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Umbrella hypotheses and parsimony in human evolution: a critique of the Aquatic Ape Hypothesis

Conventionally, anthropologists have sought to explain a multitude of unique features of modern humans as the outcome of a single adaptive breakthrough. These "umbrella hypotheses" are aesthetically appealing because they appear to be parsimonious. As internally consistent hypotheses about the past, they are very difficult to prove incorrect in an absolute sense. Anthropology has often rejected them by consensus without developing explicit reasons. This essay explores one example of these models, the Aquatic Ape Hypothesis, the proponents of which continue to argue that they have not received a fair hearing among anthropologists. The hypothesis is troubled by inconsistencies and has not been reconciled with the fossil record. More importantly, its claim to parsimony is false. The numerous "explanations" for individual anatomical traits that it generates constitute premises that are not better founded than competing terrestrial "explanations". The unifying theme of aquatic adaptation is considerably less parsimonious than the assumption that our lineage has always been terrestrial. Finally, the mosaic pattern of hominid evolution demonstrated by the fossil record will not support this or any single cause theory. Most of these criticisms have been previously voiced in one form or another, yet umbrella hypotheses ranging from mainstream science to the paranormal maintain their popularity among students, general audiences, and scholars in neighboring disciplines. One reason for this is that simple answers, however wrong, are easier to communicate and are more readily accepted than the more sound but more complex solutions. Evolutionary science must wrestle with this problem both in its own community and in the education of the public.

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Introduction

"There is always an easy solution to every human problem—neat, plausible, and wrong" (H. L. Mencken).

Orderly and far-reaching explanations have a great aesthetic appeal within the academic community, where breakthrough explanations can advance disciplines and careers. I offer the term "umbrella hypothesis" to describe a simple idea that overspreads and appears to resolve many scientific questions. Such ideas may be quickly and easily communicated and understood, and therefore extend their appeal outside academia to the general public. The many umbrella hypotheses of human evolution have another property in common. In searching for a key transforming element, they reinforce the sense of human privilege and uniqueness within the natural world by singling out for evolutionary emphasis those traits by which we differ most strikingly from other animals.

A number of umbrella hypotheses have been proposed to explain human origins over the past century based on, for example, hunting (Ardrey, 1976), sexuality and pairbonding (Morris, 1967; Fisher, 1982), aquatic life (Hardy, 1960; Morgan, 1972), and male provisioning of the family (Lovejoy, 1981). Each model evokes a reaction in the anthropological community and may stimulate new research directions. They may have a greater impact on the public. None of the past umbrella hypotheses has been or is likely to be absolutely disproven, although

they are generally set aside by the profession, most are resurrected from time to time by scholars outside the immediate disciplines of human evolution.

Of these models, the aquatic ape hypothesis encountered the coldest reception and received the least attention from anthropologists. Unlike most of the others, it continues to have a small circle of active proponents who remain outside the mainstream of the field. A cluster of non-anthropologists continues to publish supporting articles. Another handful of authors—professionals in related fields—occasionally cite the model favorably (Calvin, 1986; Horrobin & Huang, 1983; Richards, 1987; Sauer, 1962; Thong, 1982). Thus, the aquatic ape hypothesis continues to be encountered by puzzled students who wonder why mainstream paleoanthropologists overlook it. If only because of this last audience, it should not be ignored.

The aquatic ape hypothesis (AAH)

The AAH in its present form was first articulated by Alister Hardy in 1960 in an issue of *New Scientist* magazine featuring the relationship of man and the sea, past, present, and future. According to Morgan (1990), Hardy had sat on his ideas for three decades before offering them publicly. Having observed a number of anatomical parallels between distinctively human traits and marine mammals, he proposed that the human lineage had been shaped evolutionarily by a temporary phase of adaptation to a littoral habitat. In 1972, Morgan developed Hardy's scenario further in her book *The Descent of Woman*. In addition to expounding the AAH, Morgan used the book as a vehicle to attack Morris' *Naked Ape* and other male-centered models from a militant feminist perspective.

Neither of these publications evoked much studied response from the anthropological community. The reasons for this silence were certainly many. Paleoanthropologists have been accused of being closed-minded to new ideas, sexist, and prejudiced against non-anthropologists or non-academics or Europeans (Morgan, 1990; Richards, 1991; Tuomisto, pers. comm.). From the discipline's perspective, some anthropologists have regarded the ideas as not worth the trouble of a rebuttal. The contexts of the two publications, the first a popular essay and the second a politically strident tract, diverted attention from whatever serious scientific proposal they contained.

In addition, the AAH mostly concerns developments in soft tissue anatomy and physiology. Paleoanthropologists rarely speculate beyond the musculoskeletal system and brain size as revealed in fossils. Morgan reports that two leading introductory texts have no substantive discussion of the evolution of hairlessness, for example (1990: p. 69). This neglect of soft tissues does not reflect the absence of ideas on the topic nor a "conspiracy of silence", both of which Morgan infers. It reflects the unfortunate divergence of paleontologists studying hard tissues from comparative anatomy and the consequently limited scope such textbooks and many authors maintain.

