formulation of hypotheses based on specific analogies between humans and other organisms. The rationale for such comparisons can be described as follows: taking into consideration that environmental changes are a crucial factor in the evolution of terrestrial organisms, it is reasonable to assume that human ancestors are not the only organisms that were forced (by climatic and subsequent environmental changes) to abandon a particular environment A (e.g., "water" or "forest") and to adapt to a different environment B (e.g., "land" or "open plains"). Therefore, theoretically, it should be possible to identify such organisms, understand the circumstances in which they evolved, and use this information to explain critical phases in the evolution of early humans. An analysis of several early hypotheses shows that this specific method was fundamental to early paleoanthropological research.

One of the most impressive examples of anthropocentric views in the interpretation of primeval man's environment and in the use of analogies is supplied by the German zoologist Max Hilzheimer (1877-1946). Hilzheimer explicitly considered forests as "place of stagnation" and open plains as "place of development" in the evolution of humankind and other organisms. This concept was extensively treated in his paper *Aphoristische Gedanken über einen Zusammenhang zwischen Erdgeschichte, Biologie, Menschheitsgeschichte und Kulturgeschichte* (Hilzheimer 1921). He was convinced that the evolution of most terrestrial animals was mainly influenced by the expansion/reduction of wooded areas. His belief in arboreal apes as a "failure of natural experiments" was the starting point of a bizarre anthropocentric categorization of "stagnated forest fauna" and "progressive open plains fauna." He discussed in detail how forest reptiles and mammals are "less developed" than their counterparts living on open plains, without offering understandable criteria for this discrimination. Very similar to Lamarck, he saw the emergence of bipedalism in connection with the ability to scrutinize the open plains. He regarded kangaroos (because they are, like humans, adapted to open plains and able to move on their hind legs) as "the most developed marsupials" ("die höchststehendsten Beuteltiere") and used them in an analogy with humans (Hilzheimer 1921, 187). Like other early authors, he saw the forest as a comfortable place, radically different from the open plains, which he regarded as a rough environment, characterized by strong contrasts and hard interspecific competition (Hilzheimer 1921,

189-190). But why should early humans abandon the forest paradise? Like Hans Weinert some years later, Hilzheimer viewed as probable that the human ancestors did not leave the forest but the forest landscape transformed gradually and imperceptibly into open plains (Hilzheimer 1921, 194). Hilzheimer's ideas exemplify the degree of oversimplification implicit in several early theoretical concepts of early human habitats. This oversimplification reflects the need to conceive a landscape where hypothetical human ancestors could exist and behave according to the premises of the specific hypotheses.

Analogies using other organisms to illuminate still obscure phases in the evolution of early humans were characterized not only by simplistic and anthropocentric views of the evolutionary processes. They also assumed misguided ideas whereby organisms are driven to a continuous and linear evolutionary progress towards more complex forms. Such reasoning can be recognized in the ideas presented by the geologist Joseph Barrell (1869-1919), when he proposed an analogy between alleged similar evolutionary processes relevant for the emergence of early humans and the emergence of the first land vertebrates (Barrell 1916; 1917). Strongly influenced by William Diller Matthew's ideas,[9] Barrell was also convinced that the evolution of human beings took place in Central Asia and was directly connected to climatic changes in the past. He believed that recurrent epochs of semi-aridity brought conditions that severely suppressed river fish habitats (Barrell 1916, 502; 1917, 17). With increasing aridity, the rivers were reduced in flow, the content of oxygen decreased, and fish were isolated in pools, stagnant and foul from the decomposition of animal and plant remains. From primitive fish (under the constraint of severe semi-aridity of the Devonian period) emerged the amphibians, able to carry forward their activities as terrestrial animals (Barrell 1916). Barrell stressed the key role of environmental changes and natural selection in evolutionary events. "Natural selection, although discredited as a cause determining specific variations, appears nevertheless to be a major factor in evolution, the driving cause in association with changes in environment, which has forced the great advances in organic progress" (Barrell 1916, 504). These ideas, as he stated, gave him the inspiration for a new scenario on the evolution of early humans (Barrell 1916, 502-503; 1917, 17). In the paper "Probable relations of climatic change to the origin of the tertiary ape-man," after summarizing his hypotheses on the rise of air-breathing, he defended the idea that an analogous process of climatic events and natural selection

[9] See references to Matthew's *Climate and Evolution* (Matthew 1950, first published 1915) in (Barrell 1917, 17, 20).

was responsible for the emergence of the first upright human ancestors.

