CHAPTER 6

Aquatic Scenarios in the Thinking on Human Evolution: What are they and How do they Compare?

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Abstract: Missing in the literature to date is a concise description of the various scenarios proposing that human evolution was affected, to some extent, by selection from wading, swimming and diving through water. Most of it tends to focus on just one such scenario, first proposed by Hardy [1] and promoted by Morgan [2-6], which suggested that a more aquatic interlude was contemporaneous with, and probably caused, the split between *Pan* and *Homo*, and was followed by a U-turn back to a fully terrestrial life. Although theirs is still the most well-known, it is not the only one. Other scenarios, for example that proposed by Verhaegen *et al.* [7-11], differ quite markedly in timescale, the proposed degree and mode of aquatic selection, and in terms of the evidence used in support. This Chapter reports more than ten such ideas and summarizes six aquatic scenarios and clarifies the differences between them. It also identifies a common thread between them, and uses it to propose a new label and definition for them.

Keywords: Aquatic scenarios, waterside hypotheses, Hardy, Morgan, Verhaegen.

INTRODUCTION

Discussion of the *aquatic ape hypothesis* (AAH) in the scientific literature has been for the most part sparse and dismissive. The one attempted refutation in a first class anthropological journal [12] was largely a critique of Hardy's original scenario and Morgan's promotion of it [1-6], which envisaged an aquatic interlude contemporary with – and in their opinion causing – the split between chimps and humans. As discussed in Chapter **15**, Langdon's critique appears to have a number of weaknesses, which greatly damage any claim that it provides a serious rebuttal. One such weakness is that other 'more aquatic' scenarios were not even considered.

Hardy's and Morgan's ideas [1-6] have been supplemented, enhanced and sometimes challenged by competing scenarios of what might have happened, and when, and where. The most highly developed of these is presented by Marc Verhaegen *et al.* [7-11] in Chapters **4** and **5** of this volume, but there have also been others before and since. This chapter seeks to compare and contrast them, and explain where they differ in respect of timing, and location, and the envisaged life-style of the species they describe.

WATERSIDE IDEAS BEFORE HARDY

Before comparing Hardy's and Morgan's scenarios with that of Verhaegen and other ideas that followed, mention should be made of two other ideas prior to 1960. For a full review of these, see [13].

Sera (1938): 'Aquatic' Platyrrhines

Guiseppe L. Sera, an Italian biologist, was probably the first to suggest a possible aquatic phase in primate evolution [14]. On the face of it, Sera's contribution has very little relevance to the later ideas of Alister Hardy, since it was not concerned with humans, or even with apes although it should be remembered that at the time many scientists believed that our ancestors were primitive. It dealt with the evolutionary history of the Platyrrhini (broad-nosed or New World monkeys). It foreshadowed Hardy only inasmuch as it was based on anatomical comparisons between some primate species and some aquatic ones. Features such as the detailed structure of the larynx, nose, ear, female

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external genitals and the kidneys led Sera to consider the possibility that the platyrrhines might once have occupied an aquatic habitat. Other parallels with Hardy were the willingness to put forward an idea contrary to contemporary thinking, and the modest tones in which they were offered. Sera expressed the hope that "such ideas which at first sound so improbable should at least serve as a stimulus to further research."

Westenhöfer (1942): *Der Eigenweg des Menschen* (The Pathway to Mankind)

The most significant predecessor to Hardy in alluding to aquatic factors in human evolution was the German anatomist Max Westenhöfer (1871-1957) [15]. His attention, like Hardy's, was drawn to various anatomical traits in humans, such as lobulated spleens and kidneys, which he believed were somewhat analogous (*i.e.*, had similar anatomy through convergent evolution) to those present in whales, dolphins, seals, and sea otters. Other such traits mentioned in his work were hairlessness, bipedalism, subcutaneous fat, reduction of olfaction, face-to-face copulation, and brain development.

Westenhöfer's view differed most significantly from Hardy's in that it did not assume that humans had evolved from an African great ape stock, but that they descended from, relatively unchanged, a primordial animal so ancient that it predated even the emergence of primates. The assumption of this *primitivity thesis* makes any realistic comparison between Westenhöfer's and Hardy's ideas very difficult, especially in terms of time-scale. Even though the two were partly contemporaneous, neither of them apparently was aware of the other's thinking.

HARDY / MORGAN: 'MORE AQUATIC' U-TURN HYPOTHESIS

This section deals with what most people think of when they hear the term 'aquatic ape hypothesis', *i.e.*, Hardy's original idea and the promotion of it by Elaine Morgan.

Alister Hardy (1960): Was Man More Aquatic in the Past?

Alister Hardy (1896-1985) was a marine biologist at Oxford University who, in the 1930s, happened to read a comment by Professor Wood Jones [16] on the puzzling fact that the layer of fat lining the skin of *Homo sapiens* is not present in the chimpanzee. Hardy had just returned from an expedition devoted to studying the marine fauna of Antarctica. Examples of animals and birds that do possess a fat-lined skin instantly sprang to his mind, and he could not fail to notice that they were all aquatic. Was it possible that Man too was more aquatic in the past?

He had a good idea of the scepticism with which this question would be received, and waited thirty years before publishing it in *New Scientist* [1]. Fifty years later, it remains one of the most controversial subjects in palaeo-anthropology. Despite being largely ignored by scientists in that field, interest in it elsewhere has continued to grow. The reasons for this discrepancy are probably many-fold and complex (see Chapter **14**), but one possible explanation may be, simply, that it has been misunderstood. Clearly, if anyone is going evaluate this idea, let alone reject it, it is of critical importance that they understand what Hardy was proposing and, perhaps even more importantly, what he was not proposing.

