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WADING FOR FOOD THE DRIVING FORCE OF THE EVOLUTION OF BIPEDALISM?*

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ABSTRACT

Evidence is accumulating that suggests that the large human brain is most likely to have evolved in littoral and estuarine habitats rich in naturally occurring essential fatty acids. This paper adds further weight to this view, suggesting that another key human trait, our bipedality might also be best explained as an adaptation to a water-side niche.

Evidence is provided here that extant apes, although preferring to keep dry, go into water when driven to do so by hunger. The anecdotal evidence has suggested that they tend to do this bipedally. Here, a new empirical study of captive bonobos found them to exhibit 2% or less bipedality on the ground or in trees but over 90% when wading in water to collect food.

The skeletal morphology of AL 288-1 (“Lucy”) is shown to indicate a strong ability to abduct and adduct the femur. These traits, together with a remarkably platypelloid pelvis, have not yet been adequately explained by terrestrial or arboreal models for early bipedalism but are consistent with those expected in an ape that adopted a specialist side-to-side ‘ice-skating’ or sideways wading mode. It is argued that this explanation of *A. afarensis* locomotor morphology is more parsimonious than others which have plainly failed to produce a consensus. Microwear evidence of *Australopithecus* dentition is also presented as evidence that the drive for such a wading form of locomotion might well have been waterside foods. This model obtains further support from the paleo-habitats of the earliest known bipeds, which are consistent with the hypothesis that wading contributed to the adaptive pressure towards bipedality.

1. INTRODUCTION

The recent discovery of *Sahelanthropus tchadensis* Brunet *et al* (2002) has brought into focus once more questions about the factors which may have led some ape clades to begin to evolve those most distinguished human traits: large brain size and bipedality. This is the oldest hominid yet found and, dated at between 6 and 7 million years ago, must have lived at around the same time as the last common ancestor of *Homo* and *Pan*.

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From the paleo-ecology of the find it is rather clear that water was a significant part of his landscape. The fossils were found at the site of the ancient 'Mega' Lake Chad which dominated the area and included a significant number of aquatic or amphibious fauna, including an abundance of *Anthracotheriid* 'swamp pig' fossils. This clear potential association of the earliest hominid found with a water-side habit yet begs the question — what evidence is there that aquatic habitats generally might have driven human evolution?

Recent nutritional and biochemical studies have strengthened the idea that human evolution probably occurred in water-side habitats and not, as is still largely advocated in many paleo-anthropological circles, a predominantly, semi-arid savannah environment. Broadhurst *et al* (2002) show that there is a growing body of biochemical evidence suggesting that one of the key human traits, our large brain, could not have evolved on the savannah where, they argue, the quantity of certain naturally occurring essential fatty acids (EFAs) such as docosahexanoic acid (DHA) and arachidonic acid (AA) in the food chain is too meagre to have driven (or even allowed) such a dramatic increase in brain size. They argue that a water-side habitat, where such EFAs especially necessary for brain growth are very plentiful, is consequently more likely to have been the place where humans evolved.

One of the other key traits that distinguish humans from other apes is our bipedality. Since Darwin first suggested that humans and apes had evolved from a common ancestor there has been much speculation about the causative factors which might have led to the adoption of this unusual form of locomotion. However, despite its simplicity, plausibility and consistency with evolutionary paradigms (Darwinian natural selection and the Crawford/Marsh (1989) notion of substrate driven evolution—'plastic heredity') little serious scientific study has been undertaken into the plausibility that the first bipeds might have waded in water.

This paper reviews the anecdotal evidence for wading apes and offers some new empirical data from captive bonobos which supports the hypothesis that the earliest bipedal hominids may have been predominantly wading apes and that the motivation for doing so might have been the search for food. Furthermore it argues that traits in the fossil record of the most well known of the early bipeds—Lucy—which have remained controversial despite over twenty-five years of intense scrutiny—is not only consistent with the hypothesis but actually resolves some of the dilemmas and contradictions which remain if moving through water is not considered as a possible mode of locomotion. The idea that this wading might have been driven by the search for food is supported by microwear evidence from *Australopithecus* dentition which is compatible with the hypothesis that they fed of waterside sedges.

Finally it proposes that the paleoecology of the earliest hominid sites is entirely consistent with this water-side based model for the evolution of humans.

1.1 The Wading model for the origin of bipedalism

The idea that bipedalism was first practiced in wading apes is not a popular one. It was first published in an English-language journal by Sir Alister Hardy FRS (1960) but has received little attention since apart from steadfast support by a popular science writer, Elaine Morgan (e.g. 1998). A host of terrestrial or arboreal models, some which also involve food (e.g. carrying food Hewes 1961, Washburn 1967, Lovejoy 1974, 1980, picking small food items from branches Jolly 1970), have been widely discussed. (See Niemitz 2002 for a brief, recent review of the existing theories or Hunt 1994 for an older but more comprehensive review.) No true consensus has yet arisen amongst these models to explain the adoption of a bipedal mode of locomotion in hominids but one of the most promising lines of investigation in this area has been to try to find analogues of facultative bipedalism in extant apes. This approach was pioneered by Kevin Hunt who, in 1994, published a landmark paper about an extensive study of wild chimpanzees (*Pan troglodytes*) in their natural habitat in Gombe and the Mahale Mountains in Tanzania. The opening lines of his paper were ... “Contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism.” In over 700 hours of observation time he found that the chimpanzees studied spent less than 3% of their time in a bipedal posture but that foraging for food was the most common (80.4% of bipedal incidents) motivation for doing so, when they did. 59 out of 97 recorded incidents of bipedalism were due to feeding vegetation and 15 were due to insect feeding (Hunt 1994, p. 185.)

