

Langdon's Critique of the Aquatic Ape Hypothesis: It's Final Refutation, or Just Another Misunderstanding?

Algis V. Kuliukas*

Centre for Forensic Science, University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia

Abstract: Thus far, there has been no challenge to Langdon's 1997 critique [1] of the aquatic ape hypothesis (AAH), despite its having a number of weaknesses. The paper lacks scholarly quality as it does not draw upon the one published scientific investigation into the plausibility of the AAH in the literature, *i.e.*, that by Roede *et al.* [2]. Langdon's summary of "anatomical evidence for the AAH" seems to have been directed against an exaggerated interpretation of Alister Hardy's hypothesis that humans were "more aquatic in the past" [3]. Most of the critique was based on cursory and superficial comparisons with fully aquatic mammals, such as cetaceans, rather than considering whether human ancestors could have been more aquatic than those of apes. Even on this basis, Langdon considered eleven out of twenty-six traits to be "possible aquatic adaptations" or "consistent with the AAH".

It is argued here that none of the specific hypotheses of the AAH have yet been refuted. Instead, what appears to have happened, is that individuals have been left to interpret certain ambiguities in arguments put forward by proponents of the hypothesis in their own way and then reject, or accept it on that basis. More than a decade later, significant new evidence has emerged, and other AAH-based models have been published, which demand serious reconsideration.

Keywords: Langdon, AAH critique, rejection, parsimony.

INTRODUCTION

In 1991, Vernon Reynolds stated: "Overall, it will be clear that I do not think it would be correct to designate our early hominid 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." [4].

That paragraph, taken from Reynolds' concluding editorial section of the Valkenberg symposium [4], which specifically considered the so-called *aquatic ape hypothesis* (AAH), signals that the author believed that the hypothesis, although probably wrong in its extreme (and, perhaps, most commonly interpreted) form, deserved consideration in some revised, moderate reconstruction. The idea that moving through water for food might have acted as an agent of selection in human evolution has, however, remained more the target of ridicule than of research in the field of palaeo-anthropology. This state of affairs has remained to this day, possibly in part because of the critique of the AAH by Langdon [1], the only paper published in a palaeo-anthropological journal that considered, and rejected it.

Langdon justified his critique by arguing that "the aquatic ape hypothesis continues to be encountered by puzzled students who wonder why mainstream palaeo-anthropologists overlook it [1]. If only because of this last audience, it should not be ignored." Langdon makes a good point. In my experience, students and lay people who hear about the AAH for the first time tend to be open to it: "That makes sense" is a common reaction. Indeed, the negative reaction to the AAH from the field of palaeo-anthropology might be seen as interesting as the hypothesis itself, and has been the subject of a number of scholarly articles in the literature [*e.g.*, 5].

Whatever the reasons for the lack of serious attention afforded to the AAH by palaeo-anthropologists in the past, be they some kind of "perceived 'outsidership' of Elaine Morgan" [5], or be it simply bad timing, arguing for the importance of water in 1960 when the general consensus was more focused on aridity, Langdon was right to address the issue.

*Address correspondence to Algis V. Kuliukas: Centre for Forensic Science, University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia; E-mail: algis.kuliukas@uwa.edu.au

The interest by new students and the interested lay public in the AAH appears to be as real today as it was in 1997: It has remained by far the most popular topic of discussion on internet newsgroups about palaeo-anthropology for years (*e.g.*, science.anthropology.paleo). However, a student of human evolution, familiar with the literature today, might be forgiven for concluding that Langdon's critique was the final refutation of AAH, as no reply has been published since. This might also explain why so few prospective Ph.D. students have chosen AAH-related subject areas in which to conduct their research, or why most students have probably been persuaded not to waste their time looking into it.

With that audience in mind, this counter-critique has been written. Weaknesses in Langdon's paper deserve to be challenged, pro-AAH arguments not covered should be heard, and alternative interpretations of the AAH not considered by Langdon's critique should be aired for scientific 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" [6]. Tobias has been one of the few palaeo-anthropologists in the past few years, calling for his peers to reconsider the rôle that water has played in human evolution [7].

This chapter mirrors the structure of Langdon's original publication. It critiques his arguments, and outlines additional AAH-related ideas.

LANGDON'S INTERPRETATION OF THE AQUATIC APE HYPOTHESIS (AAH)

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" [1]. Most AAH-proponents probably take Hardy's paper [3] 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 is gathered. Therefore, its present form today is not the same as the one Langdon dismissed in 1997. There are now several AAH variants, differing in their proposed timescales, aquatic habits and habitats (see Chapter 6), and human traits suggested as evidence. It should also be noted that Hardy's ideas are not the only (or indeed the first) to be articulated in the literature (see Chapter 6).

Most importantly perhaps, Langdon overlooked Hardy's rather modest title: "*Was Man more aquatic in the past?*" (my emphasis). This, in my opinion, is the most common misunderstanding of the hypothesis. On first hearing the term 'aquatic ape', reviewers could be forgiven for understanding that the hypothesis postulates that humans evolved from a truly aquatic ape, in the sense that whales and sea cows are aquatic mammals. A series of publications [8-30] never made such an extreme claim.

At most, some of them have argued that a move into more littoral habitats shaped a distinct phase of human evolution, in a similar way to that which, it is postulated, must have happened in the earliest stages of the evolution of Cetacea, Sirenia and Pinnipedia. Almost every mammalian order contains at least one or two genera or species that appear to have taken advantage of, at some time in their evolution, more aquatic habitats, and human traits such as nakedness and increased subcutaneous fat, which seem to be rather unique in the primates, have analogues in more aquatic mammals [*e.g.*, 2, 10].

