LANGDON'S CRITIQUE OF THE AQUATIC APE HYPOTHESIS: NOT THE LAST WORD

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Abstract

A challenge to Langdon's 1997 critique of the Aquatic Ape Hypothesis has still not been published despite the paper appearing to have a number of weaknesses which deserve a response. Langdon's analysis of "anatomical evidence for the AAH" seems to have been directed against an interpreted hypothesis of thoroughly aquatic human ancestors and not towards Alister Hardy's (1960) original hypothesis that humans were merely "more-aquatic in the past". Therefore the critique was often superficial and largely based on false comparisons with truly aquatic mammals. Several of the arguments used to discredit the AAH's claim for greater parsimony were flawed. And criticism of the lack of fossil evidence for an 'aquatic phase' was based largely upon a single proponent's view.

Six years on, significant new evidence has emerged and other AAH-based models have been published which demand that the debate be reopened.

It is argued that the notion that water has acted as some kind of agent of selection throughout human evolution has, in fact, not yet been refuted and deserves more serious consideration than it has hitherto received.

Introduction

"Overall, it will be clear that I do not think it would be correct to designate our early hominid ancestors as 'aquatic'. But at the same time there does seem to be evidence that not only did they take to the water from time to time but that the water (and by this I mean inland lakes and rivers) was a habitat that provided enough extra food to count as an agency for selection." Vernon Reynolds (in Cold and Watery? Hot and Dusty? Our Ancestral Environment and Our Ancestors Themselves: An Overview. In Roede et al 1991 p 340.

That paragraph, taken from the concluding editorial section of the Valkenberg symposium (Roede *et al* 1991), which specifically considered the Aquatic Ape Hypothesis, signals a clear message that the hypothesis, although probably wrong in its extreme (and, perhaps, originally interpreted) form, does deserve consideration in some revised, moderate reconstruction.

That water might have acted as an agent of selection in human evolution has, however, remained more the target of ridicule than research in the field of paleoanthropology. This state of affairs has remained to this day, at least in part, because of the critique of the 'Aquatic Ape Hypothesis' (AAH) by Langdon (1997) which continues to be the only paper to be published in a scientific journal to have considered it, and rejected it.

Langdon (1997:p480) justified writing his critique by arguing "the aquatic ape hypothesis continues to be encountered by puzzled students who wonder why mainstream paleoanthropologists overlook it. If only because of this last audience, it should not be ignored."

Langdon makes a good point. Students and lay people who hear about the theory for the first time tend to be open to it. 'That makes sense' is a common reaction. Indeed, bearing this in mind, the whisperingly negative reaction to the Aquatic Ape Hypothesis from probably the great majority of professional paleoanthropologists is, perhaps, as interesting as the hypothesis itself. It has been the subject of at least two PhD theses to the knowledge of the author and warranted Graham Richards to write a whole chapter on the subject entitled "The Refutation that Never Was: The Reception of the Aquatic Ape Theory, 1972-1987" (Richards 1991) although Langdon makes no mention of this angle on the subject in his critique. Whatever the reasons for the lack of serious attention afforded the AAH by paleoanthropologists in the past, be they some kind of "perceived 'outsidership' of Elaine Morgan", as argued by Richards (1991:p124), or simply bad timing, arguing for the importance of water in 1960 when everyone else was sure it was due to aridity, Langdon was right to address the issue.

The interest by new students in the aquatic ape theory is as real today as it was in 1997. However, a student of human evolution familiar with the literature today might be forgiven for concluding that Langdon's critique was the last word on the subject, its final refutation, considering that no reply has been published since.

It is with that audience in mind that this riposte has been written: The weaknesses in Langdon's paper deserve to be

challenged, pro-AAH arguments not covered should be heard and an altered version of the AAH, modified to reflect Langdon's and others' criticisms, should be aired for public scrutiny. It also aims to respond to a recent, plea from Phillip V. Tobias "to re-examine these claims, much as Langdon (1997) has done" (Tobias 2002:p16). Tobias has been a lone voice in the field of paleoanthropology, in the past few years, calling for his peers to reconsider the role that water has played in human evolution (Tobias 1998a).

The document will mirror the structure of Langdon's original paper, critiquing his arguments but, additionally outlining some AAH-related ideas which were not covered in the paper and suggesting a new redefinition of the hypothesis.

The aquatic ape hypothesis (AAH)… Then

Langdon introduced the hypothesis thus: "The AAH in its present form was first articulated by Alister Hardy in 1960 in an issue of New Scientist magazine featuring the relationship of man and the sea, past present and future." Although the phrase 'in its present form' is probably out of date six years on, it is true that most proponents of some kind of AAH take Hardy's (1960) paper as their starting point. It should be noted however, that the AAH, like any model of human evolution, is under constant revision in response to criticisms and as new evidence emerges. Therefore its *present* form today is not the same as the one Langdon dismissed in 1997. Some of those new forms will be discussed later in this document.

One small but important point about Hardy's original paper, overlooked by Langdon, was its rather modest title: 'Was man *more* aquatic in the past?' (my emphasis). Here lies one of the most common misunderstandings of the hypothesis. On first hearing the term 'aquatic ape hypothesis', reviewers could be forgiven for understanding that this was an hypothesis which *actually postulated that humans evolved from a truly aquatic ape*, in the sense that seals are aquatic mammals, although this is clearly not the case. Hardy (1960), Morgan (1972, 1982, 1990, 1994, 1998), Cunnane (1980), Crawford & Marsh (1989), Verhaegen (1990, 1993, 1994), Knight (1991), Evans (1992), Ellis (1993), Verhaegen *et al.* (2000, 2001), Kuliukas (2002) and other proponents have never made such claims. They have only argued that some human traits may be better explained as adaptations to life by the water's edge than alternative explanations hitherto understood.

The key part to understand in Hardy's title and his thesis, then, is the word 'more'. The meaning of the AAH should merely taken to be the hypothesis that human evolution underwent a phase or phases where our ancestors were merely *more* aquatic than humans are today and also, by implication, more aquatic than our ape cousins' ancestors were, and whose extant survivors are today. Langdon did no justice to the hypothesis by avoiding this complexity and merely defining it's meaning as "having observed a number of anatomical parallels between distinctively human traits and marine animals, he [Hardy] proposed that the human lineage had been shaped evolutionarily by a temporary phase of adaptation to a littoral habitat" (1997:p480).