Hardy was puzzled by several anomalous features of human anatomy. Every species is unique by definition, but the sheer number and variety of ways in which humans differ from all other primates seemed to him to demand an explanation. He attempted to account for it by postulating that their ancestors had gone through a "more aquatic" phase in their evolutionary past. The subcutaneous fat was the feature that first put the idea into his head, but it was soon followed by others [1, 17].

A key argument in Hardy's thesis is that most mammalian taxa include at least one species that appears to have become "more aquatic", indeed some lineages, leading to entire taxa, have returned to the sea permanently. It seemed to him quite possible that the Primate Order might also contain such a species, and if so, that *Homo sapiens* might be the species in question. Clearly, Hardy argued, since humans today are by no means aquatic, this phase must have somehow been curtailed and then reversed. This reversal was later characterized as a *U-turn*, and was sometimes used as a reason for rejecting the idea. If they had gone into the water, why would they have come out again? Hardy did not regard that as a serious stumbling-block. Such U-turns are rare, but no means unknown in the history of life on earth.

When did Hardy propose this phase happened? Hardy's time-scale was in accordance with what was known from the fossil record at the time. He proposed that a "more aquatic" phase in human evolution would neatly 'plug the gap' that appeared at the time to exist in the fossil record between *Proconsul* and *Australopithecus*, namely about 15 to 10 Ma (million years ago).

Where did it happen? Hardy doesn't originally propose anything more precise, geographically, than to suggest that warm tropical coasts would have been ideal for the sort of scenario he envisaged. However, later, he did enthusiastically endorse the idea of a geologist Leon P. La Lumiere Jr. [18] that the Afar triangle generally, and the Danakil horst specifically, could have provided an ideal location for the geographical isolation that at the time was thought to be required for speciation (*allopatric speciation*).

What was Hardy ***not*** *proposing?* It's worth briefly noting, considering the controversy that has arisen surrounding this idea, what Hardy was *not* proposing. Most significantly, he was *not* proposing an 'aquatic ape', in any real sense of the word. The phrase 'aquatic mammal' has specific connotations about lifestyle and swimming and diving abilities that go far beyond what Hardy had in mind. Perhaps this is best illustrated by this statement: "It may be objected that children have to be taught to swim; but the same is true of young otters, and I should regard them as more aquatic than Man has been" [1: 643].

Hardy, then, clearly set an upper bound for the degree of aquatic adaptation he envisaged. Although some might counter that an otter is still quite an aquatically adapted mammal, (some might call it semi-aquatic), Hardy is clearly proposing we were less aquatic than they are. He spelt out, in quite precise terms, how much time he thought our ancestors might have spent in the water. "I am imagining this happening in the warmer parts of the world, in the tropical seas where Man could stand being in the water for relatively long periods, that is, several hours at a stretch" [1]. Several hours might seem a long time for a human, but not for an aquatic mammal. It is certainly not a mermaid or some kind of 'primate seal'.

Unfortunately, the response from the field of palaeo-anthropology to Hardy's idea was muted to say the least. Despite a ripple of quite positive feedback in the letters pages of New Scientist in the weeks that followed, and an elegant paper in support by the geography professor C. E. Sauer [17], the idea was all but forgotten until Desmond Morris, a former student of Hardy, in *The Naked Ape* [20], mentioned it in a way that would provoke a keen interest from someone who would become the leading proponent of the idea for some forty years.

Elaine Morgan (1972, 1982, 1990, 1997, 2008): ***The Aquatic Ape Hypothesis***

Elaine Morgan asked Hardy for permission to quote his ideas in a book she was writing. Permission was granted. He later registered some startlement on learning that the book was to be entitled, *The descent of woman* [2], but he welcomed the endorsement of his basic idea and wrote a foreword to her next book [3]. She has written three more on the subject since.

Morgan's books [2-6] have been a faithful portrayal of Hardy's original idea, but she has also made her own significant and original contributions.

She advanced further examples of the ways in which an aquatic phase might help to explain enigmatic features of human physiology. Looking at human evolution from the point of view of the woman [2], and then the child [21], she provided some new insights, from a 'more aquatic' context, that Hardy had not seen. For example, she argued that the fact that human infants are born fat simply makes more sense in a more aquatic environment than elsewhere [4]. Perhaps most significantly, Morgan picked up Hardy's almost throw-away comment: that wading in shallow water might help "our understanding how Man obtained his erect posture" [1] and developed it, over twenty years into a well-developed hypothesis of bipedal origins though half a dozen chapters containing good evidence and strong arguments [3-5].

Her main emphasis has always been on the remarkable differences between humans and chimpanzees – animals that are even more closely related to us than they are to gorillas. Even the most cursory examination of the clade of the African great apes makes it inescapably clear that *Homo* is the odd man out. Whatever may have happened in the

past to account for the features that all apes have in common, there must be some additional reason why this one particular species evolved along such strikingly different lines from its nearest kin. Whatever changes in the environment brought that about cannot have predated the chimp/human split. She was looking for a scenario that would take that into account.

In her second book, *The aquatic ape* [3], she proceeded to compare three alternative hypotheses as candidates for this 'ideal' scenario. It could be argued that one of the three (*neoteny*) was not really a scenario but a *mechanism* and shouldn't have been included, but the differences between the other two – Hardy's proposition and the officially approved savannah theory – were clearly set out.

In that book and the one that followed it, *The scars of evolution* [4], she focussed on the numerous ways in which humans are maladapted to life on the savannah. For example, being the thirstiest and sweatiest of all primates would not have helped them to survive in conditions where water was a rare and precious commodity. It was possibly the attack on the savannah hypothesis, which prompted the only attempted rebuttal to date of the AAH published in first class palaeo-anthropology [12]. Langdon's critique in the Journal of Human Evolution made the claim that "the savannah hypothesis that Morgan criticizes turns out to be straw man" [12]. That was gratefully taken up and served for years as the standard reply: "That was not what we meant." But finally there came the first admission, from one of its leading proponents, that it was indeed what they had meant, but he now believed they had been wrong [22].

