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The Aquatic Ape Evolves: Common Misconceptions and Unproven Assumptions About the So-Called Aquatic Ape Hypothesis

While some paleo-anthropologists remain skeptical, data from diverse biological and anthropological disciplines leave little doubt that human ancestors were at some point in our past semi-aquatic: wading, swimming and/or diving in shallow waters in search of waterside or aquatic foods. However, the exact scenario — how, where and when these semi-aquatic adaptations happened, how profound they were, and how they fit into the hominid fossil record — is still disputed, even among anthropologists who assume some semi-aquatic adaptations.

Here, I argue that the most intense phase(s) of semi-aquatic adaptation in human ancestry occurred when populations belonging to the genus *Homo* adapted to slow and shallow littoral diving for sessile foods such as shellfish during part(s) of the Pleistocene epoch (Ice Ages), possibly along African or South-Asian coasts.

Introduction

The term *aquatic ape* gives an incorrect impression of our semi-aquatic ancestors. Better terms are in my opinion the *coastal dispersal model* (Munro, 2010) or the *littoral theory* of human evolution, but although *littoral* seems to be a more appropriate biological term here than *aquatic*, throughout this paper I will use the well-known and commonly used term *AAH* as shorthand for all sorts of waterside and semi-aquatic hypotheses.

Popular and semi-scientific websites about AAH (e.g., Wikipedia) and even some supposedly scientific papers (e.g., Langdon, 1997) appear to contain several biased or outdated views on AAH, giving lay-people and new students of AAH wrong impressions of our ancestors' likely waterside past. Many of these unproven prejudices are widespread, not only among AAH opponents, but also among proponents. Some of these misconceptions find their origin in the original writings of the 'father of AAH' Sir Alister Hardy (e.g., on the timing of our aquatic past, and on the transition towards it), in the books of Elaine Morgan (who has done most to promote AAH) or in common interpretations of AAH proponents (e.g., on bipedalism, and on laryngeal descent). Others derive from wide-spread interpretations and unproven assumptions in popular writings on human evolution, or even in more scientific papers, for instance, on savanna adaptations, on running, hunting and meat-eating, and on australopiths being human ancestors.

This paper first briefly discusses the AAH website in Wikipedia. Then it lists a number of popular misconceptions on AAH by opponents as well as proponents. Thereafter it discusses a few important aspects of AAH, such as bipedalism and speech origins. Finally, it briefly provides a possible scenario of ape and human evolution.

Wikipedia: a reliable source?

While Wikipedia is generally a fantastic instrument, usually providing recent and reliable information to lay-people, this is perhaps not always the case in highly controversial topics like human evolution. In spite of the efforts of AAH enthusiasts to update the Wikipedia website *Aquatic Ape Hypothesis*, the editors of the website appear to take a conservative approach (which in other instances might be a safe strategy). As a result, the AAH website is considerably biased and outdated, relying chiefly on the 1987 Valkenburg conference (Roede et al., 1991), while overlooking most recent literature on AAH.

For example in the first paragraph, instead of referring to a few dozen recent peer-reviewed and detailed publications on different aspects of AAH, Wikipedia refers solely to the only anti-AAH peer-reviewed paper, now sixteen years old: “An extensive criticism appeared in a peer reviewed paper by John H. Langdon in 1997. Langdon states that the AAH is one of many hypotheses attempting to explain human evolution through a single causal mechanism, and that the evolutionary fossil record does not support such a proposal; that the hypothesis is internally inconsistent, has less explanatory power than its proponents claim, and that alternative terrestrial hypotheses are much better supported. AAH is popular among laypeople and has continued support by a minority of scholars. Langdon attributes this to the attraction of simplistic single-cause theories over the much more complex, but better-supported models with multiple causality.”

However, the article fails to mention that Langdon’s paper has been thoroughly answered in peer-reviewed publications not mentioned by the Wikipedia article. Suffice it to say that Langdon merely gives his personal thoughts without scientific argumentation. AAH is no simplistic, single-cause theory. On the contrary, waterside hypotheses provide an *extra* viewpoint to human evolution, not discussed by conventional anthropologists: AAH not only considers forest- and open plain dwelling, but also the possibility that human ancestors at some time lived along coasts, rivers, swamps etc. AAH is internally consistent, and, compared to purely terrestrial hypotheses (forests vs. plains, tropical vs. cold, scavenging vs. hunting, etc.), it offers incomparably greater explanatory power, as shown below as well as in the many recent publications not consulted by Langdon.

The Wikipedia AAH article bluntly declares: “There is no fossil evidence to support the AAH”, but fails to refer to relevant publications (e.g., Walter et al., 2000; Gutierrez et al., 2001; Joordens et al., 2009; Munro, 2010). In fact, our extensive reviews of the literature as well as the malacological (mollusc) and other paleo-environmental evidence suggest that virtually all archaic *Homo* sites are connected with abundant edible shellfish (Verhaegen et al., 2007; Munro, 2010; Table 5 in Munro & Verhaegen, 2011).

The Wikipedia article also states without argument: “Several theoretical problems have been found with the AAH.” In our opinion, the littoral theory instead offers theoretical as well as practical *solutions* to several problems in conventional paleo-anthropology, as shown below.

The site continues: “some claims made by the AAH have been challenged as having explanations aside from a period of aquatic adaptation ... most of these traits have an explanation within conventional theories of human evolution.” But the older and more conventional ideas suggest that human ancestors evolved from forests or trees to more open plains, without considering alternatives. These open plain ideas are anthropocentric just-so interpretations: uniquely-human (not seen in non-human animals) constructions attempting to fit the human condition. For instance, they ‘explain’ fur loss by heat, and subcutaneous fat by cold, not considering the possibility that human ancestors, like all mammals that are both furless and fat, could have spent a lot of time in the water. All the purported objections by conservative anthropologists have been addressed and answered in recent publications on AAH, not cited in Wikipedia’s entry (e.g., Verhaegen et al., 2007; Munro & Verhaegen, 2011).

The Wikipedia article claims that human traits such as bipedalism and laryngeal descent have been considered by proponents to be pro AAH arguments. However, this is not the general AAH opinion, currently. According to Hardy’s method (comparative biology), neither bipedalism nor laryngeal descent can be considered as pro AAH arguments. There are no bipedal (semi)aquatic animals apart from (wading) birds, and even the semi-aquatic penguins are only bipedal when *outside* the water. The same holds for laryngeal descent. For instance, Cetacea have *ascended* (intra-narial) larynges, not descended. These matters have been discussed (see also below) in several publications not mentioned in the Wikipedia article (e.g., Verhaegen, 1993; Verhaegen & Munro, 2007).

The article is also biased in citing anti-AAH comments, while failing to mention the obvious responses. One opponent claims that AAH “explains all of these features ... twice. Every one of the features encompassed by the theory still requires a reason for it to be maintained after hominids left the aquatic environment”, yet seems to be unaware of the existence of *phylogenetic inertia* as well as of *rudiments* in evolution, and has apparently not heard of the title of Elaine Morgan’s book *The Scars of Evolution*: as Morgan explained repeatedly, AAH is based on embryological, anatomical, physiological etc. remnant traits of our past that are not typically seen in terrestrial mammals. She quoted Stephen Gould: “the remnants of the past that don’t make sense in present terms—the useless, the odd, the peculiar, the incongruous—are the signs of history.”

Equally selective is the Wikipedia article’s mentioning Greg Laden’s anti-AAH comments in 2009, yet omitting Laden’s more recent and positive blog on AAH (Laden, 2013).

The Wikipedia article mentions the recent eBook on AAH (Vanechoutte et al., eds, 2011), but then cites from Langdon’s review of that book, instead of discussing the fifteen actual contributions in the eBook. The site verbosely writes about Langdon’s opinion (outdated and no longer relevant, see above), yet not about recent peer-reviewed critiques of Langdon’s publications (Kuliukas, 2011; Vanechoutte et al., 2012). It also does not mention many intriguing contributions in the eBook on different aspects of AAH, and it misrepresents or omits our own chapters on Miocene ape and australopith evolution, on Pleistocene *Homo*, and on speech origins.

These are only a few examples, but they support the idea that the Wikipedia article is prejudiced toward outdated and ill-informed opinions on what AAH is as defined and misunderstood by its critics rather than on the recent publications exploring the theory itself.

Of course, the same can be said about some similarly unscientific blogs and websites on the Internet mentioning AAH.

What is AAH—and what is it not?

In popular discussions, it is often incorrectly assumed by opponents, and even by some proponents, that AAH proposes that our most-aquatic phase happened before the time of the australopiths. Such an early phase (late Miocene), however, is unlikely. I provide a number of possible (often overlapping) pitfalls on ideas on AAH.