Both Hardy and Morgan apparently were not arguing for anything more than a semi-aquatic or littoral stage in human evolution. For example, Hardy wrote: "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" [2]. And Morgan: "At the highest point of their period of aquatic adaptation the ancestral hominids, though never as fully marine as the dolphins or sirenians, would probably have been capable of crossing wide stretches of water under their own steam; and without postulating that at such an early stage of their evolution they became boat builders, it is highly possible that they would have been aware of some of the uses of a floating log." [9]. It would appear that it was exactly how these ideas were personally interpreted that determined how well they were received. If one interpreted them as meaning that humans went through some kind of 'primate seal' or 'merman' phase, they were rejected. If one interpreted them as merely arguing that ancestors of ours included more aquatic foods in their diet and/or did more swimming and diving than we (or our ape cousins) do today, it was difficult to see what the fuss was all about.

Although Langdon began his paper by referring to Hardy's original paper, ignoring the earlier work of Max Westenhöfer [31], almost all of it subsequently appraises the work of a single proponent of the AAH, Elaine

Morgan. Morgan is certainly the most prolific proponent, but she is not the only one. Unfortunately, Langdon's critique was published in the same year as Morgan's *The aquatic ape hypothesis* [13], and could not take into account the answers to a number of weaknesses pointed out by Langdon, but already addressed by Morgan in *The aquatic ape hypothesis*.

ANATOMICAL EVIDENCE FOR THE AAH

About half of Langdon's critique discussed modern human anatomical traits which AAH proponents have suggested as evidence of a more aquatic past. Twenty-six such traits were paraded, as if for ridicule, and most were dismissed after a very cursory treatment. No attempt was made to emphasize the more important of these traits, an approach very much at odds with Morgan's, who, for example, wrote six chapters on just three of them in *The aquatic ape hypothesis* [13].

Langdon placed the traits into six categories [1]:

1. Primary evidence - possible aquatic adaptations
2. Parallelisms inadequately explained by the aquatic hypothesis
3. Traits consistent with the AAH
4. Primitive traits
5. Hypothetical reconstructions of past events
6. Secondary developments.

Even Langdon [1] categorized four traits as "possible aquatic adaptations" (voluntary-breath holding, enlarged pharynx, thermoregulatory strategy, and absence of salt hunger) and seven as "consistent with the AAH" (bipedalism, speech, protruding nose, paranasal sinuses, long scalp hair, sebaceous gland distribution and apocrine gland distribution). However, throughout the table, and the review generally, he repeatedly appears to be critiquing an extreme interpretation of the hypothesis. His one-line rebuttal "not typical of aquatic animals" was used several times, as if the AAH was arguing that human ancestors had been aquatic.

Bipedalism

In the first paragraph, Langdon discussed just one of Morgan's many arguments for a wading origin for bipedalism, *i.e.*, that medical disorders associated with bipedalism, such as increased risk of lumbar disk herniations, and vascular problems such as fainting and varicose veins, would have been reduced in water [11]. 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" [1]. No such authors were cited, but it was implied that this was Morgan's reasoning. Morgan, in fact, only compared humans to apes. Even if one assumes that she meant a medium-sized terrestrial, knuckle-walking ancestor, this is not a remarkable position to hold as many prominent palaeo-anthropologists [28] also advocated such models at the time.

Langdon then went on to suggest that climbing and suspensory specialization and the resulting increased use of bipedal posture and gait in hominids is a more likely explanation of bipedal origins. He misrepresents Morgan by arguing that she "wrongly dismisses these specializations on the grounds that brachiation is irrelevant" [1], when she only said that "as far as the spine is concerned, brachiating is at the opposite end of the spectrum to bipedalism. For the ape, the weight of the body and legs tends to stretch the spine and minimize pressure on the disks of cartilage between the vertebrae." [11].

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" [1]) merely backs the brachiationist model of bipedal origins, which is only one of many. As there are more than twelve other such models [33], arguably as many as thirty (see Chapters 3 and 6), and very little consensus exists in the field about them, Langdon's argument hardly acts as a rebuttal to the aquatic argument for bipedal origins. Indeed, he even categorized bipedality in his table as "Traits consistent with the AAH".

It is not the intention here to line up all of the twenty-six traits listed by Langdon for re-evaluation. Suffice it to suggest that most of them received an even more perfunctory consideration than did the case of bipedalism. Two other important ones will be addressed, however, as a further illustration of Langdon's method.

Reduction of Body Hair

Reduction of body hair is discussed in three sentences [1] by arguing that, although it can be explained similarly in both terrestrial and aquatic mammals, the aquatic model is not strongly favored over the terrestrial one. Again, this is hardly an adequate portrayal of an important pro-AAH argument, nor is it any kind of serious rebuttal.

Morris' *The naked ape* [34] 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*" [34]. This very odd mammalian and, even more so, primate characteristic deserves a more thorough analysis than Langdon chose to give it.

Of perhaps eleven separate evolutionary events of the loss of hair in mammals, at least four may be attributable to aquatic factors, *i.e.*, those in Cetacea, Sirenia, Hippopotamidae, and a few Pinnipedia (most male walruses and elephant seals). Two might possibly/arguably be attributed to very large and stocky body build: in Elephantidae and Rhinocerotidae (but not *Giraffa*). Three may be attributed to subterranean burrowing: the naked mole rat (*Heterocephalus glaber*) and perhaps members of Xenarthra (Armadillos) and Pholidota (Pangolins). Other instances are many newborn mammals in the nest or pouch, the naked bat (*Cheiromeles torquatus*), some naked domesticated races of dogs and pigs, the babirusa (Suidae), and *Homo sapiens*. Clearly, climate is a contributing factor as all non fully aquatic/terrestrial naked mammals are tropical.

