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University College London

Bipedal Wading
in *Hominoidae* past and present.
by

Algis Kuliukas B.Sc.

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Abstract

The factors that contributed to the origin of human bipedalism are still not understood. Many have been proposed but the idea that the earliest bipeds waded in water-side niches seems to have been overlooked. This thesis investigates the plausibility of a “wading-origins” model for bipedality by making a number of potentially controverting predictions and testing them.

It found that the wading model fulfils a number of theoretical requirements. For example in, avoiding drowning, it provides the strongest possible adaptive pressure for an upright posture.

Evidence from apes in the wild show that though preferring to keep dry, they do go into water when necessary and tend to do so bipedally. An empirical study of captive bonobos found them to exhibit 2% or less bipedality on the ground or in trees but over 90% in water.

Human subjects showed wading to be faster than swimming at depths below hip height and that speed correlated closely with submerged body profile. Apes specialised for this niche would therefore be expected to minimise this profile. A sideways wading mode was found to generate less drag in humans than frontal wading, suggesting that if our sideways propulsion were stronger it would be the optimal method. A review of AL 288-1 skeletal morphology indicates a strong ability to abduct and adduct the femur. These traits, together with a very platypelloid pelvis, are consistent with those expected in an ape that adopted a specialist sideways wading mode. It is argued that this explanation of *A. afarensis* morphology is more parsimonious than others which have plainly failed to produce a consensus. The paleo-habitats of the earliest bipeds, as with all the evidence reviewed here, are consistent with the hypothesis that wading contributed to the adaptive pressure towards bipedality.

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1. Introduction

The idea that an adaptation to a water-side habitat may have been one of the contributory factors that caused the earliest bipeds to adopt a more orthograde posture is not a popular one. University-level texts about human evolution (e.g. Boyd & Silk 2000:p331-338, Jones *et al.* 1992:p77-79, Klein 1999:p249-250, Lewin 1998:p215-229, Woolpoff 1998:p195-242) tend to review the most popular theories but none seriously consider that water might have had anything to do with it.

One worker in the field who has contemplated the idea is Chris Stringer, of the British Natural History Museum. He wrote (1997:p115) "If our ancestors did go into the water, that would force them to walk upright." Also, at Birkbeck College, London, (Nov. 2000) he gave a public lecture about the "Recent modern human origins model", which predicts that all humans alive today are descended from a small population that lived in Africa as little as 150,000 years ago. Part of his talk outlined how it would appear that many of our ancestors had migrated out of Africa along coastal routes.

At the end, a question was asked about human swimming ability. Did he think it was an adaptation to this coastal phase? He replied that he did not believe that humans were adapted to water in this regard but suggested that if you were looking for one then perhaps you might consider the possible causes of bipedalism. "What about wading?" he asked.

This work considers that question too and poses a few more of its own: Exactly what *is* the wading origins theory? What does it predict? Why is it so rarely listed as a possibility in standard texts? Has it been dismissed? If so, how? If not, how could it be scientifically tested? And, most interestingly, might the theory be plausible after all?

2. Testing the Wading-origins hypothesis

2.1 What is the wading-origins hypothesis?

The idea that bipedalism may have originated in apes that became adapted to a wading habitat is not new and has several forms.

The earliest reference to it in the literature is attributable to the marine biologist Hardy (1960). His argument was based on the belief that human erect bipedalism must have evolved gradually through intermediate stages of orthograde posture and that water would have provided the ideal medium for this to have taken place.

He postulated that the earliest wading apes might have done so because they were driven to it through competition for food or to escape predators.

Unfortunately this specific idea was not backed up by any empirical data and Hardy did not make any predictions about it other than to say the habitat was probably “coastal” and that it occurred “in the gap between *Proconsul* and *Australopithecus*.”

Most problematic for the hypothesis, perhaps, was its timing. In 1960 most paleoanthropologists had almost the exact opposite habitat in mind for early hominids, namely the savannah rather than coastal regions, and, not surprisingly some thought that the idea was “not worth the trouble of rebuttal” Langdon (1997: p480).

Zoologist Morris (1967:p40) referred to Hardy's idea positively but it was left to a non-specialist, the Oxford English graduate and former playwright Elaine Morgan, to keep alive any interest in it with a series of controversial popular science books.

Geologist La Lumiere (1981: p 105) added some detail to the Hardy-Morgan model by postulating a specific geography, scenario and timescale for it: A range of mountains that became isolated due to the flooding of the northern rift valley. He wrote “thus between 6.7

and 5.4 Ma B.P. [Million years before present] in the Miocene (Messinian), a group of apes along with other animals could have been trapped on Danakil island.”

La Lumiere (p 106) also predicted localities which “should yield fossil hominids if the hypothesis here put forward is correct.”

A different formulation of the wading-origins hypothesis has been provided by Verhaegen & Puech (2000).

They argue that wading bipedalism may have preceded the *Pan-Homo-Gorilla* split through a specialisation to a mangrove swamp habitat suggesting that it happened long before the Danakil flooding suggested by La Lumiere and further north along the Red Sea and Arabian coasts.

The main thrust of their argument is that dental microware studies suggest that australopithecines regularly fed off aquatic herbaceous vegetation. They postulate that these apes adopted a climbing-wading (or ‘aquarboreal’ pers. communication) mode of locomotion on the grounds of logical association with their putatively wooded and water-side habitats.

One conclusion of their model is that both *Pan* and *Gorilla* have reverted to quadrupedalism from an ancestor that adopted a wading form of bipedality. This ancestor may or may not have been *A. afarensis* but that phylogeny is supported by several workers (Kleindienst (1975), Goodman (1982: 260), Gribbin & Cherfas (1983), Hasegawa *et al.* (1985) and Edelstein (1987)).

2.2 Published criticisms of the theory

Considering how little material has been published in support of a wading bipedal-origins model it is not surprising that even less should have been written against it.

There have been only two main published papers criticising the model.

Langdon (1997:p481) specifically critiques Morgan for her (1990:p24-35) arguments which suggested that the health costs of human bipedalism, such as increased lumbar weight bearing, would have been reduced in water. He argued that her position was based on the assumption that our ancestors had once been fairly large, purely terrestrial quadrupeds but that there was no strong evidence that this was so.

Langdon's (1997:p489) criticism of the specific location and timescale proposed by La Lumiere (1981) seems only to be based upon a statement Morgan made in one of her earliest books that *Australopithecus* had "returned to the land." The implication Langdon drew from this was that, according to Morgan, *Australopithecus* must have been able to swim and that there was no evidence that it could.

No investigation into the localities suggested by La Lumiere (1981), providing a reasonable test for the island wading origin model, has yet been published.

In the other main work regarding the theory, at the Valkenburg symposium in 1991, Ghesquiere & Bunkens (1991:p 256-257) criticised the wading model from an energy cost perspective. Their findings showed that Oxygen consumption increased dramatically when volunteers were asked to wade at speeds that were greater than 1.5 km/h (0.42 m/sec) and that this indicated a far greater use of energy than the equivalent speed needed when walking on land.

However their subjects were “submerged to the armpits” at which depth it clearly would be faster and much more energetically efficient to swim. Their study did not investigate wading in shallower depths.

From the same symposium Reynolds (1991:p333) summarised the discussions on bipedalism but made no specific criticisms of the wading origins model.

2.3 How to test its plausibility?

It would appear that the main obstacle preventing specialists from giving serious consideration to the wading bipedal-origins hypothesis has been that those who have promoted it have, so far, not done so in a strictly scientific way. Few testable predictions have been made and no empirical data has been collected to support the ones that have. However, it is only fair to add that what published criticisms have been made have equally failed to demonstrate why it must be wrong.

It is therefore argued here that the hypothesis has not yet received the proper consideration that, perhaps, it deserves.

A framework of predictions, based upon commonly held principles of Darwinian natural selection, is now made. Although the predictions are specifically intended to find tests which may controvert the wading bipedal-origins model, they have been drawn up so that they might, with some modifications, be applied to any theory regarding bipedal origins.

Two categories of predictions are made:

The first set can (and will) be specifically tested here with a series of experiments yielding new empirical data and by investigating the literature.

The second set have to be evaluated on a purely theoretical level.

In this way the plausibility of the hypothesis might finally be properly evaluated.

Testable Predictions

1. Bipedal wading should be demonstrably observable in extant Apes.

Hunt (1994:p183) wrote “Contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism.” Specifically for any support of the wading-origins model to be implied one would expect that extant apes should move bipedally when observed in water. Moreover, considering that many semi-aquatic mammals move from a quadrupedal mode directly to swimming as water gets deeper, one would expect that apes moved bipedally in depths of water *in which they could also theoretically move on all fours*.

If apes were observed to move quadrupedally as much as possible before switching to swimming, then this would be taken as evidence against the hypothesis.

2. Bipedal wading should be demonstrably the *optimal* mode of locomotion in certain depths of water in hominoidae.

One would predict that, if specific wading traits had evolved, it must have been the optimal mode of locomotion in certain niches. Specifically it would have been a faster and more efficient way of moving than quadrupedalism or swimming. If not, one would predict that wading is unlikely to have evolved as the primary mode of locomotion in waterside niches.

3. If the earliest bipeds were wading apes one would expect to find specific traits in the fossil record to support that view. Specifically there should be evidence indicating mechanisms that could have optimised the efficiency of this mode of locomotion.

Ideally, some kind of explanation for the rather strange ‘non-human’ kind of bipedalism that appears to have manifested itself in *A. afarensis* should be possible.

If, instead, the traits of the earliest bipeds can be adequately explained as purely terrestrial or arboreal then the wading origins model would be rebutted.

4. If the earliest bipeds were wading apes one would predict that the earliest hominid fossil sites would be associated with significant bodies of water. The hypothesis would be seriously challenged if these fossil sites had been categorically designated as arid zones.

In addition to these specific, testable, predictions a further set of theoretical expectations might also be made. These could also be used to measure the general plausibility of the wading origins model against others.

Theoretical predictions

5. Whatever factors led to bipedalism should, as far as possible, explain the advantage towards it relative to the immediate alternative at every stage of its evolution and not just as a final product. It should avoid anthropocentric notions like 'it evolved to free our hands for tool use' as if it were pre-ordained to do so.

6. The factors that led to bipedalism in hominids should also explain why chimpanzees did not also succumb to this pressure and become (or stay) bipedal too but became knuckle-walkers instead. In other words it is not enough to explain why humans are bipedal if it does not simultaneously explain why chimps are not.

7. The selective factors that led to bipedalism should ideally be strong ones. Natural selection theory predicts that behavioural traits evolve to maximise the reproductive success of the individual. This can work either directly to the individual itself or indirectly via kin selection. However probability theory tells us that adaptations which offer immediate, life-or-death advantage to an individual must, logically, be ranked as more significant than more subtle ones which may give milder benefit to others, later.

8. The cost of bipedalism to an individual throughout its life should be less than the benefit. Specifically “freeing the hands” should more than compensate for “enslaving the feet.”

The costs might be measured in terms of energy needed to be expended for an early biped to achieve an upright posture.

9. Ideally, the advantage of bipedalism should apply equally to both sexes. An argument that only focused on one sex, for instance one suggesting that it arose predominantly to help mothers carry infants (Smith 1994) or for male threat displays (Jablonski & Chapman 1993) should logically be considered weaker than one that covered both sexes.

It is not the objective of this thesis to perform a comparison of the different bipedal origin models but it would appear that, in terms of these theoretic predictions, the wading model is at least as feasible as the others. The seventh prediction (about selective pressure) is particularly strong as it is difficult to conceive of a more clear-cut reason for being upright than to avoid drowning.