In summary, when comparing Hardy's original ideas with Morgan's promotion of them, one only finds differences in emphasis. Morgan's time-scale for the more aquatic phase has gradually changed from 10-15 Ma, as Hardy originally suggested, to around 6 Ma today, but this merely reflects changes to the estimate of the date of the LCA (last common ancestor) of humans and chimpanzees. Morgan believes today, as she did in the early 1970s, that the most significant 'more aquatic' phase was in and around that event.

One of us (AK) believes Morgan's contribution to Hardy's idea cannot be overstated. She resurrected an idea that had all but been forgotten and gave it enormous popularity and a new, vigorous lease of life. As Groves and Cameron put it recently: "At first, this idea was simply ignored as grotesque, and perhaps as unworthy of discussion because proposed by an amateur. But Morgan's latest arguments have reached a sophistication that simply demands to be taken seriously" [23]. Perhaps most importantly, she sparked a fascination about Hardy's idea in several others that would motivate them to study the subject themselves and make their own contributions to it. A series of aquatic scenarios proposed by such people, will be discussed next starting with arguably the most sophisticated and well-developed one, that of Verhaegen *et al.*

Some Reflections after Hardy

It is half a century since Hardy posed his question, and a quarter of a century since he died. Since then Elaine Morgan has continued actively promoting his ideas, and challenging any theories that are put forward offering new non-aquatic explanations of enigmatic human features such as the naked skin, the fat layer, and the descended larynx (see Chapter **12**).

Like Hardy, she has never been specific about dating, or locations. She asserted at one time that the water involved must have been salt, but later admitted that her reasons for declaring that were inadequate. Also like Hardy, she never quite relinquished La Lumiere's idea [18]. The flooding in the Danakil area was presumably as catastrophic as the successive flooding and desiccation of the Mediterranean, and converted the slopes of the Danakil Horst virtually into an island. Since Hardy was writing, fossil hunters have tended to forsake the South-African sites and move further North: many of the very earliest fossils have been found in the Afar region, just where La Lumiere would have predicted. However, the idea is untestable and has been disregarded.

She has been less receptive to some of the newer ideas among water theorists, such as some of those of the aquarboreal hypothesis (see below). She admits that it is theoretically possible, and would not be entirely incompatible with Hardy's theory, since the chimp/human split could have been occasioned by what Verhaegen *et al.* term the *most-aquatic phase* (Chapter **5**). But she has voiced the opinion that some of the reasoning behind it is inconclusive, and is particularly sceptical of the idea that *vertical floating* was once part of early hominid

locomotive repertoire. She points out that all vertebrates moving through water do so with their vertebral columns horizontal, in obedience to one of the basic laws of physics: "When a body moves through a resisting medium the resistance is proportional to the surface area perpendicular to the direction of motion."

For most of the last thirty-eight years her greatest efforts were devoted to questioning the belief in the savannah hypothesis that held sway for most of the last century. It was finally defeated, not by persuasive reasoning, but by improved technology. However, she is quietly pleased that she lived long enough to see it come to an end.

MARC VERHAEGEN *ET AL.*: FROM AQUARBOREAL 'APES' TO DIVING *HOMO*

A different scenario, starting from Hardy's and Morgan's waterside ideas, has been developed over the last decades by Marc Verhaegen, Pierre-François Puech, Stephen Munro and others. For a detailed description of their ideas and supporting evidence for them, see Chapters 4 and 5, and earlier publications of Verhaegen *et al.* [7-11], but here it will be summarized and compared with Hardy's, Morgan's and other waterside scenarios. Like most waterside hypotheses, their approach is based on comparative anatomy, but in addition takes into account biomolecular, geological and fossil data.

Whereas Hardy's and Morgan's models concern themselves only with human divergence from the rest of the great ape stock and propose that a 'more aquatic' phase was a key component causing that divergence, Verhaegen *et al.* seek to explain the evolution of apes too, and place human evolution inside that context. Compared to Hardy's and Morgan's scenarios, their model has a more specific ecological scenario as well as a more detailed timescale. Broadly, ape and human evolution is described as follows:

Early Hominoids (~ 20-5 Ma)

In their scenario, early Hominoidea (the superfamily of apes and humans) lived in coastal and swamp forests and other wetland habitats around the Tethys Sea and in southern Eurasia during most of the Miocene (23-5.3 Ma) and Pliocene (5.3-2.6 Ma) epochs. The locomotor repertoire of these Miocene 'apes' is labelled *aquarboreal* (from *aqua* 'water' and *arbor* 'tree'). They climbed trees in an *orthograde* manner (*i.e.*, with a vertical spine) often climbing with arms overhead, but also moved through water too, by swimming, and possibly vertical floating (perhaps using laryngeal air sacs) and wading. As a consequence, they became bigger like all (semi-)aquatic mammals, lost the tail, which caused heat loss and hindered orthograde swimming-wading and evolved vertical spines for grasping fruits and branches above the water.

Miocene apes were more widespread and diverse than living apes, many were thick-enameled omnivores, suggesting that they could have fed, at least in part, on hard-shelled foods, *e.g.*, mangrove oysters and palm nuts. Examples of these early hominoids are *Afropithecus*, *Griphopithecus*, *Dryopithecus* and *Oreopithecus*. This phase in the model is supported by the evidence that ancestral Hylobatids (today's gibbons) and pongids (including sivapiths and today's orangutans) appear to have lived in southern Asia, and the early hominids (*i.e.*, relatives of australopiths, gorillas, chimpanzees and humans, as opposed to pongids) appear to have lived around the Tethys Sea, the ancient Mediterranean Sea, and later in Africa.