Discounting very large size and a burrowing ancestry as explanations for human nakedness, and ignoring that suids (although babirusas are semi-aquatic), elephants and rhinoceroses may have also been more aquatic in the past [35], this comparative evidence does suggest that some kind of an aquatic explanation could be an important factor for nakedness in humans. This view is supported by further evidence that in competitive swimmers shaving body hair does measurably improve swimming efficiency and/or speed through drag reduction [36, 37] or through undetermined means [38].

Alternative explanations, not mentioned by Langdon, are:

1. The *parasite reduction* hypothesis [39]. Although it covers both males and females, it fails to adequately explain why only humans out of all the primates, and indeed almost all mammals, have adopted this strategy.
2. The *sexual selection* hypothesis [40]. Richard Dawkins suggests: "Sexual selection produces quirky, whimsical evolution that runs away in apparently arbitrary directions, feeding on itself to produce wild flights of evolutionary fancy." [41]. But, as Dawkins notes, sexual selection is also usually associated with increased sexual dimorphism, so the appearance of body nakedness in *both* sexes is difficult to explain by sexual selection. In some (*e.g.*, European) human groups there is a clear disparity between male and female body hair, but it does not appear to be a particularly strong universal human characteristic. Most men have little more body hair than most women. It should also be noted that fetuses of chimpanzee, and probably also of other great apes, at about seven months become naked *in utero*, except for the scalp, and after birth regrow body hairs, though no underfur [42, 43].

Wheeler [44 - 46] 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 does not make sense for several reasons. Evidence from the analysis of genes involved in melanocytes now seem to indicate that nakedness arose relatively recently, perhaps as late as 1.2 million years ago (Ma) [47], and some recent fossil findings [48] are thought to imply that bipedalism may have evolved as early as 6 Ma, possibly long before nakedness.

Nakedness as an aid to sweat cooling, could possibly make some sense, although several mammals, *e.g.*, Equidae and Camelidae, are known to sweat (although to a much lesser degree than humans) without being naked, and others, *e.g.*, Elephantidae, are naked without sweating. In any case, sweating is only plausible in the context of a habitat where there is ready access to (sources of) water. Notable thermo-actively sweating mammals are fur seals. When on land, they sweat abundantly through (eccrine and apocrine) skin glands on their naked hind-flippers when overheated [49-51].

Langdon's argument that aquatic explanations for nakedness may not be stronger than terrestrial ones [1], misses the point. It is at the *junction* between land and water where sweat cooling makes most sense, and therefore there is no contradiction with a waterside scenario. Indeed, the best possible way of rapid cooling, as witnessed by Hippopotamidae, is simply to go for a dip. In this sense, 'dip-sweat' cooling, where temporary immersion in water is used as a thermoregulatory behavior, could be justifiably claimed, by AAH-proponents, to be an aquatic adaptation.

As with the case for bipedalism, the complexity of the arguments for and against human nakedness 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

The unusual amount of subcutaneous fat in humans, especially infant humans, the trait Morgan considers possibly the most important pro-AAH argument [Morgan, personal comment 2000], receives four sentences of discussion. Langdon writes: "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." [1]. If this were correct, 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 clearly not. It would be an energetically very expensive method for any mammal, especially ones living in drier, more open habitats.

Langdon does not contradict the waterside explanation here, and does not explain why humans should, unusually, have more subcutaneous fat than any other primate. Together with sweat cooling, it is in a waterside habitat where a mammal is likely to gain most from this kind of arrangement. The specific issue of high amounts of human infant subcutaneous fat, which accumulate in the last trimester of pregnancy, accelerating in the last few weeks before birth [52], and explanations for it, such as acting as an energy buffer during the critical period of brain growth [*e.g.*, 53], were not mentioned by Langdon, leaving the impression that his rebuttal of this argument too was rather perfunctory and unsatisfactory.

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 quite diverse. For example, the enlarged pharynx is explained by speech, the nose and paranasal sinuses by climate, and "the origin of voluntary control of human breathing is to be found in bipedalism." [1]. These 'explanations' are unique to humans and therefore unlikely and Langdon fails to provide any argument as to why the non-AAH explanations would be 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, increased vaginal depth, presence of hymen, frontal sex, loss of oestrus, female breasts, tears, large brains, webbed digits, neoteny, and tool use.

For each, Langdon used the same technique: Briefly describe the aquatic argument in one or two sentences, and then dismiss it just as quickly. Taking into consideration 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 looks rather simplistic. As noted above, several of Langdon's criticisms of 'aquatic' explanations for these traits were already addressed by Morgan [13], but published too late to be included in Langdon's critique. For example, Morgan [13] openly withdrew her claim that "the employment of eccrine glands over the entire body for evaporative cooling is unique to humans" after the publication of evidence showing eccrine sweat cooling in patas monkeys (*Erythrocebus patas*) [54, 55].

Other arguments were enhanced by Morgan. She devoted a complete chapter to explain the descended larynx [13] and Langdon's claim that she "all but ignores" observations on the relationship between the pharynx and speech is countered by the fact that she wrote a whole chapter on this as well [13].

Overall, Langdon's presentation of the list of traits may leave sceptics 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 human ancestors had become adapted to a waterside 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? It should also be remembered that even Langdon considered eleven out of the twenty-six traits, and in fact the most important eleven from an AAH proponent's point of view, either "possible aquatic adaptations" or "consistent with the AAH." [1].