3. Wading in extant apes

The first testable prediction of the wading-origins model is that it should be observable in extant apes. The first part of this section looks at the anecdotal evidence for this and the second reports new empirical data from captive bonobos.

3.1 Anecdotal evidence for bipedal locomotion in great apes

There has never been a strong association between the apes and water. Indeed they have been considered so fearful of it that moats are often used to contain them in captivity.

Kortlandt (1975:p648) for instance wrote “it is a fact that anthropoid apes cannot swim. Many zoos have had experiences which prove this. I have myself observed two cases in which chimpanzees would have drown in a 5 foot deep moat if they had not been rescued by an attending scientist.”

More recently though, evidence (mainly film or photographic) has been accumulating suggesting that all of the *hominoidae* may be more comfortable in water than might have been assumed.

3.1.1 Orangutan (Pongo)

A great deal has been written about *Pongo* by workers in the field although very little documents any association with water. Despite this a growing amount of photographic evidence suggests that they do wade bipedally.

Galdikas (1980:p835) said “Orang-utans have surprisingly little fear of water.” The article was accompanied by a photograph of a female with an infant on her back wading bipedally in an Indonesian swamp. Ellis (1990:p56) includes a photograph of an instance when an orang-utan at Singapore zoo was wading in the moat bipedally. Sommer & Amman (1998) use a photograph (fig. 1) of a bipedally wading orang-utan on the front cover of their book.

Ammann (personal comment) reported “I photographed this male at Tanjung Puting crossing the river and using the stick to gauge depth or give him a better hold should it get too deep. That was my assessment.”

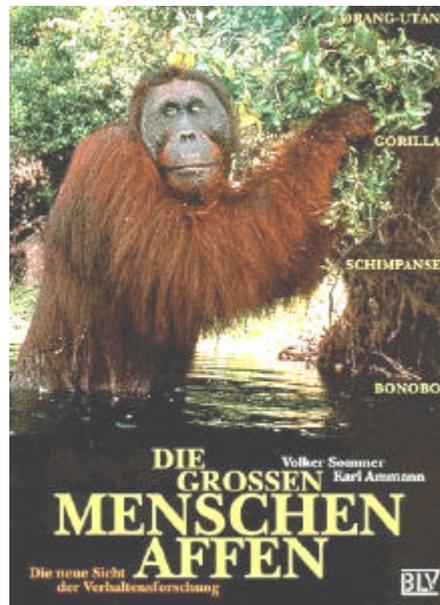


Figure 1 Male Orangutan wading at Tanjung Puting.
(Sommer & Amman 1998, Photograph by Karl Ammann)

Galdikas (1999:p72-80) includes a sequence of photographs of an orangutan wading through a swamp.

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. At Camp Leakey (situated within the park), I have seen orangutans sitting below the main walkway from the river to the camp (high ground), where they have often been viewed putting their faces under the water.

On a visit to Ragunan Zoo in Jakarta, I also saw two orangutans standing and wading in the moat surrounding the island enclosure.”

3.1.2 *Gorilla (Gorilla)*

Gorillas have also not traditionally been linked with water and many zoos use moats to contain them even though this has occasionally proved to be a mistaken policy. Ellis (1990:p57) describes a situation at the University of Ibadan Zoo where gorillas began swimming across the moat using the “breast stroke.”

However there is growing evidence and a large amount of film footage that has emerged in the past three years which directly contradicts this view.

Doran & McNeilage (1998:p121) review the ecology and behaviour of all the sub-species of gorilla and claim that of the three the lowland gorillas are the least studied. They say “it was long thought that gorillas avoided water” but “recent work has demonstrated that western lowland gorillas routinely wade into swamps in forest clearings to feed on aquatic herbs.”

Studies at Mbeli Bai, at the Nouable-Ndoki National Park have been particularly interesting and (p124) the article is illustrated with a photograph (taken by Michael Nichols) of a bipedally wading adult male.

Parnell (2001:p294) added to this evidence when he reported observations of ‘spectacular splash displays’ in male silver backs. He was working as scientific consultant for a film crew making documentaries about western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai in the Congo.

Although most of the film evidence so far indicates that western lowland gorilla wading is usually quadrupedal, as the water tends to be shallow when they move into the swamp, they clearly do wade bipedally when the need arises.



Figure 2 Male Western Lowland Gorilla “Bear” at Mbeli Bai.

Parnell 2001 (personal communication) noted thirteen incidents of bipedal wading in several weeks of observation. He noted that “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.”

3.1.3 Chimpanzee (*Pan troglodytes*)

Angus (1971:p51) documents several cases where zoos have implemented moats to constrain chimpanzees only to find that individuals soon overcame their fear of water. One such individual, Joe at Chester Zoo, is a good case in point. “At first, he never actually crossed the ditch, immersing only his legs” but about a year after the enclosure was built he crossed the water (up to 5.5m wide and 1m deep) onto another island and later onto the zoo grounds

itself. The zoo authorities were forced to install an electric wire in the centre of the waterway. After one of the chimpanzees were shocked none of them went into the water again.

This evidence suggests that chimpanzees are indeed capable and prepared to cross water barriers if they are so inclined and if there is no alternative route. Angus does not state, but logically it must be the case, that Joe waded across the moat bipedally for at least some of the distance.

Nishida's (1980) investigated chimpanzee behaviour near water at Kasoje, at the foot of the Mahale mountains in Tanzania and compared it with the behaviour of chimpanzees in similar situations in Gombe.

Nishida cites several examples of chimpanzees wading in water including one caused by heavy rain. "Muddy terrain caused temporarily by rain sometimes has influences upon chimpanzee's locomotion" states Nishida (1980:p201.) "An adult male was once observed to walk bipedally on muddy ground during moderate rain. In 6 steps he descended bipedally the steep valley slope, crossed the rocky valley bottom quadrupedally, and ascended the opposite slope bipedally again." This behaviour has also been reported by van Lawick-Goodall (1968).

In addition to this anecdotal evidence from the literature there has recently emerged some significant photographic footage of chimpanzees wading bipedally in fairly deep (chest high) water.

A research student, Jess Tombs, working at a chimpanzee sanctuary in the Conkouati reserve lagoon (See Tutin *et al.* 2001), made some observations which she captured on film. The chimpanzees are placed on three islands in a lagoon where they live semi-natural lives. Because there is not enough vegetation on the islands to sustain them, every day fresh food supplies are brought to them by boat.

Another worker in the field there, Karlovski (1996), describes what happens when the boat comes in “The biggest group of chimpanzees lives on Grand Ile which is almost 1 km long...

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.”

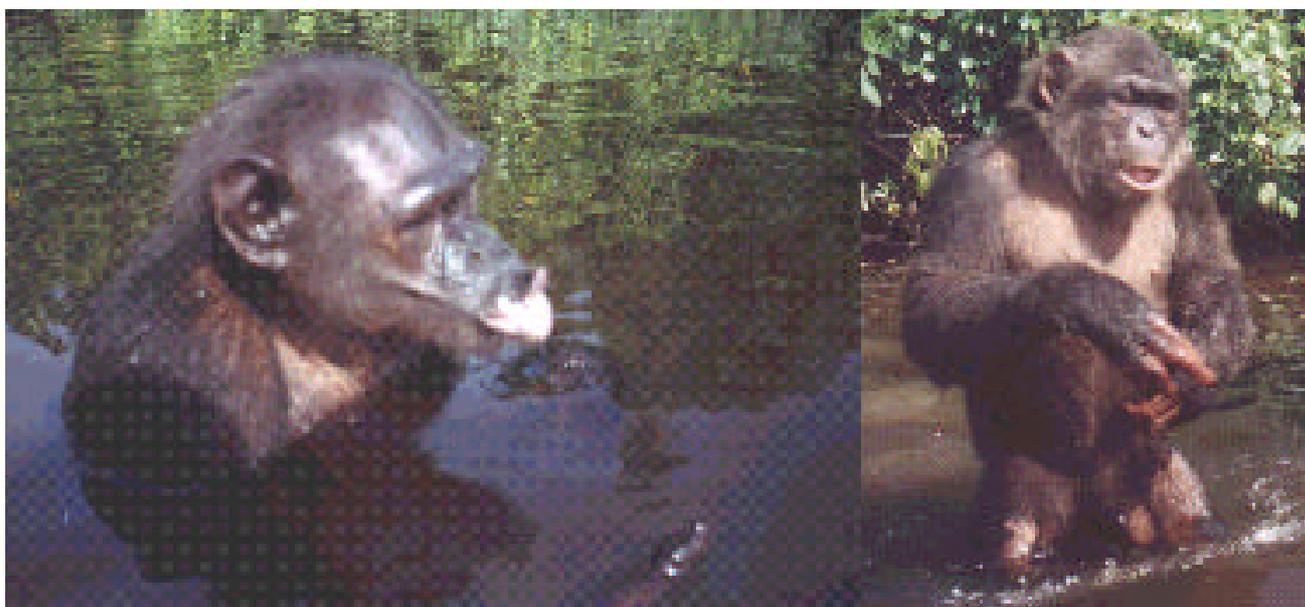


Figure 3 Two wading chimpanzees at the Conkouati reserve lagoon.

Photograph by Jess Tombs.

Angus’ (1971) studies of captive chimpanzees and the experiences of workers undertaking their rehabilitation on protected island habitats have provided strong evidence that although *Pan troglodytes* may prefer to keep away from water, they are prepared to overcome their fear when necessary.

Bearing in mind their undoubted inability to swim it is logical that in order to cross stretches of water deeper than about 50cm they would have to do so bipedally.

3.1.4 Bonobos (*Pan Paniscus*)

Relative Bipedality of Pan paniscus and P. troglodytes

There appears to be some disagreement about whether *Pan paniscus* or *Pan troglodytes* has the greater tendency for bipedalism.

If there was a difference it would be interesting to speculate about the reasons behind it considering the relatedness of the two species both to each other and to *Homo sapiens*. If bonobos were more bipedal than chimpanzees it could be used as an argument in favour of the wading origin as their habitat is generally wetter and more prone to flooding. Certainly, if bipedalism had arisen in a savannah environment, one would expect that chimpanzees and not bonobos would be the more bipedal as that species inhabits the generally more open habitat.

According to De Waal (1996:p181) “bonobos stand and walk on two legs more often, and with greater ease than chimpanzees” and (1997:p53) “are excellent bipeds.” They have certainly long been associated with increased bipedality compared to their cousins the “common” chimpanzee.

It has often been claimed that *P. paniscus* has specific anatomical traits that make them better suited to bipedal movement. As Wrangham put it (1996:p7) “small-headed, long-legged chimpanzee would be a more appropriate morphological description of *P. paniscus* than pygmy chimpanzee.” He goes on to describe other anatomical differences which might imply a greater tendency for bipedalism too: shorter arms, shorter clavicles, more horizontal back and narrower pelvis. Doran & Hunt (1996:p93) add that they also have more curved phalanges.

These traits, when put together, begin to sound rather like *Australopithecus afarensis* and the idea has not been missed. Zihlman (1978) famously compared them and concluded that of all

the living apes, bonobos are the closest in body shape. “A creature somewhat like pygmy chimpanzees may very well have directly preceded the earliest hominids.” (1978:p92)

However a comparative study of wild chimpanzees and bonobos by Doran & Hunt (1997:p106) concluded that although “bonobos are more suspensory and engage in more arboreal travel than chimpanzees” they found very little evidence for bipedal activity in either species.

