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Book review

Reply to John Langdon's review of the eBook: Was Man more aquatic in the past? Fifty years after Alister Hardy, Waterside Hypotheses of Human Evolution, Mario Vaneechoutte, Algis Kuliukas, Marc Verhaegen (Eds.). Bentham eBooks (2011). 244 pp., eISBN: 9781608052448

Introduction

We welcome the opportunity, offered by the editors of *HOMO - Journal of Comparative Human Biology*, to respond to John Langdon's review (Langdon, 2012) of our recently published eBook, *Was Man More Aquatic in the Past?* (Vaneechoutte et al., 2011).

Langdon's review, however, is not so much about the eBook itself – as he hardly discusses any of the rich data and hypotheses forwarded by the eBook – but rather represents his critical attitude towards the aquatic hypothesis (AH). His criticisms are largely rhetorical, focusing on philosophical questions about science, rather than substance, and as such they can be applied equally to science in general. Our comments address these reflections, and also highlight the fact that some of Langdon's statements are based on misinterpretations and misrepresentations, not only of the content of the eBook and of the AH, but also of some of the palaeo-anthropological and comparative biological data.

Langdon dismisses the AH as an unnecessary and extraordinary explanation for differences between humans and their closest relatives

Langdon states (line 3): "Behind the original formulations of AH was the perception that humans are so distinct from other species of primates that only a radical evolutionary process can explain our appearance on earth." and (line 50): "In the last 40 years, as comparative anatomical, fossil, genetic, and behavioural studies have eroded much of the apparent gap between humans and the African apes, there is less need for extraordinary scenarios."

This stance comprises two separate arguments. Langdon states that (1) humans do not differ significantly from their closest relatives, and that this gap has even narrowed due to new knowledge gathered during the last 40 years, and that (2) assuming a more aquatic past of our species to explain the eventual differences with apes represents a radical evolutionary process or an extraordinary explanation.

Humans do not differ all that much from apes

We strongly disagree with this opinion, on all points (anatomy, genetics, fossils, and behaviour):

- * Anatomy: African apes are still not upright bipeds, they are not naked, nor fat, and do not have very large brains, to name only a few of the most apparent differences, of which many are extensively addressed in the eBook.
- * Fossils: The pachyostotic skeleton of *Homo erectus* is totally unlike what we observe in African apes. In addition, it is now clear that archaic *Homo* fossils are found almost exclusively in association with large bodies of permanent water (Munro, 2010; Kuipers et al., 2012). While many of these asso-

ciations occur along inland river systems and lake basins, there is also ample evidence of *Homo* fossils associated with marine milieus (e.g., Joordens et al., 2009; Verhaegen et al., 2007). This association with permanent water and the presence of pachyostotic bones in the fossil record widens the gap between fossil *Homo* and African apes.

* Genetics: In opposition to Langdon's statement, our rapidly increasing genetic knowledge (with human, chimp, bonobo and gorilla genomes now fully sequenced) continues to broaden the gap between humans and apes. For example, mutations in the CMAH-enzyme make the surface of our cells look very different from that of other primates and, as far as we know, to that of all other mammals (although aquatic mammals have not been studied in this respect yet). In addition, we also have four copies of SRGAP2, a gene involved in dendritic synapse formation, whereas apes have only one copy (Geschwind and Konopka, 2012). Both CMAH and SRGAP2 mutations have been linked to the possibility of increased brain growth and are estimated to have occurred between 4 Ma and 2 Ma, i.e., preceding the appearance of the first *H. erectus* fossils.

Humans also lack a certain class of endogenous retroviruses (ERVs) that is present in all African monkeys and apes, but missing from non-African monkeys and apes, suggesting that human ancestors may have been absent from Africa when the ERV swept the African continent between 4 Ma and 3 Ma (Benveniste and Todaro, 1976; Yohn et al., 2005), i.e., at the time when *Ardipithecus* and australopithecines existed.

* Physiology: There are many physiological differences, which are profoundly discussed in the eBook, especially with regard to our wastefulness with water – a very unterrestrial-like adaptation (Tobias, 1995; Williams, 2006, 2011). There are other differences, which further broaden the gap. For instance, the normal vaginal econiche of human females has low pH (4.0–4.5), protecting against sexually transmitted pathogens and preterm birth (Manns-James, 2011), whereas all mammals studied (all terrestrial to our knowledge), including monkeys, have neutral vaginal pH (Mirmonsef et al., 2012).