There is little evidence that apes are as strong swimmers or divers as humans. Physically, they have almost no subcutaneous fat and are less buoyant than humans [56]. Zoos have traditionally used moats to keep great apes inside their enclosures. Although the river Congo has been sufficient to separate common chimpanzees and gorillas from bonobos for at least two million years [57], far larger bodies of water have not constrained human expansion [58]. To my knowledge, there is only one piece of anecdotal evidence in the literature of a single male chimpanzee reportedly swimming at Conkouati, Republic of Congo, for a few meters [59], whereas there are many such reports of chimpanzees being very reluctant to move into water and even drowning as a result of doing so [e.g., 56].

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 chimpanzees. Indeed, it is difficult to imagine any other comparison of the relative abilities of two species, where such a clear-cut differential in ability would not automatically lead a biologist to the conclusion that the discrepancy was explained by natural selection. This difference was, however, overlooked in Langdon's critique.

GENERAL CRITIQUE OF THE EVIDENCE

Having categorized the twenty-six traits into the six groupings described earlier, Langdon does go on to make some other counter-arguments to the AAH. To begin with, he outlines "two inconsistencies", which in his opinion undermine the hypothesis:

1. "The first is the contradictory evidence regarding marine or fresh-water habitat" [1]. Langdon correctly recognizes 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). Since there are arguments for both milieus, human ancestors might have lived simultaneously (e.g., migrating up rivers seasonally, dwelling in brackish waters, e.g., river deltas) or subsequently in both milieus (e.g., first evolving in coastal milieus, later near fresh water). This question is not yet solved, but is no real argument against a waterside past.
2. Langdon's second 'problem' is in regard to "the extent of the specialization for aquatic life experienced by our ancestors." [1]. He argues: "The greater the hypothesized specialization, the more improbable the rapid return to land." Many other traits that are expected to be present if human ancestors became adapted to an aquatic way of life, such as streamlining of the torso and repositioning of the nostrils, are not immediately obvious in humans. But this assumes that the AAH is proposing a singular, distinct aquatic 'phase' followed by the 'return to the land'. If one simply suggests, instead, that our ancestors lived in waterside habitats more than apes, or that our ancestors were subject to a larger number of 'more aquatic' pieces in a mosaic of evolutionary steps than were the apes, this objection of Langdon disappears.

Time, Place and the Fossil Record

Langdon states: "Whatever difficulties emerge, the AAH is unlikely ever to be disproved 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" [1]. This view is clearly incorrect: Over the years, evidence is accumulating of coastal, deltaic, lake- and riverside finds, as well as of consumption of shell fish, fish and aquatic mammals (see Chapter 5).

Langdon correctly criticizes Morgan [10] for claiming that "*Australopithecus* was the ape that returned to the land". This view would imply that all the traits used to support AAH should be present in australopithecines, in greater degrees than in humans. Langdon concludes that: "the fossil record might appear less problematic if the evolution of

aquatic adaptations were understood to continue through to the early stages of the genus *Homo*, at least to 2.0 Ma.” But he argues that, even then, the association of later *Homo* fossil sites with “water, on lake shores, streams and river channels, or caves” is probably merely due to taphonomic factors [1].

The taphonomy argument is often used to contradict assertions that the fossil record, if anything, promotes the view that human evolution was influenced by water more than apes. After all, thousands of individual fossils of human relatives have been found in depositional substrates, but very few [60] are currently specifically attributed to chimp or gorilla relatives. But even this argument might be special pleading. Let us consider just two examples. The palaeo-ecology of the Hadar site, where ‘Lucy’ AL 288-1 was discovered, was dominated by lakes, streams and swamp wetlands for some 1.4 million years [61]. Similarly, the palaeo-ecology of the site of the ‘Nariokotome Boy’ KNM-WT 15000 appears to have been a floodplain wetland habitat that was up to 60 km wide [62, 63].

If we ignore those factors, or assume that the AAH was proposing a purely coastal habitat, then it could be argued that 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 *singular and distinct aquatic phase* before the origin of the genus *Homo*. However, this objection can easily be met with a simple substitution of the model’s assumed singular, more aquatic ‘phase’ with a generally waterside habitat and/or a greater number of ‘more aquatic’ pieces in a mosaic of evolutionary steps in human evolution than the apes.

Moreover, much of the evidence emerging since the time of Langdon’s paper has added weight to the notion that many early hominins (and some hominids that are not unequivocally placed as ancestral to *Homo*) did actually specifically live in wetter habitats than we might have assumed. According to Reed “reconstructed habitats show that *Australopithecus* species existed in fairly wooded, well-watered regions.” [64]. WoldeGabriel *et al.* [64] showed “that these earliest hominids derive from relatively wet and wooded environments.” None of the latest fossil findings of *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus ramidus* or *Australopithecus anamensis* contradict this waterside model for early hominids. Indeed, the Toros-Menalla site, where *S. tchadensis* was found, was actually inside the maximum extent of the Holocene mega-Lake Chad and contained a high percentage of (semi-) aquatic fauna [65], *e.g.*, bird fauna, such as herons, aningas and swans [66]. As Langdon concedes, later *Homo* fossil sites are almost always associated with water [1]. 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 of a waterside human past. Fossil sites of gallery forest habitats, prone as they are to both flooding and desiccation, are likely to be comprised of faunal mixtures of aquatic, arboreal and open grassland species. Such mixtures do appear to be typical of hominin site assemblages [*e.g.*, 66-68]. The presence of equid fossils at such sites is no more indicative of a predisposition to life on the open plains, as the presence of a crocodylian is to life in the water.

Stringer and McKie [69] and other proponents of a recent Out of Africa exodus have argued that coastal migration routes have played a significant part in the evolution of fully modern *Homo sapiens*, thus placing them in a more aquatic habitat than those typically associated with the great apes. That those people relied on coastal foraging is evidenced by unequivocal evidence of shell middens [*e.g.*, 70, 71]. Finally, one of the most significant and possibly the earliest (at between 154 and 160 thousands of years ago) 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” [72].