> Did a similar climatic change in the Tertiary period acting on a species of large-brained and progressive anthropoid apes isolated from the regions of continued forest compel them to adapt themselves to a terrestrial life or die? Did the gradual dwindling, leading even to the extermination of forests, in a region from which the forest fauna could not escape, produce a rigorous natural selection which transformed an ape, largely arboreal and frugivorous in habits, into a powerful, terrestrial, bipedal primate, largely carnivorous in habit, banding together in the struggle for existence and by that means achieving success in chase and war? (Barrell 1917,17)

He was convinced that many of the specific elements that contributed to the evolution of early land vertebrates were also crucial in the evolution of humankind. He mentioned the alleged influence of a semi-arid climate as the most important factor in this evolutionary scenario:

> The gradual elimination, first of food of the forests, lastly of the refuge of the trees, through increasing semi-aridity, would have been a compelling cause as compelled as mandatory as the semi-aridity which compelled the emergence of vertebrates from the waters, transforming fishes into amphibians; the first of the vertebrate rulers of the land. It is the purpose of the present article to assemble the evidence which suggests this climatic cause acting upon our simian ancestors as a controlling factor in this latest of the major stages in human evolution. (Barrell 1917, 17)

According to Barrell, the primary cause for the differentiation of ape-men from the apes was "the compulsion of increasing aridity in Miocene times, by isolating anthropoids north of the Asiatic mountain systems and reducing the forests there to savannahs and open plains" (Barrell 1917, 19). He speculated about the predatory activities of early humans living in open plains. "With the use of crude weapons for the killing of animals the modifications in teeth and jaws represent a carnivorous-omnivorous adaptation fully worked out in a terrestrial and predatory primate" (Barrell 1917, 22). Barrell asked why a species of ape would choose a more hazardous life voluntarily. The answer to this question has strong similarities to Arldt's speculations (see above), published ten years earlier: human ancestors were obliged to leave the trees (Barrell 1917, 23).

A similar analogy was presented by the American paleontologist, Richard Swan Lull (1867-1957), in his book *Organic Evolution* (1917). The similarity is probably not coincident, as Barrell acknowledged his debt to Matthew and to Lull (Barrell 1917, 17). Lull believed that the drying up of central Asia in Miocene and late Pliocene times forced pre-human ancestors to descend from the trees, "a step which was absolutely essen-

tial to further human development" (Lull 1917, 672). Like Barrell, he drew a comparison with the evolution of the first terrestrial vertebrates: as the lakes and ponds of the Devonian had gradually dried up with the increased aridity, the primitive amphibians were forced to move across dry land. Analogous to this scenario, the ancestors of humankind had been forced to migrate from one shrinking patch of forest to another, until some groups of survivors were fully adapted to live permanently on the open plains (Lull 1917, 672). Interesting in this analogy, already clearly formulated by another author (Reinhardt 1906, 7), is that the tree-to-tree scenario has been essential in the hypotheses formulated by many scholars after the Modern Evolutionary Synthesis. Ideas similar to Lull's analogy were later used by influential scientists like Ellsworth Huntington (1945, 26), Gerhard Heberer (1959, 1131) and Wilfrid E. Le Gros Clark (1978, 187). The tree-to-tree scenario belongs to the most influential versions of the SHs in modern paleoanthropology.

A further popular form to corroborate scenarios of early human evolution was the direct comparison between humans and animals living on open plains, as the peculiar analogies between the evolution of humans and horses. The term "peculiar" is appropriate here, since such analogies cannot be corroborated by any anatomical or physiological convergences between these organisms but were mainly motivated by two ideas. On one hand, the fossil record of early horses was excellent in the late-nineteenth century and some scientists viewed it as natural to compare this material with the very scarce hominin fossil evidence of this time. For instance, the quality of equine fossil material inspired the British science writer Samuel Laing (1812-1897) to compare the evolution of horses with the evolution of humankind to clarify aspects related to time of emergence and tempo of evolution of both organism groups.

> The horse, whose ancestral pedigree is the best established of any of the existing mammals, was already in existence in the Pliocene period, and the Hipparion, which is the first of the links connecting him with the primitive mammal, is first found in the Miocene and not later than the Pliocene. Why should the development of man have begun later, and followed a more rapid course that that of the horse? (Laing 1893, 160)

On the other hand, reflecting the admiration of horses as magnificent and noble animals, several scholars in the past believed that they must have evolved in a similar way to our own species (note the anthropocentric view implicit in this analogy). William Diller Matthew (1871-1930), the most influential scientist in the fields of vertebrate paleontology and zoogeography of his time (Colbert 1992; Rainger 1997, 648-649), envisioned the scenario of a primeval horse deprived of its original forest

environment and forced to adapt to open plains. As curator of fossil vertebrates at the American Museum, he had access to the world's largest collection of fossil horses. In the preface of one popular guide he wrote about this collection, confessing that "[a]mong all the animals of past and present there is none so deserving of our interest and affection as the horse" (Matthew 1913, 7). In the same leaflet, he speculated about the factors he believed were crucial for the emergence of the first horses.

> The evolution of the horse, adapting it to live on the dry plains, probably went hand in hand with the evolution of the plains themselves. [...] The coming of a cold, dry climate restricted and thinned the forests and caused the appearance and extension of open, grassy plains. The ancient forests inhabitants were forced either to retreat and disappear with the forests, or to adapt themselves to the new conditions of life. (Matthew 1913, 31; see also Matthew 1926, 171)

This belief in an overwhelming and infallible climatic determinism, connected with the need to present early human evolution in a simple and convincing scenario, led to the detailed horse-human analogy expressed by Matthew's early teacher, Henry Fairfield Osborn (1857-1935), the influential American geologist, paleontologist, and director of the American Museum of Natural History in New York (Rainger 1991). Osborn believed in a very long and independent evolution of human beings and he excluded an "ape-man" as a human ancestor. The similarities between apes and humans, according to Osborn, are due either to very remote common inheritance or to the convergent evolution of the ape towards the human type (Osborn 1927, 377; see also Bender 1999a, 45-48; Bender-Oser 2004, 64-71).