Later in the paper Langdon (1997:p490) accuses Morgan of making false comparisons in positing the AAH in opposition to "the savannah theory". He states (1997:p490): "The savannah hypothesis that Morgan criticizes turns out to be a straw man", arguing that many in the field "are now discarding the savannah setting for hominid divergence." This may, or may not be correct. Many paleoanthropologists have published work (e.g. Rodman & McHenry 1980, Lovejoy 1981, Wheeler 1984, 1991, 1992, Vrba 1985, Hunt 1994) before Langdon's critique (and many before Morgan's latest books) which are very much based on the model that aridity and a greater adaptation to more open and grassy habitats was a significant driver of hominid evolution. Indeed Tobias is quite open about agreeing with Morgan on this point. He wrote "Until recently, the evolution of early hominids in the savannah has been a strongly held, prevailing hypothesis" (Tobias 2002:p15) and "the competing [with the AAH] hypothesis is no longer tenable since I presented much evidence against it in my Daryll Forde Lecture at University College London in 1995" (Tobias 2002:p16).

It does appear to be the case that since Langdon's critique fewer papers have been published arguing for a savannah setting for hominid evolution than before, but the general assumption still remains that it was the aridification of Africa since the Miocene that was the main contemporaneous ecological change going on and that a general move to more open habitats was the resulting factor that drove the process of hominization. (See, e.g., Leonard 2003.)

However, whether the savannah theory is 'dead' or not, anyone accusing the AAH of using 'straw man' arguments should be very careful not to be found guilty of doing the same thing themselves in trying to discredit it. By emphasising comparisons with fully aquatic marine mammals and avoiding areas of discussion which invoke human ancestors as being merely more exposed to water as an agent of selection than our ape cousins Langdon, and other 'aquaskeptics,' are open to accusations of using the same straw man tactics themselves. The use of such strategies on either side can only act to polarise the debate and not bring us any closer to finding a solution to the problem.

Although Langdon began his paper by referring to Hardy's original [1] paper, almost all of it appraises the work of a single proponent of that theory, Elaine Morgan. Morgan is certainly the most prolific proponent of the hypothesis but she is not the only one. It should also be noted that Langdon's critique was written too late to take into account Morgan's latest, and arguably best, work, 'The Aquatic Ape Hypothesis' (Morgan 1997), which addressed a number of the weaknesses Langdon referred to.

Anatomical evidence for the AAH

About half of Langdon's critique detailed anatomical traits drawn from modern human anatomy which proponents of some kind of AAH have suggested as evidence of a more aquatic past. Twenty-six such traits were paraded and given seemingly equal weighting of importance in his review before being placed into six categories: Primary evidence – possible aquatic adaptations; Parallelisms inadequately explained by the aquatic hypothesis; Traits consistent with the AAH; Primitive traits; Hypothetical reconstructions of past events; and Secondary developments. Langdon (1997:Table 1:p488).

It should be noted that Langdon categorised 4 traits as "possible aquatic adaptations" (voluntary-breath holding, enlarged pharynx, thermoregulatory strategy and absence of salt hunger) and 7 as "consistent with the AAH" (bipedalism, speech, protruding nose, paranasal sinuses, long scalp hair, sebaceous gland distribution, and apocrine gland distribution) (Langdon 1997:p488).

However, throughout the table, and the review generally, Langdon repeatedly makes the same kind of false comparison he accused Morgan of using. His one line rebuttal "not typical of aquatic animals" was used several times, as if the AAH was arguing that human ancestors *had been* truly aquatic.

Bipedalism

Clearly, time and space is a significant constraint in any review but most of the traits listed received a very superficial hearing. The waterside explanation for bipedalism, for example, received merely two paragraphs of discussion (Langdon 1997:p481).

In the first paragraph, Langdon chose to pick out but one piece of reasoning in favour of a wading origin for bipedalism, the one proposed by Morgan (1990: pp24-35) that common human lower-back problems, increased risk of herniation and vascular problems such as fainting and varicose veins associated with bipedalism would have been reduced in water. In the second paragraph this argument was refuted on the grounds that "authors who wish to recite the many disadvantages of bipedalism commonly do so by comparing humans to medium-sized terrestrial quadrupedal mammals" (Langdon 1997:p481). No such authors were cited but it was implied that this was Morgan's reasoning. Morgan, in fact, never made such comparisons and only compared humans to apes. Langdon's argument here is merely to dispute that we had evolved from "medium-sized terrestrial quadrupedal mammals", but other prominent paleoanthropologists (e.g. Rodman & McHenry 1980) do advocate such models.

He then went on to suggest that climbing and suspensory specialisation and the resulting increase use of bipedal posture and gait in Hominoidae is a more likely explanation of bipedal origins. Langdon misrepresents Morgan by arguing (Langdon 1997:p481) that she "wrongly dismisses these specialisations on the grounds that brachiation is irrelevant", when actually, she was merely making the point that, in terms of the associated problems with the lower back, human bipedality was the opposite of brachiation. She wrote "in fact, as far as the spine is concerned, brachiating is at the opposite end of the spectrum from bipedalism. For the ape, the weight of the body and legs tends to stretch the spine and minimise pressure on the disks of cartilage between the vertebrae" Morgan (1990:p27.)

His concluding comment on this, "the climbing/suspensory complex both removes our ancestry from conventional terrestrial quadrupedalism and helps to bridge the gap towards human bipedalism" (Langdon 1997:p481), merely emphasises the brachiationist viewpoint, one of many models, of bipedal origins. As there are at least twelve other such models (see Rose, 1991, for a review) and very little consensus exists in the field about them, Langdon's argument hardly acts as a strong rebuttal to the aquatic argument for bipedal origins.

In 1997 there was very little data in the literature about ape behaviour in water but even from a theoretical point of view it is difficult to conceive of any naturally occurring environment where an ape would be free to move in any direction it chose, but be forced to do so bipedally, other than in waist-deep water.

Since Langdon's paper, several pieces of data have emerged indicating that extant great apes do, indeed, move bipedally in water (Karlowski 1996, Doran & McNeilage 1998, Tutin *et al.* 2001, Parnell 2001, Kuliukas 2002). The wading or wading-climbing hypothesis therefore might appear to be more plausible today than it has ever been and

Langdon's critique of it should not be regarded as having any significant power of rebuttal at all.