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” are, therefore, out of date, misleading and wrong.

UMBRELLA HYPOTHESES AND THE PROBLEM OF PARSIMONY

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

Langdon’s first point, *i.e.*, ‘False comparisons’, criticizes Morgan for holding up the aquatic ape hypothesis against a competing *savannah hypothesis*, which, he claims, is “a straw man”, created by her for that purpose, arguing that many in the field “are now discarding the savannah setting for hominid divergence” [1]. Yet many palaeo-

anthropological papers [e.g., 28, 44-46, 73-75], before Langdon's critique, and before Morgan's latest books, are based on the model that more open arid habitats were a significant driver of hominin evolution. Tobias openly agrees here with Morgan: "Until recently, the evolution of early hominids in the savannah has been a strongly held, prevailing hypothesis" [4] and "the competing (with the AAH) is no longer tenable since I presented much evidence against it in my Daryll Forde Lecture at University College London in 1995." [4] (See also Chapter 1).

Even though fewer explicitly pro-savannah papers are published recently, it is still often tacitly assumed that the gradual aridification of Africa since the Miocene (23-5 Ma) was the main ecological factor towards hominization [e.g., 76-79]. Most texts on human evolution still allude to "more open habitats" (if not to "savannah" directly) as a major factor in human evolution. As Morgan put it: "It has been repeatedly asserted that there was never such a thing as the 'savannah theory', that it was simply a straw man constructed by Elaine Morgan for the pleasure of knocking it down again, and that no reputable scientist can be shown ever to have used the phrase 'savannah theory'. The last part of that statement is true. I would no more have expected them to use that phrase than I would expect a Creationist to refer to 'the God theory' – their faith in it was too strong for that." [13].

Morgan's point about the savannah hypothesis is simply that humans are so substantially different from apes, 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" [13] and that the savannah therefore at least offers a radical enough change in habitat to potentially explain those differences. Langdon's counter-argument, that it was not savannah but "a woodland or mosaic setting" [1], posits human evolution to have occurred in a habitat so similar to that of extant chimpanzees, gorillas or baboons that it is no longer clear how such a divergence in physical traits could have resulted from very similar environments.

However, whether the savannah hypothesis is *dead* or not, anyone accusing the AAH of using 'straw man' arguments should be careful not to do the same thing in trying to discredit it by making comparisons between humans and marine mammals. By doing so, Langdon and other aquaskeptics use straw man tactics themselves. The use of such strategies on either side can only result in further polarization of the debate.

Langdon's next point, the problem of parsimony, *i.e.*, use of the simplest or most frugal route of explanation available, gives four arguments trying to refute the AAH's claim to greater parsimony in explaining a cluster of different human traits in one go:

1. 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 point was actually almost the same as his third that we "should consider not only observed phenomena, but also unobserved possibilities.") This point demonstrates, once again, that Langdon is taking 'aquatic' in a black-white meaning, rather than considering Hardy's original "*more aquatic*" sense.
2. His first section was entitled 'false comparisons' and yet here, in his second, he starts by making a fundamental false comparison himself. Answering that criticism, and taking the AAH's basic assumption that Man was more aquatic in the past, one could make several broad predictions: 1) hominin fossils should be found more frequently in riverine/lacustrine/deltaic/coastal deposits than ape fossils, 2) humans should be better able to move through water (wade, swim and dive) than apes and should have a set of traits that help in that regard, 3) humans should be physiologically more dependent on water than apes, and 4) our ancestors should have procured from the aquatic food chain. Those predictions need testing thoroughly, but would appear, at first glance, to hold true, see *e.g.*, Chapter 2 (aquatic food), Chapter 5 Table 5 (near-water fossil deposits), Chapter 7 (human diving abilities), and Chapters 10 and 11 (human underwater vision).
3. His next 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 each and every trait, but if, for example, all twenty-six characters listed by Langdon could be explained by one single hypothesis – an adaptation to waterside life, then that *must be* a more parsimonious solution than invoking twenty-six separate explanations.

4. His last argument is that postulating that human ancestors 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.” [1]. 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 Langdon's “lack of parsimony” objection could be withdrawn if one understood the AAH to posit a waterside past, rather than a diversion to an aquatic phase and back again. 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 it is unlikely that all of this (multiple evolutionary steps in multiple evolutionary lineages) can 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 possibly imagine. It probably involved a bewildering mosaic of different stages, some happening in sequence, some in parallel, along different contemporaneous lines, as he suggests. Certain aspects of bipedalism might have evolved much earlier than other characteristics of human-ape divergence. But what Langdon fails to demonstrate at this, or at any, point in his review, is why some parts of that mosaic could not have involved waterside periods.

THE APPEAL OF UNORTHODOX THEORIES

Finally, Langdon completes his refutation of the AAH by drawing analogies with creationism and explanations that include invoking aliens from space. It is, like them, “only one of several ideas rejected by orthodox science that has refused to go away.” [1].

