

Terrestrial or Waterside?
A Conversation about Human Evolution

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Abstract

Communication across paradigms is impeded by different vocabulary and assumptions. The Aquatic Ape Hypothesis has been largely dismissed by anthropologists since its presentation in 1960 and debate has been impeded by misunderstanding and failure of communication. Coming from opposing paradigms, the authors identify the different premises underlying this controversy in an attempt to facilitate civil dialogue and future resolution of the controversy.

The Aquatic Ape Hypothesis, first published in English in 1960, has long been derided by paleoanthropologists as pseudoscience, and few have written seriously about it. Over the years, however, a small number of researchers have attempted to refine it and bring it more in line with the known fossil record. There are now a variety of “Waterside Hypotheses” and increasing arguments have been made on both sides of the debate, yet there continue to be misunderstandings, failures of communication, and attacks on outdated positions in both directions. As authors, we represent different sides of the debate and attempt here to compare the different models with a common language and to ask how different underlying assumptions have lead to different interpretations of evidence.

In 1960, marine biologist Alistair Hardy published his long-held idea that human ancestors had once been more aquatic in the past. He proposed that distinctive human traits, such as bipedalism, loss of body hair, and increased adiposity might be explained as adaptations for moving through water. The idea was taken up in a series of books by playwright and science

writer Elaine Morgan (1972, 1982, 1997), who promoted the “Aquatic Ape Hypothesis” (AAH), while deriding savannah-based models as male-orientated. In *The Descent of Woman* (1972), she elaborated Hardy’s coastal model as a more plausible and female-friendly alternative. One of the reasons for the neglect of the AAH by anthropological journals is that Morgan’s argument was based almost entirely on modern human anatomy and physiology rather than the fossil record. Few paleoanthropologists took the AAH seriously, as it contradicted long-held assumptions and standard interpretations. In the six decades since Hardy’s paper, the field has changed significantly, as continuing fossil discoveries and various technological advances have driven changes in our understanding of human evolution. The models of both communities have evolved in response and we take this opportunity to re-evaluate the status and nature of the arguments. What follows is a dialogue between two authors who are on record as supporting different sides of this debate (e.g., Kuliukas 2011a, 2011b, 2014; Langdon 1997, 1999, 2006, 2013). We attempt to bridge the gap by identifying and contrasting the implicit assumptions of the two paradigms; to examine the extent to which the two perspectives have converged; and to establish a groundwork for continuing conversation. We attempt to eschew rhetoric and to separate facts from subjective interpretations. This is not a debate and we do not attempt to resolve differences.

What in the past has been referred to as the “Aquatic Ape Hypothesis” is here referred to as “Waterside Hypotheses” (WH), signifying that multiple independent ideas are represented, having in common a dependent reliance on coasts and other permanent water courses and distancing them from the caricature of a dolphin-like hominin. The dominant view in textbooks and academic journals is termed “Terrestrial Models” (TM), again intentionally vague to acknowledge a diversity of subhypotheses.

1. What are the current Waterside Hypotheses?

The original AAT of Hardy and Morgan has since evolved into a radiation of ideas that vary in proposed timescale, the degree of “aquatic” selection invoked and the evidence cited in support (see Kuliukas and Morgan 2011). What they share in common is the premise that selection for wading, swimming and diving and the procurement of food from aquatic habitats led to the phenotypic divergence of *Homo sapiens* from its sister species. For the sake of argument, Kuliukas here promotes his own variant (Kuliukas 2013) as representative of the various waterside hypotheses. It proposes two broad phases with a transition period in between. In the first phase, the last common hominin ancestor in the Miocene was already a facultatively bipedal ape, living in swampy habitats conducive to a significant amount of wading through shallow water, while exhibiting vertical climbing in its locomotor repertoire.

During the transition to the second phase, East African climate grew broadly drier, albeit with dramatic cycles between wet and dry periods. The hominins that lived there were forced to retreat to waterside habitats in seasonally flooded gallery forests and lakes, and later to the coast. This transitional period is represented in the fossil record by the australopithecines. They were not yet obligate bipeds in the sense of *Homo*, but became physically adapted to more bipedalism than their wading-climbing ancestors.

Once at the coasts, the second phase would have begun. Hominins became less arboreal, more aquatic and more terrestrial and evolved the striding gait of *Homo*. Beachcombing on coastal flats helped optimize the energy efficiency of our striding gait; and the occasional need to swim and dive for (marine) food provided sufficient selection pressure to cause other phenotypic changes. The switch to a relatively high-energy diet, rich in essential brain nutrients, such as

docosahexaenoic acid (DHA) and iodine, drove our encephalisation, and the fine voluntary breath control from swimming led to the evolution of speech.