The AAH was the subject of a published symposium that represented both favorable and opposing views in Roede *et al.* (1991). The AAH has been reiterated by Morgan (1982, 1990) and received contributions by Cuanne (1980), Ellis (1986), Evans (1992), Verhaegen (1985, 1987), and LaLumiere (1981). Nonetheless, it remains in limbo, neither dead to its adherents nor acknowledged by the mainstream academic community. It is worth re-examining, so that we may better understand how we evaluate models of evolution and how rejected models thrive even within the broader scientific community.

Anatomical evidence for the AAH

The evidence for the AAH is drawn from modern human anatomy. It is unfortunate that the hypothesis has been unable to make use of the numerous fossil discoveries concerning human origins since 1960. Supporters continue to cite the large number of human features that are explained by the model; however, closer examination of individual traits considerably weakens this claim. Most of these traits have hypothetical explanations in more conventional scenarios.

Bipedalism

Morgan argues the transition to bipedalism would have been improbable without a transitional aquatic phase to counter the effects of gravity, because of the numerous health costs associated with it, including increased lumbar weight-bearing and associated lower-back problems; the necessity of supporting the visceral mass and its associated risk of herniation; and an increased variability of cerebral blood pressure and associated risks of fainting and varicose veins (Morgan, 1990: pp. 24–35). As Morgan notes, these costs are not intolerable, since they are borne by modern humans. However, they would create a serious hurdle for a quadrupedal species under selection to become bipedal. Morgan argues that an aquatic habitat would be a good transition zone since immersion in water would counteract many of the effects of gravity, while wading would have favored bipedal posture and locomotion.

Authors who wish to recite the many disadvantages of bipedalism commonly do so by comparing humans to medium-sized terrestrial quadrupedal mammals. However, hominoid ancestry has probably never included medium-sized terrestrial quadrupedal mammals. A comparative anatomy of living hominoids reveals a pattern of climbing and/or suspensory specializations across the taxon. This pattern includes relative lengthening of the upper limb and its use in suspension, increasing use of upright posture supported by the lower trunk and lower limbs, and increasing use of bipedal posture and gait (Fleagle *et al.*, 1981; Temerin & Cant, 1983). Morgan wrongly dismisses these specializations on the grounds that brachiation is irrelevant (1990: p. 27). The climbing/suspensory complex both removes our ancestry from conventional terrestrial quadrupedalism and helps to bridge the gap toward human bipedalism.

Elongated lower limbs

The human lower-limb structure is well adapted for swimming. However, modern body proportions, with elongated lower limbs, do not occur until the genus *Homo*, well after the putative aquatic phase (Aiello & Dean, 1990).

Breath-holding and speech

Humans can voluntarily override the respiratory control centers of the brainstem and suspend breathing for a limited time. This skill has not been demonstrated for other terrestrial mammals and is obviously necessary for swimming. Morgan (1982) and Verhaegen (1987) argue that only humans among primates developed speech because no other species had the necessary breath control. Morgan cites dolphin vocalizations as the closest analogy with human speech.

The origin of voluntary control of human breathing is to be found in bipedalism. Quadruped breathing is constrained by the mechanics and muscular contractions of

locomotion; thus respiration is locked in phase with gait (Bramble & Carrier, 1983). Because the human upper limbs and thorax are not involved in locomotion, we are able to breathe independently of gait.

Breath control is of obvious importance for speech and may need no other explanation. Voluntary control of the glottis and muscles of respiration permit us to modulate sound volume, voice, and cadence of speech. Could speaking itself have depended on an aquatic heritage? Probably not. The complex vocalizations of cetaceans are not typical of other aquatic species and their adaptive significance, aside from sonar used by some of these species, is not clear. The parallel with humans is superficial and only a circumstantial link to an aquatic life. Aquatic adaptations cannot explain the equally complex speech capabilities of certain birds, such as parrots.

Enlarged pharynx

Humans have separated the palate and the epiglottis by enlarging the pharynx. This enables us to gasp air rapidly through our mouths to ventilate between dives (Morgan, 1990: p. 135). However, the descent of the larynx is also an important adaptation for speech. The enlargement of the chamber, while making us more vulnerable to choking, increases our repertoire of vowels, enabling us better to shape the sounds of our speech.

Morgan (1990) is disingenuous on this count. She examines work by Crelin on the development of the pharynx at length, and all but ignores his observations on the relationship between the pharynx and speech (Crelin, 1987). She exposes the inadequacy of alternative explanations for the position of the larynx, but ignores the speech hypothesis. Only at the end of her discussion does she observe the relationship between breathing and speech and considers the respiratory changes to be preadaptations for the latter.

Nose

Morgan suggests that the projecting human nose is an adaptation to protect the nasal cavity while diving. Her argument is built in part on comparisons with the proboscis monkey and tapir, which sometimes navigate flooded habitats (1972: pp. 38–39; also Ellis, 1986), and the elephant, which Morgan believes also has an aquatic ancestry.