In conclusion, the more we learn about our morphology and physiology and more recently about our genetic makeup and biochemistry, the more intriguing differences are revealed, not only with apes, but with most (terrestrial) mammals in general. Instead of closing the gap, these differences add up to the many established morphological and physiological differences, a number of which are explicitly dealt with in the eBook.

AH is an extraordinary explanation of our past

Langdon's second argument, that the AH is an extraordinary explanation (see also further: II.3 The AH is unconventional), is already an improvement, because previously Langdon considered the AH as an unorthodox hypothesis, comparing it to creationist beliefs (Langdon, 1997).

First, at several occasions, Langdon keeps misrepresenting the AH as if it claims that we once were fully aquatic, comparable to whales and dolphins. Langdon states (line 8): "... by comparing them with the anatomy of cetaceans and a variety of semi-aquatic species.", and even more explicitly at line 92: "Dolphins and humans are similar in the loss of body hair, relatively large brains, and complex vocal capacities; but these similarities do not make us dolphins." By emphasizing 'cetaceans', Langdon continues to feed the impression that it is a claim of AH that we once were fully aquatic.

Further on (line 29), Langdon erroneously states that it is claimed that our colour vision resembles best that of cetaceans: "Chan suggests the blue shift in one of the human cone pigments resembles a blue shift in a different pigment in cetaceans (Chapter 11)." However, Chan (2011) explicitly writes that the shifts in our colour vision most closely resemble those of the manatee (a shallow water diver) with the same blue shift as ours and in the same cone (S-cone), whereas cetaceans (frequent deep water divers) are in fact almost colour-blind (even lacking the S and M-cones).

To conclude the 'issue of cetaceans', Hardy (1960) only asked: "Was Man *more* aquatic in the past?" (our italisation, and see the title of our eBook) and it has never been a claim of the AH that we were once fully aquatic cetacean-like creatures. How many times more do we have to repeat this?

Moreover, one can ask whether a switch to a more aquatic lifestyle represents a radical evolutionary process, as Langdon names it. In fact, there are numerous examples of habitat shifts from water to land (e.g., all terrestrial life stems from aquatic ancestors, including the fish-to-amphibian transition), land/water to land (e.g., amphibian to reptile), land to land/water (most numerous examples:

e.g., tortoises, aquatic snakes, crocodiles, seals, our ancestors?) and back: land/water to land (e.g., elephants, pigs, *Homo sapiens*?), land to water (e.g., cetaceans, sirenians, extinct *Mosasaurus*), land to land/air (e.g., birds, bats) and land/air to land/water (penguins). After all, adaptation to new or changing environments constitutes one of the most important processes that fuel evolution. There is nothing "unparsimonious" nor extra-ordinary about the assumption that also our ancestral founder populations adopted a waterside (predominantly wading) and/or amphibious (predominantly swimming and diving) lifestyle.

In conclusion, in opposition to Langdon, we claim that there are many apparent differences between our species and its closest relatives, which need explanation. Moreover, it should now be clear that the idea that our ancestors partially adopted an aquatic lifestyle is not extraordinary.

Philosophical considerations

Langdon's review contains many elements which we consider merely as philosophy of science in general.

The AH is unconventional

Langdon not only considers the AH as extraordinary, he also designates it several times as "unconventional", in implicit opposition to the 'conventional' (terrestrial) view. While not a direct criticism, the use of these terms gives the impression that somehow the AH has been developed outside the norms of scientific practice.

'Conventional' narratives of human evolution suggest that humans adapted to more open habitats and therefore started walking upright and lost their fur. Yet other animals that have adapted to open habitats, such as baboons, are furred, quadrupedal and pronograde, strongly prognathic, and have no drastically enlarged brain. Therefore, the only way a human evolutionary narrative of this kind can be accepted is if one assumes that the normal rules of biology (i.e., those that apply to baboons) do not apply to humans. This strikes us as unconventional.

The hypothesis that human ancestors once foraged regularly in relatively shallow waters for slow moving foods such as shellfish, which has been formulated by applying conventional biological reasoning and derived from comparative biology, is seen as unconventional from a mainstream point of view, only because it does not fit with the conventional – historical – idea, but not because it has been reached by unconventional, unscientific or unorthodox reasoning, although the latter implication follows from Langdon's statements.