Langdon categorised bipedality in his table as 'Traits consistent with the AAH' (Langdon 1997:p488) but dismissed it as "not typical of aquatic animals". This was just one example of a false comparison he made and completely ignored the phylogenetic fact that humans evolved from great apes, which are very typically bipedal in water.

The matter of bipedal origins is clearly a very complex subject and any proposed model would require far more than a couple of paragraphs to even begin to discredit it.

It is not the intention here to line up all of the twenty six traits listed by Langdon again for re-evaluation. Suffice it to suggest that most of them received even more perfunctory consideration than did the case of bipedalism.

Although Langdon chose to give each of them apparently equal weighting and list them out, rather as if to make fun of them, a proponent of the AAH would probably have chosen to emphasise two or three which seem to have most explanatory power. So with that approach in mind, in addition to bipedalism two others will be given specific attention now.

Reduction of Body Hair

'Reduction of body hair' was discussed in just three sentences (Langdon 1997:p483) by arguing that although it can be explained similarly in both terrestrial and aquatic mammals, the aquatic model is not strongly favoured over the terrestrial one. Again, this was hardly an adequate portrayal of one of the most powerful of the AAH arguments, nor was it any kind of serious rebuttal.

Morris' (1967) 'The Naked Ape' made the point very well, when it began: "There are one hundred and ninety-three living species of monkeys and apes. One hundred and ninety-two of them are covered with hair. The exception is a naked ape self-named *Homo sapiens*" (Morris 1967:p5.) This very odd mammalian characteristic deserves a more thorough analysis than Langdon chose to give it.

Of perhaps eleven separate evolutionary events of the loss of pelt in mammals, at least four may be attributable to aquatic factors: Those in Cetacea, Sirenia, Hippopotamidae and at least one species of Pinnipedia. Two might be attributed to large body size: In Elephantidae and Rhinocerotidae. Three may be attributed to subterranean burrowing: The Naked Mole Rat (*Heterocephalus glaber*) and members of Xenarthra (Armadillos) and Pholidota (Pangolins). Leaving just two other instances: Some pigs like the babirusa (Suidae) and *Homo sapiens*. It is likely that climate is a contributing factor too as virtually all terrestrial naked mammals are tropical.

Discounting large size (on the scale of a rhinoceros or above) and a burrowing ancestry as explanations for human nakedness, and ignoring any possibility that pig, elephant (although see Gaeth *et al.* 1999) and rhinoceros (but see Clements & Koch 2000), ancestry may have also been more aquatic in the past, this comparative evidence does suggest that some kind of an aquatic explanation could be the most likely causative factor for nakedness in humans. This view is supported by further evidence that in competitive male swimmers shaving body hair does significantly improve swimming efficiency through drag reduction. (Sharp & Costill 1989).

Alternative explanations have been put forward that were not mentioned by Langdon, for example sexual selection (Darwin 1879) and parasite reduction (e.g. Pagel & Bodmer 2003). However such models do not make a good case as to why only humans out of the primates would have become naked. In that regard, a link to bipedalism has been used to make the distinction. Wheeler (1984) argued that the origin of bipedalism was linked to the origin of human nakedness as an adaptation to improve thermoregulation through evaporative sweat cooling. This would appear logical, except that evidence from the analysis of genes involved in melanocytes now seem to indicate that nakedness arose relatively recently, perhaps as late as 1.2 mya (Harding, Rogers, Iltis, Wooding) and recent fossil findings (Senut *et al.* 2001) imply that bipedalism may have evolved as early as 6 mya, long before nakedness.

Nakedness as an aid to sweat cooling could make some sense, although several mammals, e.g. Equidae, are known to sweat without being naked and others, e.g. Elephantidae, are naked without sweating. But even this, rather tenuous, association is only plausible in the context of a habitat that is proximal to reliable sources of fresh water. In this regard, Langdon's argument (1997:p483) that aquatic explanations for nakedness may not be stronger than terrestrial ones, misses the point. It is at the *juncture* between land and water where sweat cooling makes most sense: There is no contradiction. Indeed the best possible way of rapid cooling, as witnessed by Hippopotamidae, is simply to go for a dip. In this sense, sweat/dip cooling could be justifiably claimed, by proponents of the AAH, to be an aquatic adaptation.

As with the case for bipedalism, the complexity of the arguments for and against a human trait being seen as some kind of aquatic adaptation was given short shrift in Langdon's critique and therefore it can hardly be taken as any valid refutation of the argument.

Subcutaneous fat

Similarly, the unusual amount of subcutaneous fat in humans, especially infant humans, the trait Morgan considers the most powerful piece of evidence in favour of a more aquatic past (personal comment 2000), receives just four sentences of discussion.

Langdon (1997:p483) explains it thus: "The fat-and-sweat strategy of thermoregulation may be adaptive for a species that is more concerned about shedding internally generated heat. Insulative fat, rather than hair, permits the bloodstream to bypass it as needed, taking hot blood from the core of the body to the surface to be radiated or lost through evaporation."

If this were true one would expect the "fat-and-sweat-strategy" to be found in other tropical terrestrial mammals concerned with shedding internally generated heat, when it is not. The notion that animals living in habitats where the shedding of internally generated heat was a priority would evolve mechanisms to do so involving the laying down of heavy layers of energy rich adipose tissue is simply absurd.

As with the argument for hair loss, Langdon's argument does not contradict the water-side explanation at all and does not explain why humans should, unusually, have this requirement more than any other primate. Together with sweat cooling, it is in a water-side habitat where a hominid is likely to gain most from this kind of arrangement. The extra buoyancy that a healthy layer of subcutaneous fat gives to people only adds further advantage to the thermoregulatory benefit Langdon describes.

The specific issue of high human infant fat, which begins to accumulate in the last trimester of pregnancy and accelerates in the last few weeks before birth (Bennet & Brown 1999:p982), and explanations for it such as acting as an energy buffer during the critical period of brain growth, were not mentioned by Langdon, leaving the impression that his rebuttal of this argument too was rather perfunctory and unsatisfactory.