The external form of the human nose is highly variable and it is difficult to characterize the species. Some of this variation has been related to climate. Since the human face and nasal cavity have been much shortened relative to those of other primates, extending the cavity externally partly compensates in the important functions of warming and moistening incoming air.

Respiratory valves

The human soft palate, unlike that of other primates, can elevate and close off the nasopharynx. This is a necessary feature of aquatic mammals that must be able to keep water out of the respiratory passage (Morgan, 1990: p. 136). According to Verhaegen (1985), this function was satisfied by external nasal muscles and internal vascular tissue on the conchae that have since become “rudimentary”. However, the “rudimentary” nasal muscles described by Verhaegen are part of the much more complex set of muscles specially developed in humans for facial expression and communication; and there is no evidence that they were ever better developed.

Paranasal sinuses

The extensively developed paranasal sinuses are postulated to create buoyancy for the upper respiratory tract (Evans, 1992). Morgan cites a review paper (Blanton & Biggs, 1968) that critiques past explanations of the sinuses as evidence that there are no better hypotheses. In fact, Blanton & Biggs make the point not that preceding hypotheses are all wrong, but that no model has been supported by thorough investigation. Certainly that criticism applies no less to Evans' model.

Diving reflex

Humans, including infants, share with all diving mammals the “diving reflex” in which immersion of the face stimulates the vagus nerve and causes a depression of heartbeat. The diving reflex appears to be adaptive for a swimming species, yet Morgan (1982) acknowledges that some terrestrial mammals also exhibit it. Other living hominoids have not been tested in this regard. The data on this subject are insufficient to support the AAH.

The diving reflex in human infants facilitates underwater birthing. Although this obstetric practice never achieved great popularity, it has demonstrated that newborns may be quite comfortable in the water and may survive several minutes of immersion. On the face of it, it is not surprising that a neonate—human or otherwise—immersed for months in amniotic fluid would find water less stressful than air.

Reduction of body hair

This most conspicuous of human features clearly parallels developments in all fully aquatic and some amphibious mammals. This and several traits discussed below including subcutaneous fat and thermally sensitive eccrine sweating relate to a strategy of thermoregulation and internalized insulation that is explained similarly in both the aquatic and terrestrial models. While it is valid to point out the parallel strategies of human and aquatic mammals, the similarity does not strongly favor one model over another.

Direction of hair follicles

Morgan observes that the hair follicles of the human trunk point caudally in a pattern that reduces drag in the water. Verhaegen (1985) proposes that scalp and facial hair, well oiled by sebaceous secretions, helped to smooth the contours of the head and neck and thus streamline the body for more efficient swimming. It is curious that the contours would not have been streamlined by reshaping skeletal and soft tissues.

Sexual dimorphism of scalp hair

Morgan (1972) speculates that long hair in women may have provided a lifeline by which a floating infant may grasp its mother and not drift away. Scalp hair does serve the function of protecting the head. Any sexual differences in length, which varies considerably among populations, are usually interpreted as reflecting sexual selection (Bruhes, 1977).

Subcutaneous fat

Humans have an unusual amount of subcutaneous fat that functions for buoyancy and to a lesser degree for insulation in place of fur. This is a parallel adaptation with many aquatic mammals. However, the fat-and-sweat strategy of thermoregulation may be adaptive for a species that is more concerned about shedding internally generated heat. Insulative fat, rather

than hair, permits the bloodstream to bypass it as needed, taking hot blood from the core of the body to the surface to be radiated or lost through evaporation.

Activity of sebaceous glands

Sebaceous glands, which produce an oily secretion to protect the fur, are very active in the human face and scalp. Morgan argues they waterproof the skin in aquatic mammals, but are useless in terrestrial humans, causing only complications such as acne.

Paucity of apocrine glands

Apocrine sweat glands have been highly reduced in number and distribution in humans. The evaporative cooling function they serve in many mammals is absent in humans, having been taken over by eccrine glands. Apocrine sweat glands secrete pheromones for sexual signalling. Their significance is lost for humans because pheromones would have been washed away in an aquatic environment (Morgan, 1990: pp. 84–85). She extends this argument to explain the reduced size of the human nasal cavity and a reduced sensitivity to smell relative to other primates and especially relative to other mammals (Morgan, 1982: pp. 96–97). Other aquatic mammals also have diminished ability to discriminate smells.

If the losses of olfactory sensitivity and pheromone effectiveness are to be interpreted primarily as due to the shift in habitat, one must infer a great deal of time spent in the water for olfaction not to be useful on land. Specifically, sexual arousal and intercourse would both have occurred in the water, according to this reasoning. This is rarely true except for fully aquatic mammals.

Eccrine sweating

Employment of the eccrine glands over the entire body for evaporative cooling is unique to humans. Human sweating is notorious for its profligate expenditure of water and salt. Under extreme conditions, the loss of either water or salt may become life-threatening. According to the aquatic hypothesis, humans evolved in circumstances in which neither water nor salt were in short supply.