In my opinion (*):

** AAH is not about becoming aquatically adapted by gradually wading deeper on two legs at the beach.*

Hardy (1960), understandably, imagined that human ancestors might have become more aquatic by wading deeper and deeper at the beach. But since early Primates were arboreal, and since Darwinian evolution generally does not make great leaps, a transition towards a more aquatic lifestyle likely happened in a milieu where both trees and water were present, rather than on open rocky or sandy shores. Flooded, swamp and mangrove forests and later wetlands are indeed where virtually all fossils of Mio-Pliocene hominoids are found: as we discuss elsewhere (e.g., Verhaegen & Puech, 2000; Verhaegen et al., 2002; Verhaegen et al., 2011), the transition towards more aquaticness therefore did not start at the beach as Hardy and other AAH advocates have suggested, but rather in densely vegetated mangrove or swamp forests—wet forests were more abundant in the Mio-Pliocene (23–5.3–2.59 Ma, million years ago) than in the Pleistocene epoch (2588–12 ka, kilo-years ago)—by descending into the water below the branches, and by spending less and less time in the trees and more in the water, for instance, collecting easily obtainable foods they found near the water surface, possibly not unlike lowland gorillas collecting *aquatic herbaceous vegetation* (AHV) in forest bais (Doran & McNeillage, 1998). Such *semi-arboreal semi-aquatic* lifestyles have been called *aquarboral* by Williams (2006). Typical hominoid features (as opposed to monkeys) such as below-branch climbing, a broad thorax with dorsal scapulae and arms aside, complete tail loss, and a more vertical and central spine (Schultz, 1969) are parsimoniously explained by *vertical aquarboralism* (Verhaegen et al., 2011). The remarkably humanlike lumbar vertebra of *Morotopithecus* (e.g., MacLachy et al., 2000; Filler, 2007) suggests that (at least some) Miocene hominoids were already *orthograde* ~18 Ma (the exact dates do not affect my

proposed scenario), i.e., with habitually-vertical lumbar spines in as well as outside the water. Since the early great hominoids acquired thick cheekteeth enamel (e.g., *Afropithecus*–*Morotopithecus*, *Griphopithecus* etc.) and since all extant great apes use and even make stone tools (Breuer et al., 2005), the diet of the great hominoid last common ancestors might have been *durophagous*, partially feeding on hard objects, for instance, nuts or hard-shelled invertebrates (HSI). Note the thick-enameled capuchin monkeys *Cebus apella* also use hard tools to open palm nuts and mangrove oysters (Fernandes, 1991; Martin et al., 2003).

* *AAH is not about why Homo and Pan split, or about what happened at the split, but about what happened during the million years after the split.*

Elaine Morgan (personal communications, Internet discussions) suggested that our ancestors becoming more aquatic caused the *Homo/Pan* split. But at the time of the *Homo/Pan* split (~5 Ma?) chimpanzee and human ancestors were identical, so the differences between them and us arose (possibly mosaic-like) *after* that time, i.e., at some time(s) between the split and today, in the *Pan* branch or in the *Homo* branch. Evolutionary turn-overs are indeed more frequent with drastic climatic changes such as during the Pleistocene through alternation of glacials and interglacials (Ice Ages). Humans are obviously a very special kind of primate: they must have walked a special or complicated evolutionary path. Indeed, most or all possibly-aquatic traits in the human fossil record (see below the huge brain, POS, ear exostoses, external nose, platycephaly, platymeria, finds in association with marine molluscs, dispersal to islands, etc.) seem to have appeared after ~2 Ma, at some time in the Pleistocene.

* *AAH is not about ‘aquatic apes’ or even australopiths, but about archaic Homo.*

Most or all traits that can possibly be explained by a (semi)aquatic past seem to be absent in apes and australopiths, and appear in the fossil record mostly or exclusively in the genus *Homo*: the spectacular brain enlargement (arguably through the abundant DHA in aquatic foods, see Crawford et al., 2002), an external nose (strongly projecting nasal bones, as in some semi-aquatic mammals), pachy-osteo-sclerosis (POS, very thick and dense bones, as in slow and shallow diving tetrapod species), platycephaly (flattened skull-caps, as in semi-aquatic Carnivora, presumably for hydrodynamic streamlining, see Curtis et al., 2012), platymeria (dorso-ventrally flattened femora, as in Pinnipedia), wide and deep thoraxes (as in most shallow-diving endotherms), ear exostoses (as in human divers in cold water), etc. In the malacological record, marine mollusc species in combination with hominid fossils are not seen with australopiths, but appear together with *Homo erectus* and relatives (Munro, 2010). This does not mean that our ancestors’ littoral adaptations could not have begun prior to that time, only that to date we have no evidence of littoral adaptations before the Pleistocene (this absence of Pliocene evidence

might or might not be due to the fluctuating sea levels of the Ice Ages). Since littoral adaptations seem to be more prominent in *Homo erectus* than in Neanderthals, later *Homo* populations might gradually have ventured more and more inland along the rivers, where their remains have been found in oxbow lakes at the time (e.g., Mauer in Germany, Lynford in the UK), frequently in paleo-landscapes with reeds and beavers. The Neanderthal diet seems to have been remarkably varied (Hardy & Moncel, 2011) and probably included salmon (Bocherens et al., 2013). How aquatic the non-archaic *Homo* fossils were, is less clear. Which of the different so-called *Homo habilis* fossils were close relatives of archaic *Homo* (e.g., many O.H. fossils?) and whether some of them might have belonged to the australopiths (e.g., KNM ER-1813?) might be difficult to answer with the present knowledge. In any case, *Sahelanthropus*, *Orrorin*, *Ardipithecus* and australopith fossils have to be studied on their own, apart from *Homo*'s littoral past: even if they can provide information on how our ancestors before their most-aquatic phase might have looked and lived, they have in my opinion little bearing on AAH in the strict sense.

** AAH is not about what happened 10 or 5 Ma, as Hardy and Morgan thought, but rather about what happened less than ~2 Ma.*

In 1960, when Hardy wrote his famous paper, it was generally thought that humans and apes split more than 10 Ma, and since it was commonly believed then (without firm evidence) that australopiths were precursors of humans and had lived on the open plains, Hardy supposed that the most-aquatic phase must have happened before that time. If that had been the case, most (semi)aquatic traits might have disappeared since then, but the abundance of these traits in humans suggests that our ancestors' most-aquatic phase happened more recently. Indeed, the first known occurrences of fossil hominids in coastal sediments are probably ~1.8 Ma (Mojokerto), as well as the first hominid fossils or tools outside Africa, so the diaspora of *Homo* to tropical, subtropical and temperate regions of the Old World (as far as England, Angola, the Cape, China and Flores, between at least 0°E and 120°E, and 52°N and 34°S) might have happened at the beginning of the Pleistocene along the coasts (*coastal dispersal model*, see Munro, 2010), and afterwards from the coasts inland along rivers.

** AAH is less about how modern humans behave in water than about erectus' differences with sapiens.*

In popular AAH discussions, proponents as well as opponents often assume that *Homo erectus* moved more or less like us (e.g., the *endurance running model*), and that if there was ever a semi-aquatic episode, this was followed by a more cursorial phase in human evolution (on savannas or elsewhere). This thinking not only underestimates the differences between *erectus* and *sapiens*, but is also based on the unproven assumption that when hominid fossils bear humanlike locomotor traits, these traits are adaptations