Both the reduced body hair trait and the subcutaneous fat were categorised as 'secondary developments' (Langdon 1997:Table 1:p488), 'secondary to thermoregulatory strategy'. It could be argued that such a 'fat-and-sweat' thermoregulatory strategy works best in water-side habitats and that, therefore, this was not a counter-argument at all but, actually, a vote of support for a modified version of the AAH.

Other Traits

There were twenty-three other human traits listed in the critique.

Some, such as 'Breath-holding and speech', 'Enlarged pharynx', 'Nose', 'Respiratory valves' and 'Paranasal sinuses' could all be grouped under 'respiratory modifications' and the AAH argument for all of them could be summed up as 'adaptations for swimming and diving'.

Langdon's counter-explanations for this group of traits are, on the other hand, quite diverse. For example, the enlarged pharynx is explained by speech (p482), the nose by climate (p482), and "the origin of voluntary control of human breathing is to be found in bipedalism" (p481.)

All of these explanations are not *a priori* impossible but Langdon does not provide any argument as to why the non-AAH explanations are better than those invoking some selection from increased swimming and diving in human ancestry or how several different explanations can be more parsimonious than a single common one.

The other traits listed were 'diving reflex', 'direction of hair follicles', 'sexual dimorphism of scalp hair', 'activity of sebaceous glands', 'paucity of apocrine glands', eccrine sweating', 'absence of "salt hunger"', 'vaginal depth', 'hymen', 'frontal sex', 'loss of oestrus', breasts', 'tears', 'large brains', 'webbed digits', 'neoteny' and 'tool use'.

For each, Langdon used the same technique: Describe the aquatic argument in one or two sentences and then dismiss it just as quickly. Considering that Morgan had written five books on the subject, each usually with a whole chapter dedicated to a cluster of such traits, Langdon's attempted rebuttal could be seen as being rather simplistic. The latest, and arguably the best, of those books (Morgan 1997), as mentioned earlier, was published too late to be included in Langdon's critique. Several of the criticisms Langdon made of arguments in favour of an aquatic explanation for these traits were addressed in this work.

A few were retracted: For instance the claim that "the employment of eccrine glands over the entire body for evaporative cooling is unique to humans" (Langdon 1997:p484) and that it was adaptive to salt excretion was openly withdrawn (Morgan 1997: pp116-117) after the publication of evidence showing eccrine sweat cooling in patas monkey (*Erythrocebus patas*) (Mahoney 1980, Elizondro 1988).

Others were enhanced: The aquatic explanation for the descended larynx was treated with a full chapter (Morgan 1997:pp123-136) and Langdon's claim that Morgan "all but ignores" observations between the relationship between the pharynx and speech can be countered by the fact that Morgan wrote a whole chapter on this too (Morgan 1997: pp137-148).

Overall, the style of Langdon's presentation of the list of traits appears to be almost comical, seemingly designed to leave someone sceptical of the hypothesis shaking their head in disbelief at the diversity of the claims made in support of this idea.

But behind the parody lies a serious point: If hominids had become adapted to a water-side habitat then isn't this exactly what one would predict? That a whole cluster of relatively small human traits would be indicative of a *more* aquatic past?

The list itself, would appear quite arbitrary and down to personal choice. Some might argue, for example, that other traits, such as human eye brows (to keep water from dripping into the eye) and the rotation of the metatarsals (as an adaptation for cupping the hands during swimming) deserved a mention too.

Perhaps a more serious approach would have been to look at the broad generality of the AAH claim: that humans show indications of past adaptation to the waterside which our ape cousins lack. This should, if true, translate into features which result in better locomotion (wading, swimming, diving) through water and a greater physiological dependence on it.

Although apes do wade bipedally rather successfully there is little evidence that they are as strong swimmers or divers as humans. Physically, they are not as buoyant as humans (Angus 1971) and Zoos have traditionally used moats to keep great apes inside their enclosures. Whereas the river Congo has, apparently, been a successful enough barrier preventing chimpanzees and gorillas co-habiting with bonobos in significant numbers for at least two million years (Gagneux *et al.* 2000), far larger bodies of water have not constrained human expansion (Morwood *et al.* 1998.)

Perhaps, then, one of the clearest indications that human ancestors had a more aquatic past than our ape cousins is the marked disparity between the swimming abilities of humans and our nearest cousins. This difference was overlooked in Langdon's critique.

General critique of the evidence

Having categorised the twenty-six traits into the six groupings described earlier, Langdon does go on to make some rather strong counter arguments to the AAH. To begin with he outlines 'two inconsistencies' which undermine the hypothesis.

"The first is the contradictory evidence regarding marine or fresh-water habitat" (p488.) Langdon correctly recognises the discrepancy in arguments that invoke marine habitats, e.g. lack of 'salt hunger' and copious salt loss through sweating and those that invoke fresh water habitats, e.g. human dependence on fresh water and infant intolerance to salt.

Langdon's second problem is regarding "the extent of the specialization for aquatic life experienced by our ancestors." (p489)

He argues that "the greater the hypothesized specialisation, the more improbable the rapid return to land" and that many other traits which might reasonably be expected to be present if had become adapted to an aquatic way of life (such as streamlining of the torso and repositioning of the nostrils) are not present in humans.

These are good counter arguments and require sophisticated responses. As Langdon argues later himself, some explanations may require more work to understand than others and just because an explanation is not simple it does not make it wrong.

A few possible solutions to these objections within the AAH framework will be outlined in the last section of this paper.

Time, place and the fossil record

Langdon states (p489) "whatever difficulties emerge, the AAH is unlikely ever to be disproven on the basis of comparative anatomy. One body of data that potentially can disprove it is the fossil record" and that "the problems of reconciling it [the AAH] to the fossil record have increased over the years."

This view would appear to be based upon the premise that the AAH is arguing for a distinct and real 'aquatic *phase*'

something which both Hardy and Morgan both explicitly did suggest but which, as we shall see shortly, is not actually necessary for the AAH.

Langdon correctly criticises Morgan for claiming that "*Australopithecus* was the ape that returned to the land" (Morgan 1982 p. 116) as this view (that the putative aquatic 'phase' had preceded *Australopithecus*) would imply that all the traits used to support it in humans would also still be present in australopithecines in greater degrees and he makes a good case that this would appear unlikely.