The increased distribution of eccrine glands over the body is a pattern observed in other higher primates. What appears to be unusual among humans is their sensitivity to temperature. Thermoregulatory sweating is a feature shared with several other large terrestrial mammals, including horses, although these animals use apocrine rather than eccrine secretions. Non-human eccrine glands respond to sympathetic arousal rather than temperature, as do those in the human palm. Morgan's explanation for the predominance of eccrine glands has several problems. There are few habitats where both water and salt are independently in plentiful supply. Fresh-water animals must conserve salt. Marine animals must excrete salt from their body fluids, but they must conserve water. Dehydration resulting from sweating would be as catastrophic in a marine mammal as it would in a terrestrial one.

Morgan speculates that eccrine glands once secreted a hypertonic solution relative to blood plasma and thus functioned to rid the body of salt (1990: pp. 95–96). She does not explain why these glands have subsequently become so wasteful of water. At present, human sweat is hypotonic because of active recovery—not excretion—of sodium from sweat by the eccrine glands. In individuals that already have low levels of sodium, the salt content of sweat can be markedly reduced (Weiner & Hellman, 1960).

Similar to the hypotonic eccrine sweating, human kidneys produce urine that is more dilute than is typical for terrestrial animals. The salt concentration of human urine (1430 mOsm/l)

is somewhat less than that for marine animals (about 1800 mOsm/l) and much less than that of savannah mammals (>2800 mOsm/l) (figures from Verhaegen, 1985). Verhaegen attempts to reconcile these contradictions by suggesting humans inhabited both fresh and salt-water environments simultaneously or successively.

Evaporative cooling would be relatively unimportant for a species with constant access to water. Morgan observes that fur seals use evaporative cooling via sweat glands in their fins, but this need would be unlikely to drive the excessive sweating observed in modern humans. The AAH does not explain the human strategy better than does a terrestrial hypothesis.

Absence of "salt hunger"

Morgan claims that humans have no "salt hunger"—i.e., no instinctive drive to consume salt based on physiological need for it—because we experienced an excess. In fact, humans do have a taste for salt that is loosely keyed to body state. Salt-deprivation studies have shown that human subjects lower their detection threshold for salt in food, show a generalized loss of sense of taste, and increase their preference for salting their meals (Denton, 1982). Subjects in one study developed intense cravings for salt. Our bodies appear to be opportunistic in other tastes, favoring fat and protein whether we need them immediately or not, and we appear to treat salt in a similar way. This is not consistent with a habitat where salt is in dangerous oversupply.

Vaginal depth

The uterus is withdrawn deeper into the body to protect it from seawater (Morgan, 1990; pp. 146–147). The penis is correspondingly lengthened. Many anthropologists have discussed the astounding length of the human penis, but few have made the eminently logical connection that Morgan does with the extraordinarily deep vagina. Morgan supports her explanation with the observations that certain aquatic birds and reptiles have acquired organs of intromission while their relatives lack them; this reduces the chance that sperm might be washed away by the water. The problem with this argument is the assumption that any increase in length/depth is equivalently adaptive. A small penis acquired by a marine reptile does not explain why the typical primate pattern, which has an even greater size, is inadequate for aquatic primates. In the terrestrial model, increased vaginal depth is most likely a secondary consequence of bipedalism (Gallup & Suarez, 1983).

Hymen

The hymen, unusual among primates, exists to protect the vagina from sea water (Morgan, 1990; p. 151). The hymen is a variable feature even among humans. It is a fetal structure usually incomplete, but varying normally from completely sealing the vestibule to completely absent. If reproduction is to occur, the hymen must be permanently stretched or broken. The ability of the hymen to protect the vagina is temporary, at best.

Frontal sex

Frontal sex occurs commonly in aquatic mammals and is unique among primates under natural conditions. Terrestrial models link frontal sex with upright posture, a connection Morgan acknowledges. Thus her observation that frontal sex is "the commonest mode [of copulation] in aquatic mammals except those which go ashore to breed" (1990: p. 151) is irrelevant. Frequent frontal sex has also been documented for non-aquatic bonobo chimpanzees (e.g., Blount, 1990; Thompson-Handler *et al.*, 1984; Wrangham, 1993).

Loss of estrus

Morgan explains that estrus swellings among catarrhines function to protect females of terrestrial species from dirt at critical times. Humans lost estrus swellings with the abandonment of a terrestrial habitat. Furthermore, estrus attraction is primarily an olfactory mechanism and has become impractical as water washes away pheromones. Morgan's description of estrus as an olfactory phenomenon ignores the standard definition of estrus as a behavioral state (Ford & Beach, 1951; Hrdy & Whitten, 1986). Estrus includes a state of mind of the female, as well as a variety of signals (olfactory, visual, or behavioral) to the male. Defined this way, estrus has been prolonged, not lost, in humans.

Breasts

In 1972, Morgan argued that human breasts evolved to make it easier for infants to reach the nipple while the mother nursed it on land, although some authors have argued that breast development interferes with nursing (Fisher, 1982). Although she discusses at length the parallel development of breasts in sireneans (pp. 33–35), she makes no attempt to connect breast development adaptively with an aquatic habitat.