The clear implication of this study is that food may well have been the major driving factor that led the first bipeds to change their main method of locomotion. Hunt’s study showed no evidence for wading bipedalism however. In that regard it merely demonstrated how, in their typical habitat, chimpanzees usually avoid water completely.

The fact that chimpanzees do not spend much time in and around water today, however, does not mean the early ancestors of humans did not do so. Indeed it does not mean other apes today do not do so either. The questions remain: how do apes behave when they *do* move in water? And what evidence is there that hominid ancestors may have done so?

The next two sections will attempt to answer one of these questions each.

2. WADING IN EXTANT APES

2.1 Anecdotal Evidence of Wading

The extant apes *Pan troglodytes* (chimpanzee), *Pan paniscus* (bonobo), *Gorilla* and *Pongo* (orang-utan) have not traditionally been associated with wet habitats and have rarely been observed wading in the wild. Indeed in the past they have been considered so fearful of water that moats are often used to contain them in

captivity. There is consequently a remarkable scarcity of scientific data about wading apes. Even anecdotal information is rare although more recently evidence (mainly film or photographic) has been accumulating that suggests that the *Hominoidae* may be more comfortable in water than might have been previously assumed.

2.1.1 *Pongo*

Galdikas (1980), Ellis (1991) and Sommer & Amman (1998) have all either commented about orang-utans (*Pongo*) wading or have published photographs showing such behaviours and Ashley Leiman of the Orangutan foundation made this statement “Since 1986 I have visited Tanjung Puting National Park in Indonesia, on numerous occasions. During this time I have frequently seen orangutans wading bipedally in the swamp and river.”

2.1.2 *Gorilla*

Gorillas have also not traditionally been linked with water but Ellis (1990: p.57) provides anecdotal evidence in captive gorillas that they can swim. Also Doran & McNeillage (1998: p. 121) and Parnell *et al.* (2001: p. 294), studying Western Lowland Gorillas in the field, provide evidence of splash displays and feeding in the marshy swamps of Mbeli Bai. Parnell (2000, personal communication) observed several bouts of bipedal wading in these animals and wrote ... “when crossing any expanse of open water too wide to bridge by reaching and clinging to swamp vegetation and dragging oneself across, in water over about 2 feet deep, most adult gorillas waded bipedally. Water up to approx 100–150cm deep has been crossed in this way.” The main motivation for this wading behavior would appear to be the search for “aquatic herbaceous vegetation”.

2.1.3 *Pan troglodytes*

Even chimpanzees, which have long been considered the most hydrophobic of all the apes, turn out to be surprisingly fearless in water when they are sufficiently driven by hunger to get their feet wet. Angus (1971: p. 51) and Nishida's (1980) both provide anecdotal evidence of chimpanzee locomotion in water. In addition to this there has recently emerged some significant photographic footage of chimpanzees wading bipedally in fairly deep (chest high) water from a research student, Jess Tombs, working at a chimpanzee sanctuary in the Conkouati reserve lagoon. Again, the motivation for these chimpanzees overcoming their undoubted fear of water and launching themselves, sometimes up to their necks, in the Congo—was hunger. A worker in the field there, Karlovski (1996), described their behaviour in the following

way. “Generally the whole group runs into the water, when the boat carrying the caretakers and the food arrives on the island—holding their arms high to keep as dry as possible. Chimpanzees usually go into water only in emergencies, but the food is so tempting that they lose their fear of water.”

2.1.4 Pan paniscus

Finally, in bonobos too (the least studied of the great apes) there seems to be growing evidence that they are less fearful of water and show a greater tendency to wade than their chimpanzee cousins. Uehara (1976), de Waal (1996: p. 185), de Waal & Lanting (1999: p. 79–82) all document anecdotal evidence of bonobos moving in water in the wild. Again much of this evidence appears to be related to gathering food (according to de Waal 1996: p.185, this included small fish from small rivers and streams.)

What is lacking in the literature, however, is a specific study into the way extant apes move in water. It is this gap in the knowledge base that this paper attempts to begin to fill.

2.2 Analysis of new empirical data of captive *Pan paniscus* wading bipedality

2.2.1 Methods

Ten captive bonobos were studied at Planckendael (near Mechelen, Belgium) wild-life park on the 12th April and 13th/14th June 2001. They have a sheltered enclosure which leads directly to a large island surrounded by a moat. Eight of the ten bonobos in the group were studied.

The principle behind the study and the methodology used was largely based upon Hunt’s (1994) work with some changes. The most obvious difference was that this study was with captive bonobos not wild chimpanzees. Secondly, the study focused on the substrate in which the bipedalism was observed rather than the behavioural context in which it occurred. In this regard it specifically undertook to identify and quantify the types of locomotion exhibited in water.

All observations were made using a Sony digital handy cam with 25 frames/sec precision. Over four hours of continual bonobo behaviour was recorded for detailed, in some cases frame-by-frame, analysis later. Thus, in three days, it was possible to generate potentially 14,400 lines of, continuous second-by-second, data to analyse. (Although actually, because the technique allowed long periods of inactivity to be ‘skipped’, the actual number of data items recorded in the database was 1,319.)