In contrast, other models such as Hardy's and Morgan's make no proposal about the lifestyle of apes that were ancestral to the chimpanzee/human split, other than a tacit assumption that they were probably somewhat chimp-like. Hardy's and Morgan's writings assume that the immediate ancestors of the LCA of *Pan* and *Homo* ~ 5 Ma were largely arboreal, quadrupedal when they had occasion to descend to ground level, and included in their locomotor repertoire, no indication of previous aquatic influence, whereas Verhaegen *et al.* argue that they had vertical spines (orthogrady) and not only climbed vertically, but also did a lot of swimming and possibly wading.

Australopithecines (~ 4-1 Ma)

Here, the model differs greatly from most orthodox as well as most other waterside models, which largely assume that australopithecines were ancestral to *Homo.* Verhaegen *et al.* are unconvinced by that view and are open to the idea that australopithecines might be ancestral to *Pan* and/or *Gorilla*. They argue that australopithecines were Plio-Pleistocene (5.33-0.012 Ma) swamp forest and wetland dwelling hominids that partly fed on hard-shelled foods and (like lowland gorillas) on aquatic herbaceous vegetation and wetland grasses such as papyrus reeds, and had a swimming-wading-armhanging locomotion.

Like Hardy and Morgan, they propose that a key factor in the evolution of *Homo* after the split with the chimpanzees (~ 5 Ma) was a reduction in climbing and an increase in a littoral lifestyle through diving and beach-combing along the Indian Ocean, African and Mediterranean coasts, from where different populations followed the rivers inland. Unlike Hardy and Morgan, they propose that the *most-aquatic phase* happened during the Pleistocene, presumably less than 1.8 Ma.

Littoral *Homo* (~ 1.8-0.1 Ma)

The Verhaegen-Puech-Munro model proposes *Homo* palaeo-species, such as *Homo erectus*, as the most aquatic in human evolution. It suggests, like most orthodox theories, that human ancestors by now were losing their arboreality, but differs from them markedly in suggesting that they lived in littoral habitats where diving for food would have been a major component in their locomotor repertoire. In this regard, it also differs from Hardy's, Morgan's, Williams' and other waterside scenarios that assume that, by the time fossils for *Homo* appear in the record, human ancestors had 'returned' to a fully terrestrial lifestyle.

Retroviral DNA evidence [24], suggesting that human ancestors were absent from Africa between 4 and 3 Ma, is offered to support the view that early *Homo* may have inhabited South-Asian seacoasts. Uniquely *Homo* features, such as increasing brain size, protruding nasal bones, a very heavy skeleton (*pachyostosis*) and ear exostoses, are explained as adaptations for shallow diving for shell fish on the now submerged continental shelves, presumably along the Indian ocean.

The Verhaegen-Puech-Munro model differs markedly from orthodox models of human evolution in rejecting arguments of terrestrial locomotor efficiency in *Homo erectus*, or more recently *endurance running*, as an explanation for human bipedalism generally and long-leggedness specifically. Indeed, they propose that a major precondition of human locomotion was a hydrodynamic *linear build* that evolved for efficient swimming and diving. They argue that there is no comparative evidence that wading was a key factor in the evolution of bipedalism. This differs from other waterside models including Morgan's [2-6] and Kuliukas', who believe that wading through shallow water was a key factor in the origin of early human bipedality and that energy efficiency of walking on land was a key factor in its optimization.

After the arrival of *Homo sapiens*, Verhaegen-Puech-Munro's model is largely in accord with orthodox, as well as other waterside, models of human evolution in that they had reduced aquatic components in their locomotor repertoire. However, it argues that early *H. sapiens* would still probably have waded significantly with harpoons, nets, reed boats and/or dugouts at coasts and rivers.

OTHER 'AQUATIC' SCENARIOS OF HUMAN EVOLUTION

The scenarios discussed so far are certainly the most well-known ideas associated with AAH, but there are several others that should be documented too.

Stephen Cunnane (1980, - 2005): *Survival of the Fattest*

Canadian nutritional scientist Stephen Cunnane, was one of the first to be sufficiently impressed by Morgan's work that it influenced his research interests. Having read *The Descent of Woman*, he decided to write a paper on the response of classical evolutionists to Hardy's idea [25].

Cunnane listed Hardy's main points, as well as those added by Morris and Morgan, and ended with a succinct summary: "Its main virtue is that the existence of so many of Man's anatomical and physiological features are put into perspective without any contradictory suggestions concerning his phylogeny. It may be difficult, if not impossible to unequivocally establish the theory, but that is not so much the point; if we are interested in learning more about our evolutionary niche the aquatic theory is a valuable step towards that goal" [25: 57].

Up until this point, Cunnane's ideas are indistinguishable from Hardy's or Morgan's, but after doing a post-doc with Michael Crawford (see below), who was also skeptical about the prevailing savannah hypothesis, the two of them began researching into the importance of omega-3 fatty acids and other nutrients in human brain chemistry and growth. Cunnane's original angle, as described in his most important work so far, *Survival of the fattest* [26], is that human infant adiposity is a key unique human aspect amongst terrestrial mammals, especially primates, and he explains it as 'fuel insurance' for infant brain growth. Where Cunnane deviates from orthodoxy is his claims that the specific nutritional input required to fuel infant

brain growth is most optimally provided from the marine food chain. He provides compelling evidence that most of the micro-nutrients associated with healthy infant brain growth are found in shell fish and fish.

Cunnane's explanation is different, at least in emphasis, from Morgan's, which also suggests that increased buoyancy and thermoregulation in water would also contributed the selective pressure for this trait.