Tears

Humans are unique among primates in weeping psychic (emotional) tears that flow in excess of what is needed to moisten the conjunctiva. Morgan cites parallels among sea birds and reptiles that have nasal salt glands to eliminate excess salt from the body and among seals, otters, and elephants that secrete in response to emotions (1982, 1990), but it is not clear how she intends to explain the human pattern. Since human tears drain across the conjunctiva and evaporate in the nasal cavity, the lacrimal gland is a very unlikely (and unparalleled) choice to secrete excess salt. Tears in her non-human parallels are just as inexplicable as they are in humans. Her cited reference (Frey & Langseth, 1985) reports anecdotal evidence of emotional tears also in many terrestrial species: dogs, wolves, rats, a gorilla, cats, cows, hogs, lambs, a horse, a turtle, and a kangaroo, but reviews all of the non-human examples skeptically. If the animal observations are meaningful, it is clear that psychic tears are not restricted to aquatic species. If they are not, tears are not relevant to the aquatic model.

Large brains

Morgan hypothesizes that the double shift in habitat presented new challenges that were met by increased intelligence, thus initiating a trend that continued much later than the return to land. The rapid expansion of the human brain is certainly one of the remarkable and inadequately explained facts of human evolution. Morgan's explanation is not significantly different or any more specific than those offered by terrestrial hypotheses—e.g., that tool use or hunting or social complexity or climatic deterioration during the Ice Ages locked hominids into a positive feedback loop—since these hypotheses are presently untestable and cannot be used as evidence supporting any particular scenario.

Morgan ties brain expansion to an ideal balance of fatty acids (a 50:50 ratio of Omega-6 to Omega-3 fatty acids) needed by the brain that is most easily obtained from the marine food chain (1990: p. 169). However, a worldwide preponderance of landlocked peoples attests to the fact that a marine diet is not nutritionally essential.

Webbed digits

Morgan cites Hardy in observing that some degree of webbing occasionally appears between toes or, less commonly, fingers. She comments,

“It is extremely rare for congenital abnormality to take the form of adding a feature (as here, the interdigital webbing) that is usually believed to have been absent from our own species and from *our whole biological order* (the Primates) throughout its evolutionary history” (1982: p. 77).

In fact, digital webbing is part of the normal tetrapod pattern of development. Digits are created in the hand and foot by the elimination of cells between them. Webbing may reflect the failure (or perhaps normal variation) of the process to proceed to its usual completeness and not the creation of new tissue.

Neoteny

In her 1982 book, Morgan criticized and rejected neoteny as a competing theory of human evolution; but in 1990, Morgan suggests that neoteny is a shared pattern between humans and aquatic mammals resulting in such features as lack of ears, reduced appendages, loss of hair, and expansion of the brain (pp. 172–173). Neoteny may or may not have been an important evolutionary mechanism in human evolution, but it is neither an adaptation nor an explanation by itself. The only relevant comparisons of neoteny in aquatic mammals and humans would be the individual consequences that may have favored selection for neoteny, many of which have been discussed. This is another gratuitous analogy.

Tool use

Hardy (1960), Morgan (1972), and Verhaegen (1985) suggested that tool use may have come about as a means to exploit shell fish. They cite parallels with the sea otter, which uses hard objects to break open abalone shells. As Morgan observed in 1982, a considerable time lag is found between the appearance of bipedalism and tools. At best, one and not both, is associated with a putative aquatic phase. Although it is conceivable that the earliest pebble tools were unmodified and thus unidentifiable in the fossil record, such a possibility does not constitute evidence for the aquatic hypothesis. Tool use itself is now recognized among a wide variety of terrestrial mammals and birds.

General critique of the evidence

Individually, terrestrially adaptive stories are at least as strong as those in the AAH, which is not to say that any are “proven”. Both aquatic and terrestrial “explanations” are built on conjecture, and evaluation of them is quite subjective. The arguments for the AAH mostly fall into six categories of evidence (Table 1). Among them, only items in the first constitute independent evidence to support the hypothesis.

(1) Primary evidence—traits in common between humans and aquatic mammals that may be understood as adaptations for aquatic habitats (e.g., breath-holding ability).

(2) Parallelisms—features evolved in parallel with aquatic mammals but which are inadequately explained by the aquatic hypothesis (e.g., breasts).

(3) Consistencies—traits not contradicting the hypothesis but not suitable as independent evidence (e.g., speech).