Osborn was the most famous proponent of the idea that Central Asia was the birthplace of humans. His concept explained the ideal environment of the ancestor of humankind not in the warm forested lowlands "but in the relatively high, invigorating uplands of a country such as central Asia" (Osborn 1929, 6). He stressed the idea of woodland and forest as places of stagnation (enough food, congenial life) and open plains as places of progression (less food, harsh conditions), both for the emergence of the primeval humans and for the development of early civilizations (Osborn 1926; 1927; 1928).

The horse analogy defended by Osborn and Matthew illustrates the tautology and subjectivity implicit in the process of identifying the places regarded as adequate to contextualize early human evolution in early-twentieth century. How could scientists in this time identify the cradle of humankind without fossil evidence? Osborn simply decided that "the home of primitive man should be looked for in the same kind of country in which the primitive horse flourished" (Osborn 1927, 377). The first

land vertebrates as "pioneer" organisms, horses as "noble" animals, Asia as a culturally, geologically, and esthetically "high standing" region – the criteria used to contextualize early human evolution demonstrate in an impressive way the fragile basis of the incipient use of synergies among disciplines during this period.

Incipient Doubts on the Savannah Paradigm

In 1925, the Australian paleoanthropologist Raymond Dart (1893-1988) described the "Taung child," a fossilized skull of a juvenile *Australopithecus africanus* discovered in South Africa in 1924 (Dart 1925). When finally accepted as a hominin a quarter-of-a-century after its discovery,[10] scientists recognized that the Taung child was the oldest recovered evidence for hominin evolution at the time and was the first fossil of a small-brained hominin ever described. This discovery brought about a paradigm shift in the discussion of human origins and prehistory (Kuykendall and Štrkalj 2007).

Dart was evidently inspired by Darwin in connection with the formulation of his SHs. He quoted Darwin's passage on an ancestor of primeval human who came "to live somewhat less on trees and more on the ground" (Darwin 1871, vol. 1, 140-141) to underline his own ideas about the role of open plains as a harsh environment in hominin evolution in his classic *Nature* paper.

> […] 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. (Dart 1925, 199)

Dart believed that the enhanced cerebral power of human ancestors made their existence possible in an "untoward environment," described as "more vast open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of this species" (Dart 1925, 199). He emphasized the desertic or semi-desertic ecology of Taung as supporting his interpretation of the status of the Taung child.

> It will appear to many a remarkable fact that an ultra-simian and pre-human stock should be discovered, in the first place, at this extreme southern point in Africa, and, secondly, in Bechuanaland, for one does not associate with the

[10] The majority of researchers gradually accepted the hominin status of australopithecines in the 1940s and 1950s (Gundling 2005, 101-140; Delisle 2007, 225-255; Kuykendall and Štrkalj 2007).

> present climatic conditions obtaining on the eastern fringe of the Kalahari desert an environment favourable to higher primate life. (Dart 1925, 198)

Although Dart definitely defended a SH, he cannot be regarded as the first author of this idea, as regularly stated in historical introductions of paleoanthropological publications (Susman 1987; Verhaegen 1991; Roede et al. 1991; Boesch-Achermann and Boesch 1994; Reed 1997; Potts 1998b). Evolutionary scenarios containing elementary arguments of modern SHs were regularly mentioned before 1925. Fossil evidence found from 1924 onwards was interpreted in the light of savannah ideas already known at the time. When discussing the alleged role of *A. africanus* in the SHs' crystallization, it is important to be aware that Dart's ideas did not have much impact in paleoanthropological discussion immediately after the first description of *A. africanus*. This is relevant for the interpretation of the following statement by Franz Weidenreich (1873-1948) by the end of the 1930s. He, who vehemently rejected some aspects of the SHs, described these ideas as an already "widely spread belief" (Weidenreich 1939, 87-88; see also Beurlen 1950, 417). This popularity of the SHs was not influenced by Dart's publications on human evolution, since the acceptance of hominin status for *A. africanus* had just begun to figure in paleoanthropology in this time and consensus on this point was reached only many years later (see, e.g., Delisle 2007, 222-265).

Today's perception of Dart's pioneering role in the SHs' emergence is not based on historical research but is strongly related to Dart's ideas that early humans developed a taste for flesh and became hunters and cannibals, characterized by a high degree of interspecific aggression (Dart 1953; 1957; Dart and Craig 1959, 157-210). The American playwrite and scientific writer, Robert Ardrey (1908-1980), became fascinated by Dart's hunting hypothesis. He met Dart in 1955, inspected his evidence at the Johannesburg Medical School (Ardrey 1961, 28), and developed his own hypotheses on the subject in several books. With detailed accounts of Dart's paleoanthropological ideas, Ardrey depicted early humans as social primates hunting in African open plains, stressing the role of climatic factors in the shrinking of the forests and the expansion of savannah (Ardrey 1961; 1966; 1970). Ardrey's books *African Genesis* (1961), *The Territorial Imperative* (1966), *The Social Contract* (1970), and *The Hunting Hypothesis* (1976), became worldwide best sellers and strongly influenced popular and scientific discourse on the role of hunting, climatic and environmental changes and open plains habitats in early hominin evolution.