Langdon provides several properties that the AAH, as he argues, has in common with such theories, in a section entitled “The appeal of unorthodox theories”:

1. 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 [2] paper was merely a question and his article ended: “My thesis is, of course, only a speculation – a hypothesis to be discussed and tested against further lines of evidence. Such ideas are useful only if they stimulate fresh inquiries that may bring us nearer the truth.” Nor does he 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’, whereas instead she merely questioned answers provided by others. Indeed, the fact that Morgan has modified and retracted various arguments over the years [e.g., 13] indicates that she is open to contradictory evidence.
2. Langdon compares the AAH with heterodox ideas that feed on suspicion against the scientific establishment, but he fails to mention that its 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 (see also Chapter 1). As well as the supporting comments published in the 2002 paper cited earlier, Tobias 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 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” [80]. 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 AAH with the early sceptical reception of the continental drift theory of Wegener, a historical fact that no-one would dispute today.
3. Langdon's third AAH 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 is based on the observation that Elaine’s first book, written more than twenty-five years earlier, “spoke with the passion of embittered and victimized feminism” [1]. 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. Moreover, Langdon fails to credit Morgan with the fact that her following books were very carefully written, without ‘feminist’ passages.

4. Langdon suggests that the AAH is popular because it is easily communicated “in simple narrative” to those “not actively engaged in the primary evidence” [1]. Putting aside the question of whether the AAH is popular or not (how many school books on human evolution show ‘Man-the-mighty-hunter’ on open, grassy plains, rather than images of women bathing infants in water?), his argument could be seen to apply more to savannah-based stories than to AAH. The 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.
5. Langdon compares the AAH’s “great emphasis on negative arguments” [1] with that of creationism, suggesting that Morgan places “a great deal of weight on the tentativeness of hypotheses in the terrestrial models” [1], as creationists do with their perceived insufficiency of evolutionary theory. This is a rather remarkable argument to make, considering that her work is full of positive ideas, attempting to explain traits that university level texts on human evolution have often avoided. To compare the AAH with creationism is particularly facile as the hypothesis has, at its core, neo-Darwinist adaptationism, the argument that every human trait must have an adaptive explanation rooted in natural selection.
6. 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” [1]. He compares two explanations for human breath control, and 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-holding control, whereas some bipeds, *e.g.*, turkeys, do not) and also a highly selective one. Where the AAH is difficult in his opinion, 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 a waterside past, then the counter-argument is that it is *too simple*. Then, Langdon encourages us, instead, to “look for complex stories with weak plots” [1]. In Langdon’s view, 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” [1].

THE VALKENBURG SYMPOSIUM

On top of all of these detailed flaws in Langdon’s arguments, yet one more must be added. Perhaps the greatest weakness of his critique of the AAH was the fact that it all but ignored the findings of the Valkenburg symposium, published six years earlier. Langdon did know about it (he wrote: “The AAH was the subject of a published symposium that represented both favorable and opposing views” [1]), but then failed to cite a single comment or piece of data from any of the twenty-two contributions. The four editors of the publication were given the unenviable task to trying to summarize the symposium, and to produce some kind of concluding statement on the merits of the AAH. Overall, in my opinion they decided against the AAH, but, as with Langdon, it should be clearly understood what it was they thought they were rejecting: They wrote: “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 there are a number of arguments favouring the aquatic ape theory, they are not sufficiently convincing to counteract the arguments against it” [3]. They did further suggest that “it may well be rewarding to reconsider the issue once further evidence – for instance from palaeontology – becomes available.” [3].

Of the four editors, Jan Wind wrote a piece against the AAH, Machteld Roede herself wrote one in favor, 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.” [3]. And Reynolds’ summary of the symposium, included the opening paragraph used in this chapter, was arguing most clearly that he thought there was evidence that water may have provided enough food to act as an agency of selection in human evolution.

It would appear that the review by Roede *et al.* [2], just as Langdon’s critique six years later, was considering the idea that there was actually an ‘aquatic ape’ in a literal sense. If the AAH is defined in tune with Hardy’s original idea, that Man was merely *more* aquatic in the past, then it would appear, from the arguments in their papers, that at least three out of four editors were clearly endorsing that view.

This certainly was the impression of Colin Groves. In his book review of Roede *et al.* [81], he also picked out some of the same words in Vernon Reynolds’ statement this paper begins with. Taking into consideration those words: “Not only did they take to water from time to time but ... the water ... was a habitat that provided enough extra food to count as an agency for selection” [5], Groves commented: “Is this, perhaps, all that was necessary all along? Might Hardy and Morgan have seen their ideas discussed if they had taken them just this far? I suspect it might.” [81].

CONCLUSIONS

But Roede *et al.* [2] 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, only makes the power of his refutation that much weaker. If an undergraduate student had submitted an essay on the AAH and not significantly drawn upon Roede *et al.* [2], his/her tutor might have been justified in putting a red line through it and asking for it to be re-written. Yet, Langdon’s paper was peer reviewed and made it into the esteemed pages of the *Journal of Human Evolution* and remains today the unchallenged refutation of the aquatic ape hypothesis.

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 caricature of an ‘aquatic ape’, at almost every juncture, demonstrates that, like many in the field, he assumed an unrealistic interpretation of what the hypothesis was proposing. If Langdon refuted anything, it was merely a cartoon image of an aquatic ape, something no-one has ever seriously considered.