Michael Crawford (1989, -2007): DHA, the Driving Force of Encephalization?

Michael Crawford is a nutritional chemist whose ideas and research interests have much in common with Stephen Cunnane. Crawford was one of the earliest to warn of the dangers from eating too much red meat and the wrong sorts of fat, and was a pioneer in promoting those foods high in the omega-3 fatty acid DHA, as healthier choices. It was this dietary health angle that led Crawford, independently to the same conclusion as did Elaine Morgan, at about the same time, that coastal scenarios were more plausible in explaining the human condition than savannah ones.

Crawford's major work on human evolution, co-written with David Marsh and published in 1989 [27], promotes the view that changes in diet drive are at least as significant for phenotypic change, as changes in habitat and basically argues that the remarkable phenomenon of human encephalization simply could not have occurred if it were not for a significant shift in diet towards foods rich in certain brain-rich nutrients such as DHA and iodine, which are most plentiful in the marine food chain. This area has been the focus of research for Crawford and his collaborators since [*e.g.*, 28-31].

Crawford's view of human evolution, like Cunnane's, appears to be very much along the lines of Hardy's 'a more aquatic phase, followed by a U-turn' model. Where it differs, again, is in a matter of emphasis. Crawford argues that a switch to a coastal diet was as much a factor in our evolution as any selection from wading, swimming or diving.

Derek Ellis (1986, -1995): Wetland Apes

In the late 1980s and early 1990s the Canadian field ecologist, Professor Derek Ellis, wrote a number of papers [32-35] based on his growing interest that early human ancestors may have lived in coastal wetlands. Put simply, his argument was that, on ecological grounds, such habitats would have been ideal places for hominids to have inhabited.

As an ecologist with experience with primates he was already sceptical that humans had evolved on the savannah on the grounds that any hominin newcomers there would have to survive by out-competing the species that were already there, notably the already well-adapted primate immigrants, the aggressive, fast, four-legged baboons, in addition to avoiding being preyed upon by the even better grassland-adapted lions, leopards and hyenas. Ellis decided that in order to survive, the human species would have needed to have already evolved appropriate adaptations to grasslands, in advance of populating them. The only way human ancestors could have done this, he thought, was if they first inhabited a totally new ecosystem, which enabled the evolution of increased brain-power, complex vocalizations and foresight. And he believed the most likely place for this to have happened were coastal wetland and shorelines. These, he argues, have ample and easily available sedentary and sessile foods such as clams and fish. They are also characterized by few dangerous parasites and pests. Ellis got into exploring these issues and decided that a marine wetland phase was appropriate for the evolution of two-leggedness and reduced body hair as well as the cultural pre-adaptations needed for them to take on the savannah competitors and predators. An obvious suitable location for this to have happened, Ellis argues, was the North end of the Rift Valley.

Arguably the fullest account important of Ellis' scenario is found in Roede *et al.* [35] where he proposes a thorough waterside scenario of human evolution. Some of Ellis' key points in favor of a coastal wetland scenario were:

- Despite the fact that the idea originated with a marine biologist, Hardy, there had really been very little discussion so far of marine or coastal ecological factors for a putative 'aquatic ape'.
- An impressive audit of different coastal marine wetlands is given, comparing then on various ecological attributes in terms of their suitability to early humans. Coastal mangrove forests, embayed and reef-back-channelled lagoons, near-shore islands, rocky shore and tide pools, surf beaches, sand dunes including dune slacks, deltas and estuaries were compared by environmental stresses (salinity, temperature and waves), competition severity, predation risk as well as 'adaptation demands' (sleeping, night food periodic low-tide night-food gathering, utilization of complex vocalization, and

potential for tool use). All of these are presented as plausible habitats for an inquisitive omnivorous ape based on cited scientific data. Ellis concluded, for example, that near-shore islands have the lowest predation risk, whereas embayed lagoons have the highest potential for tool use.

- Ellis considered the coastal habitats of the Red Sea, during the dramatic rifting there, around 5 Ma, as potentially habitats for early hominins to have evolved. He notes that the changing habitat there during this time would have provided a wide variety of coastal wetland habitats ideal for providing a range of habitats suitable for human evolution. The timing and location are perfect for this.
- A comprehensive (at the time) audit of wading and swimming locomotion in extant apes and other large primates was provided, suggesting that chimpanzees and (especially) gorillas were perhaps better able to swim than we had been led to believe.
- Ellis goes into some detail analysing the potential behavioral repertoire of putative coastal apes.

Although we label Ellis' scenario *wetland apes* here, he actually referred to it as the "unorthodox descent theory," proposing that humans moved from forest to grassland not directly, but *via* a third, coastal, habitat. Ellis describes his model with a detailed timeline in three phases.

Phase 1. Coastal and Riverine Forest Ape Stock

Phase 1 is proposed to have been "in rift valley and coastal wetlands" up to and around 5 Ma. Ellis proposes that some of this ape stock would have been sufficiently isolated in these coastal habitats for sub-speciation to have occurred. This part of the model is rather closer to Verhaegen *et al.* than to Hardy's or Morgan's in that it proposes some aquatic adaptation even before the *Homo/Pan* split.

Phase 2. An Aquatic Ape

Phase 2 proposes that Red Sea rifting would have provided a variety of coastal wetland habitats (islands, marsh, lagoons, beaches, rocky shores *etc.*) from around 5 Ma that could have led to some of the ape stock sub-species to have become genetically isolated from the more terrestrial forms. This phase, Ellis proposes, would be the most "extreme" in terms of aquatic adaptation resulting in what he calls "a unique primate aquatic ESS" (Evolutionary Stable Strategy) [35]. This phase is very much like Hardy's and Morgan's original idea, albeit with a much more specific proposed palaeo-habitat and ecology.