2. What is the standard Terrestrial Model?

Again, we must avoid details on which there may be variant models, but there is a premise that hominin lineage has always been and remains a clade of terrestrial species. Since the 1980s, australopithecines are portrayed as ecological apes with a unique but incompletely understood blend of terrestrial bipedalism and arboreality. Aside from the tools discovered recently at Lomekwi, there is no evidence of more sophisticated behavior or mental capacity. Consistent tool behavior, hunting and carcass processing, and brain expansion began about the same time as genus *Homo*, between 3.0 and 2.0 Ma. A second remodeling of the postcranium produced the modern striding gait, first apparent shortly after 2.0 Ma. By then, humans were spread widely across Asia.

Conflicting Premises/Ideas

There is no disagreement about the paleoenvironments of the hominin fossil record other than a general shift in emphasis. Probably all East African fossil assemblages were deposited in water, else they would not have preserved. They are therefore usually accompanied by both aquatic fauna, such as remains of fish and crocodiles, and also terrestrial fauna representing varying proportions of woodland and grassland communities. Likewise, humans, more than most mammals, are dependent on drinking water and would have lived within daily range of fresh water, whether it be a spring, seasonal pan, permanent lake, or river. Thus, the fossil record may be seen to associate hominins with water.

TM arguments tend to emphasize the terrestrial flora and fauna in paleoecological reconstructions; WH the aquatic species. TM emphasizes that many known hominin sites are away from coasts and permanent water-courses; WH stress that coastal habitats are not conducive to fossilization due to erosion and changes in sea level. During the period of increasing instability after 3.0 Ma, TM emphasizes temporal and spatial environmental instability and complexity due primarily to changing rainfall patterns, whereas WH models stress that it was largely the changing degree of surface water that was critical.

Both models agree on the two-phase evolution of bipedalism. Likewise there is agreement on the significance of the relatively late development of enlarged brains, language, and progressive technological development that resulted in a species that is a very adaptable eclectic omnivore, capable of expanding into numerous niches across the planet. Beyond these points of agreement, our conversations have revealed underlying differences of perspective and different premises that are explored here.

1. Do human origins require an extraordinary explanation?

At the heart of the classic narratives on human evolution, whether they be TM or WH, is a prime mover, a key factor leading to the divergence of the hominin lineage from that of the other great apes. Proposed prime movers have included a switch to the open plains, hunting and gathering or, in the AAH, a switch to a more aquatic life style. Whether or not modern narratives should espouse a prime mover is a point of debate.

TM. Historically, anthropologists considered humans far removed from other animals and inferred from that a long separate ancestry, at least since the Miocene. Grand narratives have sought special circumstances that would explain our outstanding characteristics of bipedalism,

tools, intelligence, and language as interrelated phenomena. Landau (1991) used narrative analysis to compare such storytelling with folk tales, in which the protagonist acquires a special gift to help him or her conclude a quest. Hunting emerged in the 1960s as the “gift” in the dominant narrative (Washburn and Devore 1967), but with a few exceptions such speculation has been relegated more to popular literature than academic journals in recent decades. The AAT in its first incarnation was a part of this genre. Morgan used a habitat shift from land to water as the narrative device to acquire the “gift” (a suite of unusual anatomical traits).

A model that invokes a discontinuity in behavior or ecology beyond normal repertoire – particularly one that has no contemporary evidence – may be considered extraordinary. The gift of tools in Darwin’s model was extraordinary in 1871; but now that we understand tool use and culture to be widespread among other species, it is less so. Some anthropologists continue to evoke extraordinary events, such as cooking (Wrangham et al. 1999) or sudden changes in levels of intelligence (Coolidge and Wynn 2009); however, if the same outcomes can be accounted for through more gradual shifts in behavior, such explanations are unparsimonious. By this standard, WS proposes an extraordinary explanation.

Since the acceptance of the molecular clock in the late 1970s, anthropologists have been impressed by the close relatedness of humans and chimpanzees – about 98% identity in DNA – and have emphasized the similarities between australopithecines and ape anatomy. Field and laboratory studies have likewise made it difficult to draw distinct boundaries between the mental abilities of humans and other animals. Consequently, hominin exceptionalism is now downplayed in the evolutionary narrative of early hominins in favor of continuity. Since we now know that the first appearance of bipedalism is far removed in time from the later appearance of

distinctive human cultural and social traits, it is no longer reasonable to seek a single prime mover to tie all of these traits together.