REFERENCES

- [1] Langdon JH. Umbrella hypotheses and parsimony in human evolution: A critique of the aquatic ape hypothesis. *J Human Evol* 1997; 33: 479-94.
- [2] Roede M, Wind J, Patrick J, Reynolds V. Aquatic ape: Fact or fiction. Proceedings from the Valkenburg Conference. London: Souvenir Press 1991.
- [3] Hardy A. Was Man more aquatic in the past? *New Sci* 1960; 7: 642-5.
- [4] Reynolds V. Cold and watery? Hot and dusty? Our ancestral environment and our ancestors themselves: An overview. In: Roede M, Wind J, Patrick J, Reynolds V, Eds. *The aquatic ape: Fact or fiction?* London: Souvenir Press 1991; pp. 331-41.
- [5] Richards G. The refutation that never was: The reception of the aquatic ape theory. In: Roede M, Wind J, Patrick J, Reynolds V, Eds. *The aquatic ape: Fact or fiction?* London: Souvenir Press 1991; pp. 1972-87.
- [6] Tobias PV. Some aspects of the multifaceted dependence of early humanity on water. *Nutr Health* 2002; 16: 13-7.
- [7] Tobias PV. Water and human evolution. *Out There* 1998; 3: 38-44.
- [8] Sauer CO. Seashore - Primitive home of Man? *Proc Am Phil Soc* 1962; 106: 41-7.
- [9] Morgan E. *The descent of woman*. London: Souvenir Press 1972.
- [10] Morgan E. *The aquatic ape*. London: Souvenir Press 1982.
- [11] Morgan E. *The scars of evolution*. Oxford: Oxford University Press 1990.
- [12] Morgan E. *The descent of the child*. London: Penguin Books 1994.
- [13] Morgan E. *The aquatic ape hypothesis*. London: Souvenir Press 1997.
- [14] Verhaegen M. African ape ancestry. *Hum Evol* 1990; 5: 295-7.
- [15] Verhaegen M. Aquatic *versus* savannah: Comparative and palaeo-environmental evidence. *Nutr Health* 1993; 9: 165-91.

- [16] Verhaegen M. Australopithecines: Ancestors of the African apes? *Hum Evol* 1994; 9: 121-5.
- [17] Puech PF, Munro S, Verhaegen M. Aquarboreal ancestors? *Trends Ecol Evol* 2002; 17: 212-7.
- [18] Verhaegen M, Puech PF. Hominid lifestyle and diet reconsidered: paleo-environmental and comparative data. *Hum Evol* 2001; 15: 175-86.
- [19] Kuliukas AV. Wading for food: The driving force of the evolution of bipedalism? *Nutr Health* 2002; 16: 267-89.
- [20] Cunnane SC. The aquatic ape theory reconsidered. *Med Hypoth* 1980; 6: 49-58.
- [21] Evans PHR. The paranasal sinuses and other enigmas: An aquatic evolutionary theory. *J Laryngol Otol* 1992; 106: 214-25.
- [22] Ellis DV. Human ancestors in wetland ecosystems. *ReVision* 1995; 18: 8-12.
- [23] Ellis DV. Wetlands or aquatic ape? Availability of food resources. *Nutr Health* 1993; 9: 205-17.
- [24] Ellis DV. Is an aquatic ape viable in terms of marine ecology and primate behaviour? In: Roede M, Wind J, Patrick J, Reynolds V, Eds. *The aquatic ape: Fact or fiction?* London: Souvenir Press 1991; pp. 36-74.
- [25] Ellis DV. Proboscis monkey and aquatic ape. *Sarawak Mus J* 1986; 36: 251-62.
- [26] Ellis DV. Swimming monkeys and apes - Know their biology. Fresno, Ca: Proceedings Western Regional Meeting Conference, American Association of Zoological Parks and Aquariums April 5-8 1987.
- [27] Knight C. *Blood relations*. London: Yale University Press 1991.
- [28] Wescott RW. Aquaticism and quantalism. *ReVision* 1995; 18: 40-43.
- [29] Marsh D, Crawford MA. *The driving force*. New York: Harper & Row 1989.
- [30] Crawford MA, Wang Y, Cunnane SC, Parkington JE, Broadhurst CL, Schmidt WF. Brain-specific lipids from marine, lacustrine, or terrestrial food resources: Potential impact on early African *Homo sapiens*. *Comp Bioch* 2002; 131: 653-73.
- [31] Westenhöfer M. *Der Eigenweg des Menschen*. Berlin: Mannstaedt 1942.
- [32] Rodman PS, McHenry H. Bioenergetics and the origin of hominid bipedalism. *Am J Phys Anthropol* 1980; 52: 103-6.
- [33] Rose MD. The process of bipedalization in hominids. In: Coppens Y, Senut B, Eds. *Origine(s) de la bipédie chez les hominides*. Paris: CNRS Cah Paleoanthrop 1991; pp. 37-48.
- [34] Morris D. *The naked ape: A zoologist's study of the human animal*. New York: McGraw-Hill 1967.
- [35] Short RV, Renfree MB, Gaeth AP. The developing renal, reproductive and respiratory systems of the African elephant suggest an aquatic ancestry. *Proc Natl Acad Sci USA* 1999; 96: 5555-8.
- [36] Sharp RL, Cain SM, Ness RJ, Hackney AC. The effect of shaving body hair on the physiological cost of freestyle swimming. *J Swim Res* 1988; 4: 9-13.
- [37] Sharp RL, Costill DL. Influence of body hair removal on physiological responses during breaststroke swimming. *Med Sci Sport Exerc* 1989; 21: 576-80.
- [38] Krüger J, Heck H, Mikoleit J. The influence of total body shaving on performance and lactic acid behaviour in swimming. *Deutsche Zeit Sports* 2000; 51: 55-8.
- [39] Pagel M, Bodmer W. A naked ape would have fewer parasites. *Proc Roy Soc Series B-Biol Sci* 2003; 270: S117-9.
- [40] Darwin C. *The descent of Man and selection in relation to sex*. London: Murray 1879.
- [41] Dawkins R. *The ancestor's tales*. London: Weidenfeld & Nicolson 2004.
- [42] Schultz AH. Chimpanzee fetuses. *Am J Phys Anthropol* 1933; 18: 61-79.
- [43] Bolk L. *Das Problem der Menschwerdung*. Jena: Fischer 1926.
- [44] Wheeler PE. The evolution of bipedality and loss of functional body hair in hominoids. *J Hum Evol* 1984; 13: 91-8.
- [45] Wheeler PE. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: The contribution of increased convective heat loss and cutaneous evaporative cooling. *J Hum Evol* 1991; 21: 107-15.
- [46] Wheeler PE. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *J Hum Evol* 1992; 23: 351-62.
- [47] Jablonski NG. The evolution of human skin and skin color. *Ann Rev Anthropol* 2004; 33: 585-623.
- [48] Senut B. Paleontological approach to the evolution of hominid bipedalism: The evidence revisited. *Cours Forsch Inst Senckenberg* 2003; 243: 125-34.
- [49] Rotherham LS, van der Merwe M, Oosthuizen WH. Morphology and distribution of sweat glands in the Cape fur seal, *Arctocephalus pusillus pusillus* (Carnivora: Otariidae). *Aust J Zool* 2005; 53: 295-300.
- [50] Masuura DT, Whittow GC. Evaporative heat loss in the California sea lion and harbor seal. *Comp Biochem Physiol* 1974; 48a: 9-20.
- [51] Bartholemew GA, Wilke F. Body temperature in the northern fur seal *Callorhinus ursinus*. *J Mammal* 1956; 37: 327-33.
- [52] Bennett VR, Brown LK. *Myer's textbook for midwives*. Edinburgh: Churchill Livingstone 1999.
- [53] Mota PG, Correia ER, Correia HR, Balseiro SC, de Areia ML. Why are human newborns so fat? Relationship between fatness and brain size at birth. *Am J Hum Biol* 2004; 16: 24-30.
- [54] Mahoney SA. Cost of locomotion and heat balance during rest and running from 0 to 55 degrees C in a patas monkey. *J Appl Physiol* 1980; 49: 789-800.