for humanlike locomotion ('bipedalism'). For instance, the human plantar arch is believed to be an adaptation to running, whereas it should be noted in the first place that cursorial mammals are not plantigrade, but unguli- or digitigrade. Extant humans are in fact very atypical runners: we are relatively slow, on short as well on long distances, we are fully plantigrade, have remarkably short toes, a wide body build, archaic *Homo* had very heavy skeletons (ballast in running), etc. Virtually all purportedly 'running' features of *Homo* (i.e., where humans locomotorically differ from chimps) can more parsimoniously be explained by non-running adaptations (Table 4 in Verhaegen et al., 2007): by diving and/or wading locomotions and/or vertical climbing. Conservative views often suppose that there was a more or less straight evolutionary line from apelike towards human locomotion, and that most locomotor differences between humans and apes are adaptations to bipedal walking or running. But primates that evolve from forests to more open terrain typically become *more* pronograde and quadrupedal, not less. This contradiction has been called the *baboon paradox* (Bender, 1999). On the other hand, many AAH proponents assume that wading led to bipedalism, although bipedalism did not evolve in non-primate wading mammals such as tapirs, hippos or capibaras. Obviously, the different *erectus*-like fossils should be studied on their own. My quantitative comparative study of extant and fossil hominoid cranio-dental traits showed that the sum of differences between *Australopithecus africanus* and *Homo erectus* was only marginally higher than those between *H. sapiens* and *H. erectus* (Verhaegen, 1996). There were indeed a lot of differences between *Homo sapiens* and archaic *Homo*, and even between different fossils of archaic *Homo*. The following list is not exhaustive. Some archaic *Homo* specimens were very heavy creatures (e.g., *heidelbergensis*), and archaic men weighed in some populations much more than the women (e.g., *georgicus*). The brain size was initially (already in *modjokertensis* ~1.8 Ma, which exceeded *georgicus*) intermediate between australopiths and later *Homo*. In archaic *Homo* skulls, the frontal braincase was placed behind the eyes rather than above as in *sapiens*, and the inferior part of the brain skull was relative wider (notably in *neanderthalensis*). The skull-cap was remarkably flattened and ventrodorsally long (platycephaly), with a heavy eye-protecting ridge (torus) above the orbits (in *neanderthalensis* largely filled by frontal air sinuses, though not in *erectus*), and sometimes with parasagittal 'keeling' (especially in *erectus*). *Homo erectus* s.s. had smaller, but some other archaics (e.g., *heidelbergensis*) had larger paranasal sinuses than *sapiens* (see also below Table 2). The dorsal skull (occiput) and many other skeletal parts such as most long limb bones had typically extraordinarily thick cortices (often more than twice as in gorillas), dense bone and narrow medullary canals (POS). Some Javanese *erectus* specimens had canine diastemata in the maxilla of ~4 mm, about as large as in female orangutans (G.H.R. von Koenigswald in Puech, 1983). Tooth enamel was generally thicker than in *sapiens*, although some archaic specimens showed enamel dysplasias and even tooth loss (e.g., Margvelashvili et al., 2013). Teeth from Atapuerca (cf. *heidelbergensis*) were strongly worn as by plant foods such as roots, stems and seeds (Pérez-Pérez et al., 1999). Postcranially, the palms of the hands

and soles of the feet were generally wide, the fingers and toes were relatively short, but the fifth digital rays were relatively long compared to the other rays (*neanderthalensis*). In the shoulder, the glenoid fossae were directed more upwards (possibly for climbing arms-overhead) in the early-Pleistocene *georgicus* and *ergaster*. In most archaics, the femur was dorsoventrally flattened (platymeria). The vertebrae were craniocaudally ‘low’ (platyspondyly) in *ergaster* (Walker & Leakey, 1993). The femoral neck, as in australopiths, was relatively longer than in humans and certainly apes, which fits the iliac flaring and wide pelvis (platypelloidy) as well as the more valgus knees than in *sapiens* and certainly apes. The long leg bones and especially the tibiae were relatively shorter than in *sapiens*. Etcetera. For possible explanations of these differences with *sapiens*, see below, but it is clear that archaic skeletons (too heavy and too wide) were even less adapted to cursorialism than *sapiens*.

* *AAH is less about bipedal wading (except in later phases <200 ka?) than about slow and shallow diving.*

As explained in the previous paragraphs, but not commonly acknowledged by AAH opponents and some proponents, archaic *Homo* fossils displayed a number of features that are often seen in shallow-diving mammals: brain expansion, ear exostoses (in some *erectus* and many *neanderthalensis*), POS, platymeria, platycephaly and keeling, relatively wide bodies and extremities, midfacial prognathism with projecting nose, etc., whereas in *H. sapiens* (in the fossil record after ~200 ka) these possibly-littoral features disappear or become reduced. This does not imply that most or all archaic *Homo* populations did not frequently wade or walk bipedally, only that we do not have enough evidence to make firm conclusions about how often they waded. Although archaic *Homo* had relatively larger femoral heads than apes and australopithecines, which suggests more frequent bipedalism (standing, wading or walking), they had very heavy skeletons, and at least some of them (e.g., *heidelbergensis* and *neanderthalensis*, especially the males) seem to have had larger bodies than most extant humans. Thick and dense skulls (POS), on the other hand, are exclusively seen in slow and shallow diving tetrapods (e.g., Laurin et al., 2011): there is no reason—apart from conservatism—why archaic *Homo* should be unlike other animals with POS (Munro & Verhaegen, 2011; Verhaegen & Munro, 2011). POS, ear exostoses, abundant edible shellfish, human slow-diving skills (Schagatay, 2010) etc. all independently point into the same direction: our Pleistocene ancestors were no cursorial runners, but—at least parttime—littoral divers.

* *AAH is not about surface-swimming, but about shallow bottom-diving, where Homo's foods such as shellfish could be found.*

Many AAH proponents do not discern clearly between *surface-dwelling* (which can be called a terrestrial—keeping the head outside the water—rather than an aquatic adaptation) and *underwater foraging*, and among the latter, between *fast swimming* (e.g., in open or even oceanic waters) and *littoral diving* (e.g., in search of sessile foods). In all endotherms that spend time in the water, hydrostatic adaptations are essential. Buoyancy, especially of the airway entrances, is very important: terrestrial ungulates that live in wetlands, or even only twice a year have to cross dangerous rivers, typically have very large paranasal air sinuses; elephants have huge paranasal sinus around the trunk origin, and swine around the snout origin, as opposed to hippos (who usually stand and walk on the bottom); and salt water dwellers such as most marine mammals (sea water is ~2.4 % heavier than fresh water) also have reduced or absent air sinuses (Farke, 2010; Curtis et al., 2012; and refs in Verhaegen, 1991). *Homo erectus*' dense and thick skeletons (POS) and small paranasal sinuses are typical of salt-water littoral bottom-diving mammals, and *erectus*-like fossils are indeed the first hominid fossils that are sometimes found in association with marine molluscs (Munro, 2010). In this respect, the East African australopiths *Australopithecus afarensis*, *aethiopicus* and *boisei* were the opposite of *Homo*. Their more lightly built skull bones with large basicranial air sinuses as well as their large laryngeal airsacs (as still seen in extant gorillas) are not unexpected in surface-feeders in fresh water habitats such as papyrus swamps, where indeed their fossils have been found (Conroy, 1990; Reed, 1997): a wetland diet with a lot of papyrus sedges (AHV), possibly supplemented by hard-shelled invertebrates (HSI) found in reedbeds etc. (Shabel, 2010), is confirmed by their dentitional molarization (with super-thick enamel protecting against HSI), glossy polished micro-wear (Puech, 1992), and isotopic evidence (van der Merwe et al., 2008).

* *AAH is less about what happened in Africa or even the Rift Valley than about what happened on the Indian Ocean or Mediterranean shores.*

As opposed to the presence of australopiths in Africa, *Homo* fossils and tools are found at (sub)tropical and temperate coasts all over the Old World throughout the Pleistocene, and indeed many of the earliest known archaic *Homo* fossils come from Java and Georgia (~1.8 Ma), both outside Africa. During the Ice Ages, sea levels dropped, and vast territories, presumably tree-poor and shellfish-rich, became accessible for handy tool-using omnivores, and since Pleistocene *Homo* fossils are found in coastal sediments from different latitudes and longitudes (Indonesia, the Cape, England), the most parsimonious solution is that *Homo* populations dispersed along the coasts between those sites, possibly during the glacial periods on the then exposed continental shelves (Verhaegen & Munro, 2002). From the coasts, different populations in parallel followed the

rivers inland, arguably at first seasonally (e.g., following anadromous species such as salmon), later sometimes permanently. Joordens et al. (2013) “propose that the Indian Ocean coastal strip should be considered as a possible source area for one or more of the multiple *Homo* species in the Turkana Basin from over 2 Ma onwards.” Since glacial coasts are now far below the present sea level, fossilization of *Homo* might be biased towards inland lakes or riverbeds such as Lake Turkana in the East African Rift Valley.

* *AAH is less about out of or into Africa or Asia scenarios than about coastal dispersal.*

Paleo-anthropologists often discuss when early *Homo* left Africa, but if Pleistocene *Homo* was originally littoral, the question whether they lived, for instance, on the African or the Asian side of the Red Sea is not very relevant. If Pleistocene *Homo* dispersed along the coasts, it should be noted that the East-African coasts do not have extensive continental shelves, as opposed to Sunda in Southeast Asia. Some of the oldest archaic fossils (~1.8 Ma) come from coastal and deltaic sediments in Indonesia (Mojokerto, amid shellfish and barnacles) and from a site in Georgia “rich in lacustrine resources” (Dmanisi, at a confluence of rivers, not so far from the Black–Caspian Sea connection at the time). Both sites are Asian. Yohn et al. (2005) provide DNA evidence (retroviral data) that human ancestors (this does not necessarily mean all *Homo* populations then) were outside Africa at least between ~4 and 3 Ma. If this is correct, they might have been in southern Asia then, but it does not say where they lived after ~3 Ma. (In fact, theoretically, part of our genome might even have been in Africa at the same time when another part was perhaps in Asia.)