Around the time Ardrey published his first hunting hypothesis book,

the British marine biologist Alister Hardy (1896-1985) proposed a completely different scenario on early hominin evolution, the so-called aquatic hypothesis (AH;[11] Hardy 1960). Hardy pointed to some alleged anatomical, physiological, and behavioral similarities between humans and aquatic mammals, suggesting that reduced body hair,[12] a layer of subcutaneous fat, erect posture, and underwater swimming abilities evolved when early hominins exploited food resources in lakes, rivers, or coastal environments. The AH was not the first scenario that criticized the open plains ideas. For instance, the Austrian paleontologist and paleobiologist, Othenio Abel (1875-1946), regarded the open plains idea as not specially insightful. He proposed that between the arboreal phase and the terrestrial phase primeval humankind lived as a creature adapted to climbing in a mountainous region (Abel 1931, 379). Other authors defended the idea that climatic and environmental changes did not play a crucial role as driving factors in hominin evolution. Instead, the earliest humans descended from the trees because they were allegedly too heavy to stay in them (Weidenreich 1939; Beurlen 1950; Rensch 1972, 325). However, the AH introduced a new component in the way that scientists perceived the SHs. For the first time in paleoanthropological discourse, classical ideas were challenged by a scenario which implied hominins interacting intensively with water, a view that was often perceived as diametrically opposed to the open plains ideas.

The first reaction to the AH began soon after Hardy's publication of his paper, "Was man more aquatic in the past?" in *The New Scientist*, a science magazine (Hardy 1960). It was no one less than Raymond Dart who addressed a criticism to this new scenario in the same magazine. As the title of his paper suggests, "The recency of man's aquatic past," Dart also considered human relation to water as significant. However, in opposition to Hardy, he regarded it not as product of an early hominin semi-aquatic phase but rather as a recent innovation in human evolution (Dart 1960).

Despite the fact that the AH was perceived as highly controversial,

[11] The *Aquatile Hypothese* was first proposed by the German pathologist Max Westenhöfer (1871-1957) in several publications between 1923 and 1942 (e.g., Westenhöfer 1923; 1924; 1942, 311-312). For an historical analysis of the aquatic hypotheses, see Bender 1999a and Bender-Oser 2004.

[12] Charles Darwin, when discussing the hair reduction in humans in his *Descent of Man*, noted that a naked skin and a large amount of subcutaneous fat are features of a number of aquatic mammals (Darwin 1871, vol. 1, 148). Both features were used in Westenhöfer's and Hardy's AHs, giving the same aquatic organisms as examples for hairless animals. Although Darwin was not quoted by these authors in this specific context and although the historical background of Westenhöfer's and Hardy's ideas were analyzed in detail (Bender 1999a, 88-99; Bender-Oser 2004), we cannot exclude the possibility that the first insights on the AHs were directly or indirectly inspired by Darwin's side note.

not all SHs' proponents were inclined to refuse it *a priori*. Some authors regarded it as possible to integrate the aquatic scenario in the SHs' framework, instead of seeing it as an attempt to replace the open plains ideas. For instance, when the British zoologist and popular author Desmond Morris (born 1928), presented his own interpretation of the role of hunting on open plains in early hominin evolution in his best seller, *The Naked Ape,* he provided a fair summary of Hardy's aquatic hypothesis, characterizing its indirect evidence "appealing" but without "solid support" (Morris 1967, 45). Inspired by Hardy's attempts to envision the aquatic ape as a predecessor of a hunting hominin adapted to open plains (Hardy 1960), Morris decided to assume a neutral and conciliatory position.

> Even if eventually it does turn out to be true, it will not clash seriously with the general picture of the hunting ape's evolution out of a ground ape. It will simply mean that the ground ape went through a rather salutary "christening" ceremony! (Morris 1967, 45)

In a footnote in his book, *The Biology of God*, Hardy agreed with Morris's conciliatory comments but did not accept the hypothetical aquatic phase's secondary role squeezed between an arboreal ancestor and a savannah adapted hominin. Inspired by Morris's Christian metaphor, he argued: "[…] if [the AH is] true, I think it was rather more than a mere christening – it was the all-important weaning from the fruits of the trees to flesh by way of succulent bivalves and other tender 'fruits of the sea'" (Hardy 1975, 158).

The AH would probably have become a bizarre footnote in the history of paleoanthropology without recognizable impact on the SHs' reception if it had not become entangled with developments which initially took place outside of scientific debate. Until the middle 1960s, paleoanthropological discussion was characterized by the idea that male hominins had the active role in early hominin evolution, a concept historically connected to the dominant role of male hunters as seen in today's hunter-gatherer societies. Although Dart and Ardrey did not initiate the discussion on the role of hunting in early hominin evolution (see Cartmill 1997, 509; Stoczkowski 2002, 71-72), Ardrey's skills in depicting early humans as hunters in open plains and the popularity of his books contributed to instigate a fundamental discussion on the role of women in hominin evolution. On one hand, ethnological and paleoanthropological publications increasingly stressed the female contribution to reproductive success through gathering and preparing food, mitigating the role of hunting in early hominin evolution (see Zihlman 1981; Tanner 1987). However, as these concepts stressed the role of females

in food acquisition in savannah woodlands and grasslands, they did not challenge the general framework of the savannah paradigm.