Postural categories were based upon the work of Hunt (1994).
The most significant ones for this study were:

TABLE 1

Description of Postural Modes

Postural Mode	Description
Bipedal	Unsupported bipedalism. Subject stood or walked without the aid of upper limbs.
Upright	Supported bipedalism. Subject stood or walked with most of the body mass on the hind legs but using upper limbs for balance.
Knuckle-walking	Quadrupedal posture or movement.
Swinging	Brachiating whilst above the ground.
Sitting	Sitting



Figure 1. Wading Bonobo Exhibiting Unsupported Bipedalism

A mixture of observation techniques was used. Five focal studies were undertaken when one animal was followed continually for a half-hour slot. One hour's worth of observations were recorded of isolated, real or anticipated instances of contextual wading behaviour.

Inducing Wading Behaviour

It is well known to staff at Planckendael that visitors to the bonobos often throw food items to them. This behaviour is strongly discouraged, but nonetheless the food is keenly accepted. Often these pieces of food fall short of their intended destination and instead, drop into the large moat which surrounds it. When this happens the bonobos simply wade in and claim it.

One difficulty was that although it would undoubtedly have been very easy to induce the bonobos to wade into the moat, the authorities at Planckendael did not permit any such experimentation as they did not want to be seen condoning the widely held practice of visitors throwing food to the animals. Also they are getting increasingly nervous about the prospect of the bonobos escaping the enclosure as they get more comfortable in the water. This policy inevitably had an impact on this study. Instead of controlling the wading events, the observations had to be predominantly reactive: waiting for and anticipating children (usually) to throw in pieces of food into the moat. This meant that the overall amount of time that bonobos were observed in water was very small (only about two minutes.) However, workers at Planckendael have gone on record stating that the wading behaviour observed is very typical. Also the actual type of the food being given to the apes was not controlled and was largely unknown. It appeared that most of the children appeared to be throwing small pieces of bread and fruit to them.

This study was primarily focused on the substrate that the bipedalism took place so four substrates were defined:

- *Terrestrial*, where the individual was at least partly touching land.
- *Arboreal*, where he or she was above the ground and not touching it. At Planckendael there are not many trees in the enclosure but there are a variety of climbing apparatus which were classified as arboreal nonetheless.
- *"In Water"*, where no part of it was still touching dry ground.
- *"Partly in water"*, where at least one part of the body was touching dry ground.

2.2.2 Results

Substrates used

As expected, analysis of focal study data (only) clearly showed that bonobos prefer the terrestrial substrate (72.63%) with arboreality taking up almost all the other time (27%). Only 0.37% of time was spent in contact with water (See Fig. 1).

The results here confirm the accepted wisdom that bonobos generally prefer not to enter the water.