He states (p. 490) "the fossil record might appear less problematic if the evolution of aquatic adaptations were understood to continue through to the early stages of genus *Homo*, at least to 2.0 million years ago" but argues that even then, the association of later hominid fossil sites with "water, on lake shores, streams and river channels, or caves" (p. 490) is probably merely due to taphonomic factors.

So, Langdon does make a good case for dismissing the AAH on the grounds of fossil evidence *if* the AAH is taken as the hypothesis that human ancestors went through a *distinct aquatic phase* before the origin of the genus *Homo*. If, however, one postulated that no such 'phase' occurred but rather that human ancestors merely lived in water-side habitats more than their ape cousins did and that, as a consequence of this relatively mild selection, aquatic-like traits evolved, then Langdon's fossil record objection could be withdrawn.

Moreover, much of the evidence emerging around the time of Langdon's paper and since has added weight to the notion that early hominids did specifically live in wetter habitats. According to Reed (1997:p289) "reconstructed habitats show that Australopithecus species existed in fairly wooded, well-watered regions." WoldeGabriel *et al.* (2001) showed "that these earliest hominids derive from relatively wet and wooded environments." None of the latest fossil findings of *Sahelanthropus tchadensis, Orrorin tugenensis, Kenyanthropus platyops, Ardipithecus ramidus* and *Australopithecus anamensis* contradict this water-side model for early hominids.

As Langdon concedes himself (p490), later *Homo* fossil sites are almost always associated with water. Although this might be due to taphonomic bias and many of these sites have significant faunal assemblages from more open grassland species this hardly amounts to a refutation that water could have acted as an agent of selection in late human evolution. Indeed the rather remarkable absence of a single fossil fragment of either *Pan* or *Gorilla* from the same time period, if anything, adds weight to the argument that the distinguishing factor between hominids and other African great apes may have been their relative exposure to water.

Stringer & McKie (1997) and others have argued that coastal migration routes have played a significant part in the evolution of fully modern *Homo sapiens*, thus clearly placing them in a more aquatic habitat.

Finally, one of the most significant and possibly the earliest (at between 154 and 160 kya) modern *Homo sapiens* finds has recently, unambiguously placed them not only next to water sources but also reliant on aquatic food sources when they noted that "associated faunal remains indicate repeated, systematic butchery of hippopotamus carcasses" (Clark *et al.* 2003:p748).

Langdon's concluding remarks on the fossil record, that "subsequent years have made the fossil record much more complete and less compatible with the aquatic hypothesis" would, therefore, seem out of date and potentially quite misleading.

Umbrella hypotheses and the problem of parsimony

In his final section, Langdon takes a more general line against hypotheses which attempt to explain a whole group of features in one fell swoop.

His first point 'False comparisons' criticises Morgan for holding up the aquatic ape hypothesis against a competing 'savannah hypothesis' which, he argues, is "a straw man" created by her for that purpose. This, again, is not a fair portrayal of her argument. Whether or not other models can truly be referred to as supporting 'the savannah hypothesis', many of the more popular models of human evolution, even today, depend upon an assumption of increased aridity causing a change in habitat from forested to more open woodland (e.g. Rodman & McHenry 1980, Lovejoy 1978, Jolly 1960, Hunt 1994, Wheeler 1984).

Morgan's point is simply that humans are so substantially different from our ape cousins, considering how closely related we are, "that something must have happened to our ancestors which did not happen to the ancestors of the other apes" (Morgan 1997 p 13). She argues that it has been a widely held view for years that a change in habitat, from dense forest to more open woodland with increasingly large patches of grassland was the "something" that was used to explain these differences. Langdon's argument, that it was not savannah but "a woodland or mosaic setting" (Langdon 1997:p490) posits human evolution to have occurred in a habitat so close to that of chimpanzees and gorillas that it is no longer clear how such a divergence in physical traits could have resulted on just our line.

His next point, headed 'Parsimony', attempts to refute the AAH's claim to greater parsimony in explaining a cluster of human traits in one go. He provides four reasons for this:

Firstly, he argues that the AAH explains certain human traits "without predicting them". Specifically, he questioned why "with such diverse examples of seals, otters, manatees, and porpoises before us, one must explain why observed human traits and not others were selected." This demonstrates, once again, that Langdon has misunderstood what the hypothesis is postulating. *More* aquatic does not mean "aquatic". His first section was entitled 'false comparisons' and yet here, in his second, he starts by making a fundamental false comparison himself.

Taking the AAH's basic assumption, that hominid ancestors lived in water-side habitats more than did the ancestors of apes, one could make three broad predictions: That more hominid fossils would be found in riverine/lacustrine /coastal deposits than ape fossils; That humans would be better able to move through water (wade, swim and dive) than apes are and have a set of traits which helped in that regard; And, that humans would be more physiologically dependent on water than apes. Those predictions need testing thoroughly but would appear, at first glance, to hold true.

His second argument is less clear. He appears to argue that because explanations for individual traits are not free from conjecture, then grouping them under an umbrella together with other explanations does not make them more parsimonious. This seems to contradict the definition of the word 'parsimony'. Of course there is a great deal of conjecture about all of the traits but if, for example, all twenty-three Langdon listed could be explained by one single hypothesis – an adaptation to water-side life, then that *must be* a more parsimonious solution than invoking twenty-three separate explanations.

His third point, merely repeats his first: That any hypothesis "should consider not only observed phenomena, but also unobserved possibilities."

Finally, his fourth reason is a logical one: That postulating hominids moved from a terrestrial to a marine habitat and then back again is less parsimonious than "the assumption that a lineage that was terrestrial in the Middle Miocene and terrestrial in the Middle Pliocene was terrestrial in the intervening time." (p 491). He argues that it is the "unnecessary complication of the narrative that has led many anthropologists to reject the hypothesis out of hand."

However, even this objection could be withdrawn if one understood the AAH to posit, not an aquatic phase as such, but as a general, constant pattern of hominids living in water-side habitats more than their ape cousins did. It is an objection, in any case, which Langdon contradicts himself in the next section when he argues that human evolution probably involved a very complex mosaic of steps, far more complex than the Hardy/Morgan putative 'aquatic phase' and subsequent 'return to land'.