Table 1 Summary critique of the anatomical arguments for the AAH

Primary evidence—possible aquatic adaptations	Voluntary breath-holding and enlarged pharynx—probably secondary to speech Thermoregulatory strategy—also adaptive in terrestrial environments Absence of salt hunger—questionable
Parallelisms inadequately explained by the aquatic hypothesis	Complex vocalizations Olfactory reduction Emotional tears—parallels are questionable Loss of estrus Breast development Enlarged brain Neoteny Tool use
Traits consistent with the AAH	Bipedalism—not typical of aquatic animals Speech—not typical of aquatic animals Protruding nose—variably expressed in humans Paranasal sinuses Long scalp hair—not typical of aquatic animals Sebaceous gland distribution Apocrine gland distribution
Primitive traits	Diving reflex Infant tolerance of immersion Hymen Webbed digits
Hypothetical reconstructions of past traits	Respiratory valves—not currently present Hair follicle orientation—not currently functional Dilute urine production—not currently present
Secondary developments	Elongated lower limbs—secondary to bipedalism Body hair reduction—secondary to thermoregulatory strategy Subcutaneous fat—secondary to thermoregulatory strategy Eccrine gland development—secondary to thermoregulatory strategy Increased vaginal depth—probably secondary to bipedalism Increased penis length—secondary to vaginal depth Frontal sex—secondary to upright posture

(4) Primitive traits—common to many mammals, both terrestrial and aquatic, and which therefore cannot support one model or the other (e.g., diving reflex).

(5) Hypothetical characteristics—traits or functional states not currently observed (e.g., salt excretion).

(6) Secondary traits—consequences of adaptations in the above categories (e.g., frontal intercourse).

Two internal inconsistencies undermine the hypothesis. The first is the contradictory evidence regarding marine or fresh-water habitat. Morgan argues that the copious salt loss during sweating and absence of a “salt thirst” are maladaptive in any habitat except salt-water. The copious water loss during sweating would be maladaptive in a marine habitat, and the presence of a dietary salt preference is also not consistent with a marine habitat. Moreover, the terrestrial distribution of hominid fossils has been explained by their association with fresh-water deposits. The most reasonable interpretation within the AAH would be the assumption that sweating evolved after a return to land from a fresh-water habitat, but this surrenders a major part of the aquatic argument constructed from the unique skin and lacrimal glands.

The second problem is an ambivalence regarding the extent of specialization for aquatic life experienced by our ancestors. The greater the hypothesized specialization, the more improbable the rapid return to land. Many specific interpretations point to extensive commitment to the sea—e.g., respiratory adaptations, reduced olfaction, mating (loss of pheromones, reproductive system alterations), and child care (long hair, breasts) in the water. Many other reasonable specializations, such as streamlining of the torso and repositioning the nostrils, are not present in our species. The typical quadrupedal head form with an elongated face that is directed forward while swimming would have been adaptive, but hominids more than any other primate have eliminated this. Much has been made of behavioral parallels with species such as the proboscis monkey that show little, if any, morphological adaptation (Ellis, 1986). If human ancestors were no more adapted to water than *Nasalis*, as Morgan's discussion sometimes implies, the entire list of anatomical traits would be irrelevant.

Time, place, and the fossil record

Whatever difficulties emerge, the AAH is unlikely ever to be disproven on the basis of comparative anatomy. One body of data that potentially can disprove it is the fossil record. To the credit of the proponents of the AAH, the model has become much more specific as to the time and place of the aquatic phase. However, the problems of reconciling it to the fossil record have increased over the years.

Morgan's 1972 book was quite vague concerning which phase of hominid ancestry was aquatic. Before that time, it was widely believed that the human–ape split occurred 14 million years ago, leaving plenty of time for such adaptive shifts. In the following years, the majority of paleoanthropologists accepted the molecular clock data pointing to a much later divergence of the lineages and presently would place this event at about six million years ago. Most recently, Morgan dates the aquatic phase, “between six and seven million years ago and three-and-one-half million years ago” (1990: p. 22). Morgan argues that this time window does not need to be very large since strict isolation of a small population with an abrupt change in the habitat can cause rapid evolution.

Aquatic theorists (e.g., LaLumiere, 1981; Morgan, 1982, 1990) favor the geological setting of the Danakil region of eastern Ethiopia. This corner of Africa among the Red Sea appears to have been surrounded by a marine basin from six million to 70,000 years ago. The resulting island is a site where an isolated population could have responded to a shifting habitat by rapid evolutionary change and speciation. Furthermore, this region of Africa is the general vicinity of the earliest known australopithecine fossils beginning shortly after five million years ago.

Morgan stated explicitly in 1982 that “*Australopithecus* was the ape that returned to the land” (p. 116). This implies incorrectly that all of the adaptations cited as evidence for the AAH are present in *Australopithecus*, as well as later *Homo*, and that australopithecines were at least as well adapted for swimming and diving as ourselves. Their postcranial structure is unique and is not simply a direct intermediate between those of chimpanzees and humans. Anthropologists have been unable to agree how to interpret their pattern, mostly debating the extent to which australopithecines continued to live in trees; but there does not appear to be any aspect of their adaptations that suggests swimming. A high intermembral index, flared ilia for strong hip abduction, a powerful peroneal complex, a knee possibly incapable of full extension, and a conical rib cage indicate a body less well designed for swimming than that of modern humans. Reconstructions of the head depict an ape-like upper respiratory tract lacking “aquatic” adaptations (Laitman, 1982).