* *AAH is less about a riverine evolution in fresh-water than about a coastal life possibly followed by a riverine life.*

Homo erectus’ POS suggests that they, as all other pachyosteosclerotic tetrapods, collected a considerable part of their food in near-shore salt-water habitats. Two ontological data might confirm this. The human newborn’s *vernix caseosa* has only been observed among other species in newborn common seals (Don Bowen, personal communication, and Odent, 2011). And newborn humans have *renculated kidneys* (each kidney consisting of numerous small kidneys, from Latin *reniculus* or *renculus*, the diminutive of *ren*), a trait that is most often seen in marine mammals (Williams, 2006), but this renculization disappears during childhood, when human kidneys and renal concentration powers become more like those of mammals with free access to fresh water, such as pigs (Verhaegen, 1991b). This seems to suggest that a littoral phase in the early Pleistocene (with frequent diving apparently) might have been followed by a more freshwater phase in the late Pleistocene (with more frequent wading presumably).

** AAH is not in the first place about an isolated evolution on an island.*

LaLumiere (1981) suggested that the semi-aquatic phase happened on an isolated island (he proposed Danakil, a Miocene island in the southern Red Sea). Islandization, however, generally leads to drastic brain reduction in mammals. More likely, AAH is about a littoral and estuarine evolution on African and Eurasian coasts (possibly including near-shore, but not isolated, islands) during most of the Pleistocene. Near-shore islands may have been involved, but a long isolation on one island, such as Danakil, seems unlikely.

** AAH is not about unique anthropocentric explanations, but about universally valid biological correlations.*

Hardy (1960) based this theory on comparative anatomy. As an illustration, the combination of fur loss and abundant subcutaneous fat is only seen in (semi)aquatic mammals. (The reverse is not true. Some illogical opponents reject AAH saying that not all (semi)aquatic mammals are fat and furless.) Some AAH proponents and many opponents, however, use just-so purportedly-functional explanations for ‘unique’ human features. For instance, bipedalism is believed to have evolved for running over open plains (opponents) or for wading (proponents), subcutaneous fat for thermo-isolation during cold savanna nights in furless mammals (opponents) or for buoyancy in surface-swimming (proponents), laryngeal descent for breathing large amounts of air for open plain running (opponents) or for diving (proponents). But when we use comparative data, and if necessary and possible, analyse these features into more elementary traits, we discover more realistic and fool-proof, although at first sight sometimes unexpected, correlations. Human locomotion includes, for instance, orthogrady (e.g., seen in gibbons hanging from branches, and in penguins on land), full plantigrady (e.g., as in sealions and ducks on land), very long and straight legs (e.g., in herons and flamingoes more than ostriches) etc. Human laryngeal descent also is composed of at least two different elements (Nishimura, 2003, 2006, 2008; Nishimura et al., 2003, 2006, 2008): laryngeal descent against the hyoid bone (also in other hominoids, and extremely in e.g. hammer-head bats *Hypsignathus monstrosus*), and the typically human hyoidal descent against the mandible (whereas Cetacea have ascended larynges). Below I discuss bipedalism and laryngeal descent in somewhat more detail.

** AAH is not about sudden mutations, macro-evolution, saltations or evolutionary jumps from ape- to human-like, but about a mosaic-like evolution in small steps.*

AAH is not about a sudden evolutionary shift as thought by many opponents (some even reason: humans are unlike aquatic Cetacea and Pinnipedia, hence AAH is wrong) and some proponents (Wescott, 1995). Our ancestors’ evolution is not a straight line, for

instance, from forest to open plain dwellers. Rather, there were a lot of small (mosaic-like) steps in different directions, as discussed below: in my opinion schematically from pronograde arborealism (above-branch) to pronograde and later orthograde aquarborealism (below-branch) to slow and shallow littoral diving (archaic *Homo*) to bipedal wading in very shallow waters (early *sapiens*) and to walking on terra firma (Table 1).

* *AAH is even less about the hominid fossil record than about our own rudiments.*

Some opponents criticize AAH for being untestable, as most of the evolutionary adaptations described by AAH proponents would not have fossilized. But AAH is in the first place a *biological* hypothesis, based on comparisons of extant humans with other animals (parallels) and with chimpanzees (differences): “the remnants of the past that don’t make sense in present terms—the useless, the odd, the peculiar, the incongruous—are the signs of history” (Gould, 1977). Although the hominid fossil record can provide relevant information on African ape (australopith) and human (*Homo*) evolution that would otherwise be unknown (e.g., that most archaic *Homo* displayed POS, or that many early great hominoids had thick enamel), AAH is based on the anatomy, embryology, physiology, biochemistry and DNA of extant humans compared to our close relatives (chimpanzees and other primates) as well as to animals of different lifestyles (including arboreal, terrestrial, littoral, pelagic, and freshwater). Human ‘odd’ traits—ill-adapted to our present way of life (fur loss, fatness, low speed etc. are unexpected in terrestrial mammals)—give clues to how our ancestors lived.

Analytical comparative approach

AAH is in the first place based on comparative biology, but not all features can easily be compared to comparable features in other animals. Moreover, human features such as language and bipedal locomotion are considered to be unique. Consequently, paleo-anthropologists tend to rely on functional interpretations rather than on comparative arguments. However, functional interpretations are often subjective. For instance, since quadrupedal non-human primates live in forests, and bipedal humans live on terra firma, it is easily concluded that the transition from forest to open plain resulted in the adoption of bipedalism (this logical mistake, confusing *since* and *because*, is known as *post hoc ergo propter hoc* ‘after this, therefore because of this’). Once this seemingly-logical interpretation is considered a fact, other misinterpretations follow: since we ‘know’ our ancestors lived on the open plains, it is easy to conclude that in humans, unlike typical open plain mammals, the function of subcutaneous fat was, for instance, thermal insulation in the cool savanna night, or energy depot during endurance running, or for the dry season. And because it is ‘known’ that human ancestors were living on the open plains, there is no need to consider that subcutaneous fat tissues (often seen in

(semi)aquatic but not open plain mammals) could have been a (semi)aquatic adaptation (no matter for what reason: energy storage in the water, thermo-insulation, streamlining, buoyancy, sexual selection, or some other reason). In the same way, conventional paleo-anthropologists who find fossil hominid footbones or footprints automatically assume that such feet evolved ‘for’ running bipedally over open plains, without considering that ostriches (cursorial bipeds) have feet that are higher and shorter than ours, with only two toes, which are spread widely apart and are unequal in length. In still the same way, since we ‘know’ that we lived on the open plains and that our brains need high-quality nutrients (e.g., DHA), and since these nutrients are scarce on the open plain and almost exclusively obtainable from animal food there, it was concluded that our ancestors must have eaten a lot of meat, bone marrow or brains from ‘prey’. This conclusion was corroborated by discoveries of ‘butchering sites’—without considering that all these sites were lake- or riverside, that archaeological materials could have been washed together there, that stones and bones conserve incomparably better than fish or plant foods (biasing the archaeological record), and that virtually all sites where archaic *Homo* tools or fossils have been discovered were near abundant (and sometimes marine) edible shellfish. Also, the fact that some humans can successfully throw spears at ungulates, in combination with the idea that archaic *Homo* regularly scavenged or even hunted, recently led to the conclusion that all human features that allow throwing were developed ‘for’ throwing (Roach et al., 2013)—without considering that (part of) our throwing skills could have evolved stepwise (preadaptations) over long periods in different contexts (e.g., ‘arms overhead’ movements in vertical climbing and/or surface-swimming), and that throwing-skills could at least as easily have evolved for throwing harpoons or nets when wading in shallow water.

Just because some of our features (e.g., human locomotion, language) can appear to be unique, it does not mean that comparisons with other animals cannot be made at all. What is required is to separate these features into as many individual (more elementary) components as possible (ideally these components should be independent from each other). The finer the distinctions, the more detailed reconstructions can be obtained. Since biological features are inherited largely independently of each other (Mendel’s Laws, due to chromosomal recombination and crossing-over during meiosis), there is no reason not to use an analytic approach.

I provide two illustrations, already discussed elsewhere: bipedalism (e.g., Verhaegen & Munro, 2007) and speech (e.g., Vanechoutte et al., 2011).