A completely different development was initiated by the Welsh writer and journalist, Elaine Morgan (born 1920). She felt immediately attracted to the AH – when she read about it she felt "as if the whole evolutionary landscape had been transformed by a blinding flash of light" (Morgan 1972, 31). Another factor which rendered this scenario attractive to her was the possibility to interpret human evolution without the androcentry implied in classical hunting hypotheses. Morgan's own evolutionary scenario mitigated the relevance of hunting technology and male hunters as main meat deliverers, since animal protein could also be provided by early hominin females and children when gathering shells in a coastal environment. In a book insightfully entitled *The Descent of Woman* (1972), Morgan pointed out several problems related to an incipient hominin adaptation to open plains, addressing specifically Ardrey's, Dart's, and Morris's ideas (Morgan 1972, 11-17). In later publications Morgan reinforced her criticism of the SHs, using a more scientific approach and abandoning the feminist discourse (e.g., Morgan 1972, 11-17; 1982, 19-20; 1984). She named the open plains idea "savannah theory" (Morgan 1982, 19-20), a term used regularly in paleoanthropological publications since the 1990s (e.g., Roede et al. 1991; Langdon 1997).

Adverse Attitude toward Topics Associating Early Hominin Interaction with Water

The AH never gained widespread acceptance and was mostly rejected (Dart 1960; Gowlett 1984, 17; Pickford 1991; Wheeler 1991; Langdon 1997) or ignored in paleoanthropological debate. However, it contributed significantly to show how the savannah scenario was perceived in popular and scientific discourse on human evolution since the 1980s. In opposition to early publications, which treated the savannah idea as mere description of facts, the open plains scenario became increasingly perceived as a hypothetical construct, subjected to the normal process of scientific validation.

Having in mind the strong influence of the aquatic ideas in the SHs' crystallization, it is probably not surprising that one of the first attempts to define the SH by a paleoanthropologist was formulated in connection with an attempt to falsify the AHs. In a paper published in the *Journal of Human Evolution,* the anthropologist John Langdon wrote:

> The savannah theory is, in fact, the collective discipline of paleoanthropology.

> It encompasses all the frequently proposed and rejected models, discussions, debates, and hypotheses that assume a terrestrial habitat for all stages of human evolution. (Langdon 1997, 490)

This definition is peculiar, since theories and disciplines cannot be used to define each other. Scientists working within a discipline formulate, defend, and reject different hypotheses, and paleoanthropology is not an exception to this process. Even if Langdon intended to explain the savannah theory as the product of the collective discipline of paleoanthropology, this definition still does not hold with evident historical facts. Previously mentioned Othenio Abel's "cliff hypothesis" (1931) was formulated as an alternative to the classical SHs. Another example is the influential model proposed by the Swiss primatologists Christophe and Hedwige Boesch, in which early hominin evolution is contextualized in a forest environment (Boesch and Boesch 1984a; 1984b).

Langdon's definition implies a clear distinction between SHs as related to research carried out within "the collective discipline of paleoanthropology" and AHs as models defended by non-scientists or scientists working outside of paleoanthropology. This distinction is misleading for several reasons. First, we saw the crucial role of science writer Robert Ardrey in the popularization of the SHs in the 1960s and the role of science writer Elaine Morgan in the process through which the savannah model was recognized as a hypothetical construct. Second, not all proponents of the aquatic model regarded it as completely incompatible with the classical views. We saw that Alister Hardy proposed his AH as a phase between forest and savannah. On the other hand, not all scientists working within paleoanthropology or engaged in the popularization or development of classical paleoanthropological ideas saw the SHs and AHs as completely incompatible models. We saw above that Hardy's narrative inspired Desmond Morris's attempt to squeeze the aquatic phase between an arboreal and savannah phase. Later, the Dutch evolutionary biologist, Sarah B.M. Kraak, undertook an attempt to fuse the AH and SH in a book chapter insightfully entitled "The answer: the Aquatic Ape Theory and the Savannah Theory combined" (Kraak 1991; see also Knight 1991, 235-244). Furthermore, AHs' critics give more attention to the ideas proposed by non-academics than to publications by specialists who recognize the need for a scientific study of early hominins' interaction with water (e.g., Richards 1987, 193-204; Crawford and Marsh 1989; Cunnane et al. 1993; Schagatay 1996; Wrangham 2005; Wrangham et al. 2009; Tobias 2010). Finally, little attention is given to paleoanthropological scenarios for early hominin evolution that diverged considerably from the SHs exposed in textbooks by depicting

early hominins exploiting coastal environment, wet savannah, or marsh communities (see, e.g., Hewes 1972, 22-23; Geist 1978, 215-218).