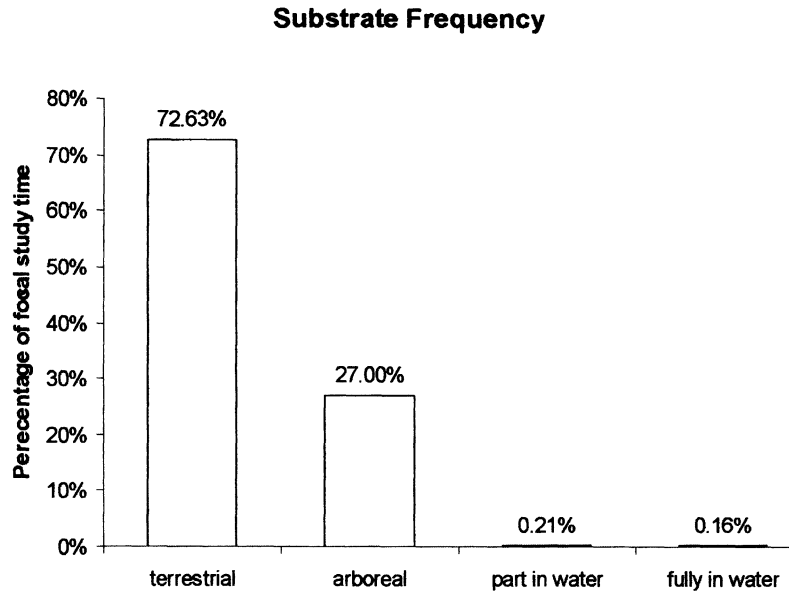


Figure 2. Time spent in various substrates

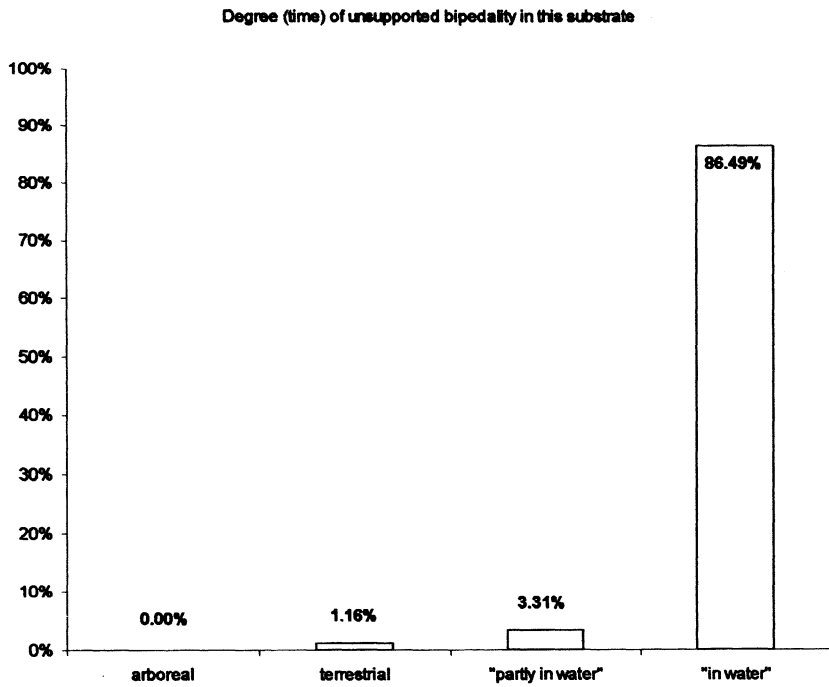


Figure 3. Unsupported (only) Bipedality by substrate

Mode of posture and locomotion in water

The contextual data and focal data together were used to determine the levels of bipedality in different substrates.

Although only 37 seconds was spent in water with no contact with dry land at all, almost all of it (34 seconds, 92%) was spent in an upright (supported or unsupported bipedal) posture. A larger proportion of time (121 seconds) was spent in water with some part of the body touching dry land. Apes in this substrate were upright for over 50% of the time. When terrestrial or arboreal, accounting for more than 99% of observed time for the group, the level of bipedality dropped to around or below 2%.

2.2.3 Discussion

The bonobos observed at Planckendael spent very little time in water and only did so at all because visitors threw food items (itself not encouraged) too weakly to reach them. However there is no doubt that the amount of time they spent in the water was, very much, determined by human behaviour and it would seem that at least some individuals could have been induced into the water at will in response to being offered food. Bonobos almost always entered the water feet first and adopted a bipedal posture even when the moat was shallow enough for them to have done so quadrupedally.

2.3 Conclusions

The anecdotal and observational evidence presented here indicates that, although extant apes prefer not to get wet, they are more than prepared to do so if they are given a strong enough incentive and that the drive for food is usually sufficient reason. In answer to the question 'how do extant apes move in water?' the answer would appear, in general, to be: bipedally. Or at least, their mode of locomotion is far more likely to be bipedal than on land. Equally clear is that in deep enough water, they have little choice but to move bipedally or swim. As only *Gorilla* out of the four great apes have been reported to be able to swim (Ellis 1991: p. 55) it would seem that wading may occasionally be a life-saving behaviour in the wild.

It is difficult to imagine any other scenario with such a clear-cut, immediate survival benefit for moving bipedally as the one provided by waist deep water but it does beg a serious question: If a putative ancestor did wade regularly, where is the fossil evidence to support that theory.

The next section investigates this problem and attempts to answer the question 'what evidence is there that the earliest bipedal hominids waded'

3. WAS *AUSTRALOPITHECUS AFARENSIS* A WADING APE?

In the 1970s Oxnard (e.g. 1975) through the use of new techniques, such as multivariate, morphometric analyses, became sceptical of the prevailing view that placed Australopithecines ancestral to *Homo*. Using such techniques he demonstrated how their post-cranial skeletons differed so markedly from *Homo* as well as from the African apes that he had to conclude that they were probably of a different lineage altogether or, as he put it, (1983: p. 331)—“that human bipedality was not the only experiment in this direction. The australopithecines are displaying for us another experiment, and, given that they are now extinct, one that failed.”

Oxnard agreed (p. 329) that *Australopithecus*, *Homo*, *Pan* and *Gorilla* are (or were) all closer to one another than any of them are to *Pongo* and that they are most similar to *Homo* in exhibiting a propensity for “a type of bipedality.” However, he argued against the notion that it was an intermediate form of bipedalism, “close to the pathway of the evolution of bipedality as expressed in the evolution of man.” Instead he suggested that Australopithecines in displaying uniqueness in their morphology may have been functionally unique too. He wrote (p. 329) “They therefore displaced *either* a totally new and unknown manner of locomotion which would be unique in its own right (and which we will judge unlikely), *or* they possessed such a mixture of locomotor abilities, therefore anatomical adaptations, and therefore, in turn, bony morphologies, as to be rendered unique through being curious functional and morphological mosaics.”

The objective of this section is to reopen the question on this curious morphology. Specifically, it is to consider Oxnard’s first option, the one he dismissed as unlikely, that it was the result of an unknown mode of locomotion, and simply ask: Was *Australopithecus afarensis* a wading ape?

Before doing so it should first be considered if the *A. afarensis* morphology has already been adequately explained in terms of its locomotor repertoire by existing models. This will be tackled in three parts. In the first, the debate about the general locomotor repertoire of *A. afarensis* is discussed. In the second the attempts to relate her peculiar pelvic morphology to its potential functionality, and specifically her gait, are reviewed. Finally the third discusses the possibility that if *A. afarensis* did wade bipedally perhaps they had a way of doing so that was different to extant hominoids today.

3.1 In which ways did *A. afarensis* move: two modes or three?

The question must be asked: Was Lucy arboreal, terrestrial, a bit of both *or what*? The debate thus far about the way *A. afarensis* (e.g. as summarised by Stern 2001) has been primarily focused on how arboreal she was and how human-like her undoubted bipedality manifested itself. It seemed that she walked on the ground and/or climbed in the trees, the only question was: how

much in each? Recently however, evidence of another mode to her locomotory repertoire may have been found that might complicate this picture. Richmond & Strait (2000) found notches on distal radii that were analogous to similar structures found in chimpanzees and gorillas associated with knuckle-walking. Their findings suggest that “bipedal hominids evolved from a knuckle-walking ancestor that was already terrestrial” (p. 382).