Increased arboreality in bonobos would still be analogous to the most widely held views of *A. afarensis*.

Further doubts about their increased bipedality were raised by a recent study of the two species in captivity by Videan & McGrew (2001).

Their study of paired captive individuals of similar age, sex and background from the two species found the levels of terrestrial bipedality were not significantly different quantitatively but qualitatively. They concluded (p238) “Bonobos showed more bipedality in carrying and vigilance; chimpanzees showed more bipedality in display.”

Bonobos have generally been studied less than the other great apes. However there does seem to be evidence that they are less fearful of water and show a greater tendency to wade than their chimpanzee cousins.

According to Uehara’s (1976) field study in the Congo, bonobos were observed to feed on aquatic plants for at least two consecutive months. In doing so, they immersed themselves in water up to the shoulders.

De Waal (1996:p185) reports findings that bonobos had entered streams wading bipedally. Referring to fellow primatologists, he wrote “On a recent field trip, however, the Badrians

saw two female bonobos walking upstream, in the water. They snatched handfuls of floating dead leaves, picking out things to eat.” Later he added “Susman has observed that the numerous tracks along streambeds lack knuckle prints. This suggests to him that bonobos avoid getting their hands wet by assuming bipedal postures when crossing streams.”

In a published interview with Barbara Fruth and Gottfried Hohmann, who had worked in Lomako, Congo from 1990 (de Waal & Lanting 1999:p79-82), de Waal asks them about the phenomenon of bonobo wading.

Fruth replied “There is no fishing but perhaps they eat a sort of shrimp. They walk through the water and stare into their hand while they let the water flow away through their fingers. Then they eat something. They are tiny, transparent crustaceans in the water. The local people also eat them. It’s a delicacy. The apes sometimes wade for hours through the stream bed.”

De Waal then asked “Bipedally?”

He described her reply in this way: “Fruth: [*Laughing, knowing the wild idea I’m referring to.*] No, they simply wade through the water on all fours; these little rivers are very shallow.”

Captive bonobos at Planckendael

This thesis includes new empirical data from observational studies of captive bonobos as the Planckendael wildlife park, Michelen, near Brussels, Belgium. Details of that study follow in the next section. Talking to the staff at Planckendael there seemed little doubt that they frequently went into the moat which surrounds their spacious enclosure.



Figure 4 Kidogo, Redy and Hermien wading at Planckendael

One worker, who had been tracking a single female bonobo, Dzeeta, daily for sixty days confirmed this.

Interview with Maarten De Rouck. 13th June 2001 at Planckendael. 9:28 am. (Full transcript available on request)

AK - How long have you been here?

MR - 2 months

AK - How many hours do you think you have spent watching the bonobos?

MR - Hundreds.

AK - Have you ever seen any of them get into the water?

MR - Well I've seen three of them getting into the water. 2 males : Redy and Vifjo and one female Dzeeta but Dzeeta isn't keen on getting in the water.

AK - How frequently would you say that occurs?

MR - Rather frequent. Almost every time that visitors are throwing food or sweets they are always dropping something in the water and the two males I named mostly go and get it out of the water.

AK - How do they get into the water?

MR - Bipedally.

AK - Have you ever seen them knuckle-walk in the water?

MR - No. I have never seen it. So I don't know if it ever happens sometimes but I don't know.

AK - Could you give me an estimate of how many times you have seen these males get into the water?

MR - In those two months? Yes. I have seen it practically daily.

AK - So, sixty times?

MR - Yes, maybe.

3.2 Analysis of empirical data of captive *Pan paniscus* bipedality

Videan & McGrew (2001:p233) suggest, as did Hunt (1994) before them, that studying extant apes may lead “to a better understanding of the influence of various hypothesised selection pressures and anatomical correlates on the evolution of bipedalism in hominids.”

In this section the results of a set of observational studies of captive bonobos with the same objective in mind is reported.

3.2.1 Materials and methods

Ten captive bonobos were studied at Planckendael 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 as listed below in table 1.

Table 1 Bonobos Studied

Name	DOB	Sex	Born	Data Items	Total Observed Time (sec)	Total observed Unsupported Bipedality (sec)
Dzeeta	1971?	F	Congo	104	3479	0
Hermien	1978?	F	Congo	452	4828	146
Hortense	1978?	F	Congo	47	1441	10
Kidogo	28-Feb-83	M	Stuttgart	123	2426	3
Redy	24-Nov-90	M	Planckendael	342	3331	28
Vifijo	23-Jul-94	M	Planckendael	42	130	5
Zamba	16-Apr-98	M	Planckendael	164	2348	1
Zomi	28-Jan-98	F	Planckendael	45	148	3

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.

This study quantified the amount of time that was spent in different locomotor modes in different substrates whereas Hunt (1994) and Videan & McGrew (2001) measured “instances” of bipedalism according to Altmann’s (1974) method (or “observer’s guide”) of using instantaneous focal-subject observations at definite, frequent, intervals for fixed lengths of time

Hunt (1994:p184) used 2-minute sampling for a whole day at a time, if possible. Hunt studied chimps for 701 hours in all providing him with 21,030 data items in all (30 samples /hour x 701).

The same method was used by Videan & McGrew (2001:p236) who used a 30 second sampling interval for 45 minute observation periods. 28 individuals were tracked for an average of 8.95 hours providing them with 30,072 lines of data.

Due to time constraints, and in order to record and time precisely the incidents of bipedality, it was decided to adopt a different technique in this study following Bauer (1977:p914) who used video recording equipment to study chimpanzee bipedalism.

All observations were made via this method (a Sony digital handycam 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.)

This approach had a number of advantages:

- Altmann’s technique, may become a little ‘hit-or-miss’ when tracking behaviours that may only last a second and might be missed whilst recording a previous behaviour. It thus relies on a mass of data to average out sampling errors. With the aid of a video camera even the shortest behaviours (even of multiple animals) are reliably recorded allowing for shorter focal study lengths.
- Every recording is automatically timed allowing the analysis to be more quantitative. The problem with the ‘bout recording technique’ is that it gives equal weighting to an incident of bipedalism that lasted a second to one that lasted twenty seconds.
- Bipedal incidents can be studied frame by frame if necessary. This makes it possible to record data such as the number of bipedal steps taken and the actual use of upper limbs for supported bipedalism and stills can be made for presentations.
- The original data can be re-used many times. In the field this could potentially provide an invaluable resource for future generations of researchers, considering the gloomy trend of destruction of primate habitats.
- Finally the source data can be analysed at leisure safeguarding against mistakes and can be verified later by others increasing confidence in its accuracy including with regard to identifying of individuals. This is useful when there is not much time to get acquainted with every face and rear end.

Postural categories were based upon the work of Hunt (1994).

The most significant ones for this study were:

Table 2 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.

A mixture of observation techniques were 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. Their reasoning was understandable: 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 impacted 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 was far from ideal. On the first day the weather was too cold for the group to leave their indoor enclosure. On the second day no children came so no food was thrown into the water and consequently no wading events were recorded. However on the third day, a large number of visitors arrived and obligingly provided many opportunities to record incidents of bipedal wading.

The observations were carefully transcribed into a Microsoft Access database after which various Visual Basic programs were written to perform numerous data preparation procedures, for example for calculating the time between postural changes and assigning each postural event to a substrate.

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. (See fig. 5 for an illustration of the difference between the last two.)



Figure 5 Kidogo (left) is showing supported bipedalism partly in water,
Hermien (right) is showing unsupported bipedalism totally “in water.”

3.2.2 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 (38 seconds) was spent in contact with water. (See Fig. 6)

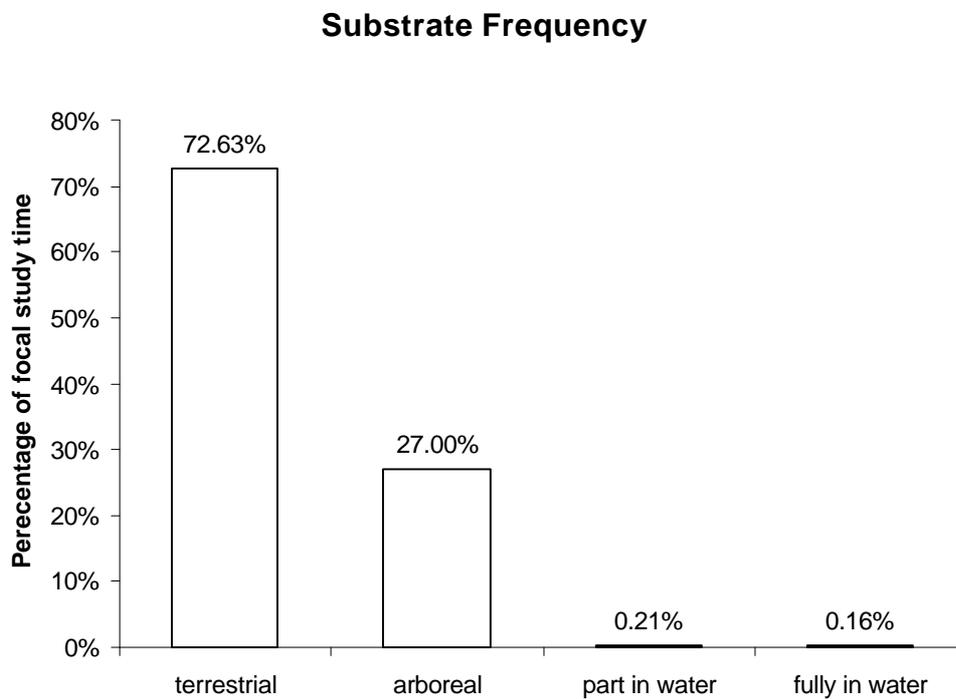


Figure 6 Time spent in various substrates

The results should be read with caution and are only shown here to provide a reference against the more significant contextual observations made of bonobos in water, which are described next.

The first of the three days was so cold that the group stayed in doors all day and so the recordings made then gave results more in favour of the arboreal substrate. On the other two

days, almost all observations were made outside giving the opposite effect. Visitors only came to the park on one of the days which is significant because it is the occasional throwing of food into the moat by children that is the primary incentive for the bonobos to enter the water.

Although the absolute percentages displayed here should not be taken literally, there is no doubting the reliability of the finding that bonobos prefer not to enter the water.