Phase 3. The Return Inland

Phase 3 follows the U-turn approach and is similarly timed, *before* the genus *Homo*. Ellis offers two means of "extinguishing" the aquatic ape ancestor. Either it was anagenesis – where the aquatic ape gradually evolved into us, effectively making us the aquatic ape ourselves, or that there was an extinction of that clade, perhaps by some catastrophic change like a tsunami, or simply by competition from early human forms.

With the benefit of hindsight Ellis now thinks he undervalued the role that climate changes, interacting with population pressure, would have had on human evolution [36]. However, he remains convinced that humans must have inhabited, and become adapted to, an ecosystem very different from forest and savannah, sometime on our descent from apes and he thinks that the only such different ecosystem which has mammals with adaptive characteristics similar to some of ours (and unique for a primate) is marine wetlands, particularly seawater lagoons and sheltered coasts. The extent of these ecosystems, particularly tidal wetlands, would have been affected by climate changes, as there would have been accompanying sea level changes. Rising sea levels would have extended marine wetlands and sheltered coastlines slowly inshore, where they could have encompassed ape-human groups, which would have had time to adapt to the seawater ecosystems. Then with reversed climate changes, sea level dropping and wetlands drying out, plus population pressure, our by then more active, dextrous, intelligent, vocalising ancestors could survive in the encroaching parkland and eventually savannah.

Marcel Williams (2005): Hominin Palaeogeography and the Island Hypothesis

Marcel Williams, a San Francisco Bay area science writer, is another proponent of more aquatic scenarios of human evolution. He is the managing editor of the Paleoprimatology and Human Evolution forum [37,38]. He first encountered the

aquatic ape hypothesis in 1970 when he read Morris' *The Naked Ape* [20] and became a proponent from 1973 after he encountered Elaine Morgan's *The Descent of Woman* [2]. It was Williams who first coined the term *aquarboreal* to describe a wading-climbing component to the locomotor repertoire, used by Verhaegen *et al.* in the early part of their model.

Williams' early scenario is based on Hürzeler's [39] belief that *Oreopithecus* parallels humans to a degree in their morphology, a view Williams has also held for about a decade, when he made some phylogenetic comparisons of *Oreopithecus* with humans and other hominoids [40].

There are two major phases to the model:

Phase 1. Miocene apes (~ 20-5 Ma)

The first occurred on the island of Tuscany-Sardinia between 9 and 7.3 Ma. The descendants of some African apes became trapped there and became semi-aquatic freshwater folivores, feeding on aquatic plants and freshwater invertebrates in the crocodile infested swamps of the island. This phase ended, Williams suggests, during the Messinian crisis, when what is now Italy became a geographical extension of north Africa and *Oreopithecus* radiated into the African continent and evolved into *Sahelanthropus* and *Ardipithecus*. This part of the model is very similar to that of Verhaegen *et al.*

Phase 2. Island Hominins (~ 5-2.6 Ma)

The second phase started between 5.8 and 5.5 Ma, when global sea levels may have approached 50 meters above the present ones. The marine re-flooding of the Red Sea through the Gulf of Aden and the Bab al-Mandeb Channel also flooded the region of northern Afar. The Danakil Alps were converted into a large peninsula with Red Sea waters surrounding it from the West, North and East. A small geographic area to the North of the Danakil Alps was also flooded, becoming a small island with a geographic area at least 500 km^2 [38].

Williams believes a small population of *Ardipithecus* became isolated on such islands for nearly 3 million years. He thinks this 'more marine' phase forced the dramatic modification of the medullary morphology of the human kidneys [41]. It was in such habitats, Williams suggests, that *Ardipithecus* evolved into *Homo*, and it was there that the Oldowan stool tool culture first evolved to pry open sea shells, scrape out the meat, maybe even slice of the meat of large clams for jerking (solar dehydration for meat preservation). They may have also used these stone tools to make spears for spear fishing. 2.6 Ma is about the time when the first Oldowan tools appear in the archaeological record. The extremely limited terrestrial food resources on the small island could have prompted to the geographically isolated population to intensely exploit coastal marine resources of the Red Sea such as crustaceans, molluscs, fish, turtles, turtle eggs, and dugongs.

Island isolation in hominin evolution could explain the relative loss of genetic variation in humans and the lack of gammaretroviral exposure by humans relative to other African hominoids. And the end of island isolation during the lowering of sea levels after 2.7 Ma could also explain the sudden emergence of the Oldowan culture and the sudden appearance of *Homo* on the African continent after 2.7 Ma.

There is the possibility that other coastal islands in sub-Saharan Africa along the Atlantic or the Indian Ocean could have been the place of origin for *Homo*. However, over a period of approximately ~ 2.6 million years, such ocean islands would have been exposed catastrophic tsunami activity approximately every 190,000 years with tsunami run up heights of 10 meters or higher. For a 2.6 million year period, a population of hominins on such islands would have to endure approximately/about 13 such events. However, hominins located within an inland sea such as the Mediterranean or the Red Sea, would have been protected from such catastrophic oceanic events.

This phase of the model shares the same geographical location as the Hardy/Morgan, in the Afar triangle, but is slightly later in time-scale arguing that the phase occurred after the human split with the chimpanzee.

Phase 3. Homo (~ 2.6-0 Ma)

Williams suggests that when sea levels lowered around 2.6 Ma, *Homo* radiated back into the African continent where it encountered its relatives who had evolved to australopithecines and *Paranthropus*-like robust hominids. and

Homo brought their novel tool using culture with them. *Homo*'s relatively specialized semi aquatic phase ended 2.6 Ma, according to William's model, largely in agreement with the Hardy-Morgan scenario. Any semi-aquatic behavior displayed by *Homo* afterwards was *and is* according to Williams, just a remnant of their 2.7-million-year-long highly specialized semi-aquatic marine phase on Afar Island in East Africa from 5.3 until 2.6 Ma.