In the same journal Collard & Aiello (2000) review the finding and discuss the dilemma posed by it. On the one hand it could be argued that the knuckle-walking traits are “non-functional retentions from the common ancestor of hominoids and African apes,” “The alternative idea” they reason “that *A. afarensis* combined knuckle-walking, bipedalism and climbing—is somewhat counterintuitive, because it implies the use of two entirely different modes of terrestrial locomotion.”

It is argued here that the most parsimonious explanation for the knuckle-walking traits of *A. afarensis* has to be, simply, that *A. afarensis* was, at least partially, a *knuckle walker*. This indeed *would be* counterintuitive if one assumes that *A. afarensis* moved only in the terrestrial and arboreal substrates. However, if one considers that its bipedality was primarily for moving in water, then the dilemma disappears. Seen this way *A. afarensis* had three modes of locomotion for three different substrates: climbing and brachiating for the trees; knuckle-walking on solid ground and wading in water.

3.2 Predicting Lucy's bipedal gait

Whether *A. afarensis* had two or three modes of locomotion nobody doubts that it was, at least in some way, bipedal. Lucy's (AL 289-1) post-cranial remains are remarkably complete, especially those structures associated with her bipedality. It is reasonable, therefore, that accurate inferences might be made into the way she moved and there have been no shortage of attempts to do so. Aiello & Dean (1999: Chs.14, 19, 20–21), for example provide a good summary of what is known about human, great ape and australopithecine bipedal morphology in a systematic and clear way.

Possible functional significance of the australopith femuro-pelvic complex

One of the most remarkable aspects of the *A. afarensis* pelvis is its pronounced iliac crest. A thorough morphometric study (Marchal 1999) comparing hominid pelvis morphologies concluded this was the clearest difference between them, noting that it was “very different from the human condition.” (p. 355). This and other differences are reviewed by Aiello & Dean (1999: p. 451–453) where it was further observed that the *A. afarensis* pelvis further differs from the human condition “in their extreme width” with a very platypelloid (flattened dorso-ventrally) pelvic inlet.

It has been difficult to explain convincing functional reasons for these features. Aiello & Dean (p. 451) suggest “there are two current interpretations” and then go on to describe the morphological features that the proponents of human-like upright walking and the so-called “bent-hip, bent-knee gait” (from now on referred to as ‘BHBK’) use to back their arguments.

BHBK versus Fully Upright versus Wading

The first commentators on Lucy’s structure (e.g. Lovejoy 1974) concluded that she was a fully-upright human-like biped arguing that the wide lateral flare of the pelvis indicated that they were used as abductors of the pelvis on an extended thigh, as with humans during walking. This became accepted even though its femuro-pelvic complex was quite different, morphologically, from that of modern humans.

Later, Stern & Susman (1983) stressed that other traits, such as curved phalanges, indicated a strong adaptation to arborealism. They suggested therefore that *A. afarensis* could not have been fully adapted to the kind of bipedalism we understand and suggested that instead it exhibited a more chimp-like, intermediate form, BHBK.

Further evidence in favour of BHBK was found by workers such as Tardieu (1991), Berge (1994) and Abitbol (1994).

Those in favour of a fully-upright mode were bolstered, however, by Crompton *et al.* (1998). Through predictive dynamic computer modelling, they were able to suggest that BHBK would have been energetically very inefficient and would also have generated an excessive heat load to the individual.

Stern (1999, p. 567) and others have replied to this but the debate rages on today with no prospect of consensus in sight about the way Lucy walked in the 28 years since she was discovered. Perhaps some progress might be made by questioning their common assumption that the lifestyle of *A. afarensis* was not influenced by water.

Human-like Model

In the paper by Crompton *et al.* (1998), BHBK was suggested to have been energetically less efficient and lead to overheating but this was based upon the unspoken assumption that her bipedality was *purely terrestrial*. None of their computer models were devised to test how BHBK would have performed in water. If they had, they might have come to a very different conclusion. Whilst wading, it is likely that a significant amount of Lucy’s body weight would have been supported by inherent hydrostatic buoyancy, reducing the assumed (terrestrial) costs of maintaining that posture and overheating would have been avoided simply because of the significant cooling effect of water. Thus if *A. afarensis* was at least in part a wading ape, Crompton *et al.*’s published specific objections to the BHBK gait could be withdrawn.

BHBK Model

Ironically Berge (1994) used the same terrestrial assumption in arriving at the opposite conclusion. Her argument for BHBK or “waddling” was based largely on the belief that Lucy’s pelvic morphology would have made it difficult to maintain hip extension during walking and therefore that a fully-upright mode was unlikely. Again, she clearly did not consider if this would have also been the case in water. For the same reason as above, it would seem logical that a totally human-like posture would have been far easier to maintain in water than on land for an early biped as long as it was deep enough.

3.3 Evidence for a Wading Mode of Bipedalism for Lucy

In this section a putative mode of locomotion for *A. afarensis* is outlined which, it is argued here, uniquely explains its curious morphology and which supports the theory that bipedalism resulted from a wading ancestry.

Experiments with humans (Kuliukas 2001) reveal that strong adduction and abduction (pushing out and pulling back sideways) of the thigh is important in wading through water, especially deeper water. It was found that, surprisingly, sideways wading was as fast as any other method in the deepest ranges, due to the reduced resistance when moving in the lateral plane. This led to the idea that if human subjects, who had never even tried to wade sideways before, could do so as fast as fully frontal wading in deep water, perhaps an ape that was fully adapted to such a habitat might do so optimally in all depths.