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. (See fig. 7)

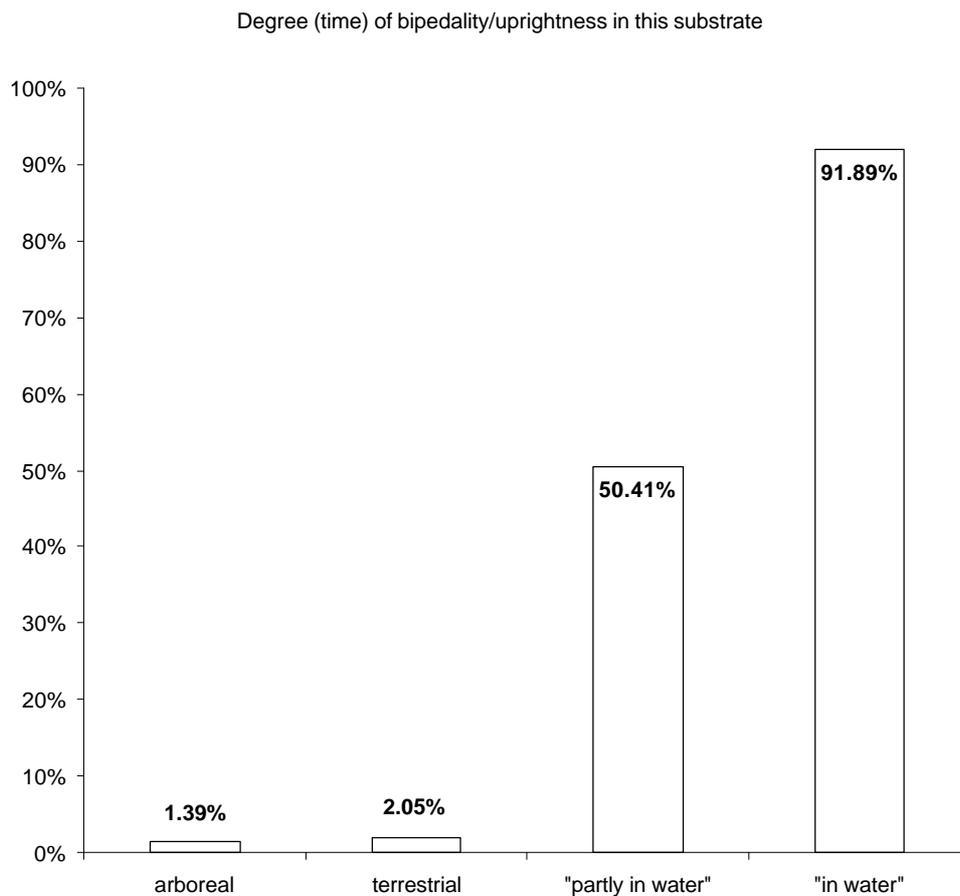


Figure 7 Time spent upright (supported & unsupported bipedalism) in different substrates

Although only 37 seconds was spent in water in total, almost 92% of this time was spent in an upright (supported or unsupported bipedal) posture.

A slightly 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, which accounted for over 99% of time for the group, the level of bipedality dropped to around or below 2%.

This affect of water was, if anything, even more pronounced when only unsupported bipedalism was taken into account. (See Fig. 8)

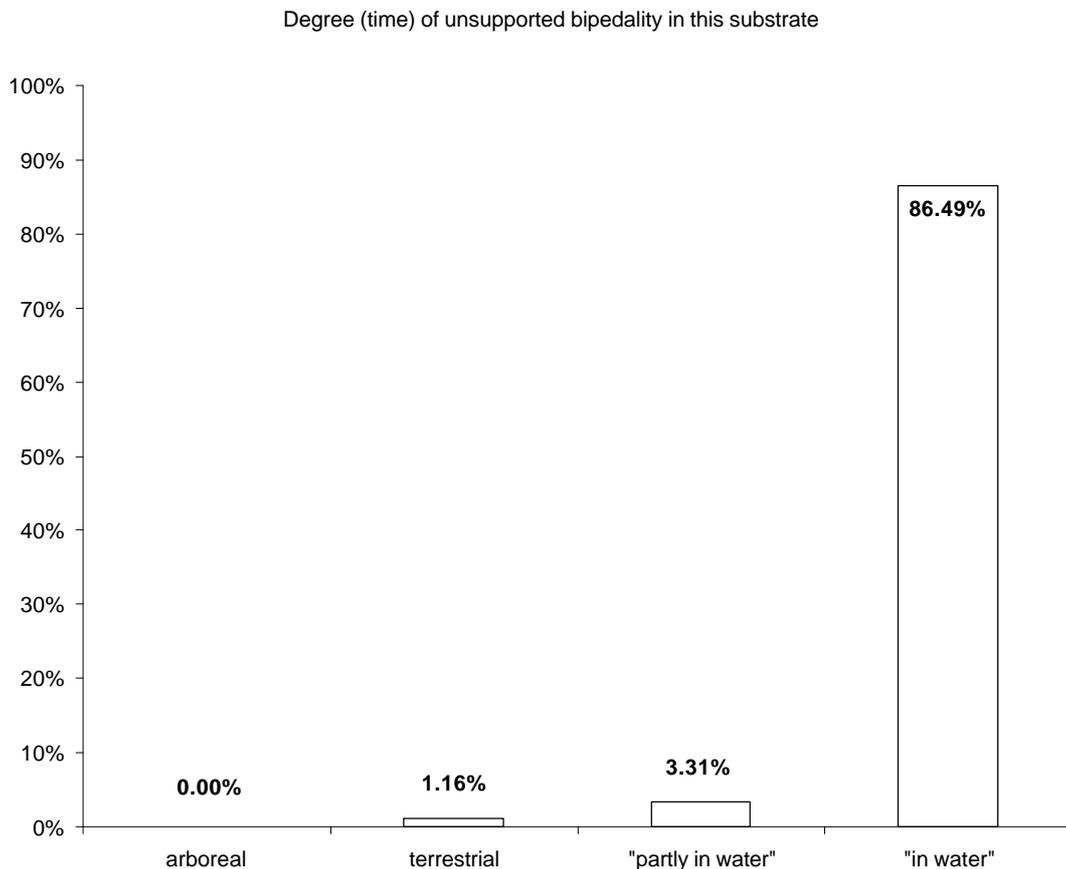


Figure 8 Unsupported Bipedality by substrate

Of the time bonobos spent in water with no contact at all with dry land, over 86% was spent in an unsupported biped posture. Only 3% of time was spent fully bipedal whilst partly in

water, meaning that the subject would in effect have to be standing upright, unsupported, with one foot in the water and one foot on land. An even smaller fraction of terrestrial time was spent in a fully bipedal posture and no observations of it were made at all in an arboreal substrate.

Analysis of instances of unsupported bipedalism

The fact that every observation was recorded allows a highly detailed study to be performed on the actual instances of unsupported bipedalism. By means of an example, below is a segment of one of observation case.

Table 3 Detailed analysis of Case 12: Hermien 14/6/01:8:06-9:30am

Time	Type	Event	Comment	Seconds	Substrate	Steps
08:36:32	P	S	Posture Sits with infant on Terrestrial substrate.	24	T	0
08:36:56	P	K	Knuckle-walks with infant clinging underneath to get food from mother.	11	T	0
08:37:07	P	B	Fully Bipedal on bank 'begging' for food.	5	T	0
08:37:12	P	K	Down on all-fours again (Knuckle-walk)	1	T	0
08:37:13	P	S	Sits	21	T	0
08:37:34	P	K	Knuckle-walks to get food thrown in moat	1	T	0
08:37:35	P	U	Upright posture adopted as right foot to moat. Three steps taken whilst in this posture.	5	T	3
08:37:36	L	LF	Left Foot in water - almost to knee (18cm?)	0	T	0
08:37:36	L	RH	right knuckle placed on bank for support	0	T	0
08:37:38	L	RF	now right foot moving across into water - above knee (20 cm?)	0	S	0
08:37:39	L	LF	left foot makes a step still right hand on bank	0	S	0
08:37:40	P	B	Now fully bipedal and fully in water as hand releases bank. 4 steps taken whilst in this posture	9	W	4
08:37:41	L	RF	right foot takes further step	0	W	0
08:37:42	L	LF	small step with left foot. water now 22cm? deep	0	W	0

08:37:42	L	LH	Bends down and stretches for food	0	W	0
08:37:43	L	LH	attempts to grab food from fish	0	W	0
08:37:46	L	LF	brings left foot back to regain upright posture	0	W	0
08:37:46	L	LH	grabs at 2nd attempt and brings food to mouth	0	W	0
08:37:48	L	RF	makes the first step out with right foot	0	W	0
08:37:49	P	U	both knuckles on ground simultaneously but body still upright and weight on feet	1	S	1
08:37:50	P	K	body thrusts forward weight taken on knuckles	2	S	1
08:37:50	L	LF	left foot first to leave water	0	S	0
08:37:51	L	RF	right foot leaves water	0	S	0
08:37:51	S	T	totally on land again	0	T	0

Table 4 Images of Case 12: Hermien 14th June 2001

08:37:36



08:37:37



08:37:39



08:37:40



08:37:41



08:37:42



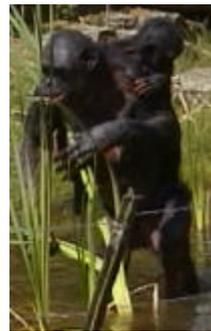
08:37:43



08:37:46



08:37:47



08:37:48



08:37:49



08:37:50



Quadrupedal Wading

Of the nine observed instances of individuals being classed as fully “in water” there was only one where quadrupedal wading was seen (fig. 9).



Figure 9 The only instance of quadrupedal wading

It happened at 14-Jun-01 08:42:53 when Hermien was reaching out for food and put her left knuckle under the water to take her weight. This instance of knuckle-walking in water lasted 3 seconds and the depth of water where her hand was placed was estimated to be at most 20cm.

3.2.3 Discussion

The bonobos observed at Planckendaël 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.

The prediction tested by this experiment, that extant apes would show a greater bipedal tendency in water was strongly supported. 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.

As Fig. 10 shows, if the water was deeper than 0.5 m (1.14 x hip height) the individual would have little choice in its postural mode in any case although no instance of quadrupedal wading was observed in depths greater than 0.2 m. (or about 0.45 x hip height.)

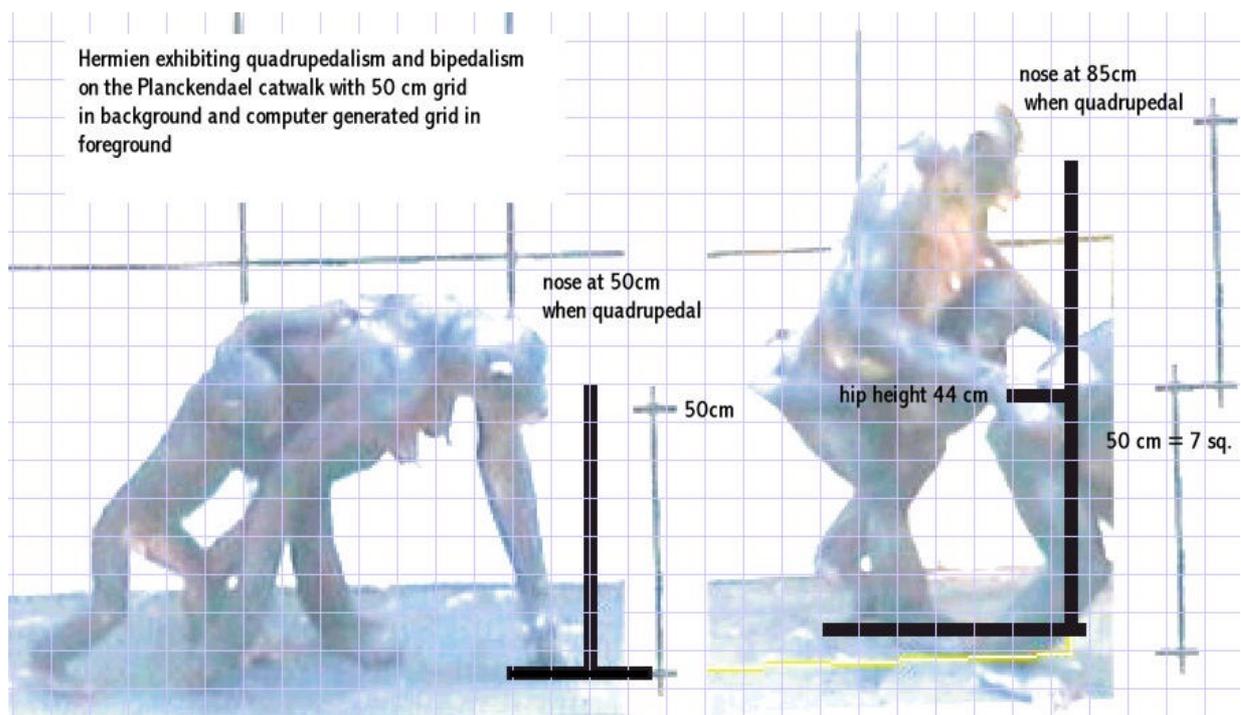


Figure 10 Hermien in quadrupedal and bipedal locomotory modes

In the background is the “cat-walk” at Planckendael with 50cm squares.