Niemitz (2002 – 2009): Amphibische Generalistentheorie

Another scenario in this audit is that by the German anthropologist, Carsten Niemitz. He reached a professorial level in academia (of Human Biology at the Georg-August-University Göttingen) at the remarkably young age of 32. In the 30 years that followed, he has been a prolific worker in various specific aspects of physical anthropology as well as zoology generally. One key paper that he wrote in 2000 was published in *Anthropologischer Anzeiger*, "A theory on the evolution of the habitual orthograde human bipedalism – The 'Amphibische Generalistentheorie'" [42]. It was followed, four years later, by a significant book on the subject of bipedal origins, *Das Geheimnis des aufrechten Gangs – Unsere Evolution verlief anders* (The Secret of the Upright Gait – Our evolution was different) [43], and other papers since [*e.g.*, 44].

Niemitz has distanced himself from being associated with the AAH, but there is no doubt that some of his latest work is very much under the same waterside umbrella.

The *Amphibische Generalistentheorie* (Amphibious Generalists Theory, or Shore Dweller Hypothesis) [42] considers that humans evolved from ancestors that were ecologically non-specialized and opportunistic in their feeding habits or in any specific locomotor habits, as a semi-terrestrial ecological generalist.

Niemitz's scenario is mainly concerned with explaining the evolution of human bipedalism. He uses biomechanical arguments to support this. For example, when wading bipedally, he argues, the hip, and knee joints of an otherwise quadrupedal ape would be relieved in the water from some of the weight bearing stresses that it would otherwise be exposed to on land. If the water is deep enough, this benefit would also include the joints of the lower back too.

The Amphibious Generalists Theory proposes a quadrupedal semi-terrestrial ancestor based on the genus *Proconsul*, which then evolved longer legs as an adaptation to wading. Niemitz is explicit in listing specific advantages that having longer legs would bestow, namely reducing drag whilst moving through water; allowing a better view into the water; increasing ground reaction force by mitigating the effects of buoyancy; and raising the threshold when the more costly and riskier mode of locomotion of swimming is required. [Carsten Niemitz, personal communication].

Niemitz's scenario therefore shares a degree of aquatic adaptation (through bipedal wading) with Hardy-Morgan's, but not with those elements that propose swimming and diving adaptations led to human phenotypic divergence away from the other great apes.

Kuliukas (2002 - 2010): River Apes... and Coastal People

Kuliukas approaches the 'aquatic ape' idea by asking the question: How *much* selection would be required to have caused the phenotypic changes under discussion? It turns out, from Kimura's work [45] on population genetics, that the answer is: "very little indeed." To overcome drift, selection need only be greater than the reciprocal of twice the effective population size:

$s > 1 / (2 N_e)$ s = selection, N_e = effective population size

With this in mind, a biphasic model of human evolution, called "River apes... Coastal people", is proposed.

Miocene Apes

The model does not depend on any particular lifestyle assumption for the LCA of *Gorilla-Pan-Homo* and its immediate ancestors, although Kuliukas favors a wading-climbing model, not unlike Verhaegen *et al.*

River Apes: From the Pan/Homo LCA (~ 5 Ma) to the Genus Homo (2.6 Ma)

The first phase concerns itself with hominids between the LCA of *Pan*/*Homo*, up to the arrival of the genus *Homo*. Like Coppens' *East Side Story* [46], it assumes that climate change caused tropical rainforest habitat to give way to open savannah East of the Rift Valley, but not to the West. Unlike Verhaegen *et al.*'s model, it concurs with others that palaeospecies such as *Australopithecus afarensis* were plausibly human ancestors. Unlike the orthodox savannah hypothesis, however, the River Apes phase does not assume that early hominins became adapted to open plains habitats. Rather, they clung to shrinking gallery forest refugia prone to seasonal flooding and other wetland microhabitats.

Such habitats provide a compulsion to move bipedally during wet seasons, as well as an incentive to do so efficiently during dry periods. Wading reduces the cost differential between human-like bipedal gaits and ape-like ones [47]. It encourages bipedal locomotion in apes more strongly than any other naturally occurring factor. Therefore, as efficient terrestrial bipedal locomotion is also dependent on flat, firm, vegetation free substrates [48, 49], and remembering Kimura's point of slight selection above [45], - it is argued that adding a wading component in the locomotor repertoire of early hominins can help to explain the evolution of human bipedalism. Seasonally and during longer wet-dry cycles, flooded gallery forests could have provided a powerful mix of factors of selection to have push humans up to and beyond a Rubicon where bipedalism became the default mode on dry land as well as in water.

This phase of the model differs from Hardy's and Morgan's in that it does not assume that this happened around the time of the split of humans from chimpanzees. In that sense it is closer to the Verhaegen *et al.* model. It is also closer to it in assuming that climbing, as well as wading, were key components of the locomotor repertoire of early hominids. It differs from both of these more aquatic scenarios in that it does not assume a littoral scenario for bipedal origins, but a riparian one. In that regard it is actually much closer to, and quite compatible with, the orthodox savannah hypothesis. It is in full agreement with those orthodox ideas which stress terrestrial energy efficiency as force to optimize the bipedalism of the genus *Homo*.