The fossil record might appear less problematic if the evolution of aquatic adaptations were understood to continue through the early stages of genus *Homo*, at least to 2.0 million years ago. By this time, however, hominid fossils are widely scattered in East and South Africa in a greater variety of habitats. It is true that these fossil deposits are consistently associated with water (Morgan, 1990; Verhaegen, 1985), on lake shores, stream and river channels, or "caves" (fissure fills); but this is because such conditions provide the rapid burial usually necessary for fossilization. Hominid fossils always occur with those of terrestrial species, and the simultaneous presence of fresh-water fauna does not support the notion that the hominids were themselves water-dwelling, much less marine.

Morgan stated in 1982, "... in the absence of any complete fossil record, none of [the competing hypotheses] is any more or less susceptible to 'proof' than any of the others" (1982: p. 21). While this statement might have been disputed in 1982, the subsequent years have made the fossil record much more complete and less compatible with the aquatic hypothesis.

Umbrella hypotheses and the problem of parsimony

False comparisons

Morgan offers the aquatic hypothesis in opposition to "the savannah theory." The savannah hypothesis is described briefly in her 1982 book as a series of hypotheses that, by their vagueness, would have found general agreement with a large number of anthropologists but would have been considered sufficient by none. The savannah theory is, in fact, the collective discipline of paleoanthropology. It encompasses all the frequently proposed and rejected models, discussions, debates, and hypotheses that assume a terrestrial habitat for all stages of human evolution. Within this corpus of work are, of course, many contradictory ideas and numerous alternative hypotheses for nearly any question that has been posed.

Morgan extracts from this process of science a profession of ignorance. Regarding the problems of (1) bipedalism, (2) hair reduction, (3) large brains, and (4) speech:

The orthodox answers to these questions are: (1) "We do not yet know"; (2) "We do not yet know"; (3) "We do not yet know"; and (4) "We do not yet know." The list of questions could be considerably lengthened without affecting the monotony of the answers (1990: p. 5).

At one level, this is an accurate admission of the limitations of science. Neither paleoanthropologists nor proponents of the AAH can presume to hold final answers to questions of causes of evolutionary events. On the other hand, this is a very unfair depiction of legitimate science. To state "we do not yet know" is not to admit total bafflement. Anthropologists may concur on a single model or they may debate two or more serious hypotheses without insisting they have found the final answers. This aspect of the argument for the aquatic hypothesis greatly resembles the approach that "creation science" takes to evolutionary biology. In comparing a single model to an entire academic field, there is an illusion of contrasting order with chaos.

The savannah hypothesis that Morgan criticizes turns out to be a straw man. Anyone who dredges up a century of hypotheses can find many to ridicule; but if the field has already rejected them, the exercise is pointless. In fact, scholars are now discarding the savannah setting for hominid divergence. Recent paleoecological work favors a woodland or mosaic habitat for early australopithecines (e.g., Kingston *et al.*, 1994; Sikes, 1994; WoldeGabriel *et al.*,

1994). Although Morgan's book reflects the growing evidence for this (1990: pp. 17–18), she nonetheless directs criticisms at an older savannah model.

Parsimony

This false comparison produces an appearance of parsimony for the AAH that continues to make it appealing. The parsimony of a hypothesis—its making few untested assumptions—is not an issue of validity. However, in the absence of absolute knowledge, science favors parsimony and informally relies upon it to evaluate alternative hypotheses. Umbrella explanations appear to be parsimonious. Given an initial scenario—intense sexual selection, the advantages of a male bringing food to his mate, the advantages of cooperative hunting, adaptation to aquatic life—the principal characteristics of human uniqueness can be paraded as logical consequences. The very fact that competing umbrella models exist tells us that logical connections are not sufficient.

Morgan states that her AAH “accounts for more of the difference between man and the other primates than does any alternative theory” (1982: p. 122). She understands parsimony in terms of embracing many observations under a single premise. However, there are at least two levels of premises or assumptions to be considered, the evolution of individual traits and the habitat scenario itself. At neither level is the AAH more parsimonious than other models. There are several reasons for this:

(1) Most evolutionary scenarios are weakened because they explain traits without predicting them. Surmising an aquatic phase does not predict that the human form would evolve. With the diverse examples of seals, otters, manatees, and porpoises before us, one must explain why observed human traits and not other ones were selected. Thus evolutionary explanations for individual traits must still be surmised.

(2) Explanations for individual traits are no more free from conjecture in the AAH than they are in competing models. Umbrella hypotheses link a series of individual explanations, but a given hypothesis—for hairlessness, for example—is not more parsimonious within the AAT than within a terrestrial scenario.

(3) The evaluation of parsimony should consider not only observed phenomena, but also unobserved possibilities. The AAH must explain why humans do not have a fusiform torso and dorsally oriented nostrils, among other traits.

(4) The larger premise of the AAH—that terrestrial hominoids adapted to a marine habitat and then adapted back to a terrestrial one—is a much more complicated and less parsimonious scenario than the assumption that a lineage that was terrestrial in the Middle Miocene and terrestrial in the Middle Pliocene was terrestrial in the intervening time. It is this unnecessary complication of the narrative that has led many anthropologists to reject the hypothesis out of hand.