3.3 Conclusions

There is still very little published evidence for bipedal wading in extant apes. Searching the literature revealed just how little work had been done in this area.

However, what little evidence there is clearly indicates that, although apes prefer not to get wet, they are more than prepared to do so if they are given a strong enough incentive. 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:p55) it would seem that wading may occasionally be a life-saving behaviour.

It is difficult to imagine any other scenario with such a clear-cut, immediate survival benefit (one of the theoretical tests for the wading-origins model) for moving bipedally as the one provided by waist deep water but it does beg a serious question: If a putative ancestor was regularly exposed to such a life-threatening habitat, wouldn't they have been more likely, instead, to have evolved the ability to swim?

The next section investigates this problem.

4. Analysis of empirical data of wading in humans

4.1 Hypotheses tested

The wading-origins model predicts (2nd prediction) that there are certain semi-aquatic niches where wading would be the optimal mode of locomotion. Specifically, wading should be faster, safer and probably also more energy efficient than swimming at certain depths.

If, however, swimming was found to be faster than wading at depths significantly shallower than a putative ape ancestor would have been able to move quadrupedally it would call into question the wading origins theory.

A group of simple experiments were designed to test this prediction in human subjects of different sizes.

The model also predicts (3rd prediction) that an ape that was well adapted to a habitat where it regularly waded would adopt strategies to improve its wading efficiency. Although this can never be tested directly, at least the efficiencies of different wading techniques in humans can be studied to determine if such strategies may have been open to a putative wading ancestor.

4.2 Materials and methods

A series of simple experiments were held in a variable depth swimming pool (see fig. 11) at Amersham multi-pool, Amersham, Buckinghamshire between 11th and 18th June 2001.

The pool, 12m in length has been designed so that the bottom can be raised hydraulically to any required depth which was always done by a qualified lifeguard.



Figure 11 Amersham multi-pool

A variable depth pool ideal for wading experiments.

Fifteen volunteers, of different ages and sizes, took part in a series of timed races. Firstly everyone swam their fastest stroke to get a benchmark with which to compare wading times. Then, with the pool repeatedly set to different depths, a series of timed races, using different wading gaits, were undertaken. Each individual's times were recorded using a video camera that was focused in on the finish line so that the results could be taken later, at leisure, more accurately and verifiably.

The three wading gaits were: “frontal wading” where the subject ploughed through the water head on as if walking; “waddling” where the person pushed through the water from side to side, rather like an ice-skater, with bent knees and bent hips and thirdly “sideways” where the subject moved through the water side-on. People were told to keep their arms above water as much as possible whilst wading.

It was subsequently decided to only use the “frontal wading” results from children, as their reliability at performing waddling was a little suspect. It is worth noting that very little time was available for the volunteers to practice the two ‘new’ wading techniques (everyone knew how to wade frontally.) This inevitably affected the results. With hindsight it would have

been better to have booked enough time in the pool for volunteers to spend much longer practicing.

The races started at the deeper end of the scale and then the pool depth was lowered. This was to counter the possibility that the speeds were getting progressively slower due to tiredness. A short break of a couple of minutes was given between each race. Perhaps if the experiment was repeated this should have been longer. At each depth the sequence was “frontal”, then “waddling” and then “sideways.”

Later, individuals were measured for their full standing height and then sitting down. By subtracting one from the other each individual's hip height could be calculated. This figure was used to express the depths for individual recorded wading times as a fraction of their hip height.

Note: The term *hip height* is often abbreviated to the unit h in the rest of this discussion.

4.3 Results

The Wade-Swim Threshold

Perhaps unsurprisingly, these experiments showed that, for all individuals, there are depths of water at which wading is faster than swimming. On average this threshold was found to be around hip-height. None of the volunteers could be described as athletes but several were strong and experienced swimmers.

For each volunteer, their individual wading performances were plotted against their swimming speed.

Then a linear (for simplicity) regression analysis was used to calculate the wade-swim cut off point for each individual. The swimming speed, (0.96 m/s in the example in Fig 12) was used

in the regression formula to calculate the threshold at which swimming becomes faster than wading. For this individual it was calculated at $1.1h$.

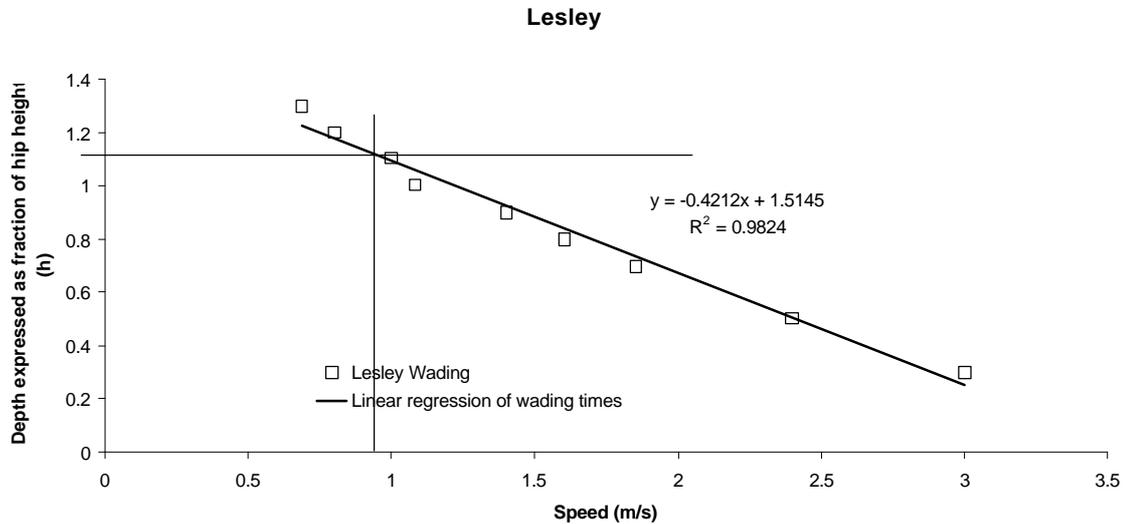


Figure 12 An example plot of individual wading speeds

The same analysis was carried out for all 14 individuals resulting in a table of swimming speeds and wade-swim cut off points.

This data was collated and compared as shown in fig 13. The chart shows the relationship between swimming speed and the wade-swim threshold, the depth at which wading becomes the faster mode of locomotion.

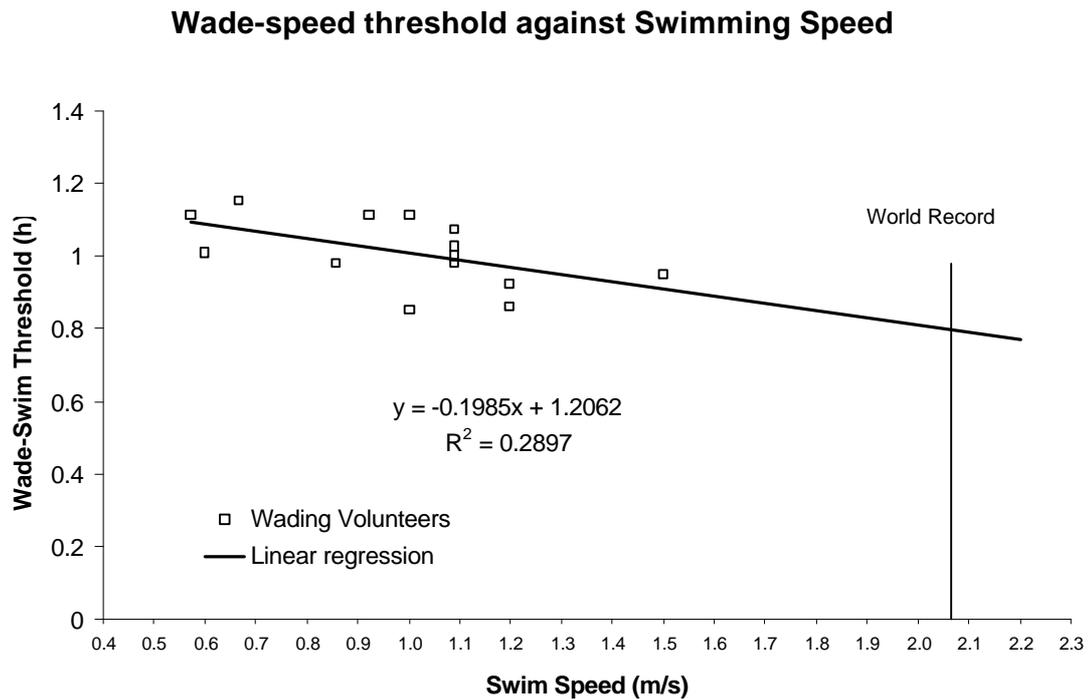


Figure 13 Wade-Swim Threshold against Wading Speed

There would appear to be a slight tendency for faster swimmers to have a lower threshold but generally the cut off point where wading becomes faster is:

$$1.01 \pm 0.09 h \quad (n = 14)$$

Using linear regression analysis this chart would predict that even the fastest swimmer in the world (at the time of writing Michael George Klim, at 48.18 seconds, is the men's 100 metres freestyle world record holder) would still have a wade-swim threshold at $0.79h$.

Wading Speed against Depth

As might be expected, the results showed a very clear correlation between wading speed (frontal wading only here) and h (pool depth expressed as a fraction of hip height): The deeper the water, the slower the wading.

What is less clear is the precise nature of the correlation. It appeared that the relationship here was a squared one (this idea was confirmed by personal communication with Vogel) but another possibility considered was that the relationship only cut in after a certain point.

Children and adults were plotted separately in order to show that the relationship held up for both groups although, with one or two exceptions, the children's speeds were predictably a little slower than the adults.

It was decided to show both a linear and a polynomial (order 2) regression against each group as shown below in Fig 14. The adult linear data regression line was generated using wading results only from depths greater than $0.75h$.