Perhaps a sideways, or at least a side-to-side “ice-skater” like wading gait might explain *A. afarensis*’ curious morphology.

3.3.1 Features for adduction & abduction of the thigh

The most dramatic aspects of the *A. afarensis* femuro-pelvis are those that give it a very platypelloid (flat front-to-back) shape and much extended iliac arches. See Aiello & Dean (1999: pp. 395–482) for a comprehensive review of these features. It is argued here that these traits would be conducive to strong adduction and abduction of the thigh and a streamlined hip shape combine to allow powerful wading through water.

According to Aiello & Dean’s summary of Lovejoy’s (1974) interpretation of the pelvis (1999: p. 451). “The length of the iliac blade, together with the corresponding length of the femoral neck, would give the muscles an *even more favourable lever advantage in abduction than human* [my emphasis] iliac-femoral morphology, and considerably reduce the force on the femoral head at the tip joint.” Also Berge (1994: p. 267) notes that “it appears that the australopithecine adductor musculature must have been more powerful than that of humans” because of longer lever arms.

A number of workers (e.g. Berge 1994: p. 261, Aiello & Dean 1999: p. 452, Rak 1991) have commentated on the platypeloid (wide laterally but thin dorso-ventrally) form of its pelvis. Aiello & Dean for example identify that the pelvic inlet sagittal diameter is 58% of the transverse diameter in *A. afarensis* compared with 78% in humans.

In Fig. 4 (below) a photograph of pelvises from both *A. afarensis* and *H. sapiens* together was scanned and measured using CorelDraw 8 software to estimate the relative widths of the pelvis both dorso-ventrally and laterally.

The findings were:

H. sapiens v *A. afarensis* lateral width 103.7%

H. sapiens v *A. afarensis* dorso-ventral width 155.3%

A. afarensis lateral:dorso-ventral ratio: 2.16

H. sapiens lateral:dorso-ventral ratio: 1.44

This shows that *this* human pelvis, at least, was slightly wider than Lucy's but was more than 50% deeper dorso-ventrally. Inferring body shape from skeletal remains is not an exact science but it would seem logical that Lucy was much flatter front-to-back at the hip than either humans or extant apes.

The Bonobo's sideways gallop

One peculiar incident was reported by the field worker Maarten De Rouck at Planckendael which adds weight to the sideways wading idea. He described the behaviour of two of the bonobos he was studying thus: "Last week it was a rather rainy day and Kidogo and Hortense were sitting outside and when it started raining rather hard those two ran inside bipedally and they ran sideways toward the enclosure." He also observed this on one other occasion. One might

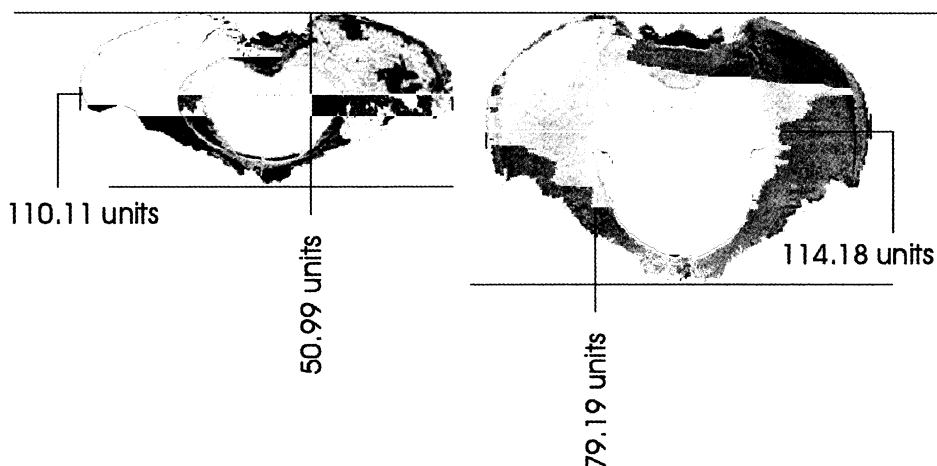


Figure 4. Pelvis of AL 288-1 compared with Human

speculate about whether this behaviour has been reported elsewhere and, if so, about its functional significance.

3.4 Conclusions

Any suggestions about how *A. afarensis* might have moved are of course speculative. However, it is suggested here that, considering Lucy's remarkably shallow pelvis and her apparently highly adapted skeletal structures for abduction and adduction, she would have been able to wade very quickly indeed, especially if she did so *sideways*.

In this section several controversies and arguments that have arisen in interpreting the *A. afarensis* fossil record have been discussed. A consensus view about them has clearly not emerged and so, it is argued here, that the morphology of AL 288-1 has not been adequately explained in terms of its locomotory repertoire by the non-wading models. Several of these points of contention have been shown to be resolvable if the assumption that water had no effect on the evolution of hominids is reconsidered.

On the basis of these preliminary findings it would appear that *A. afarensis* would indeed have been able to propel itself with sufficient force and would have been sufficiently streamlined to make sideways wading a plausible mode of locomotion in waist deep water.

All that remains is to review the paleo-habitats and paleo-ecology of the earliest bipeds to see if that is conducive with the wading-origins model.