Bipedalism

It is often stated that human locomotion was an adaptation to running on the open plains, which is illustrated by expressions such as ‘Savannahstan’, ‘endurance running’, ‘born to run’, ‘le singe coureur’ etc., even on the cover of the most influential scientific

journals. Verhaegen et al. (2007) disproved in detail all *endurance running* arguments (Bramble & Lieberman, 2004) that our *Homo* ancestors during most of the Pleistocene were adapted to running over open plains. When we analyse human locomotion into more elementary components, the running ‘explanation’ appears to be a just-so interpretation (cherry-picking): Bramble & Lieberman (2004) interpret every locomotor trait in humans as having evolved ‘for’ running, without even considering possible wading or swimming scenarios. A comparative approach shows that, for each trait, semi-aquatic scenarios provide more parsimonious explanations (Table 4 in Verhaegen et al., 2007), and that extant human running is a secondary and conspicuously imperfect adaptation which evolved late in the human past, for instance, we run maximally 32 km/hr over short and 20 km/hr over long distances, about half as fast as typical open plain mammals.

Typical for human locomotion, as opposed to chimpanzee and other primate locomotion, is not only our habitual two-leggedness (bipedalism s.s.), but also our long and flat foot soles, our very long and habitually stretched legs, our vertical trunk, etc., which we now discuss in somewhat greater detail. The list overlaps, but is not exhaustive:

a) Two-leggedness is seen in birds (including ostriches, flamingoes, and penguins on land), many dinosaurs, and diverse mammals, including kangaroos and hopping-mice on the savanna, tarsiers, indris and gibbons upon branches, and lowland gorillas and proboscis monkeys *Nasalis larvatus* while wading. Large pangolins *Smutsia temminckii* regularly walk on their hindlimbs with horizontal (pronograde) bodies (McCormick, 2007). Most mammals that frequently or occasionally wade, however, are quadrupedal, such as tapirs, hippos and many suids, wetland antelopes or ungulates that seasonally have to cross rivers: they wade into the rivers on four legs, and when the water deepens, they do not proceed on two legs, but simply swim pronogradely. This suggests that human bipedal wading did not cause our bipedal locomotion. Instead, it might have *resulted* from earlier orthograde, see (b) and (c).

b) A more or less aligned body (with head, trunk and hindlimbs in one line) is typically seen in animals that have to swim regularly, probably as a hydrodynamic adaptation. Atelids (e.g., spider monkey) and hylobatids (e.g., gibbons), however, also frequently have more or less elongated bodies when hanging or swinging vertically from branches, and I will argue below that early *sapiens* might possibly have evolved very long and straight legs and a fully upright posture to spot prey from above in very shallow water, for instance, wading with harpoons or nets.

c) Orthograde (‘upright’ truncal erectness, with a vertical lumbar spine) is rare in tetrapods, but is regularly seen in some arboreal species (especially tarsiers, sifakas, atelids and gibbons), meerkats on the look-out, gerunuks eating leaves from branches, gorillas, giant anteaters and kangaroos intimidating or threatening rivals, penguins on land, partly in herons in search for prey in shallow water, etc. Orthograde is very atypical of running tetrapods, for instance, ostriches have horizontal spines. It is not independent from the two previous ones, (a) and (b): walking bipedally with spine and head in the extension of the legs (as in humans and penguins on land, as opposed to ostriches) implies orthograde.

d) Very long hind-limbs in tetrapods relative to forelimb and/or trunk length are typical of frogs, kangaroos, indris and tarsiers (which are hopping, with hips and knees bent in rest, not striding), giraffes, ostriches, and especially flamingoes and other wading-birds, to name a few typical examples. Many swimming tetrapods have short (penguins on land walk orthogradely) or even absent legs.

e) Straight legs (as opposed to bent-knees-bent-hips in rest) are seen from wading-birds to giraffes, and especially in large and heavily-built species.

f) A striding gait (i.e., with alternating limbs, as opposed to hopping or jumping), bi- or quadrupedally, is more frequent in large tetrapods than in smaller ones, more in ground-dwelling than in arboreal species, and possibly more in slow species than in fast ones.

g) Valgus knees are very atypical for cursorial mammals: most or all cursorials have the hindlimb joints in a vertical sagittal plane (Hildebrand, 1974). Among anthropoid primates (reviewed in Verhaegen, 1991a), knees are more valgus in 3–4-year old human children ($\sim 165^\circ$) than in adults ($\sim 170^\circ$), in smaller ($\sim 165^\circ$) than in larger ($\sim 170^\circ$) Hadar specimens (*afarensis*), and in orangutans and spider-monkeys ($\sim 175^\circ$) than in most monkeys and apes ($\sim 180^\circ$).

h) A medio-laterally wide trunk is typically seen in beavers and platypuses, and to a lesser degree in hippopotami, river dolphins as well as suspensory and/or brachiating primates (apes and atelids). Fossil hominids (australopiths as well as archaic *Homo*) typically show iliac flaring, which broadens the pelvis and hence the trunk. Iliac flaring and long femoral necks facilitate femoral abduction through the action of the gluteus medius and gluteus minimus muscles (Aiello & Dean, 1990), an adaptation which is not seen in cursorial mammals. The longer and more horizontal the femoral neck, the more effective femoral abduction is, but also the more valgus the knees have to be in order to have the hip, knee and ankle joints in one line, which might be required in a standing position for a stronger stance. If this is the case, the valgus knee might suggest an often vertical leg stance (possibly for wading) and/or a relatively very heavy body weight. (Note archaic and modern *Homo* have relatively larger femoral heads than apes and australopiths. This too might suggest more bipedalism (with the body weight on two instead of four legs) and/or relatively heavier body weights.)

i) Relatively long and strong outer pedal digital rays, resulting in subequal toe-lengths, are seen in pinnipeds and wading and swimming birds. Cursorial mammals typically have long and strong central digital rays (ray 3, or rays 3–4), never the first or last digital rays.

j) Toe shortening together with hindfoot lengthening as seen in humans is rare or absent in nonhuman animals, cursorial as well as swimming ones. Cursorial tetrapods typically show drastic lengthening of distal hindlimb parts, especially the central digital rays (Hildebrand, 1974).

k) Very flat feet and full plantigrady (i.e., with the heels usually touching the ground or branch) is, for instance, seen in sealions, water opossums, and wading and swimming

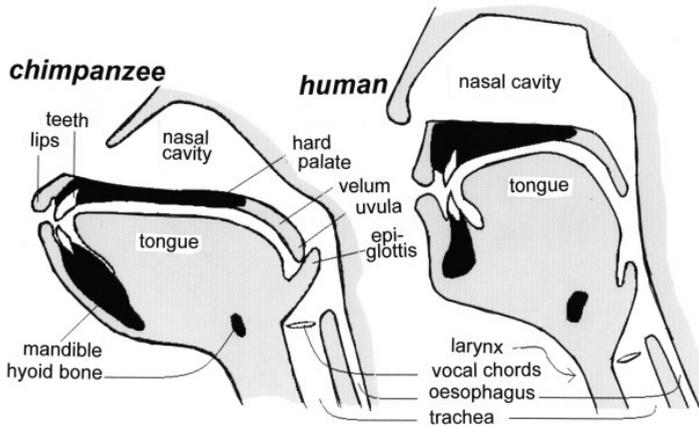


Figure 1. Mid-sagittal view of mouth and throat of chimpanzee and human (schematically). After Laitman (1977), Aiello & Dean (1990), and Vaneechoutte et al. (2011).

birds. Cursorial mammals, however, run on their toes or hooves (digitigrady or unguligrady).

l) Non-grasping feet (with loss of the typical primate grasping) are seen in most non-arboreal mammals. This feature is not independent from the previous ones.

These comparisons are often based on subjective resemblances, sometimes do not seem to allow clear conclusions (j, f), and are preliminary and limited, nevertheless they indicate that humans partly resemble cursorials in leg length (d), less than humans resemble arboreals (a, c, d, g), waders (d, e, i, k) and swimmers (b, h, i, k). One group of adaptations alone (either climbing, or wading, or swimming) cannot explain all the different elements of human ('unique') locomotion, which suggests that human ancestors underwent a rather complex evolution. Taken together, this seems to corroborate our scenario (based on the convergence of other lines of evidence) that human ancestors were originally tree climbers who gradually learned to swim and dive, wade, walk and run.

Speech

This exercise can be repeated with all other features in which humans differ from our closest relatives the chimpanzees, such as the human skin (fur loss, subcutaneous fat, superficial veins, sebaceous glands, sweat glands etc.), nose (poor olfaction, external nose, protruding midface, conchal cavernous tissue, paranasal sinuses etc.) and mouth (philtrum, red lips, small mouth opening, closed parabolic tooth row, masticatory reduction, incisiform canines, vaulted palate, globular tongue etc.).