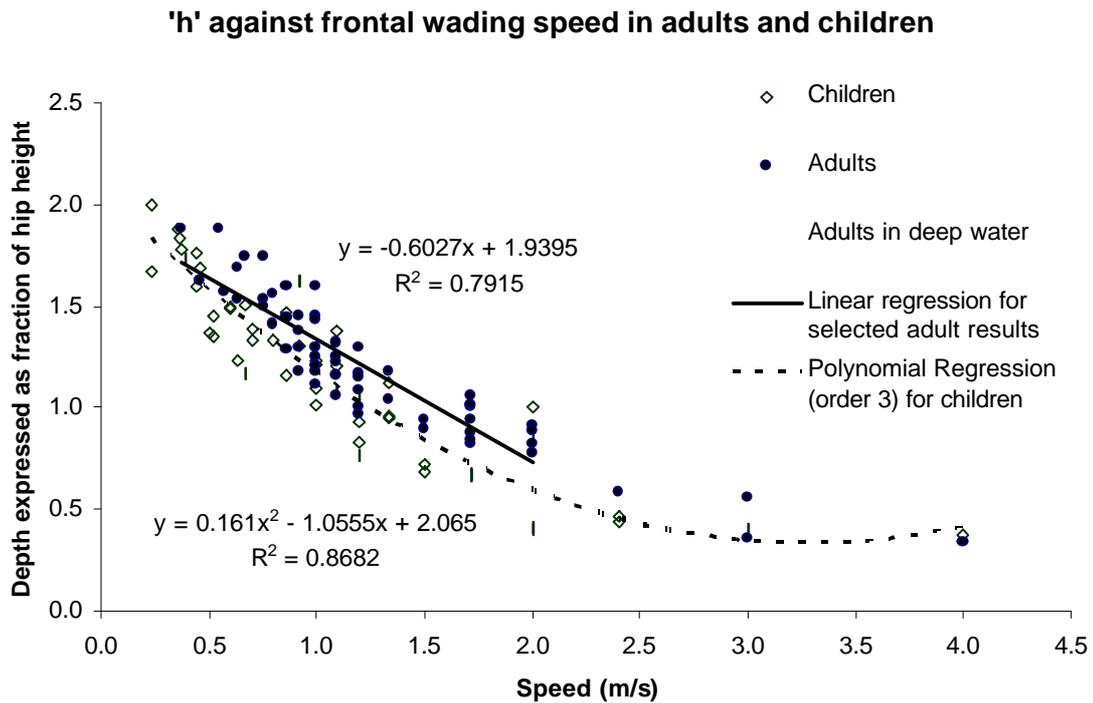


Figure 14 Comparison of wading speed against depth for frontal wading only.

The results of children for the next part of the experiment were excluded because of difficulties they had performing the waddling wading method correctly. (My demonstration of a bent-hip, bent-knee gait seemed only to make them giggle.) The sideways wading method had not even been considered for the first session, when the children took part.

Comparison of Wading Methods

The next set of results analysed the three different wading methods performed by adults:

- Frontal Wading
- Waddling
- Sideways

Firstly all the individual adult results were plotted to see if a pattern emerged. A polynomial (order 2) regression was selected as a trend line for each. Although the confidence (R^2) figure

for the regressions were never greater than 0.84, they nonetheless showed a difference in gradient that reflected the results and the volunteers' experience that it was easier to move sideways when it got deep.

The results indicate that frontal wading is significantly faster at shallower depths, although when it got deeper (> 1.7h) the advantage appeared to be lost. Both waddling and sideways wading were as fast (or slow) as frontal wading at these depths.

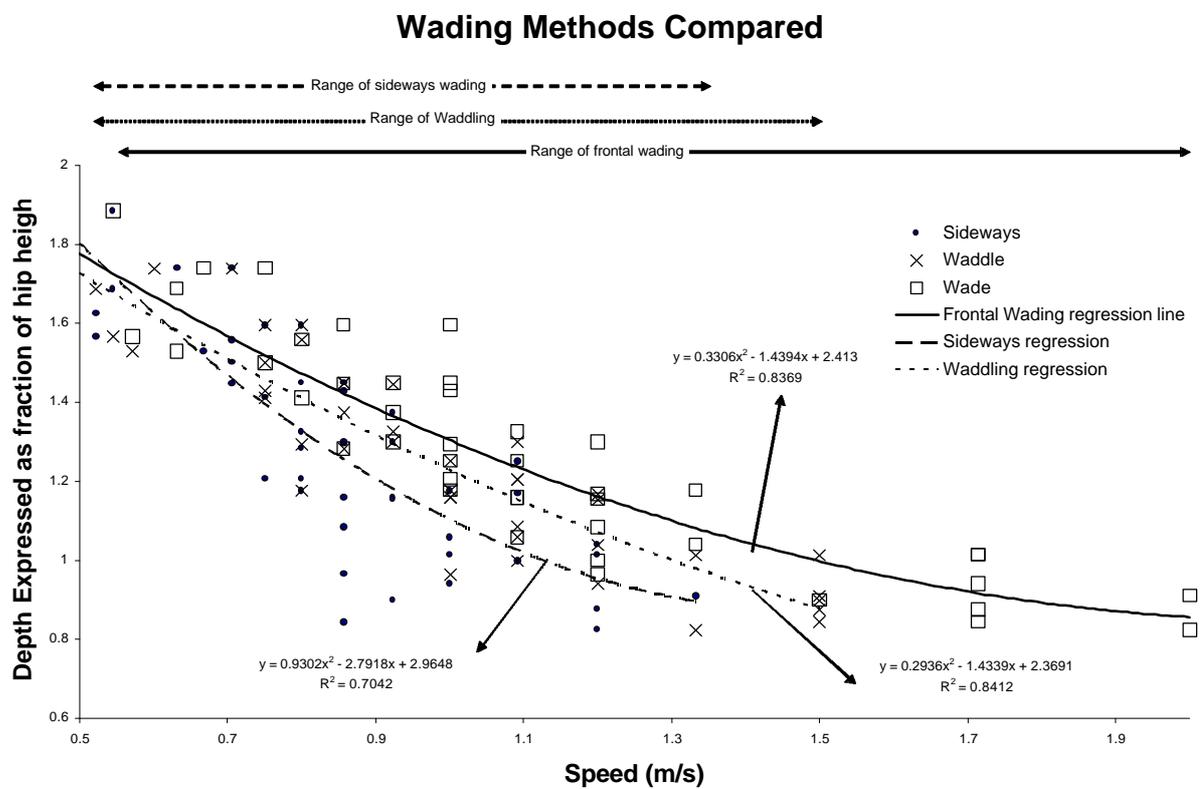


Figure 15 Comparison of different wading methods

In order to try to illustrate the trends better, the data were grouped on h values (rounded to 1 decimal place) and average speeds were calculated for each group. The same trends were found as in Fig 15 but the individual data points become much simpler.

Again polynomial (2nd order) regressions were used to identify trends, which are shown in Fig 16 below.

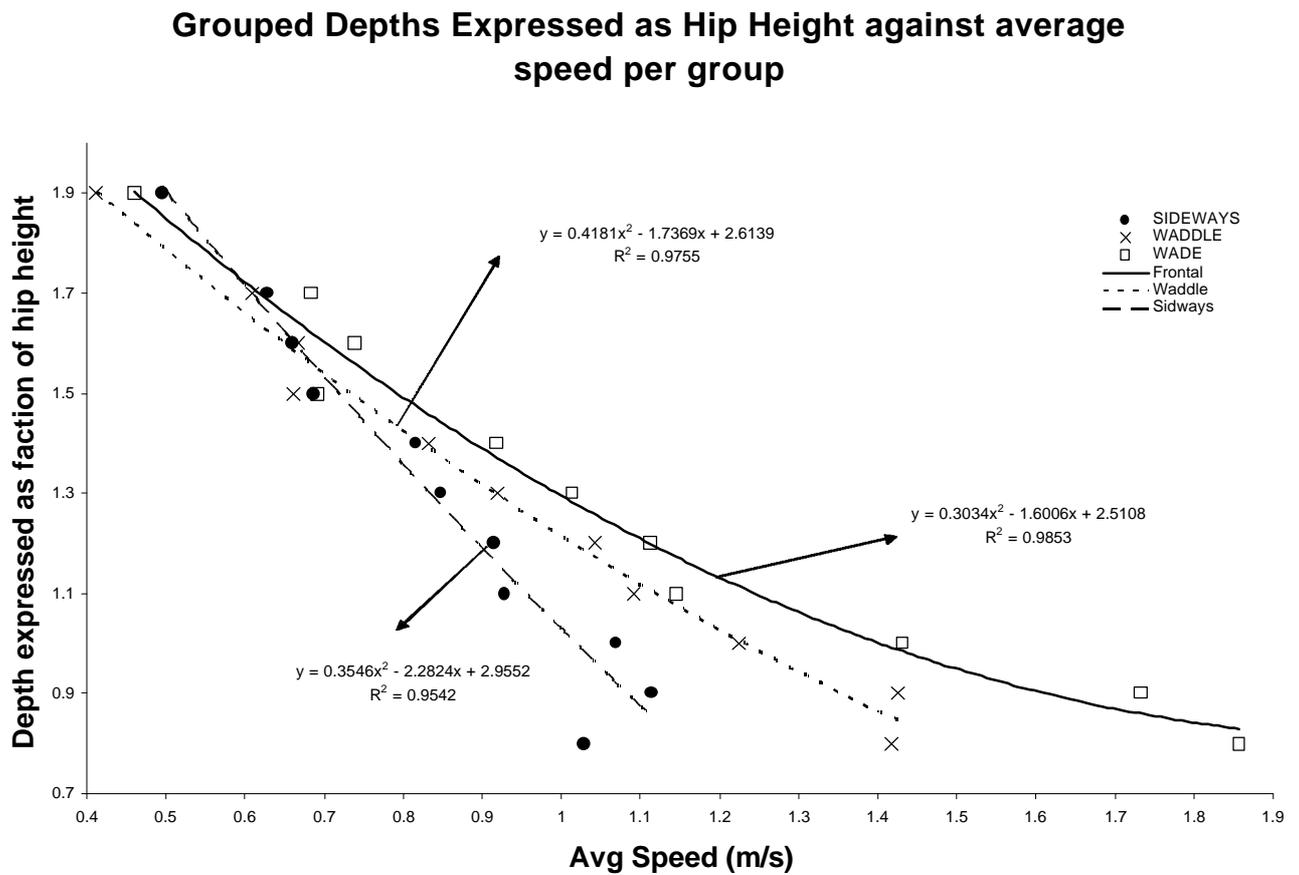


Figure 16 Grouped depths against average speed per group

The submerged body area factor

Although there is clearly a relationship between wading speed and water depth, expressed as hip height, it was considered that perhaps water depth was not the precise factor determining (or rather limiting) the speed. At least if it was, it might be an indirect relationship. A more likely candidate appeared to be the actual submerged body area.

Using a method based upon the ideas of Wheeler (1988:p64 & 1991:p110) which he used to show that bodies are cooler the further they are from the ground, human subjects were measured for their areas in given 'slices' of water at different depths. To calculate these 'slices' of body area, digital photographs were taken of individuals in full frontal and sideways wading modes. Family members were used, to avoid embarrassing the other volunteers. From these, estimated for body profiles were this obtained for everyone.

This generated a significant potential source of error because people have different body shapes. However good estimates were obtained by correlating body area (unknown value) with height (known value).

Fig 17 shows one such individual and the computer generated grid from which the area in frontal and sideways profile was calculated. The adjacent chart shows the plot of areas at different depth segments. A cumulative plot (fig. 18) of these areas was derived and from that a polynomial regression equation was generated to calculate percentage body area submerged at given depths, expressed as a percentage of body height.