Mosaic evolution revisited

The AAH, like other umbrella hypotheses, proposes specific linkages in the evolution of disparate traits. The hominid fossil record continues to demonstrate that key traits appear at different times and therefore probably for different reasons.

Bipedalism arose more than four million years ago and appears to have been evolutionarily static until *Homo* significantly reconfigured the postcrania about two million years. At least two different events with two different explanations are required to achieve the modern human gait.

The size of posterior dentition and related anatomical features increased as the australopithecine lineage diversified, was reduced in the earliest *Homo*, and continued to decline at varying rates until the present. At least two different adaptive shifts producing opposite results are indicated.

Relative brain size was expanded slightly in *Australopithecus* but began an accelerated rate of growth in *Homo* after 2.5 million years. It is not clear whether the expansion of the brain in *Homo* is gradual or episodic, but the later factors encouraging brain expansion do not appear to have acted on *Australopithecus*.

The basicranium, indicating something of the shape of the upper respiratory tract, changed between earliest *Homo* and *Homo erectus*, perhaps between 2.0 and 1.5 million years. This is the best evidence at present for the development of speech capabilities, but is not clearly linked to the evolutionary events listed above.

The evolution of different traits at different rates is a familiar pattern of mosaic evolution. The fossil evidence demonstrates that the shaping of the human species was not a single event, nor did it represent a linear pattern of change. Moreover, with as many as five or six hominid species existing at one time (Tattersall, 1996), hominid evolution is not one evolutionary story, but many different ones. It is unlikely that all of the story will fit under a single umbrella hypothesis.

The appeal of unorthodox theories

The aquatic hypothesis is only one of several ideas rejected by orthodox science that has refused to go away. Unorthodox hypotheses have been fiercely maintained by respected researchers in their fields (e.g., Peter Duesberg, Linus Pauling). More are supported by peripheral scholars (e.g., melanin studies, homeopathy) and by primarily non-academics (e.g., Creationism, "Chariots of the Gods"). While such issues arise in different contexts, those that generate lay support have certain properties in common.

First, they offer absolute answers that may not be available from orthodox science. Science is presented to pupils and the public at large as a series of answers concerning what is. Although much is made of discovery at the frontiers of science, little is noted of the ignorance that defines that frontier because the process of science is largely hidden from view. Science loses face when it fails to give absolute answers, and opportunities for unsupportable models appear.

Second, heterodox ideas feed on a suspicion of and rebellion against establishment science and other authority. The role of science in society has shifted in the past century and especially in the last generation. Instead of offering hope for societal problems, science and technology are accused of being their cause. Media have emphasized stories of egocentrism and dishonesty in the sciences while academics themselves challenge objectivity. Scientists may be accused of conspiring to suppress free investigation into unwanted truths from Africanist history to Gulf War syndrome. While past histories of science have glorified the underdog status of Galileo and Darwin in challenging conservative religious authority, modern writers celebrate those who triumph over scientific authority. Morgan's 1990 book three times compares the poor reception of the aquatic hypothesis with that of the continental drift theory of Wegener.

Third, there is a special appeal for peripheralized segments of the population in rejecting the authority that science and academia represent. For some of the examples above the attraction is to acquired immunodeficiency syndrome (AIDS) victims, African Americans, and fundamentalists. Morgan's first book spoke with the passion of embittered and victimized feminism.

Fourth, popular models, whether orthodox or otherwise, are easily communicated in simple narrative. This is an attractive mode of explanation and most easily satisfies those not actively engaged in the primary evidence. Popular narratives hide the messiness even from other scientists in which nearly all scientific ideas are born and debated.

Fifth, the models are supported by a great emphasis on negative arguments. Even though Duesberg offers only general ideas on how AIDS might be caused, he challenges mainstream medicine by asserting the human immunodeficiency virus (HIV) link has not been proven. Creationism argues almost entirely from a perceived insufficiency of evolution. While Morgan's explanations for human anatomy are no more rigorous than alternatives, she places a great deal of weight on the tentativeness of hypotheses in the terrestrial models.

Finally, unorthodox models are especially successful when consensus views are not easily communicated to the public. Many questions of evolution, for example, are easy for people of any background to ask. Responsible scientific answers are much more difficult to deliver. It is much easier for a lay person to believe an "expert" who misstates the Second Law of Thermodynamics than to understand what constitutes a closed thermodynamic system and why complex life forms do not necessarily indicate a decrease in entropy. It is much easier for that lay person to be told that evolution of the eye is impossibly complex than to ask that person to understand it. Lay audiences do not readily sit still for a recitation of technical details, especially when they come with an honest disclaimer of final solutions. Similarly, within evolutionary studies, simple narratives of adaptation, however far-fetched, are easier to recite than non-adaptive answers. "We can hold our breath because we adapted for diving" is a simple statement. "We can hold our breath because respiration is independent of locomotion in a biped" requires more understanding.

These difficulties assail mainstream science. Professionals and lay persons alike are reluctant to look for complex stories with weak plots. Until we do, however, we will resemble the proverbial drunk looking for his keys not where he lost them, but where the light is best.

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