The AH is composed of narrative and just-so stories

Beside the designation of the AH as extraordinary and unconventional, Langdon states that it is composed of subjective narrative, assumptions, and just-so stories. He admits that this is the case for the conventional terrestrial hypothesis as well. But the conventional open plain story is itself built on the unproven supposition that humans evolved in an open terrestrial environment. The assumption that we started walking upright as an adaptation to open plains has been formulated partly on the basis of at least two other wrong assumptions, i.e., that the first discovered australopithecine (the Taung child) lived in an arid open area (Dart, 1925) and that the open savannah originated at the dawn of mankind. See Bender et al. (2012) for a recent review on the history of this hypothesis. Although this idea has for some time been abandoned by several of its initial proponents, when recognizing that these assumptions are wrong (Leakey and Lewontin, 1992; Tobias, 1995; Hunt, 1994; Wood, 1993), the same narrative continues to be published in high impact journals (e.g., Bramble and Lieberman, 2004). See below also: IV. *Us* versus *Them*.

In conclusion, it is not (semi)aquatic models, but rather terrestrial, open plain models that are based on just-so assumptions, of which several have been proven wrong. The only difference is that the terrestrial assumptions have been repeated so many times and published in high-impact journals, that they have achieved the status of established fact (see below also: IV. *Us* versus *Them*).

AH proponents are not (careful) scientists

Langdon states (line 126): "... the AH literature picks from the anthropology literature only observations that can be linked to water. It has not engaged with the extensive research literature on palaeo-diet and locomotor behaviour, on hunting weaponry and butchery of terrestrial animals." Again, on the contrary, these items have been addressed extensively by AH literature and in the eBook: butchering of animals is explicitly dealt with in Chapter 5 of the eBook (Munro and Verhaegen, 2011), the palaeo-diet is referred to in Chapter 4 (Verhaegen et al., 2011) and in Verhaegen and Puech (2000), and the locomotor behaviour of hominins, as explained by Bramble and Lieberman (2004), has been critically addressed by Verhaegen et al. (2007).

Furthermore, Langdon dismisses comparative data, upon which AH proponents – and, as we assume, most authors publishing in the *Journal of Comparative Human Biology* – rely extensively, as unreliable, and suggests that aquatic proponents base their view on similarities of feature as proof of shared habitat exposure, without investigating the features in detail, e.g., at line 89: "Evolutionary convergence – structural similarity – by itself is a metaphor for functional similarity. Metaphors are useful, but they demand that we examine points of resemblance closely in order to learn whether they are meaningful." Langdon thereby ignores the work of numerous contributors (e.g., Morgan, 1982; Verhaegen, 1993), who have discussed in great detail the different explanations (savannah, aquatic and others) that have been put forward for various features. In fact, a number of AH proponents have taken care to present the published arguments of the conventional hypotheses in detail to enable comparison with the arguments for a more aquatic past of our species.

The review of Langdon contains some misrepresentations of the content of the eBook or of archaeological facts in general, and some inconsistencies.

The eBook contains few original data

Langdon states about the eBook (line 14): "... there are few original data presented here." First, it should be clear that books usually do not contain journal articles, presenting original data and research, but they are composed of chapters, which try to give the reader an overview of current knowledge gathered in the field. Nevertheless, the eBook contains very original information (see below). Langdon's claim that it does not, gives the impression that the majority of the subject matter has been dealt with by critics previously, but this is not the case. Langdon's last publication addressing the AH was in 1997, but to our knowledge there has not been any response, apart from an occasional supportive mentioning (e.g., Wrangham, 2005), to the aquarboreal model (Verhaegen et al., 2002), the pachyostosis papers (e.g., Verhaegen et al., 2011), the kidney research (e.g., Williams, 2006, 2011), the wading hypothesis (e.g., Kuliukas, 2011), our diving abilities (Schagatay, 2011), our underwater vision abilities (Gislén and Schagatay, 2011), and the very intriguing contribution in the eBook (not mentioned as original by Langdon) regarding our colour vision (Chan, 2011). Furthermore, we consider the rebuttal of Kuliukas (2011) – eBook chapter 15 – to Langdon's 1997 paper as original work, as it replies in specific detail to every previous claim by Langdon.

Different opinions regarding timing: there are many AHs

Langdon points to major disagreement among AH proponents with regard to the timing of our aquatic past.