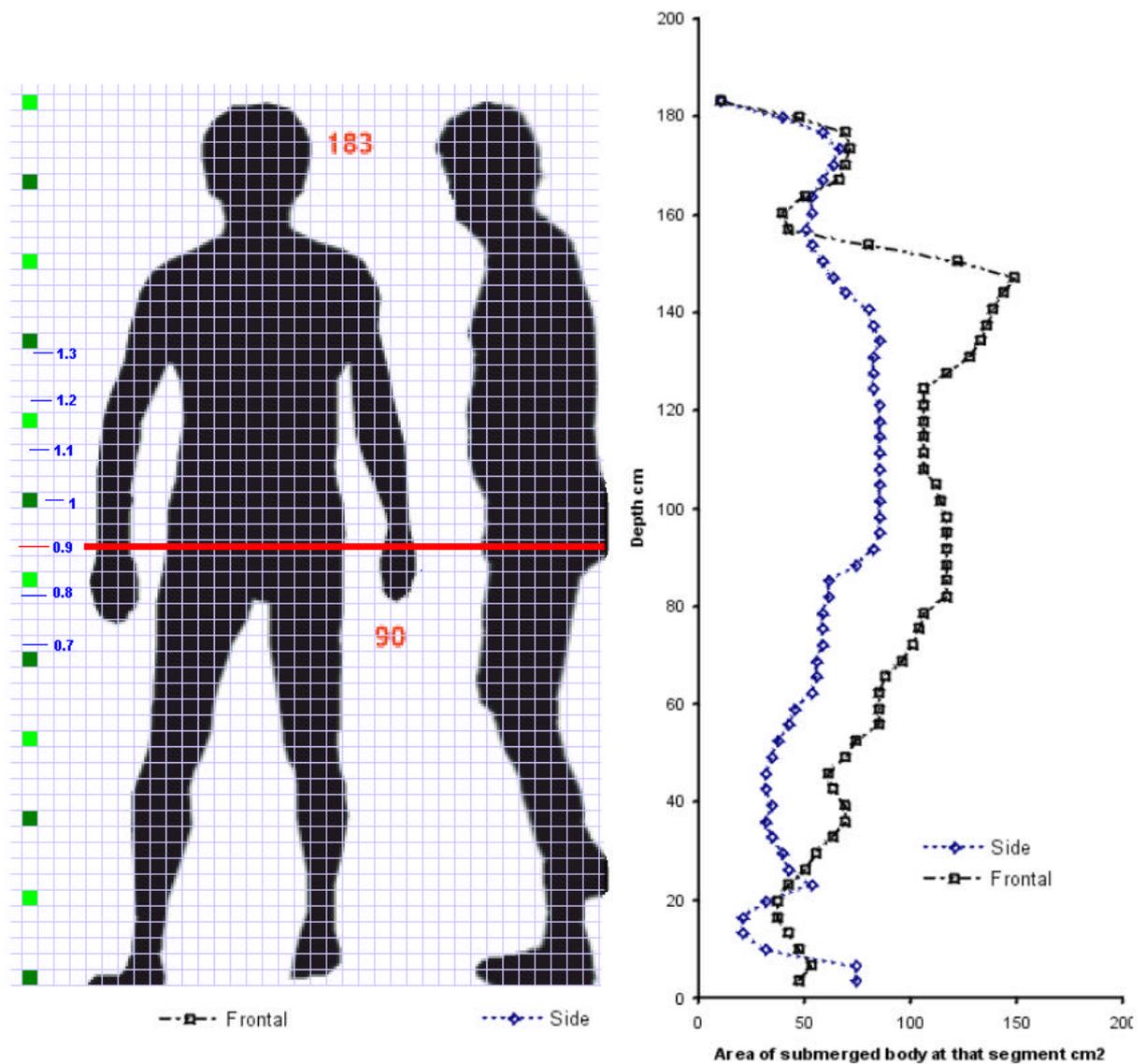


Figure 17 Example Human profiles used to calculate submerged areas. (1 square = 10.68 cm³. Note that the arms were not included in the frontal profile calculation. Thick horizontal line marks wade-swim threshold.)

It was found that frontal profile was between 46% and 28% greater than the sideways profile in those family members measured. The most conservative figure (the lower figure of 28%) was used when estimating the areas of volunteers that were not measured directly.

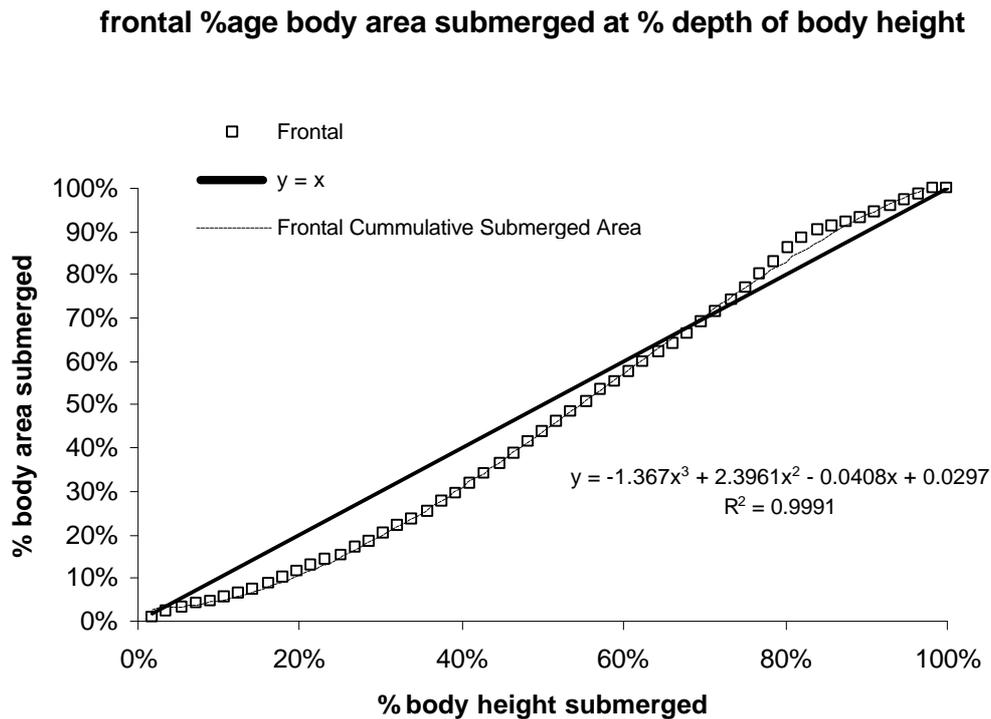


Figure 18 Cumulative plot of area segments at different depths
with $y=x$ plot for comparison

Using the same method a (3rd order) polynomial regression formula was also generated for the sideways body profile. Both formulae were quite similar and did not, in any case, deviate very much from the linear formula:

$$y = x$$

These formulas were then used to calculate the estimated submerged area of the body as seen in the plane of the direction of their movement (or “projected area” Vogel 1994:p88) for frontal and sideways wading for each individual race.

This was then plotted against wading speed for frontal and sideways wading. ‘Waddling’ was no longer included because of the complexities of that form of locomotion in determining which profile to measure.

When submerged body area was plotted against wading speed (Fig. 19) a much clearer relationship was seen and a far better distinction between frontal and sideways wading could be made.

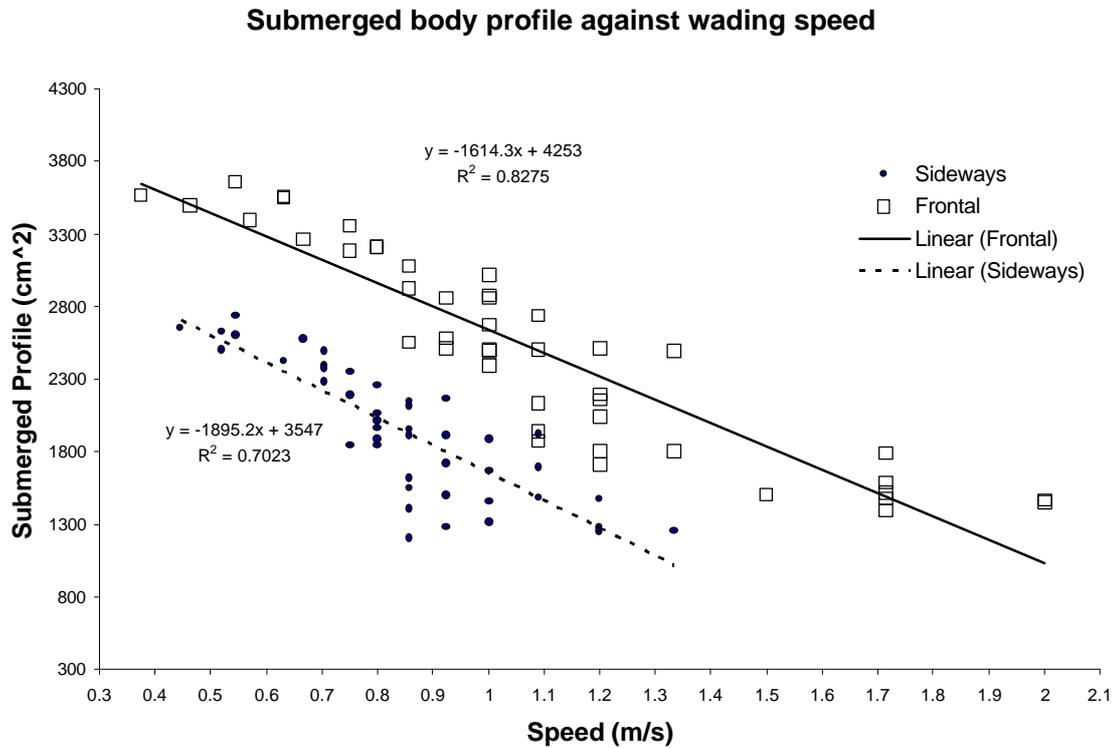


Figure 19 Submerged area of body against wading speed

The chart above is actually showing the same data as fig 15, except that *water depth expressed as hip height* has now been replaced with the more relevant figure of *submerged profile area*. This simply emphasises that, even at greater depths, sideways wading still results in a smaller body profile than frontal wading, a point that was not as clear on the previous chart.

Although the precise relationship between submerged body profile area and wading speed is undoubtedly extremely complicated and, from consultation with people who know fluid mechanics, almost impossible to predict accurately in such a complex body as a wading human, the general correlation would seem clear enough and, on the face of it, fairly obvious.

Wading volunteers certainly felt that wading sideways “was easier” than frontal wading at greater depths but at the same time frustrating at shallower depths because they weren’t physically able to move themselves as quickly.

The logical next step was to try to estimate the amount of drag each volunteer was pushing against at different depths using the different methods. This proved far more problematic than had been envisaged. Vogel (1994:p3) hints at the reason with his understatement “fluid mechanics is intimidating” although his excellent book does go on to explain the subject very clearly for biologists.

There are, apparently, at least three components of drag acting upon a person wading through water. Each one is complicated enough in its own right.

Firstly the drag created from skin friction (or viscous drag). These would be the viscous or “sticky” forces on the actual surfaces of the individual waders. It is the numeric expression of the feeling that water is “clinging” to the side of your body.

Secondly, form (or “pressure”) drag. This is caused by the pressure difference between the front and the rear of the body pushing against a fluid. It is related to the viscosity of the fluid and highly complex issues of streamlining, which affect the boundary layer separating fluid from the surface of the body with the stagnant mass just ahead.

And thirdly, wave drag. This is the most difficult of all to predict, especially in an object as dynamic and complicated as a human being wading through water. At the surface of the water, the body generates gravity waves and the energy they require is provided by an additional force on the body.

The first two are, at least, largely dependant on submerged body area although the second would be greatly complicated if one were to try to estimate, from body shape, the degree of streamlining taking place. The third was so problematic it was not even worth considering

especially as “surface waves ought to impose negligible force” (Vogel pers. comment in response to specific question about this experiment.)