As it is clear in the examples above, Langdon's definition of SHs is based on an artificial delimitation of what belongs to paleoanthropological discipline. All these problems with the SH's definition can be circumvented by focusing on the common components of these ideas. Although there are several deviations among the different savannah scenarios concerning geographical and temporal frameworks, specific ecological settings and sequence of evolutionary events, all these hypotheses share the evident characteristics of early humans evolving several key features in the context of an open or semi-open environment (Bender 1999a, 35-80). These common features supply the rationale for the definition of the SHs used in the present paper (see introduction).

Langdon's SHs definition reflects an interesting dilemma in paleoanthropology that is present to date. Based on paleoclimatic and fossil data, several paleoanthropologists in the 1990s[13] expressed doubts on the SHs. Although this evidence formerly confirmed Elaine Morgan's objections to this model, paleoanthropologists had difficulties accepting Morgan's criticism of the SHs as useful contribution to paleoanthropological discussion without promoting the AHs. This attitude is clearly recognizable in the following statement by Langdon:

> The savannah hypothesis that Morgan criticizes turns out to be a straw man. Anyone who dredges up a century of hypotheses can find many to ridicule; but if the field has already rejected them, the exercise is pointless. In fact, scholars are now discarding the savannah setting for hominin divergence. (Langdon 1997, 490)

Langdon's straw-man statement stands in stark contrast to the following sentences by Roger Lewin and Robert A. Foley:

> Paleoanthropology has a reputation for controversies and arguments, with major disagreements about who is who, and who is related to whom, among the fossil hominins. However, although there is considerable debate about the details, *there is nonetheless remarkable consensus about the major aspects of human evolution* – that our ancestors were derived from a population of African apes, adapting in increasingly open and savannah environments to the changing conditions. Most

[13] This topic will be reviewed elsewhere. Briefly, criticisms of certain aspects of the SHs were punctually expressed by paleoanthropologists in the 1980s and more emphatically from the 1990s onwards (see, e.g., Tobias 1995). Specialists today are more and more convinced that earliest bipedalism occurred in a forest context and a shift to more open country occurred two million years after the appearance of first bipedal hominins. In opposition to the classical SHs, to date there are no clear concepts about the factors influencing the emergence of bipedalism (Bender and Bender, in preparation).

> features, especially bipedalism, are seen as related to this change. (Lewin and Foley 2004, 282, our italics)

The contradiction between Langdon's and Lewin's and Foley's statements reflects the divergence in their basic attitudes. Langdon attempted to exclude the AHs from paleoanthropological discussion, while Lewin and Foley, as we will see later, mentioned the AHs when asking basic questions on the process of evaluation of alternative hypotheses in paleoanthropology.

Lewin and Foley are correct in emphasizing the SHs' influence in modern paleoanthropology. Although the SHs as a general model to contextualize early hominin evolution has been increasingly criticized in the last two decades, this model is still influential in different hypotheses using the same arguments and narrative expressed in classical savannah scenarios. For example, in the *Journal of Human Evolution* (the same journal where Langdon published his paper), the zoologist Peter Wheeler published a series of papers between 1984 and 1996 defending his ideas on the thermoregulatory advantages of hominin bipedalism, naked skin, and larger body size in the context of open plains or mosaic landscapes (see Wheeler 1994 and references therein). Wheeler's specific SHs belong to the most-quoted models on human bipedalism in contemporary paleoanthropology. It is paradoxical that this remains true even after researchers are increasingly reaching consensus that the evolution of bipedalism cannot be contextualized in open plains (see footnote 13).

An interesting example of the complexity of processes involved in the evaluation of ideas in paleoanthropology is supplied by publications which positively mentioned Wheeler's hypotheses and, at the same time, deliberately pointed out that there is little evidence for a sudden shift from more forested to more grassland habitats during an early phase of hominin evolution (e.g., Conroy 2005, 51-54, 337-341).[14] Additional evidence for the complex hypotheses evaluation is supplied by the specific views on early hominins defended by AHs' critics. For instance, Wheeler challenged the aquatic hypotheses on thermoregulatory grounds alone, emphasizing his own ideas on this topic (Wheeler 1991; see also Preuschoft and Preuschoft 1991, who similarly quoted Wheeler's view in their criticism towards the AHs). However, Langdon coined Wheeler's hypothesis as "entirely speculative," since this scenario "is also rooted in the assumption that a savannah environment had a key role in hominin origins," a concept that he regards as wrong (Langdon

[14] It is fair to note that the same author (Conroy 2005, 337, footnote 12) also refers to views challenging Wheeler's ideas.

2005, 125). This is only one of many examples demonstrating that defending paleoanthropology from the intrusion of alternative ideas does not necessarily imply a consensus on classical views.

To return to the question formulated in the introduction of the present paper, "Which factors are influential in the process leading to consensus in paleoanthropology?" In their book *Principles of Human Evolution* (2004) Lewin and Foley touch this question by referring specifically to the savannah and aquatic hypotheses.[15] These statements deserve a full quotation, since this is one of few cases in which authors with impeccable reputations in paleoanthropology refer to the AH to formulate fundamental questions on the evaluative process of alternative ideas in this field.