WH. A key point for WH is that the position of *Homo sapiens*, deeply embedded in the great ape clade, and yet so very phenotypically different, suggests that something significantly different must have happened in the evolution of our lineage. WH proponents argue that a single prime mover (i.e., a waterside habitat) *does indeed* appear to tie all of these traits together, irrespective of the timescale. Moving in shallow water encourages an otherwise quadrupedal ape to move bipedally in the first place. Seasonally flooded gallery forests, through wet/dry cycles of changing climate, should induce more frequent wading in these facultative bipeds. Riparian zones provide an elegant conduit to a habitat that explains modern human traits. We are remarkably different from all other primates and therefore, it is argued, require a remarkably different, but still plausible adaptive explanation. Where better, or more plausible, than waist deep water in swamps for this process to begin? And where better or more plausible for it to end, than at the coast? The “gift” is merely placing a large ape in a waterside niche.

2. Do modern humans express a degree of adaptation to the water that cannot be explained except as the outcome of natural selection for it?

There is no dispute that humans are better able to move through water and are more dependent on access to it than are apes. The point of contention is whether this was the result of natural selection specifically for a waterside lifestyle, or merely an exaptation for something else.

WH. A cluster of major physical differences between *Homo sapiens* and *Pan/Gorilla* are most parsimoniously explained as adaptations to moving through water. A significant caveat must be inserted here: If one is making comparisons with fully aquatic mammals such as those in

Cetacea, Pinnipedia, or Sirenia, humans are poorly adapted to swimming and diving. Waterside hypotheses are merely suggesting that since the last common ancestor of *Pan*, *Gorilla* and *Homo* our ancestors became relatively better adapted to moving through water than theirs.

Hardy (1960) noted that there are a number of additional observations about humans that a more aquatic phase in our evolution might explain. “First and foremost is the exceptional human ability to swim.” There can be little doubt that, compared to *Pan* and *Gorilla*, humans have far greater ability to dive and swim. Millions of humans have been observed swimming. From an early age, perhaps even before walking, infants can learn to propel themselves in water. Every year, in Perth, thousands of enthusiasts swim 20 km or so across open water. The world record for a human swimming without flippers is 225 km; yet the river Congo has been sufficient to geographically isolate bonobos from gorillas and chimpanzees for millions of years.

WH stress that there is no scenario that can induce unsupported habitual bipedal locomotion in great apes as well as wading in shallow water (Kuliukas et al. 2009; Kuliukas 2013). Wading is thus an ideal model for the earliest adoption of hominid bipedalism and a swamp-dwelling wading-climbing last common ancestor makes a logical precursor to both human bipedalism and the peculiar knuckle-walking quadrupedalism. As for the second transformation that undoubtedly led to greater terrestrial locomotor efficiency, waterside habitats suit that phase too, as the human striding gait can only work at optimal efficiency on flat, firm, vegetation-free substrates, as found at the water’s edge in dried-out river beds and beaches at low tide.

TM. Humans are not by nature well-adapted to deep water and must be taught how to swim efficiently. However, the issue here is not whether humans swim and chimpanzees do not, but whether humans have any adaptations specifically to enhance swimming ability. The features that enable humans to perform better in water are mostly secondary to effective bipedalism. A

linear body form reduces drag in the water, and is achieved through full extension of the lower limb joints. Joint extension is essential for efficient bipedal walking on land; however, it reduces efficiency while wading against water resistance. Increasing the length of the lower limb and shifting a greater proportion of body mass there increases efficiency of terrestrial bipedalism. Even the WS outlined in this paper assumes early *Homo* was mostly walking on land. The fundamentals of endurance that enable swimmers to cross the English Channel – regulated oxygen flow, energy storage – have equal value on land; while the thermoregulatory adaptations that enable terrestrial endurance have no value in swimming. In short, a parsimonious approach finds no special swimming adaptations that are not better explained by terrestrial bipedalism.

Could bipedalism itself be a wading adaptation? Since the 1970s, anthropologists have explored the link between hominoid climbing and bipedalism and noted many anatomical and physiological continuities (e.g., Fleagle et al. 1981). The similarities are great enough that arboreal behavior could account for increasing reliance on bipedalism in the trees (e.g., Thorpe et al. 2014). A subtle shift to more terrestrial travel or feeding may have nudged ancestors toward the australopithecine condition. This is the most parsimonious model.

These different perspectives between WS and TM extend to other aspects of soft tissue anatomy and our interpretations of them.