Even human speech can be analysed into smaller elements. In short, we argue (Verhaegen & Munro, 2004; Vaneechoutte et al., 2011):

m) that musical elements of human speech (e.g., melodic, rhythmic and prosodic sounds, in different voices) originated in the territorial song of the early hominoids (>18

Ma?), comparable to the duetting of hylobatids and some other monogamous animals living in dense vegetation, such as *Indri*, *Tarsius* and *Callicebus* primates, and many bird species (Geissmann, 2000),

n) that our voluntary breathing musculature and breath-holding originated in littoral frequently-diving ancestors (<2 Ma?) who had to hyperventilate just before they wanted to dive, as well as between dives, and to hold their breath at free will during dives,

o) that the typically-human fine control of lips, tongue, velum and throat (now used e.g. in pronouncing labial, dental, palatal, velar etc. consonants) originally evolved for the swallowing (not impossibly also underwater) of soft, wet and/or slippery foods such as molluscs without much biting or chewing,

p) and that our huge brain (possibly indispensable at some time for the development of language, e.g. for attributing an arbitrary meaning to a morpheme or ‘word’) was facilitated by the brain-specific nutrients that are abundant in aquatic foods (e.g., docosahexaenoic acid or DHA, see Crawford et al., 2002).

Laryngeal descent in adult humans has sometimes been interpreted as an adaptation for inhaling large quantities of air—for running (Geoffrey Laitman, personal communication), or to the contrary for diving in human ancestors (Morgan & Verhaegen, 1986)—but both these interpretations are contradicted by comparative data. Once more, we have to analyse human laryngeal descent into smaller elements. Nishimura (2003) described two components of laryngeal descent: hominoids, as opposed to monkeys, have the larynx descended in relation to the hyoid bone, but only in *Homo* (and possibly partly in chimpanzees, see Nishimura et al., 2006) is the hyoid descended in relation to the mandible, so that the larynx in adult humans (Adam’s apple) is lower in the neck



Figure 2. Gorilla in forest swamp, feeding on floating vegetation (AHV). The silverback gorilla “soaks in a swamp for hours, methodically stripping and rinsing dirt from herb roots before munching.”

Note its laryngeal airsac (covered with naked skin, visible in the neck) is partly inflated.

Photo by Ian Nichols, National Geographic Society http://blog.al.com/spotnews/2010/09/malaria_jumped_from_gorillas_t.html <http://nationalgeographicdaily.tumblr.com/image/4692798335>.

Table 1
Proposed Hypothetical Schema of Ape and Human Evolution

Hypothesis	Begin?	Epoch	Animal group	Example	Localization?	Locomotion?	Diet?	Tools?
Aquar-boreal Mio-Pliocene hominoids	~30 Ma	Late Oligocene – early Miocene	early Catarrhini	<i>Saadanus?</i>	Afro-Arabian hot & wet forests	pronograde above-branch + some surface- swimming?	arboreal fruits, nuts etc.	few or none
	~20 Ma	Miocene	early Hominoidea	<i>Morotopithecus</i> & other Mio-Pliocene hominoids	diaspora from Africa to Eurasia in (para)Tethys coastal forests	vertical aquar-boreal: below-branch + frequent floating? wading?	ripe fruits, omnivory ... durophagy + nuts, mangrove oysters	stone tools of capuchin monkeys?
	~10 Ma	Late Miocene – Pliocene	early hominids (relatives of <i>Pan-Homo- Gorilla</i>)	<i>Sahelanthropus</i> , <i>Orrorin</i> , australopiths	African swamp forests, reed- & wetlands?	idem + more frequent wading?	surface- feeding + HSI, floating AHV ...	Oldowan?
Littoral Pleistocene <i>Homo</i>	~2 Ma	Early Pleistocene	archaic <i>Homo</i>	<i>Homo modjokertensis</i> , <i>erectus</i>	continental shelves of Africa & S- Eurasia?	including littoral slow & shallow diving	shellfish, seaweeds? coconuts? ...	Oldowan + later Acheulian
	~1 Ma	Middle – Late Pleistocene	archaic <i>Homo</i>	<i>Homo heidelbergensis</i> , <i>neanderthalensis</i>	idem, littoral, glacials vs interglacials?	idem + seasonally following rivers inland	shallow aquatic animal & plant foods ...	composite & throwing tools, fire?
	~200 ka	Late Pleistocene	anatomically modern humans	early <i>Homo sapiens</i>	Afro-Arabian coasts & rivers	frequent wading, rarely diving, more freshwater	waterside foods, more fish & fowl ...	spears, nets? floating reed huts? boats?
	~60 ka	Late Pleisto – Holocene	idem	extant humans	Africa + out of Afro-Arabia	mostly walking on terra firma	waterside & terrestrial foods ...	domesticated dogs?

than in apes, and much lower than in monkeys. Vaneechoutte et al. (2011) argued, based on comparative data, that, schematically, the first descent was for fine and varied and/or loud phonation in territorial singing (m), whereas the second descent might have been part of a group of adaptations for suction or deglutition of littoral foods that could be swallowed whole without biting or chewing, possibly also underwater (o), such as the small mouth with fleshy lips (red mucosa), shorter mandible, short and globular tongue, vaulted and smooth palate with few transverse palatal ridges, closed parabolic tooth row with incisiform canine teeth, and myosin heavy-chain 16 (MYH16) inactivation in the masticatory musculature (Figure 1).

By using all these comparative results, in combination with the fossil and archeological data, we can try to reconstruct ancient diets and locomotions, as well as possible scenarios of African ape and human evolution (Table 1).

Early hominoids: peri-Tethys dispersal in coastal forests?

Although Mio-Pliocene hominoids were quite diverse, their fossils typically lay in coastal, flooded or gallery forests, lagoons or wetlands (surveyed in Verhaegen et al., 2011). Monkeys dominate extant African primate communities while apes are species-poor, but in the early Miocene, when catarrhine monkeys and apes appeared, the climate was hotter and wetter than today, apes were very diverse, and monkeys were not speciose (Grossman, 2013), which suggests that the flooded and mangrove forests were occupied by early hominoids rather than early cercopithecoid monkeys. The hottest and wettest forests today still have the highest densities of lowland gorillas (Blom et al., 1995), who feed parttime with erect bodies on floating vegetation in the swamp or bai today (Doran & McNeilage, 1998; Nishihara, 1995). In a comparable way, Miocene hominoids in flooded forests could have fed on floating herbs and aquatic herbaceous vegetation (AHV), cane, sedges or papyrus, eggs or frogs, crabs, snails, bivalves or other hard-shelled invertebrates (HSI) between reeds or mangroves etc. Such *aquarboreal* lifestyles (*aqua*=water, *arbor*=tree, see Figure 2) could have included climbing and hanging vertically (all extant apes), grasping branches above the water (lowland gorillas and orangutans in forest swamps), wading on two legs (lowland gorillas in forest bays) and possibly floating vertically for AHV and/or HSI collection (Verhaegen et al., 2011).

Spending a lot of time in the swamp helps explain hominoid body enlargement (as in most mammals becoming more aquatic), tail loss (discarding a superfluous organ), vertical and centrally-placed spine (for vertical wading, hanging and possibly floating), dorsal scapulae with the arms aside (for collecting floating AHV around the body, or grasping branches above the head), and wide thorax and pelvis (as in other shallow water dwelling animals). Some paleo-anthropologists argue that medio-laterally broad thoraxes might be a suspensory or brachiating adaptation (Esteban Sarmiento, personal communication), but New World brachiators such as atelids (e.g., spider monkeys) have

relatively less broad thoraxes than the about equally-large hominoid gibbons (although broader than in most monkeys). Tail loss is even more difficult to explain by pure arborealism, although the hopping indris have very short tails. Even the slow sloths as well as sloth bears and pottos still have short, not absent, tails. Tail shortening is frequently seen in primates that spend some time in the water, for instance, the simakobu *Simias concolor* and three species of *Macaca* that reached the island of Sulawesi. The uniquely-hominoid complete tail loss (incorporating the diminutive caudal vertebrae into the pelvic bottom), however, is not unexpected if they spent a lot of time vertically in forest swamps or wetlands: in an orthograde posture, the tail has no locomotor function, it was hydrodynamically (drag) and possibly thermoregulatorily (heat loss) disadvantageous in water, and could be infected by different sorts of water-born parasites, or bitten by fishes or turtles. It is easy to imagine that an early hominoid wading or floating in a swamp gradually evolved a shorter tail, which it most of the time held between the legs, protecting the body openings and/or supporting the viscera in a habitually erect posture, so that eventually it grew into the pelvic bottom. Note that the vertically brachiating atelids have lengthened, not shortened, tails. Several 'reasons' can theoretically be found to explain hominoid tail reduction (e.g., body enlargement, very slow locomotion, loss of arboreality, cold ambient temperatures, higher latitudes, and need to conserve energy in homeotherms with slow metabolism), but, as far as I know, these have not been able to cause complete tail loss in any other mammals, and, apart from body enlargement, are unlikely to have been present in hominoid ancestors. Aquatic mammals such as beavers, otters, manatees, cetaceans, water shrews etc. have kept the tail or evolved a new one, but they are pronograde swimmers (unlike orthograde hominoids), and most of them live in presumably much more open waters (requiring faster swimming speeds) than the early hominoids.