4. PALEOECOLOGICAL AND GEOGRAPHICAL EVIDENCE

Every fossil gives a reliable location for where its one previous owner died, a good estimate of when it lived and a fairly good idea of the paleo-climate and paleo-ecology of their habitat. If the bipedal wading-origins model was wrong all that would be needed was to demonstrate that the earliest bipeds lived in habitats where wading could not have been practiced.

This section reviews the evidence about where the earliest bipeds lived and what they might have ate. First their habitats.

4.1 Paleo-habitat of the earliest bipeds

In the following section the sites in which the earliest fossils of putative bipedal hominid have been found are reviewed. For a more comprehensive review (for instance including later hominids) see Verhaegen and Peuch (2000, pp. 177–180.)

4.2.1 *Sahelanthropus tchadensis*

The most recent hominid find at the time of writing is also the oldest: *Sahelanthropus tchadensis*, Brunet *et al.* (2002.) Although no post-cranial remains have been found, the early indication is that the anterior position of the foramen magnum indicates that it adopted a more upright posture and had a greater tendency towards bipedalism than modern chimpanzees do. According to the sister paper (Vignaud *et al* 2002) the habitat was dominated by a large lake ('Mega' Lake Chad) and 28% of the fauna found alongside the hominid were aquatic or amphibious animals. Indeed the whole member was named 'The anthrocotheriid unit' because of the unusual abundance of a type of ancient 'swamp pig' which is thought to be ancestral to hippopotamus and a sister clade to the ancestor of the whale.

If *Sahelanthropus tchadensis* was at all bipedal, the evidence certainly does not contradict the hypothesis that wading was a factor in its adoption of that method of locomotion.

TABLE 2

Sahelanthropus tchadensis site

Site	Site	Ecology	Age (mya)
Toros-Menalla site 266, Chad.	"The fauna suggests that <i>S. tchadensis</i> lived close to a lake, but not far from a sandy desert" Vignaud <i>et al</i> (2002: p. 152)	"The frequency of piscivorous crocodilians, including <i>Euthecodon</i> and a new species of gavial, also clearly indicates large and permanent water bodies." Vignaud <i>et al</i> (2002): p. 155)	6–7

TABLE 3

Orrorin tugenensis site

Site	Site	Ecology	Age (mya)
Tugen Hills (Lukeino Formation)	"Fluvial and shallow lacustrine deposits" Pickford & Senut (2001: p. 145)	"open woodland" or "denser strands of trees in the vicinity, possibly fringing the lake margin and streams that drained into the lake" Pickford & Senut (2001: p. 149)	5.6–6.3

4.2.2 *Orrorin tugenensis*

The discovery of *Orrorin tugenensis* from the Lukeino formation in Kenya at the end of 2000 (Senut & Pickford 2001) is the second oldest putative hominid yet found. It is almost old enough to question the long held assumption that bipedality evolved only on the hominid line since the *Pan/Homo* split.

The evidence for this hominid's bipedality is stronger than for *Sahelanthropus* and, although its paleohabitats was not as aquatic, there is again nothing in its paleo-habitat to suggest that it could not have waded.

TABLE 4

Ardipithecus ramidus sites

Site	Site	Ecology	Age (mya)
Middle Awash (Aramis)	Lacustrine silts	"Relatively Wooded" Klein (1999: p. 185)	4.4
Lothagam, Baringo & Tabarin	"Lacustrine (lake) sediments and fluvial (river) deposits" Klein (1999: p. 173)		5.0–5.6
A.r. kadabba (Haile-Selassie 2001)		"Relatively wet and wooded environments"	5.2–5.8

4.2.3 *Ardipithecus ramidus*

Before the discovery of *Orrorin* this was the oldest putative biped. This table shows the sites where *A. ramidus* has been identified. Klein (1999: p. 188).

TABLE 5

Australopithecus anamensis sites

Site	Site	Ecology	Age (mya)
East Turkana Kanapoi & Allia Bay (Moiti Tuff)	Fluvial unit overlain by lacustrine deposits	Fauna suggests: Open woodland or bushland. Klein (1999: p. 173)	3.9

TABLE 6 *Australopithecus afarensis* sites

Site	Fossils/Geology	Ecology	Age (mya)
Hadar (Denen Dora)	AL 288, AL 333 Sediments accumulated from streams in a basin periodically flooded by a lake Klein (1999: p. 182)	"Lakeshore or river floodplain." Leakey et al. (2001 p. 439) "Evidence of lake with marshes in the early part of this member but this changes to flood plains and deltas later." "Other reconstructions of habitats for Hadar suggest woodland to treeless savannah." Reed (1997: p. 309)	3.2–3.18
Hadar (Sidi Hakoma)	AL 417	"Medium to open density woodland" or "riparian" Reed (1997: p. 308)	3.4–3.2
Middle Awash (Belohdelie) Maka		Less wooded than Aramis	3.8
Middle Awash (Maka)		Less wooded than Aramis	3.4
Laetoli	Eolian (wind-driven) and air-fall volcanic tuffs	"Not located near a water source; no aquatic taxa nor terrestrial mammals indicative of swamp or grassy wetlands." Leakey et al. (2001 p. 439) Reed (1997: p. 307) "closed to medium density woodland"	3.86–3.46
Fejej	Fluvio-lacustrine (river/lake) deposits		4.1
Omo (Usno)	Fluvial unit overlain by lacustrine deposits	"Woodland riverine habitat" "there were probably bushland and thicket areas." Reed (1997: p. 310)	2.68–3.32
Omo (Shungura B)	"Deposits were formed from a perennial river system with occasional riverine flooding which created flood plains." Reed (1997: p. 310)	"Mostly closed woodland with riverine forest and edaphic grasslands." "Other habitat reconstructions include a riverine forest and ... a wooded savannah and forest." Reed (1997: p. 310)	3.36–2.8
Koobi Fora (Tulu Bor)	Stream sediments overlain by lacustrine deposits. Vulcanism and tectonic movement determined the alternation between lake and river. Klein (1999: p. 174)	"Scrub woodland region with a flooding river. Wetlands were probably extensive." Reed (1997: p. 309)	2.68–3.32
West Turkana (Lower Lomekwi)	Fluvial unit overlain by lacustrine deposits	"Lakeshore or river floodplain." Leakey et al. (2001: p. 439)	3.3–3.2 (p. 181)