WS models posit that the evolution of the human body hair pattern and follicle orientation is an adaptation to reduce drag in water whilst swimming. **WH** note that in observations of breast stroke swimming, the part of the body most likely to be covered in hair, the scalp, is also the part most likely to be above the surface of the water, and vice versa. An increase in body fat, especially in infants and mothers, is seen as an adaptation for improved buoyancy, and hence

reducing the risk of drowning. **TM** observes that human loss of an insulating layer of fur is a dangerous strategy, exposing us to hypothermia at night, heatstroke in the day, and risk of skin burns and cancers. There must have been compelling reasons to make such a change specifically, a strategy that permits us to be active in the heat of the tropical sun and to endure extended periods of exercise. The loss of hair, along with sweat, and skin vascularity combine to create superior mechanism of body cooling than is possessed by other mammals of comparable body size. (Langdon 2004). Human accumulation of body fat is most consistent and apparent among women of reproductive age and their infants, where fat provides a buffer of energy for reproduction and especially for a developing brain.

Brain expansion required a change to a diet that supported its high energy demands. **WH** models stress that brain-specific nutrients, such as DHA and iodine, are particularly rich in the marine food chain and would have been conducive to its high energy demands. **TM** argues a marine diet is sufficient, but not necessary for human brain development (Langdon 2006). The adaptive value of brain expansion is a separate but equally important problem. The presence of sufficient nutrients for the brain is necessary, but not sufficient, to account for encephalization.

WH explains the adoption of stone tools by stressing the plethora of pebbles found near beaches and other permanent water courses, along with the incentive to use them in the consumption of shellfish. From the **TM** perspective, the use of stones and other tools in extractive foraging are widespread among primates and other animals and thus no more useful in waterside than in terrestrial habitats.

Speech is one of the most significant traits distinguishing us. Modern human speech has a number of anatomical correlates, including brain processing of thought and expression, voluntary motor control over respiration, the physical apparatus to shape sound, and the neural control over

that apparatus. **WH** models stress that a key exaptation required for speech is fine voluntary breath control and that swimming and diving provide this remarkably easily. **TM** observes that, unlike the quadrupedal spine the upright human axial skeleton is minimally involved in locomotion (Bramble and Carrier 1983) and thus pre-adaptive for fine-tuning of its neural control.

3. How do we assess parsimony in evaluating these models?

Parsimony is a standard means of evaluating scientific models. However, both sides of this discussion claim to present a more parsimonious model.

TM. Langdon (1997) coined the term “umbrella hypotheses” to describe models that seemed to gather many lesser explanations under one cover. Morgan’s model was a classic umbrella hypothesis. Counterintuitively, umbrella hypotheses are not inherently parsimonious because each related “explanation” is a separate hypothesis that needs to be investigated and tested on its own merit. For example, it seems reasonable that hunters would benefit from being more intelligent; but from that surmise, the fact that humans are intelligent does not strengthen the argument that we were hunters. Nor does evidence of hunting solve the mystery of brain evolution.

WH. Morgan (1997) argued that it was more parsimonious if a cluster of traits could all be explained with one hypothesis than several. She argued that both the savannah theory and the AAH attempted to do this; however her “U-Turn” element – a shift to a more aquatic lifestyle, and then back – made it less parsimonious than models with fewer habitat shifts. The WS version used here posits that our lineage has always lived in waterside habitats and attempts to combine

stronger aspects of both terrestrial, and “aquatic ape” theories into a single model that better fits the evidence.

4. Is there evidence for habitat shifts that would support a WS scenario?

TM. Given the weak fossil record, the paleoenvironment of the Miocene LCA is unknown. The emergence of australopithecine bipedalism suggests increasing terrestriality in a primitively arboreal lineage. Arguably, early *Homo* may have operated within any or, more probably, many of the indicated niches. As humans left Africa shortly after 2.0 Ma, they began to occupy an increasing diversity of complex habitats. By the Middle Pleistocene, human activity is found in tropical forest, deciduous forest, scrub forest, savanna, steppe, mountains, swamp, lakeside, and coastal environments (Langdon, 2013). Before the end of the Middle Paleolithic, that extended to tundra and desert, as well. There is no reason to believe that humans were ever dependent on any one habitat. Adaptability rather than specialization, has long been the hallmark of human culture.

WS. Some early Miocene hominids are associated with swampy habitats and it is possible that the LCA of the great apes was as well. As climate changed in the Late Miocene and Plio-Pleistocene, our ancestors clung to their habitats. During times of aridity, large swathes of forest would likely have shrunk closer to permanent water courses. These riparian habitats, which would have been subject to regular seasonal flooding, are strongly associated with transitional hominins, such as australopithecines. It is perfectly plausible that gallery forest-dwelling hominins would have followed the drainage to coastal habitats. The evidence that human ancestors did live at the coast is patchy and equivocal; however, the arrival of *Homo erectus* in Asia and Java, in particular, suggests coastal migrations. Coasts are notoriously poor

places for fossilization. As the adage goes: absence of evidence is not necessarily evidence of absence. Most significantly, there is strong evidence from the Blombos sites in South Africa that by 167Ka, modern humans did indeed live at the coast. This is tantalizingly close to the consensus dates for the speciation event of *Homo sapiens*, and is consistent with waterside models that posit a coastal origin for our peculiar walking, talking, sometimes swimming and diving, species – a small, smart, population that expanded into vastly diverse niches across the world.