> The issue: the idea that human evolution was triggered by an aquatic phase is widely supported and discussed outside the mainstream of paleoanthropology, but is dismissed by most scientists working in the field. How do we determine what models are reasonable and plausible, and which ones are worthy of serious scientific study? (Lewin and Foley 2004, 282)

After an outline of the AH they continue:

> Indeed, it is one of Elaine Morgan's complaints that her ideas have been ignored rather than criticized or dismissed, and that this is a case of "normal science," in the terms of philosophers of science Thomas Kuhn, ignoring the radical alternative paradigm rather than engaging with it. (Lewin and Foley 2004, 283)

After pointing out that the AH is "one among many 'alternative theories' of human origins, and indeed in that light is one of the most cogent and best argued" (Lewin and Foley 2004, 283), they continue:

> The existence of such models does raise the question of what it is that distinguishes a plausible model from an implausible one. What is it that makes it reasonable to discuss one model and to dismiss another out of hand? Is the aquatic ape hypothesis a reasonable explanation for many unique features of humanity, and ignored because it is a challenge to scientific orthodoxy, or is it a crackpot theory? If it is the latter, then should the scientific community spend time and resources refuting it? If it is the former, how can it become accepted as a good model? (Lewin and Foley 2004, 283)

[15] Lewin and Foley wrote about the AHs in a "Beyond the Facts" section of their textbook, which was conceived as a didactic tool to stimulate students to think about how to assess alternative ideas in paleoanthropology. As such, the quoted pieces reflect the state of the debate more than their own personal views on this topic (Foley, personal communication).

New Evidence on Water-Contact in Non-Human Hominoids

It is impossible to give an objective answer to the above questions without an in-depth analysis of the role of water in early hominin evolution. Paradoxically, as long as topics related to hominin interaction with water are regarded as a domain of the AHs, paleoanthropologists have little motivation to undertake such analyses. As a result of this stalemate situation, a serious imbalance can be detected in early and modern paleoanthropological research. Aspects of the reconstruction of human's past directly related to well-established models proposed to contextualize early hominin evolution are much better studied than those topics which seem to contradict traditional models. We supply two actual, but still unknown examples of this disequilibrium, both related to non-human hominoids' interaction with water.

Few biologists will deny that the use of water (e.g., to exploit aquatic food resources, for thermoregulatory purposes, to escape from predators, to overcome bodies of water that act as barriers to their dispersal) is an essential topic in the study of land vertebrates' interaction with their environment. Although the ability to swim is a crucial and widespread feature in terrestrial vertebrates, non-human hominoids are universally regarded as unable to swim. Non-human hominoids and some other primates are reluctant to enter water bodies, although a broad spectrum of intraspecific variation can be identified in most species (Bender and Bender, paper in preparation). The conviction of non-human hominoids' inability to swim relies on the fact that they were never observed swimming either in the wild or in captivity (normally they can be constrained by deep water moats in zoos). This conviction is constantly reinforced by the numerous deaths by drowning in captive apes, especially orangutans, gorillas, and common chimpanzees. Based on our own observation, literature review, and a questionnaire survey, Bender and Bender (2011) showed that orangutans (*Pongo pygmaeus*) and common chimpanzees (*Pan troglodytes*) are able to learn to swim under specific circumstances. Four captive or semi-free ranging common chimpanzees and one captive orangutan were repeatedly observed swimming between three and six meters at the water surface or underwater using a variety of swimming patterns. Some individuals were able to hold their breath underwater up to 15 seconds or longer. This and other examples contrast dramatically with the general assumption of common chimpanzees as highly hydrophobic animals and show that apes under some conditions behave much like humans in their behavior towards water.

The second example concerns a widely ignored use of water for thermoregulatory purposes by non-human hominoids in the wild. At Fon-

goli (Senegal), male, female, and juvenile savannah chimpanzees (*Pan troglodytes verus*) were regularly observed spending time in ponds filled with rain water or in the riverbed of a small stream (Jill Pruetz, personal communication). The chimpanzees stay 30-45 minutes in the water, "sometimes they do some grooming, or just sit there" (Paco Bertolani, personal communication). This behavior is documented in a video footage.[16] Six adult chimpanzees hanging on vines, entered carefully into a pool (Sakoto pool) created by recent rainfall. They sit immersed up to their chests, holding onto the vines for safety, although the pool is evidently not deep.

The reason this interesting behaviour is still not reported in publications is related to the absence of a theoretical framework in which this knowledge can be easily processed. Compare for instance the well-known discovery reported by the same research group on savannah chimpanzees at Fongoli using sticks to hunt prosimians' prey, a behaviour that was considered to be a uniquely human trait (Pruetz and Bertolani 2007). In opposition to hominoid's interaction with water, hypotheses on tool use and hunting in the context of an open environment have a long tradition in classical paleoanthropological research and stay, therefore, in the centre of interest in this field.

The discovery of new behavioral patterns in well-studied species illustrates the importance of an unbiased formulation of research questions. These examples show that both proponents of the AHs and their critics developed their pro and contra arguments without careful analyses of the historical and epistemological aspects related to these ideas and without considering elementary empirical evidence about fundamental aspects of the debate.