Did this aquarboreal phase begin before or after the split (~18 Ma?) with the hylobatids (the lesser apes gibbons and siamang)? The hylobatids have complete tail loss as well as broad thoraxes (as all hominoids), habitually upright postures (for hanging from or walking over branches), and gestation times unexpectedly long for their body size, and although they weigh less than other apes, body weight reduction is not unexpected if they became acrobatic brachiators after the great/lesser ape split, so arguably they too had orthograde aquarboreal ancestors. Later Mio-Pliocene hominoids presumably colonized different sorts of aquarboreal niches: coastal (salt water) or inland (usually fresh water), more arboreal (vertical climbing, below-branch hanging or later brachiating) or more aquatic (wading, surface-swimming or/and floating), feeding on softer (AHV) or harder foods (HSI) in the water or the trees, etc.

In this view, the *Homo-Pan* last common ancestor (6 or 5 Ma?), like the australopiths and other fossil hominoids, was still aquarboreal, possibly somewhat resembling lowland gorillas today (Figure 2), but spending more time in the swamps. If the Mio-Pliocene hominids and pongids lived in the Tethys and para-Tethys coastal forests, different lineages including the australopiths might have followed the rivers inland (where

fossilization might have been more likely than in coastal forests). In the australopiths, aquarborealism can explain the unexpected combination of curved hand phalanges (suggesting branch-hanging or climbing arms overhead), a vertical and centrally-placed spine (suggesting orthogrady), and flat foot soles and flat footprints suggesting wading and/or swimming (instead of digitigrady): Pliocene australopiths “existed in fairly wooded, well-watered regions” and Pleistocene robust australopiths “in similar environments and also in more open regions, but always in habitats that include wetlands” (Reed 1997) such as swamp and riverine forests, papyrus swamps, lagoons and wetlands with sedges or cattails (e.g., Shabel, 2010; Stewart, 2010; Munro, 2010; Verhaegen & Puech, 2000). The South-African australopiths seem to have been more omnivorous generally, the East-African australopiths more herbivorous. Paleo-environmental, dento-gnathic, micro-wear and isotopic data independently suggest that East-African australopiths, not unlike extant lowland gorillas in forest bays, might frequently have fed partly or largely on papyrus sedges in the swamps where their fossils lay (Puech et al., 1986; Conroy, 1990; Puech, 1992; van der Merwe et al., 2008; Stewart, 2010; Sponheimer et al., 2013).

***Homo*: from diving to wading?**

According to retroviral data, our direct human ancestors between about 4 and 3 Ma (at least) might not have been in Africa (Yohn et al., 2005). If early *Homo* populations already before ~4 Ma followed the southern Eurasian littoral forests, this could help explain that by ~1.8 Ma archaic *Homo* fossils were found at places as far apart as Java (Mojokerto, amid barnacles and shellfish in a river delta), Georgia (Dmanisi, amid “rich lacustrine resources” David Lordkipanidze informed me), Algeria (Aïn-Hanech, at a coastal floodplain) and Kenya (Lake Turkana, where *erectus* appeared at about the time stingrays did, suggesting a marine connection, possibly already ~2 Ma, see Feibel, 1993; Joordens et al., 2013). A coastal dispersal (likely followed by riverine dispersals) easily explains this longitudinally and latitudinally diverse distribution ~1.8 Ma, as well as the subsequent finds of Pleistocene *Homo* fossils and tools as far as the Cape, Angola, England, China, Flores etc.

However, one very knowledgeable correspondent wrote, and this may reflect a general opinion among conservative paleo-anthropologists: “... we can travel inland to go from Dmanisi to Mojokerto. At least when it came to movement between Dmanisi and Africa, humans could have followed the same routes giraffes, ostriches and hyenas did. There is no direct evidence either the animals or humans followed coastal routes.” But giraffes, ostriches and hyenas do not need as much water as humans do (Verhaegen, 1987, 1991b), they are not typically found next to marine molluscs (Munro, 2010), and an inland route cannot explain the Flores remains (>800 ka?), nor the numerous human traits (fossil, anatomical, embryological, physiological, nutritional, behavioral etc.) that

are easier or even exclusively to understand within a waterside dispersal. That mid-Pleistocene *Homo* reached Flores (>18 km overseas) is not unexpected in the littoral theory (Tobias, 2011), and does not need two hardly credible assumptions, which are moreover mutually hardly compatible: that ancient people were ‘born to run’ yet built sea-worthy rafts or boats ~800 ka. As another correspondent wrote from his own experiences: “... the savannas are not the best place for two feet, the gopher holes and pits and boulders are pretty treacherous, four legs would be a distinct advantage [whereas] in the Caribbean, tourists throw coins into the ocean, and the young guys dive from the rocks to catch the coins as they fall through the water. Their ability to see underwater, to control their breath, to maneuver and dive and to nimbly and delicately grasp a tiny object falling through the warm water: how on earth does an animal have the ability to develop such subtle skills from evolving as a creature running around on the grasslands?”

Sea-levels repeatedly dropped more than one hundred metres during glacials, and on the continental shelves, vast territories (~15 % of today’s land surface)—arguably tree-poor and shellfish-rich—became available for intelligent, dextrous, tool-using, thick-enameled, coastal forest-dwelling hominoids, who could open mangrove oysters (like capuchin monkeys do) and coconuts (containing fresh water) and beach-comb for turtles and their eggs, mussels and crabs. Pleistocene *Homo* fossils (but no other hominoid fossils) are often found in association with marine molluscs (e.g., Munro, 2010; Joordens et al., 2009; Choi & Driwantoro, 2007; Gutierrez et al., 2001), and virtually all known archaic *Homo* sites, including those in savannas, were associated with permanent water and edible shellfish (Munro, 2010). Not unexpectedly, these handy beach-combers on their diaspora to different continents and islands learned to dip and later dive, deeper and deeper, for molluscs and presumably seaweeds. We called this the *continental shelf hypothesis* (Verhaegen & Munro, 2002).

In fact, only frequent diving can biologically explain archaic *Homo*’s POS, the extraordinary thickness and density of many cranial and postcranial bones of most *erectus*-like and other archaic *Homo* fossils (Munro & Verhaegen, 2011; Verhaegen & Munro, 2011). In tetrapods, generalized POS of both cranial and postcranial bones is exclusively seen in littoral, slow and shallow diving species (e.g., dugong and manatee, walrus, *Kolponomos*, pakicetids, *Odobenocetops*, and some *Thalassocnus* spp), and marine biologists agree POS has a hydrostatic ballast function (Taylor, 2000; Madar, 2007; Laurin et al., 2011). The calcium makes the skeleton heavier, but too much calcium as in osteosclerosis renders it brittle and prone to fracture, as in sirenians (Leismer, 2007) and the human disease of Albers-Schonberg.

Some conservative paleo-anthropologists, however, deny this and believe that archaic *Homo* must be an exception among heavy-boned animals and cannot have been littoral. They say that some archaic *Homo* fossils are found far inland, and they sometimes bring far-fetched ‘explanations’ for POS, such as head-banging (Knuckey, 1992) although POS bones are in fact more brittle, and flat skull-caps are more vulnerable to blows than vaulted ones. We discussed these non-aquatic hypotheses for POS at length in Munro & Verhaegen (2011).

Table 2
'Archaic' Features in Pleistocene *Homo* Skulls: Littoral or Freshwater?

Skull of	brain size	flat skull + heavy brow-ridge	orbits very large	projecting mid-face + nose	paranasal sinuses	pachyosteo-sclerosis (POS)
<i>Homo erectus</i>	+	++	?	++	-	++
<i>heidelbergensis</i>	+++	++	?	++	++(+?)	+
<i>neanderthalensis</i>	+++(+?)	+	+	++	+	+
<i>sapiens</i>	+++	-	-	-	+	-
suggesting (see text)	(semi)aquatic & varied diet? DHA?	swimming (streamline)	(semi) aquatic? (dark)	semi-aquatic	freshwater (floating or emerging)	littoral slow & shallow diving

KNM-LO 45500, an *erectus*-like fossil found in freshwater wetlands, had thin cranial bones (Potts et al., 2004), and many heavy-boned *Homo* finds throughout most of the Pleistocene were deltaic or littoral (e.g., Mojokerto ~1.8 Ma, Gibraltar ~40 ka), but other heavy-boned *Homo* fossils were probably found far from the sea. How to explain the archaic features, especially POS, in inland fossils?