- [55] Avlonitou E, Elizondo R. Effects of atropine and pyridostigmine in heat-stressed patas monkeys. *Aviat Space Environ Med* 1988; 59: 544-8.
- [56] Angus S. Water-contact behaviour of chimpanzees. *Fol Primatol* 1971; 14: 51-8.
- [57] Woodruff DS, Ryder OA, Hohman G, *et al.* Mitochondrial sequences show diverse evolutionary histories of African hominoids. *Proc Natl Acad Sci USA* 1999; 96: 5077-82.
- [58] Morwood MJ, O'Sullivan PB, Aziz F, Raza A. Fission-track ages of stone tools and fossils on the East Indonesian island of Flores. *Nature* 1998; 392: 173-6.
- [59] Attenborough D. *Life of mammals*. St Helier: Domino 2002.
- [60] McBrearty S, Jablonski N. First fossil chimpanzee. *Nature* 2005; 437: 105-8.
- [61] Edey M, Johanson DC. *Lucy: The beginnings of humankind*. New York: Simon & Schuster 1981.
- [62] Feibel CS, Brown FH. Microstratigraphy and paleoenvironments. In: Walker A, Leakey REF, Eds. *The Nariokotome Homo erectus skeleton*. Cambridge: Harvard University Press 1993; pp. 21-39.
- [63] Reed KE. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J Human Evol* 1997; 32: 289-322.
- [64] WoldeGabriel G, Haile-Selassie Y, Renne P, *et al.* Geology and palaeontology of the late Miocene Middle Awash valley, Afar rift, Ethiopia. *Nature* 2001; 412: 175-8.
- [65] Lopez-Martinez N, Rage JC, Lehmann T, *et al.* Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 2002; 418: 152-5.
- [66] Louchart A, Haile-Selassie Y, Vignaud P, Likius A, Brunet M. Fossil birds from the late Miocene of Chad and Ethiopia and zoogeographical implications. *Oryctos* 2008; 7: 147-67.
- [67] Frost SR, Delson E. Fossil Cercopithecidae from the Hadar formation and surrounding areas of the Afar depression, Ethiopia. *J Hum Evol* 2002; 43: 687-748.
- [68] Harris JM, Leakey M. The faunal context. In: Walker A, Leakey REF, Eds. *The Nariokotome Homo erectus skeleton*. Cambridge: Harvard University Press 1993; pp. 55-60.
- [69] Stringer C, McKie R. *African exodus*. London: Pimlico 1997.
- [70] Berhe SM, Bruggermann H, Walter RC, *et al.* Early human occupation of the Red Sea coast of Eritrea during the last interglacial. *Nature* 2000; 405: 65-9.
- [71] Jerardino A, Watts I, Thompson E, *et al.* Early human use of marine resources and pigment in South Africa during the middle Pleistocene. *Nature* 2007; 449: 905.
- [72] WoldeGabriel G, Defleur A, Suwa G, *et al.* Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 2003; 423: 747-52.
- [73] Lovejoy CO. The origin of Man. *Science* 1981; 211: 341-50.
- [74] Hunt KD. The evolution of human bipedality: Ecology and functional morphology. *J Hum Evol* 1994; 26: 183-202.
- [75] Vrba ES. Ecological and adaptive changes associated with early hominid evolution. In: Delson E, Ed. *Ancestors: The hard evidence*. New York: Alan Liss 1985; pp. 63-71.
- [76] Oppenheimer S. *Out of Eden: The peopling of the World*. London: Robinson 2004.
- [77] Stanford CB. *Upright - The evolutionary key to becoming human*. Boston: Houghton Mifflin 2003.
- [78] Leonard WR. Food for thought. *Sci Am* 2003; Aug: 62-71.
- [79] Wynn JG. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. *Am J Phys Anthropol* 2004; 123: 106-18.
- [80] Tobias PV. *The aquatic ape*. BBC/Discover documentary 1998.
- [81] Groves CP. Book review: *The aquatic ape: Fact or fiction?* *Hum Biol* 1993; 65: 1038-40.