In that next section, 'Mosaic evolution revisited', Langdon argues that as the hominid fossil record demonstrates that key traits appear at different times they probably appear for different reasons. Furthermore, as several hominids existed contemporaneously, he suggests that hominid evolution is not one story but many different ones. Langdon argues that is unlikely that all of this (multiple evolutionary steps in multiple evolutionary lineages) is unlikely to be explained by a single factor.

This is almost certainly true. In fact the 'real truth' of human evolution is, in all likelihood, far more complex than we can imagine. It probably involved a mosaic of different stages, some happening in sequence, some in parallel, along different contemporaneous lines, as he suggests. But what Langdon fails to demonstrate at this, or at any, point in his review, is why parts of that mosaic could not have involved periods of evolution where some apes were exposed to water as an agent of selection more than others.

Finally, Langdon completes his refutation of the AAH by drawing analogies with creationism and explanations which include invoking aliens from space. It is, like them, "only one of several ideas rejected by orthodox science that has refused to go away" he writes (p 492).

Langdon provides several properties which the AAH, he argues, has in common with such theories in a section entitled 'The appeal of unorthodox theories'.

First, he suggests, that such theories offer "absolute answers that may not be available from orthodox science." Langdon makes no mention that the title of Hardy's (1960) paper was merely a question and his article ended: "My thesis is, of course, only a speculation – an hypothesis to 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." Nor does this give a fair portrayal of Morgan's work, which very much followed in Hardy's modest footsteps. It can hardly be claimed that Morgan tried to provide absolute answers, merely to question those answers provided by others.

Indeed, the fact that Morgan has modified and retracted various arguments over the years (e.g. Morgan 1997: pp 116-117) indicates that she is one proponent of the AAH who is open to contradictory evidence.

Secondly, Langdon compares the AAH with heterodox ideas which feed on suspicion against the scientific establishment but fails to mention that it's core proponent (Sir Alister Hardy) was a Fellow of the Royal Society: a body that in 1960, at least, was the very elite of the scientific establishment and that another such fellow, Phillip V. Tobias, has recently called for his peers to be more open to the hypothesis. As well the supporting comments published in the 2002 paper cited earlier, he also said in a 1998 documentary interview "I see Elaine Morgan, through her series of superbly written books, presenting a challenge to the scientists to take an interest in this thing, to look at the evidence dispassionately. Not to avert your gaze as though it were something you that you hadn't ought to hear about or hadn't ought to see. And those that are honest with themselves are going to dispassionately examine the evidence. We've got to if we are going to be true to our calling as scientists" (Tobias 1998b).

Langdon's evidence for his claim that the AAH feeds on suspicion against the establishment was merely that Morgan has consistently compared the poor reception of the aquatic ape hypothesis with the early sceptical reception of the continental drift theory of Wegener, a historical fact that no-one would dispute today.

His third property, which sounds very much like his second, was that "there is a special appeal for peripheral segments of the population in rejecting the authority that science and academia represent." The evidence for this claim was that Elaine's first book, written over twenty-five years earlier, "spoke with the passion of embittered and victimised feminism." Many would say "and good for her that she did" because that book was a major, early contribution to the feminist movement which has helped improve the lives of millions of women in the years since. Langdon fails to credit Morgan with the fact that her following books were very carefully written so to not provoke such reactionary criticism.

Fourthly, Langdon suggests that the AAH is popular because it is easily communicated "in simple narrative" to those "not actively engaged in the primary evidence" (p. 493). Putting aside the question of whether the AAH is popular or not (how many school books on the subject of human evolution show pictures of early man as 'man-the-mighty-hunter' on open, grassy plains rather than images of women bathing infants in water?) it is not clear that this argument uniquely applies to the AAH. In the same way, the so-called savannah hypothesis probably became popular in the 1960s because it 'made sense' from the view of man's ancestry prevalent at the time: another umbrella hypothesis. If the AAH does become popular because it explains many human traits through a simple narrative, it should hardly be used as an argument against it.

Fifthly, Langdon compares the AAH's "great emphasis on negative arguments" (p 493) with that of creationism, suggesting that Morgan places "a great deal of weight on the tentativeness of hypotheses in the terrestrial models" (p 493) as creationists do with their perceived insufficiency of evolutionary theory. This is a rather remarkable argument to make considering that most of her work is full of positive ideas, attempting to explain traits that university level texts on human evolution have often avoided completely. To compare the AAH with creationism is particularly facile as the hypothesis has, at it's core, fundamental neo-Darwinist adaptationism, the argument that every human trait must have an adaptive explanation rooted in natural selection.

Langdon's final point, which sounds very much like his fourth, is that "unorthodox models are especially successful when consensus views are not easily communicated to the public" (p. 493). He makes the point by comparing two explanations for human breath control. He argues that explaining that "we can hold our breath because we are adapted for diving" is a simple statement to hear but that "we can hold our breath because respiration is independent of locomotion in a biped" requires more understanding.

This argument is rather simplistic in itself (some quadrupeds, e.g. otters, have excellent breath control, whereas some bipeds, e.g. turkeys, do not) and also a highly selective one. Where the AAH is difficult, for example when coming up with a plausible timescale, then the 'simplicity' of the orthodox interpretation of the fossil record is cited. Where the AAH is simple, perhaps arguing that human bipedality, nakedness, subcutaneous fat and breathing control are all explained by an adaptation to water-side living, then the counter-argument is that it is *too simple.* Then, Langdon encourages us, instead, to "look for complex stories with weak plots" (p 493). In Langdon's view, it seems, the AAH just cannot win. He ends with a charming analogy of proponents of such umbrella hypotheses acting like drunks "looking for lost keys not where they lost them, but where the light is best" (p 493).

Perhaps the greatest weakness of this critique of the AAH, however, was the fact that it all but ignored the findings of the Valkenberg symposium, published six years earlier. Langdon did know about it. He wrote "The AAH was the subject of a published symposium that represented both favourable and opposing views." (Langdon 1997:p480.) But then failed to cite a single comment or piece of data from any of the twenty-two participants.

The four editors of the publication were given the task to summarise the symposium, and to produce some kind of concluding statement on the merits of the AAH. Overall, they decided against the AAH but, as with Langdon, it should be understood what it was they thought were rejecting: They wrote (Roede *et al* 1991:p342) "it is clearly impossible to provide a conclusive answer to the question of whether there was an *aquatic ape*..." [my emphasis]

but that "Our general conclusion is that, while their are a number of arguments favouring the AAT, they are not sufficiently convincing to counteract the arguments against it." They did further suggest that 'it may well be rewarding to reconsider the issue once further evidence - for instance from palaeontology - becomes available.' (Roede et al 1991 p342.)