Although Hardy placed the most aquatic phase around the time of the LCA, an opinion that was followed by Elaine Morgan, and wherefrom the disputable term 'Aquatic Ape Hypothesis' is derived, the most prominent aquatic phase, according to e.g., Verhaegen and Kuliukas, occurred more recently. In agreement with Langdon and with the subtitle of the eBook (Waterside Hypotheses) and with the more recent opinions (Verhaegen, Kuliukas) that the most important aquatic adaptations are not ape but *Homo*-related, we use the term 'Aquatic Hypothesis' (AH) throughout this reply. This more recent occurrence of the most aquatic phase also may explain better why humans are such peculiar beings, whereas an earlier aquatic phase (around the split with *Pan*, dated at 7–5 Ma, or even earlier, e.g.,

Langergraber et al., 2012), as defended by e.g., Morgan (1972, 1982, 1990, 1997), might not have left such clear 'scars of evolution'.

Algis Kuliukas thinks that humans were at their most 'aquatic' at around the time of the *Homo sapiens* speciation (\sim 250 ka), evolving in a waterside habitat with a limited amount of swimming and diving, combined with walking/running along the beaches for foraging, whereas Marc Verhaegen and Stephen Munro argue that the most aquatic phase was for *H. erectus*, which they deduce from, amongst other features, the presence of dense bones (pachyostosis), as discussed in Chapter 5 of the eBook and in a recent paper in this journal (Verhaegen and Munro, 2011).

We also wonder about the relevance of referring to upper palaeolithic art, "showing obsessive focus on land animals" (line 127), when the AH is about archaic *H. sapiens* (Kuliukas), or *H. erectus* (Munro, Verhaegen). By the way, in opposition to what Langdon asserts, palaeolithic cave art also has a strong emphasis on aquatic animals (see, e.g., Mithen, 1988).

In conclusion, AH proponents generally agree on the importance of water to explain our morphology and physiology, as stated in the eBook (p. 118): "Waterside hypotheses of human evolution assert that selection from wading, swimming and diving and procurement of food from aquatic habitats have significantly affected the evolution of the lineage leading to *Homo sapiens* as distinct from that leading to *Pan*." It is true that there are some disagreements with regard to the timing and nature of the most aquatic phase, but as Langdon states himself, there are different terrestrial views as well, and therefore this 'critique' is a general one of science, not specifically applicable to the AH. After all, it is differences in opinion that make scientific knowledge proceed.

Fossils in the vicinity of water mean very little in favour of the AH

At line 134, Langdon writes that the authors of the eBook "make strong claims about fossil locales." Interestingly, he hurries to continue that "these claims mean very little" (line 140).

The fact that Langdon no longer denies the strong claims is again a point of view that already has moved substantially into the direction of the AH, because in his previous critique, Langdon (1997) stated: "The hypothesis... has not been reconciled with the fossil record", and "One body of data that potentially can disprove it is the fossil record.... However, the problems of reconciling it to the fossil record have increased over the years."

Thus, Langdon no longer denies that the fossil records do not disprove a possible semi-aquatic past, but now downplays the importance of these fossil indications for the AH. However, we contend that these are indeed strong claims and that these are well-founded: there are no archaeological or fossil sites that contradict semi-aquatic models of human evolution. Indeed, there are numerous examples of fossil sites that do not show any evidence of permanent water, but none of these are associated with archaic *Homo* (Munro, 2010), as also illustrated in Table 5 of Chapter 5 of the eBook (Munro and Verhaegen, 2011).

Terrestrial models have been developed as well

In terms of Langdon's alternative to the AH, as mentioned above, he favours a terrestrial model (line 104): "hypotheses have been conceived that are consistent with the AH. However, hypotheses have also been conceived that are consistent with a terrestrial model." Langdon here suggests that terrestrial models have been put forward that explain the various ways in which humans differ from the other apes (e.g., fur loss, subcutaneous fat, large brains, a 'linear' body, external nose, reduced olfaction, well developed slow-diving abilities, etc.), but this is not the case: The combination of these traits is not explained by any terrestrial model. If it were, Langdon could point to these models, with a level of detail similar to that contained in the eBook.

The AH is an umbrella hypothesis

One of Langdon's main arguments is that the AH is made up of independent untested hypotheses (line 97–98): "In 1997, I argued that a model that encompasses long lists of independent untested

hypotheses does not constitute parsimony. I coined the term 'umbrella hypothesis' for such an approach."