4.2.4 *Australopithecus anamensis*

This hominid was so-named because it was found by Lake Turkana. The word ‘anam’ means “lake” in the Turkana language (Niemitz 2002, p. 39). Like Lake Chad, Turkana is an ancient lake and certainly was a prominent feature in the habitat of this hominid.

4.2.5 *Australopithecus afarensis*

The most complete hypodigms of the early bipeds. Table 6 shows the earliest members in sites where *A. afarensis* has been identified (Klein, 1999: p. 188).

4.2.6 *Kenyanthropus platyops*

Another recent new hominid find. Table 6 shows the sites where *K. platyops* has been identified. Data from Leakey *et al.* (2001).

TABLE 7

Kenyanthropus platyops

Site	Site	Ecology	Age (mya)
West Turkana (Kataboi)	Fluvial unit overlain by lacustrine deposits	Leakey <i>et al.</i> (2001: p. 439) “Lakeshore or river floodplain. Relatively well watered and vegetated” and Leakey <i>et al.</i> (2001: p. 440) “more vegetated and wetter than Hadar”	3.3–3.5

4.2 Dietary inferences of the early bipeds from their dental evidence

Teeth provide invaluable fossil evidence. Firstly, because they are among the hardest living materials they are remarkably durable after death and tend to be the most commonly found type of fossil. Secondly, because the shape and size of teeth are generally indicative of the type of food the animal ate, they can be used to infer quite a lot about the lifestyles of such long-dead animals.

Puech (1992, p. 1083) wrote “in paleoanthropology the subject of dental wear continues to generate interest because of its relevance to dietary interpretations of early members of the human family. Dietary reconstruction is ultimately based on a combination of evidence including analogical arguments concerning anatomical, structural and behavioural specializations of living species, and experimental evidence of modifications of enamel and dentine with a variety of substances.” His electron microscopic study of the dental microwear of *Australopithecines* from two locations (Hadar and Laetoli) and *Homo habilis* from Olduvai found a variety of striations, small pits and micro-

flakes. By comparing these patterns with those found in modern animals and *Homo* Puech attempted to suggest dietary explanations to which accounted for them.

This line of enquiry is fraught with difficulties. Unique problems provided by the sparse fossil record (e.g. the inability to ever perform invasive tests) forced Puech to admit that his “studies on the rates of wear of early hominid teeth are inconclusive” (p. 1086). Nonetheless, the comparative evidence was sufficient for him to suggest that the “lower incidence of striations on the teeth of the Hadar hominids [*Australopithecus afarensis*] may have been due to the consumption of swamp margin plants” (p. 1084) and to conclude: The evidence of dental microwear supports the paleoecological reconstruction of the way of life that places “handy man” at Olduvai [*Homo habilis*] in flood plain settings with swamp vegetation.” And finally that “Early hominids from Hadar and Olduvai both lived in well-watered savanna woodland, near a lake. Consequently, differences in tooth wear observed in *Australopithecus* and *Homo* from Olduvai mainly depend on cultural behaviour.”

4.3 Paleo-ecological conclusions

There appears to be a chronological trend in the general nature of the paleohabitats of early hominids. The earlier ones are, generally wetter and more wooded whilst the later ones are drier and more open. This mirrors the macro-climatic changes that have long been recognised to have happened in Africa from the Miocene into the Pleistocene and the idea that “tree cover declines as mean annual rainfall decreases” (Reed 1997: p. 292). The only early hominid sites that are not associated with riverine or lacustrine deposits, and therefore are unlikely to have been places where wading could have taken place, are the Southern African limestone cave sites and Laetoli both of which were not covered here because of their relatively late dates.

The fact that the sites of the very earliest bipeds, especially of *Orrorin* and *Ardipithecus*, were predominantly “wet and wooded” is consistent with the expectation of the wading-origins model.

Although the dental microwear evidence is far from conclusive, the indications from Puech’s (1992) studies is certainly consistent with the model that the early bipeds waded and did so in order to obtain food.

5. OVERALL DISCUSSION

It is probable that no one, single factor was responsible for the origin of habitual bipedalism, but up until now the possibility that water might have even been one of them has not been given much serious consideration by workers in the field. The only people to do so have been non-specialists who have been criticised for their lack of objectivity and use of the scientific method. This work has attempted to start to fill that void.

Apes have not, traditionally, been associated with water and therefore it could be argued that it is unlikely that this would have been a significant enough part of the daily repertoire of our ancestors for natural selection to have influenced them in this way.

However, there is growing evidence that great apes do tend to wade bipedally in water whenever they have sufficient motivation to do so. Hunger has been seen to be usually sufficient motivation.

It would appear that the two most well known human physical traits: large brains and bipedalism may well have both evolved in a water-side habitat.

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