Of the four editors, it should also be noted, that Jan Wind wrote a piece against the AAH, Machteld Roede herself wrote one in favour and the other two, John Patrick and Vernon Reynolds, wrote papers somewhere in between. It might, then, be enlightening to note the type of arguments used by Patrick and Reynolds as they must have, in the end, come down against the hypothesis.

Patrick wrote in his summary on 'Human Respiratory Adaptations for Swimming and Diving': "No conclusive evidence is available to link the respiratory characteristics of modern Homo with those that might have provided selective advantages to earlier hominids living in an aquatic habitat. However, the ability to control breathing from the cerebral cortex rather than from the brain stem could be regarded as a respiratory adaptation suiting hominids to life in shallow water." (Roede et al 1991 p236.) And Vernon Reynolds' summary of the symposium included the opening paragraph used in this paper arguing, most clearly, that he though there was evidence that water may have acted as an agency of selection in human evolution.

It would appear that Roede *et al*'s (1991) review, like Langdon's critique six years later, was considering the idea that there was actually an 'aquatic ape.' If the AAH is defined more moderately and more in tune with what Hardy originally argued, that water has acted as an agency of selection more in the evolution of humans than it did in the evolution of apes, then it would appear, from the arguments in their papers, that at least three out of four editors were clearly endorsing that view.

But Roede *et al* (1991) is not the work in question here, it is Langdon's. Suffice it to say that by choosing not to draw on that body of work can only make the power of his refutation that much weaker.

It is argued here that whatever view is held on the so-called aquatic ape hypothesis, Langdon's critique falls well short of any kind of valid rebuttal. His use of false comparisons with true aquatic mammals at almost every juncture demonstrates that, like many in the field, he had a gross misunderstanding of what the hypothesis actually is all about. Perhaps the cause of this misunderstanding lies with Hardy and Morgan, perhaps not. But it would appear to be rather clear that if this issue is ever going to be resolved one way or the other, people supportive or critical of the hypothesis should, at least, agree to a basic understanding on what it is they are arguing about. Six years after Langdon's attempt at a rebuttal, perhaps it is time such a working definition was actually published.

The AAH... Now

The AAH as it was perceived by Langdon in 1997 is not the same as it is today. Like any model of human evolution, it evolves in response to criticism and new emerging evidence. Even in 1997, it was wrong to assume that there was only one aquatic model. As Langdon accused Morgan of creating a monolithic straw doll, a caricature that all opponents of the aquatic hypothesis believed in the 'savannah theory', so the same accusation can be made to him in choosing to critique only Morgan's work.

Langdon gave little or no reference to the work of Ellis, Verhaegen, Crawford and others who, even before 1997, had already began to formulate alternative aquatic-based models of human evolution which met several of the objections laid out in his paper.

Ellis' Ecological Argument for a 'Wetland Ape'

In a series of papers published in the late 1980s and early 1990s, Derek Ellis promoted a moderate version of the AAH based on an ecological hypothesis that wetland habitats could have been populated by apes leading to their adaptation to a more aquatic lifestyle (Ellis 1986, 1987, 1991, 1993).

The hypothesis rests on the argument that if hominids moved out from woodland into more open habitats "they were not moving to an environment where there was less, or no competition. The baboon was a highly successful savannah species already well adapted to a grassland environment…" (Ellis 1993:p209). In addition to the baboon there were "also fierce, fast predators on the grasslands, and limited protection from them for a slow biped, especially from the predators that hunted at night" (Ellis 1993:p209).

Ellis argues that if savannah habitats would have been relatively barren and harsh for a hominid newcomer, wetland habitats, by contrast, would have been relatively food rich (especially in the high energy foods postulated for large brain growth) and safe from predators. He writes "some shift away from a diet of foliage would have been imposed on a savannah ape, but on the grasslands animal-food replacements would have been scarce, elusive, and hotly contended for. Baboons have not managed it. The initial incorporation of animal food into the diet would be very

much easier via the tropical marine food chain, where the supply of seafood was plentiful and available all year round, and gathering it called for no skill, incurred little danger, and encountered no serious competition" (Ellis 1993:p212).

The 'aquarboreal' ape model

Unlike Hardy and Morgan, who postulated that apes underwent a definite 'phase' when they were exposed to a water-side habitat, perhaps through being marooned on a island after sudden flooding before returning to a fully terrestrial existence, Verhaegen *et al.* (e.g. 2000) propose a very different scenario.

For the commencement of greater exposure to water, they propose that it actually happenned *before* the *Pan-Homo* split and even before the *Gorilla-Homo* split.

According to their model, all African great apes and *Homo* evolved from a common ancestor that was already a wading-climbing ape. They hypothesise that such apes might have inhabited coastal forests and would have, in particular, have thrived possibly in the coasts along the Tethys / Mediterranean and Red seas in the Mid and/or Late-Miocene epoch.

They argue that "a combination of fossil (including the newly discovered *Orrorin*, *Ardipithecus* and *Kenyanthropus* hominids) and comparative data now provides evidence showing that: (1) the earliest hominids waded and climbed in swampy or coastal forests in Africa–Arabia and fed partly on hard-shelled fruits and molluscs; (2) their australopith descendants in Africa had a comparable locomotion but generally preferred a diet including wetland plants; and (3) the Homo descendants migrated to or remained near the Indian Ocean coasts, lost most climbing abilities, and exploited waterside resources." Verhaegen *et al.* (2002).

The model predicts that *Gorilla* and, somewhat later, *Pan* were off-shoots from this coastal inhabiting swamp ape that migrated inland, up river systems and eventually, as Africa became drier, began to adopt more terrestrial lives and a quadrupedal form of locomotion. *Homo*, meanwhile, stayed on or returned to the coasts but eventually began to inhabit less forested coastal areas. Verhaegen *et al.* predict that from this hominid stock *Homo* populations evolved to become coastal omnivores partly relying on marine food sources as they migrated along the Indian Ocean and Mediterranean coastlines.