One can designate the AH as a model with different hypotheses, and consider it as a negative trait that a number of independent features of human anatomy, physiology and behaviour can all be accommodated under the one hypothesis of a semi-aquatic past. But in fact this is exactly the kind of explanatory hypothesis that is the hallmark of progress in scientific insight. If one chooses to invent a term like 'umbrella hypothesis' for a vision that offers a coherent view on many problems that beg for an answer, and to consider this as a negative trait, then we assume that some of the fundamental, explanatory scientific theories, such as the theory of evolution through natural selection, are to be named 'umbrella theories' as well.

That humans are naked might be explained by water, but by itself the explanatory power of this fact is not strong. "Truth is the intersection of independent lines", said Richard Levins, and therefore the fact that humans are naked, fat, have large brains, an external nose, reduced olfaction, slow diving abilities and numerous other, mutually independent, characteristics – all very anomalous for any terrestrial mammal, let alone for a terrestrial hominoid – indicates that our ancestors' evolutionary history was strongly influenced by time spent in water. This is moreover still reflected in our – and especially our children's – present preferences and behaviours.

We should abandon the Us versus Them attitude

We very much welcome more open debates, such as the one offered by this journal, and Langdon seems to agree (line 152): "Possibly the time has come to bring the 'paradigms' together; to step out of the 'Us versus Them' mentality held by both sides of this debate . . ."

We also can only agree with Langdon, when he states: "...more attention is given to stories composed by scholars who have already established themselves through a career of solid empirical research in the field. This does not make their ideas correct, but they are more likely to draw an audience." But this is simply a sound general critique of the scientific process. It cannot be a criticism of the AH itself, and emphasizes that this hampers the consideration of views that are not shared by the establishment.

This is best illustrated by the recent experience of the editors of the eBook on Wikipedia: When trying to update the page *Aquatic ape hypothesis*, to reflect the fact that a major new eBook on the subject had been published, anonymous editors blocked every attempt, claiming it would give undue weight to a theory not accepted by mainstream scholarship. Later the same editors claimed that Bentham eBooks was not a reliable publisher and therefore could not be cited on Wiki pages (sic) – moreover overlooking that most if not all of the anti-AH 'references' (except Langdon's) came from unreliable sources such as websites and blogs. All of this is rather ironic, considering that it happened on a web page designed to provide the most updated information on the AH, but it nicely illustrates how difficult it can be for non-mainstream ideas to find a foothold within mainstream discourse.

Langdon also explains the lack of attention that the AH has received, as if there is no interest at all for whatever kind of adaptive scenarios (line 110): "Many of the authors in this volume repeat the persistent complaint that their models are ignored by conventional anthropologists and their textbooks. The truth is, most published adaptive scenarios are ignored from the time the print is dry." If this were true indeed, one wonders why adaptive stories that rely on an open plain assumption, themselves often no more than just-so stories (such as: achieving big brains by digging up tubers, standing tall to overlook the savannah grass or for postural feeding or throwing – see Table 1, Chapter 3 of the eBook), continue to be published in high impact journals, whereas our experience during the last decades shows that almost every comment referring to an aquatic past fails to get published. While we agree with the general critique of Langdon that adaptive explanations in palaeo-anthropology are intrinsically based on assumptions, we keep wondering why is it that generally only manuscripts based on terrestrial origin assumptions (e.g., Bramble and Lieberman, 2004; Hunt, 1996; Ruxton and Wilkinson, 2011; Young, 2003) are accepted for publication. In other words, the *Us* versus *Them* mentality is a reality, but it is not AH proponents that are to be blamed for this situation.

Conclusions

The majority of John Langdon's remarks are rhetorical, whereas the eBook provides numerous indications for a semi-aquatic past of our species, based on fossil evidence and on comparative biology, which could have been the subject of concrete debate. Although his review is overall very critical, Langdon does not specifically engage with any of the arguments put forward in favour of the aquatic hypothesis, and offers no alternative explanation, except for the vaguely termed, but nowhere explained 'terrestrial model(s)'.

We are convinced that the eBook illustrates how the AH has developed as a consistent framework with strong explanatory power for a range of very different and very specifically human characteristics, unseen in other hominoids and terrestrial animals, and in agreement with the fossil record. Finally, we would like to voice our agreement with Langdon's sentiment of ending the *Us* versus *Them* approach. Only through open, rational discussion of the competing evidence will scientific progress be made.

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