There might be fossilization biases. The sea level today is lower than some interglacial Pleistocene sea levels (possibly explaining some 'inland' coastal finds, or marine connections at the time, see Joordens et al., 2013), and is generally much higher than during glacial periods (presumably hiding many archaic littoral fossils). The possibility should be considered that the major part of our ancestors' semi-aquatic adaptations might have happened during the glacials, far below the sea level today, and that during warmer periods they more often followed the rivers inland, but we do not know how fast POS can appear or disappear evolutionarily when moving from salt to fresh water or vice versa (phylogenetic inertia). Some archaic populations could have been littoral during certain seasons (explaining their POS), and during other seasons trekked inland along the rivers (e.g., following anadromous fish), where their fossilization chances might have been higher.

Although the fully marine sea otters use stone tools, the late-Pleistocene composite tools suggest their manufacturers spent at least part of their time outside the water, but what about the early Pleistocene? Although many traditional paleo-anthropologists (e.g., Will et al., 2013) assume without argumentation that the Middle Stone Age shellfish collection in South Africa was a late-Pleistocene innovation (~130 ka), all available data concur to suggest that this 'coastal colonization' was only a left-over of a much more pronounced littoral phase earlier in the Pleistocene, or possibly a recent re-colonization of the coasts. In any case, although there are still numerous uncertainties, there is no reason why POS in archaic *Homo* should be explained in a unique way, different from POS in other mammals.

Regular slow and shallow littoral diving parsimoniously explains many other ‘odd’ features seen in *Homo*—fossil (e.g., ear exostoses, projecting nasals and mid-face, low and long braincases with pronounced frontal ridges, flattened femora, huge brain size) and living (e.g., fur loss, SC fat, head–spine–legs in one line, and in human newborns vernix caseosa and reniculi). The fossil *Homo* traits that are more typical of diving species (e.g., POS, platycephaly, platymeria, ear exostoses, external nose) apparently did not appear before the Pleistocene epoch: arguably, our ancestors’ most-littoral phase began with the Ice Ages, when *Homo* during glacials could colonize the drying continental shelves (Table 2). It is to be expected that these dextrous primates intensified their handedness (like clawless otters *Aonyx capensis*, who seek prey in reedbeds and under rocks) and stone tool use (in parallel with sea-otters *Enhydra lutris* in kelp beds), and that this superior handedness, together with the growing brain, led to the beginning of technological skills (stone and later wooden tool use and manufacture) which preadapted these littoral creatures to following the rivers inland. The abundant brain-specific nutrients in aquatic foods (DHA, iodine etc.) presumably facilitated brain growth. (In *Homo sapiens*, the ‘poorer’ post-aquatic diet possibly required a longer youth to grow the same brain size.) From the coasts and estuaries, different *Homo* populations gradually (presumably seasonally, and later more permanently) ventured inland along rivers, and many late-Pleistocene *Homo* populations might have been more freshwaterside than littoral. Neanderthals and pre-neanderthals generally had less POS but larger paranasal sinuses than *erectus* (Table 2), their bones had been washed into the caves according to the discoverers of the Neanderthal fossils of Engis and Neanderthal (Huxley, 1863), their fossils often lay just above those of beavers (*Castor* as well as *Trogotherium*), their dental calculus sometimes contained traces of waterlilies (Henry et al., 2011), and some of their tools bore traces of cattails (Paunovic & Smith, 2002; Shreeve, 1996), so perhaps (if their C and N isotopic values are to be explained by meat-eating, as paleo-anthropologists traditionally propose) they hunted or scavenged ungulates in shallow water, reedbeds, mud or amid water(side) vegetation in beaver ponds or oxbow lakes, whereas at the coast they still collected shellfish and butchered whales and seals (e.g., at Gibraltar, see Stringer et al., 2008).

Homo sapiens’ gracile skulls (with higher and shorter vaults, and reduced POS) appeared in the fossil record at Omo and Herto in East Africa after 0.2 Ma, and humans developed longer tibias and presumably straighter legs, they got shorter and less horizontal femoral necks, a narrower pelvis, and relatively long and more vertical spinous processes of the mid-thoracal vertebrae (stabilising the orthograde spine). This suggests our ancestors (~0.2 Ma?) abandoned regular diving, but more frequently waded upright and beach-combed on two legs, possibly to spot edible foods in very shallow water such as cray- and shellfish and/or to spear fishes from above or perhaps to use nets. The remarkably high frequency of varicose veins on the hindlimbs but not arms in humans (a very variable trait) suggests that this wading-adaptation (superficial veins are ideal to discharge superfluous body heat to the surrounding water, and the water pressure

prevented varices) is disappearing. Not impossibly, these modern-looking people might usually have slept in some primitive sort of floating reed huts (far more primitive than what is seen in Marsh Arabs) above the water (safer from predators), used reed boats or dugouts, and possibly nets, and spent more and more time outside the water, walking on land plantigradely as they did in very shallow water. Maps of human population densities show that, although we have become fully terrestrial today, we are still a waterside species, and perhaps half of human dietary calories still come from the water: fish, shell- and crayfish, rice, aquaculture, etc.

The nowadays popular ideas about Pleistocene human ancestors running in open plains ('endurance running', 'dogged pursuit of swifter animals', 'born to run', 'le singe coureur', 'Savannahstan') are among the worst scientific hypotheses ever proposed. The surprising frequency and diversity of foot problems (e.g., hammertoes, hallux valgus and bunions, ingrown nails, heelspurs, athlete's feet, corns and calluses—some of these due to wearing shoes) and the need to protect our feet with shoes prove that human feet are not made in the first place for running. Moreover, humans are physiologically ill-adapted to dry open milieus: "We have a water- and sodium-wasting cooling system of abundant sweat glands, totally unfit for a dry environment. Our maximal urine concentration is much too low for a savanna-dwelling mammal. We need much more water than other primates, and have to drink more often than savanna inhabitants, yet we cannot drink large quantities at a time" (Verhaegen, 1987). This does not imply to say that human ancestors or relatives never lived on savannas, only that if they did, it was at the wetlands and rivers there. Apparently we evolved running—only lately, and only about half as fast as equids, bovids, felids or canids, and even slower than arboreal primates—in *spite of* our broad build, short toes and plantigrade feet, profuse sweating, and large subcutaneous fat tissues (a burden of ~10 kg in most people). Of course, healthy adult men can sometimes outrun ungulates (the usual 'argument' of conventional paleo-anthropologists) and provide a limited part of the calories for the group, but this dogged pursuit is largely confined to a few inland populations in East Africa today, is derived and probably very recent (less than a few thousands of years), and it requires a rather specialized technology with water bags, weapons and poisons. Quadrupedal chimps can hunt colobus monkeys and even eat them raw, but archaic *Homo* with their heavy bones (POS), very broad pelves and valgus knees, shorter legs and flat feet were much too slow on land. Humans have a remarkably poor olfaction (Gilad et al., 2003) and low muscularity, which make regular scavenging, and a fortiori hunting, unlikely. In fact, our small mouth, spatulated canines and closed tooth-row, short tongue and smoothly vaulted palate are ill-designed for meat-eating, but ideal for consumption of slippery foods (and preadaptive to the evolution of human speech).

Conclusions

Many scientific as well as popular publications on the so-called *aquatic ape theory* or *aquatic ape hypothesis* give incorrect impressions of how, when and where our semi-aquatic ancestors could have evolved. This paper provides arguments from diverse biological subdisciplines for the following three hypotheses, which to conservative anthropologists might seem unexpected at first sight, but are based on what is known from other animals: the comparative evidence.

(1) The *aquarboreal theory* of Mio-Pliocene hominoids suggests that our Miocene and Pliocene more apelike ancestors and relatives, including the australopiths, led an aquarboreal life, living in wet forests such as flooded, mangrove or swamp forests and later in more open wetlands, and fed on hard-shelled and other plant and animal foods at the water surface and the waterside as well as in the trees.

(2) The *littoral theory* of Pleistocene *Homo* (AAH sensu stricto) suggests that early-Pleistocene archaic *Homo* populations dispersed along the coasts, where they reduced climbing adaptations, but frequently dived and used stone and other tools for feeding on shallow-water and water-side foods including shellfish.

(3) The wading hypothesis of early *Homo sapiens* suggests that, later in the Pleistocene, *Homo* populations gradually ventured inland along the rivers, reduced diving skills, and frequently waded with very long and stretched legs and fully upright body to spot prey in very shallow water and used complex tools to collect different sorts of aquatic and waterside foods.

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