Coastal People: From the Genus Homo (2.6 Ma) to the Out of Africa II Diaspora

The second phase of the model concerns itself with the time period after the arrival of the genus *Homo* around 2.6 Ma up to the *Out of Africa II* diaspora, around 130-80 ka. The basic principle behind this idea is simply that rivers flow into the sea or, as in the case of the Rift Valley, into large inland lakes. It is proposed that as the climate became more erratic and increasingly arid during the Pliocene [50], those hominins that found themselves on the lake shores or coasts would have had a key selective advantage because the aquatic food chain is far less vulnerable to seasonal variation. In this sense it agrees with the views of Crawford *et al.*

The *coastal people* phase of the model is very close to Hardy's original idea in that it proposes that swimming and diving for food in coastal shallows was a key driver of human evolution. It differs mainly in thinking that the timescale was much more recent – more recent even, than Verhaegen *et al.*'s. It is proposed that human ancestors reached the 'peak' of their 'more aquatic' adaptation – and even then, not very much – at around the time of the *Homo sapiens* speciation event, ~ 200 ka. It also differs in proposing that long-distant, efficient walking (and even *endurance running*) would have been adaptive in a coastal foraging niche.

Unlike other 'more aquatic' scenarios, it stresses minimal degrees of selection. Computer simulations [unpublished data] show that as little as one drowning per year in a population of 1,000 and only a 1% reduction in the risk of drowning from a given allele would still result in such alleles becoming fixed in the population within a few tens of thousands of years, assuming such alleles were neutral in terrestrial scenarios. Seen in this light, even very modest procurement of food from coastal shallows could still account for all the major phenotypic differences between humans and chimpanzees noted by Hardy and Morgan.

Skeptics are advised to consider the relatively weak levels of selection that undoubtedly have shaped genetic traits of human subpopulations in the last 20-40 ka, such as levels of skin pigmentation in response to balancing selection, for protection from UV light and Vitamin D/Follate production. In comparison, even a slight exposure to such a severe potential mode of selection as drowning would have influenced our phenotype at least as greatly in more than 2 million years.

Others

Many others have written on this subject and contributed to the debate, but their work has not always involved creating a 'scenario' with putative dates and sequences of possible events. The question about timing has tended to focus more on "When did the period of being water-adapted begin?" and rather less on "When did it end?" But Erika Schagatay was interested in the second query, and responded to it by questioning the premise. She pointed out that it has not ended everywhere. Our ancestors' lifestyle is almost invariably described as that of 'hunter-gatherers', so that tribes still leading that kind of existence are held up as living examples. Schagatay travelled the world getting acquainted with the fast-dwindling number of fisher-gatherer tribes, such as the Moken (Sea Gypsy) people of Indonesia, whose way of life is just as ancient, and her subsequent research have thrown light on how much of our ability to operate under water is not lost, but latent. For example, Schagatay and her Swedish colleagues have published several papers [*e.g.*, 51-53] reporting documenting some remarkable diving abilities in humans (see Chapter **7**). A somewhat similar approach is apparent in books by Michel Odent and Jacques Mayol.

Phillip Tobias's contribution to this debate was also important, but not in proposing a particularly aquatic scenario of his own. Perhaps his biggest influence consisted of clearing the ground for new thinking by criticising the old paradigm, and suggesting: "We must go back to Square One." However, Tobias has published a number of papers highlighting the potential rôle that water played in human evolution [*e.g.*, 54,55].

Another contribution to the thinking on aquatic scenarios of human evolution is currently being developed by Renato and Nicole Bender. Unfortunately their work was not ready for inclusion in this chapter at the time of submission.

SUMMARY OF WATERSIDE SCENARIOS OF HUMAN EVOLUTION

For clarity, Table **1** below summarizes six scenarios proposed by various proponents.

Table 1: Different Aquatic Scenarios

Proponents	**Timescale**	**Geographical location**	**Ecological scenario**
Hardy [1]	Between *Proconsul* and *Australopithecus*, ~15-10 Ma	African and Indian Ocean coast	Coastal niche provided food
Morgan [2-6]	Around the time of the *Pan*/*Homo* split, ~6 Ma	Unspecified waterside habitats (sea coasts, lakes, rivers)	Food procurement after inundation
Verhaegen *et al.* [8-11]	Pleistocene *Homo* < 2.5 Ma, especially during Glacials?	African and Indian Ocean coastal shallows including continental shelves now submerged	Littoral diving and beach-combing for shell fish and other sea food
Ellis [32-35]	~5 Ma	Red Sea and East-African coasts	Various coastal wetlands
Williams [40, 41]	10-2.6 Ma	Mediterranean islands, then Danakil and Afar triangle	Coastal food procurement
Kuliukas [47]	River apes: 5-2.6 Ma, Coastal people: 2.6-0.2 Ma	Seasonally flooded riparian habitats east of the Rift, then Indian Ocean coasts	Seasonally flooded gallery forests, then coastal shallows

One of the ways the aquatic ape hypothesis has been misrepresented over the years has been by portraying 'it' as if it were a single idea proposing a single scenario. Here, more than ten such ideas have been reported, and six quite distinct possible aquatic scenarios have been described in some detail and compared.

It can be seen that many of them differ quite markedly in time-scale, geographic location, the mode and degree of 'more aquatic' selection proposed and the type of evidence that is used to support them. It should also be noted,

however, that most of them overlap very closely with one or more of the other scenarios to a greater or lesser extent, and that they all share the underlying belief that aquatic scenarios are largely responsible for explaining why human beings are so remarkably different from our closest cousins, the chimpanzee.

It is proposed that labelling these ideas the aquatic ape hypothesis has not helped the scientific community to take them seriously, and that a new label, and a simple, broad definition might help to clarify these ideas so that, finally, as Hardy hoped 50 years ago, they might be "…discussed and tested against further lines of evidence. Such ideas are useful only if they stimulate fresh inquiries which may bring us nearer the truth" [1].

Waterside hypotheses of human evolution assert that selection from wading, swimming and diving and procurement of food from aquatic habitats have significantly affected the evolution of the lineage leading to *Homo sapiens* as distinct from that leading to *Pan*.

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