Summary and Conclusion

Historians of paleoanthropology are skeptical when researchers identify alleged forerunners of ideas discussed in current paleoanthropology without careful consideration of historical contextualization (Bowler 2001). However, this justified skepticism rarely applies to established views in which the description of relevant early hominin fossil evidence is regarded as decisive in the formulation of influential hypotheses. In the present paper we have shown that the first description of *Australopithecus africanus* by Raymond Dart in 1925 was not the beginning of

[16] Retrieved from http://ngm.nationalgeographic.com/video/player?titleID=1420186582, accessed 7 December 2011.

the savannah model. This view could only have been established in paleoanthropology through excessive focus on the role of fossil evidence in the formulation of hypotheses. This interpretation, ignores the historical context in which the savannah ideas were developed. The idea of primeval humans abandoning the trees and adapting to open plains was outlined by Jean Baptiste de Lamarck in 1809 and by Charles Darwin in 1871. In the first decades of the twentieth century, several authors included new elements in the open plains scenario, paving the way for arguments which since then are commonplace in current paleoanthropological discourse. The most influential component of paleoanthropological discussion at this time was the idea that early human evolution is intrinsically related to climatic and environmental changes. The concept of "the forest abandoning proto-humans" instead of "proto-humans abandoning the forest" became popular in the early-twentieth century and became the most characteristic feature of the SHs propagated in modern paleoanthropology.

In the present paper, we demonstrated that the consolidation, popularization, and rejection of the open plains ideas were not the result of research carried out exclusively in paleoanthropology but were largely influenced by science writers or by scientists working outside of this field. The aquatic model played a meaningful role in this process. The first intensive discussions on the SHs' validity began with the debate around the AHs, especially after they were continually defended and extended by Elaine Morgan from 1972. However, the AHs were not commonly regarded as a refreshing or insightful challenge of classical ideas but mainly as noise in scientific debate and an unwelcome intrusion of non-specialists (e.g., Turner 1991; Wilson 2000 [1975], 28-29). The discussion "savannah versus aquatic hypotheses" implies the conviction that both models are diametrically opposed scenarios, embedded in different historical contexts, using strongly divergent narratives, defending and corroborating the hominization process through different arguments.[17] However, the similarities between the AHs and SHs are numerous and conspicuous. For instance, both models present a simple, at first glance, highly convincing scenario apparently supplying the explanation for several divergences between humans and non-human hominoids. Both scenarios relate widespread climatic and associated en-

[17] This polarized discussion is carried out not only in printed works (see, e.g., Richards 1991; Bender 1999a, 99-104, and references therein), but also on websites (see, e.g., http://www.riverapes.com/ and http://www.aquaticape.org/), online discussion forums, newsgroups (see, e.g., http://www.waterside-hypotheses.com/, http://tech.groups.yahoo.com/group/AAT/ and http://www.thescienceforum.com/pseudoscience/23693-aquatic-ape-hypothesis.html) and online encyclopaedias (see, e.g., http://en.wikipedia.org/wiki/Aquatic_ape_theory).

vironmental changes to pivotal events in hominin evolution, without acknowledging the problems of such alleged causal relationships. In fact, both models generally do not consider theoretical aspects related to the predictability and falsifiability of their basic premises. This applies for example to analogies between humans and other animals, without formulating objective criteria to corroborate such comparative approaches[18] and to the constantly adapted scenarios needed to integrate new fossil or paleoenvironmental data. Finally, proponents of both models formulated several specific arguments based on oversimplified or "idealized" habitats. These concepts usually stress single hominin features and conceive a landscape in which a hypothetical early hominin could exist and behave according to the premises of the hypothesis. This approach contains a strong tautological component and leads to one-sided hominization scenarios.

Having in mind that specialists are good at picking apart in detail any general synthesis (McHenry 1974, 436), it is remarkable that the several weaknesses in the classical SHs were ignored for so many decades, while the analogous weaknesses in the AHs were constantly used to criticize these models. The application of these double standards is related to the fact that AHs were proposed to replace what seemed to be a plausible scenario corroborated by vast empirical data. When in the last 20 years paleoanthropologists began to doubt the origin of early hominins as an adaptive response to the transition from forest to a more open scenario, the rejection of the AHs was already regarded as an established fact in paleoanthropology. As a by-product of this rejection, topics related to early hominins' interaction with water became strongly identified with the realm of the AHs and were therefore stigmatized in paleoanthropology. As we demonstrated by presenting two examples, the biased treatment of topics related to hominoids' interaction with water represents one of the most serious hindrances in contemporary attempts to reconstruct human past.

To conclude, an objective evaluation of all relevant aspects of human evolution should not be constrained by the inertia of classical hominization scenarios formulated several decades ago. It should also not be constrained by alternative scenarios which were formulated without in-depth analyses of historical and epistemological problems related to the hypotheses they intended to replace. The lack of such analyses conceals the danger of repeating the same mistakes of old hypotheses in new context. Additionally, progression in paleoanthropology is dependent on a

[18] For the use of analogies in the SHs, see above; for the use of similar analogies in the AHs, see Westenhöfer 1942; Hardy 1960; Morgan 1982.

clear differentiation between hypotheses proposed to contextualize early hominin evolution and research topics which address questions related to early hominins' interaction with complex landscapes. We predict that future investigations addressing the problems outlined in this paper will pave the way for a fundamental reorganization of paleoanthropological research.

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