Marsh-Crawford Brain Growth Model

Crawford and Marsh (1989) outlined a very wide ranging model for how the evolution of life itself happenned on earth, stressing the importance of food as a driver at every stage and for every form of life, including human evolution. Specifically, they argue that the large human brain has been able to evolve only as a result of a change in diet of human ancestors to those from the marine food chain, which are rich in omega-3 essential fatty acids. These fatty acids are strongly implicated in the development of brain tissue (Broadhurst *et al.* 2002). Crawford and Marsh promote a moderate level of aquaticism in their work, arguing that hominids "most probably evolved at the land-water interface." (Crawford & Marsh 1989 p. 163).

Fresh-water 'River Ape' Model

It is the view of the author that all the existing models of human evolution, whether AAH-based or more orthodox in their leanings, are deficient in some way and that what may be required, is some kind of a hybrid of models based upon the orthodox paradigm, but which combines the best of the original Hardy/Morgan ideas with the strengths of those of Ellis, Crawford and Verhaegen *et al.* whilst simultaneously addressing as many of Langdon's and others' objections to the AAH.

A basic outline of what would be included in this hybrid of models is provided below:

- The most significant event in the early evolution of hominids is their bipedality. As extant African great apes appear to be at their most bipedal in shallow water (Kuliukas 2002) and as arm-hanging or suspensory primates appear to move bipedally when on the ground (see, e.g. Hirasaki 2000) it is argued that some wading-climbing model not unlike that of Verhaegen *et al.* (2000) provides a case for some sort of short-legged, partial bipedalism at least in African hominoids. This argues that the, as yet undetermined, last common ancestor of *Gorilla, Pan* and *Homo* was a rather unspecialised swamp forest (coastal or inland, unspecified) ape that exhibited facultative bipedalism whilst in water but was also a very competent suspensory climber. It is argued that this is a logical precursor to both fully terrestrial bipedalism (in *Homo*) and to quadrupedal knuckle-walking (in *Pan/Gorilla*). This is consistent with the recent early hominid finds of *Sahelanthropus tchadensis* and *Orrorin tugenensis.*
- In the Late Miocene/Early Pliocene, the aridification of Africa, particularly the region east of the rift would have caused the forested habitats to shrink not in a random, patchy way, but rather systematically, closer to sources of water. This next phase of hominid evolution then, is postulated, to have happenned in strips of

riparian forests along extensive rivers and lakes of East Africa as promoted, albeit for a very different model, by Kingdon (2003). Once again, here is an environment where the hominids would be pressurised to move through water more than they had before and more than their cousins which still lived contemporaneously in dense western tropical forests. The model postulates that during this phase hominids increasingly moved bipedally even in shallow water and even on dry land, thus perfecting their bipedality. This phase is consistent with the vast bulk of the hominid fossil record – of early *Australopithecines* through to early *Homo.*

- The next broad phase of this model suggests that, later, some hominids migrated to coastal regions and became more adapted to swimming and diving for food. This might have been through loss of habitat after further aridification or through competition for food. It is argued that this hominid, *Homo erectus* (*sensu lato*) became very successful in exploiting a wide variety of niches and food supplies and accounts for its diaspora across Africa and Eurasia from around 2 mya.
- Finally, the model proposes that a radical novel change in the human genotype caused the speciation of fully modern *Homo sapiens* in East Africa around 250 kya. This change may have been some kind of mutation leading to a gross neural change, as espoused by Richard Klein (1999:p515) or, as favoured by this author, a hybridization event of two hominid groups separated for between 1 and three million years, possibly around the Danakil depression after the inland sea there started to desiccate. Such a reticulation event could account for the change in the number of human chromosomes, from 48 to 46, which would effectively isolate the nascent species genetically from its parental groups and account for some of the rather saltatory changes in our evolution (e.g. rapid brain growth, full syntactic speech and culture). After the speciation, probably in Africa, it is proposed that fully modern *Homo sapiens* was uniquely equipped to expand and ultimately replace all other hominids on the planet, in accord with the Out of Africa replacement model of human evolution (e.g. Stringer & McKie 1997).

Clearly, as Langdon has shown, the AAH as it was originally interpreted (but perhaps not intended) has a number of flaws. However we have seen that even this interpretation is not the only one. Verhaegen *et al.*'s 'aquarboreal' model is a clear, alternative, water-side-based model of human evolution which avoids some of Langdon's criticisms but attracts other new ones. Ellis' ecological arguments for a wetland ape are very strong, and Crawford *et al.* have shown that marine and lakeside food chains may well have been the only ones suitably rich for the large human brain to have evolved.

The study of human evolution is very much subject to interpretation of evidence and open to speculation but the part that water played in that evolution appears to have been overlooked. Tobias (2002:p16) calls "for the heavy, earth-bound view of hominid evolution to be lightened and leavened by a greater emphasis upon the role of water and waterways in hominid development, survival, diversification and dissemination." This paper is an attempt to respond to that plea. It is claimed here that there is actually no significant contradiction between the existing paradigm of human origins and those espousing a greater role for water if one merely emphasises more the importance of fresh water sources such as inland rivers and lakes.

The orthodox view, that the aridification of Africa since the Miocene was the main ecological change going on during human evolution, may actually be correct but perhaps it the assumption of the consequence of that change that needs reconsidering. Rather that a general move to more open habitats, the resulting factor that drove the process of hominization could have been, paradoxically, the adoption of habitats ever closer to reliable sources of water and its rich food supply.

The AAH – A Definition

This document will end as Langdon's, it is argued, should have started: with a clear, unambiguous definition of what the aquatic ape hypothesis actually is. The working definition below is taken as the lowest common denominator of all the aquatic models discussed here and, it is proposed, should be used in all future assessments of the plausibility of the model.

The aquatic ape hypothesis (AAH): *The hypothesis that water has acted as an agent of selection in the evolution of humans more than it has in the evolution of our ape cousins and that, as a result, many of the major physical differences between humans and the other apes may be explained, at least in part, as adaptations to moving (wading, swimming and/or diving) better through various aquatic media.*

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[1] Although Hardy's 1960 article in New Scientist is the most widely attributed original AAH source and is certainly the first reference to it in an English language scientific journal, the first published work which irrefutably makes a claim that human ancestry was greatly influenced by water was that of Max Westenhöffer (1942) – *Der eigenweg des menschen*.