5. What level of selection intensity would account for the WS?

Hardy's analogy with cetaceans and Morgan's initial presentation of the AAT suggest a degree of adaptation to water that has been ridiculed; however, they are not representative of later WS models, a point poorly understood by anthropologists. How committed were our ancestors to water, such that selection could reshape our bodies?

WH. Population genetics 101 tells us that for selection to overcome the effects of random genetic drift it needs to be greater than the reciprocal of twice the effective population size. In other words, assuming a breeding population of 1,000 individuals, the degree of selection need only be 0.0005, or 0.05%. Computer simulations demonstrate that with even such small advantage for a given allele, fixation may occur in a remarkably short time in evolutionary terms – around 10,000 generations. There are several well-known examples in modern human populations which show that slight selection has rather clear phenotypic effects: lactose and alcohol tolerance, altitude tolerance and the way that skin pigmentation adapts to latitude. It seems an unremarkable conclusion to assume that if hominin ancestors lived in waterside

habitats where they would occasionally wade, swim and dive, then even slight levels of selection would have profound effects in relatively short evolutionary timescales.

TM. Such simple population genetics models come with the conditional phrase “all else being equal.” The examples of lactose tolerance, etc., are rare examples of single-gene traits simple enough for us to understand. None of the traits under discussion in this article fit that category. Redesigning the lower limb and body proportions and respiratory controls and skin structure and brain size involve alterations in developmental pathways and multigene traits likely to have widespread consequences across the body. Each of those effects may have positive or negative consequences that must balance. How would a given change affect the most consistent and important challenges to human life, such as walking efficiency or thermoregulation? Are the hypothetical genes in question linked to others with critical functions? For example, The WS suggests humans lost their hair to increase efficiency while occasionally swimming in water. Would the small saving in expenditure there compensate for the extra energy spent to keep the body warm the rest of the day and night out of water? “All else” is not equal and adaptationist arguments that identify one benefit for a given trait are incomplete if they do not encompass the bigger picture.

Conclusions – Can These Ideas Be Reconciled?

Is either hypothesis testable?

Can we identify evidence that could conclusively reject one or the other position? Scientific hypotheses can never be *proven*, but certain predictions can be made on both sides that are testable and potentially falsifiable through future discoveries.

WH. WH make a number of predictions that are testable.

1. Further fossil evidence will arise, placing *Homo* in coastal habitats earlier than we see at present. The WS model proposed here predicts that early *Homo* first lived on African (Indian Ocean) coasts ca 2.6 Ma.
2. As understanding of the human genome progresses, it is predicted that developmental mechanisms involved in infant brain growth will become more unequivocally tied to the marine food chain and micro-nutrients.
3. Studies should show that an ape-like body hair pattern causes more drag than the modern human one, and that specific human hair patterns are adaptive when using specific swimming strokes such as the breast stroke.
4. The distribution of body fat in human infants is consistent with that which one would predict as a buoyancy aid to reduce the risk of drowning.
5. Further findings from the human genome and fossil record should reveal a stronger link between voluntary breath control and swimming and diving.

TM. Predictions of the terrestrial model:

1. When the geographical origin of genus *Homo* is identified, it will be in a spatially and ecologically complex environment.
2. Fossil hominin discoveries will continue to show that human populations pursued a broad range of resources and habitats and were not dependent on or specialized for a single habitat or food resource.
3. No human traits differing from those of other primates will be identified that are demonstrably specific to activities in water.

Last Words

For nearly 60 years, those who have chosen to engage on either side of the debates about aquatic apes or waterside hypotheses, have found themselves talking past their opponents, accused of misrepresentation, and arguing in circles. The authors have sought out and conversed directly with those holding opposing views so that we may move beyond fruitless exchanges and find areas where we can agree to disagree. We hope this might be a useful model for guiding other conversations that cross paradigms. We have found the following practices to be important to maintain a civil and productive exchange of ideas:

- Leave behind historical and political aspects to focus on the science itself.
- Listen to what the other side has put forward even if disagreement remains.
- Be as clear as possible with arguments, and use the same language to avoid misunderstanding.
- Identify the premises that underlie differing interpretations.

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