It was therefore decided to proceed with an admittedly rough estimate of drag purely using the submerged surface area alone and making no attempt to estimate any streamlining. Fluid Mechanics that model airplanes and ships for drag might use the following formula to do this (See, Vogel 1994: p88-89 for an excellent background to these matters):

$$D = C_D (0.5 \tilde{n} v^2) A$$

Where D is the drag being calculated

C_D is the coefficient of drag (a function of the shape and the Reynolds number.)

v is the velocity

\tilde{n} is the density of water (1000g/m³) and

A is the reference area or a cross sectional area for form drag and a surface area for skin friction.

The ratio of pressure drag to skin friction, is called the Reynolds number. The Reynolds number is very important when considering the effect of scaling an aircraft (or model of an aircraft) up or down but not so important for the purposes of this study because the comparisons being made were not between models and real life objects but between the same individuals in the same pool just a few minutes later. Also for purposes of simplicity it was assumed that the streamlining was *the same* for both frontal and sideways wading. This is clearly not the case but made it considerably easier to get some kind of estimate for drag.

A simplified formula was thus used...

$$D = 500Av^2$$

Where

D is an estimation of drag

v is the velocity of an individual and

A is their submerged area

This estimate of drag would normally be measured in Newtons/m² although the absolute value is of no concern to us here as we are interested only in comparing the relative drag forces of frontal and sideways wading and not absolute values. Without the C_D (coefficient of drag) function such absolute values would be likely to be inaccurate in any case.

This calculation therefore gives an *overestimate* of drag because we have assumed that the body moving through the water is not streamlined in any way. Specifically, the drag for sideways wading will be even more of an overestimate than frontal because it would logically be expected to be more streamlined than frontal wading. Recall also that when the individual body profiles were estimated the most *conservative* figure (28%) was used to estimate sideways profile in those not explicitly measured.

Consequently, it is argued that an estimate of the drag forces acting upon someone wading can be calculated by multiplying this formula by the submerged body area for each wading mode.

This estimate of drag force was then be plotted against speed for the different wading methods (fig. 20).

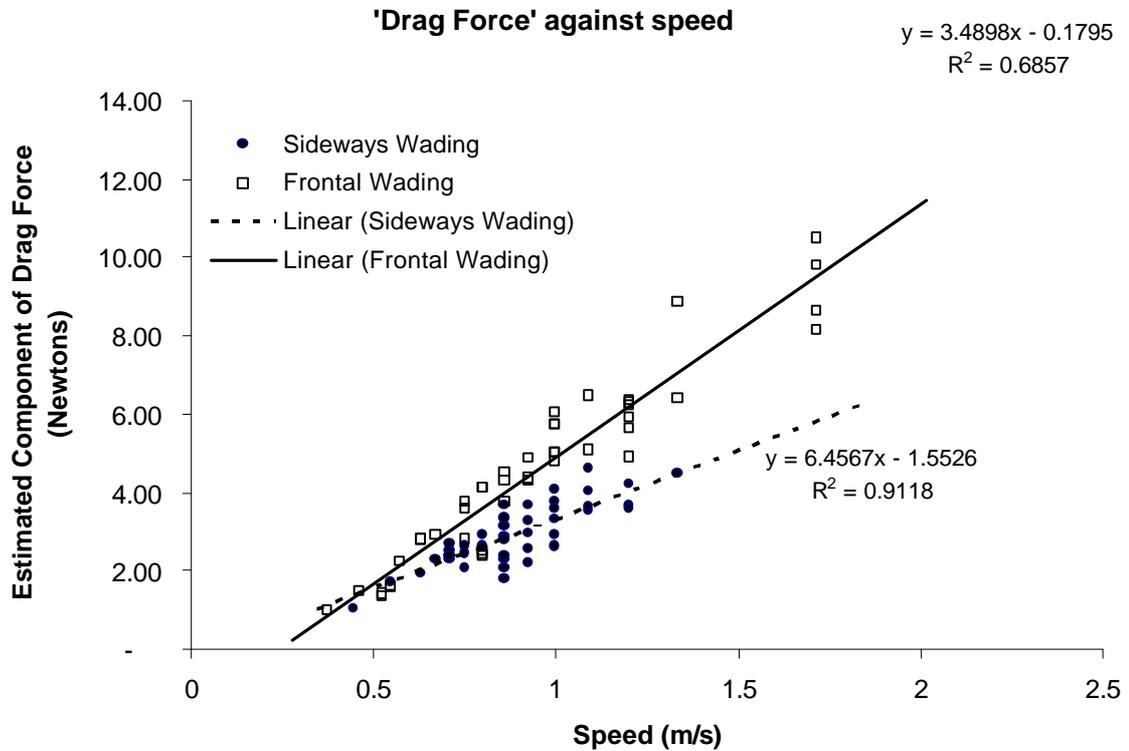


Figure 20 Estimated Drag Force against wading speed for Frontal and Sideways wading

The steeper curve for frontal wading suggests that this mode is the least efficient in terms of energy use. If streamlining would have been taken into consideration and the actual body profiles of individuals measured the difference between the slopes of the curves would certainly have been even greater.

Although some of the fluid mechanics in arriving at this conclusion might appear naïvely oversimplified to some and bafflingly complex to others it is contended that the basic principle on which it is based is fairly intuitive. Just as fish and birds have evolved streamlined shapes in nature and boats and airplanes are designed with them in civic life it is only to be expected that a reduced body profile would be more efficient in terms of drag. The

difference between frontal and sideways wading is perhaps most clearly demonstrated when you place your hand outside a moving car. When it's held out flat it is buffeted heavily by the wind but when it's twisted through 90° it cuts through the air like a hot knife through butter.

4.4 Discussion

There are a number of findings from these simple experiments that are relevant to the discussion on a wading origin for bipedalism.

Firstly the experiments supported the (2nd) prediction that wading should be the optimal mode of locomotion at certain depths. The range of wade-swim cut off points was rather narrow (0.85 - 1.15) with a mean of 1.01 (\pm 0.09 s.d.) suggesting that as water gets shallower, hip height is generally the depth at which wading becomes faster than swimming in humans.

In the previous section it was found that predominantly quadrupedal apes still tend to wade bipedally even at shallow depths (above about 0.45 *h*) and that there are clearly depths at which it has little choice but to move bipedally (at around 1.14 *h* or deeper.)

To this it can now be added that even for a biped that can swim (i.e. humans) there are ranges of water depth that still favour bipedal wading as the optimal mode of locomotion.

One could start to use this data to build an estimated range of optimal wading depths for a putative ancestor, assuming their body shape and wading abilities were somewhat intermediate between *Homo* and *Pan*. Summarised below in Fig 21.

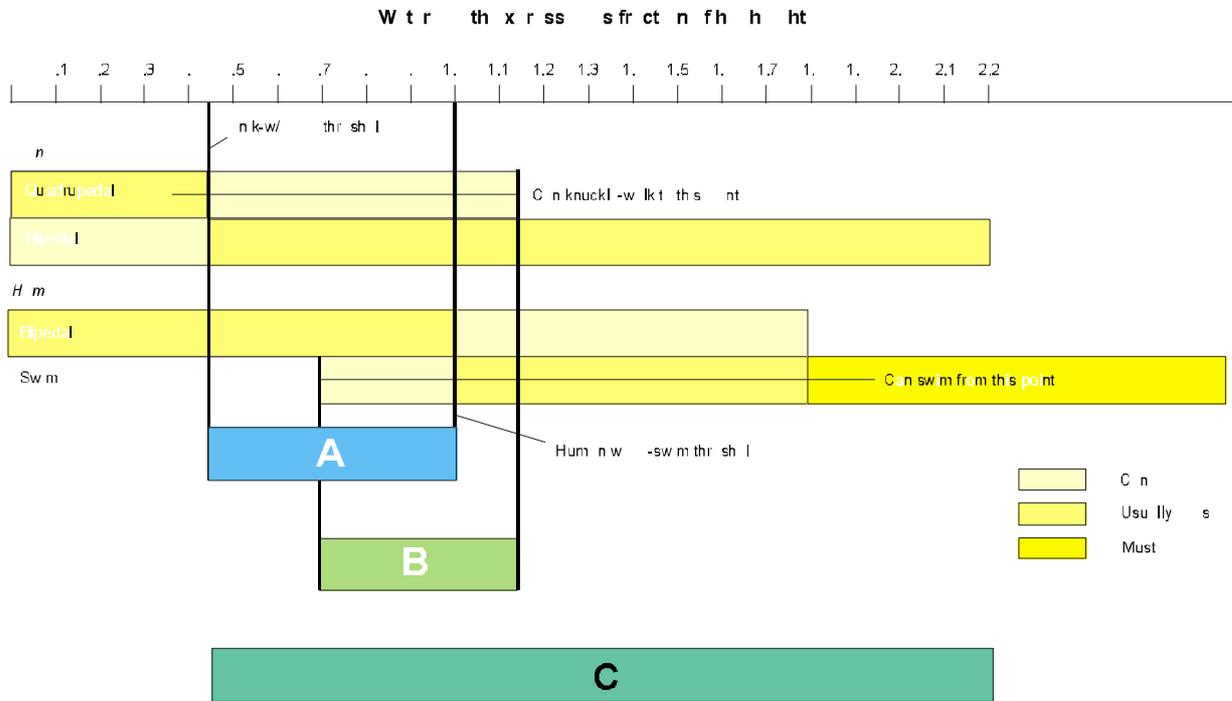


Figure 21 Knuckle-walking / Wading / Swimming thresholds of Pan & Homo indicating possible range of optimality for wading and possible overlap of swimming and quadrupedalism.

The figure shows that there is a potential overlap of ranges (**B**) where knuckle-walking could, theoretically, be used in depths up to 1.1 *h* and swimming could be used in depths as low as 0.7 *h*. This is clearly the case with most semi-aquatic quadrupedal animals, which tend to swim rather than wade bipedally. It also argues against the wading-origins model because it would suggest that swimming would become the predominant mode of locomotion in water that approached the depths where a quadrupedal mode could not be used.

However, putting theory to one side, there is no doubt that extant apes adopt bipedal wading rather than swimming. Indeed for all but *Gorilla* (Ellis 1991:p55) swimming is not even an option. If we assume that, for whatever reason, the same was true of the earliest bipeds then

they too would be more likely to use bipedalism rather than swimming in suitable depths. Taking this assumption as a benchmark provides a range (A) at which depths bipedal wading would be the optimal mode of locomotion. It should be noted that the ability to swim is therefore key in this debate. If one assumed that the earliest bipeds could not swim at all then the range of optimality extends the full range of depths (C). (Note the theoretical bipedal range is greater for *Pan* is greater than *Homo* only because human leg length is greater than that of *Pan*.)

If the 2nd prediction of the wading origins model has been fulfilled, what about the 3rd?

Recall that this predicted that any ape that was well adapted to a wading habitat should find the most efficient method of doing so. This experiment could hardly test such an hypothesis. However it did show that the area of submerged body profile was closely correlated with wading speed and it is therefore logical that a putative ape specialised to this niche would use a mode of wading that minimised this profile.

The experiments with sideways wading provided an intriguing insight as to what mode of locomotion might have evolved. A sideways wading profile reduced the submerged body area by between 25% and 45% (compared to a frontal mode) and consequently the drag in water would be decreased by at least that amount. Although the speed comparisons showed that frontal wading was faster for all but the deepest pool depths, this is clearly only because humans are not adapted to (or even used to) walking sideways. If our musculature could propel us as strongly sideways as it does frontally there would seem little doubt that sideways wading would be the optimal mode for all depths.

5. 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:p331) “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 (p329) 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 displayed *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.”

It is not the objective of this study to concern itself with the phylogeny of the Australopithecines, although that is clearly of some relevance. The objective, in this section, is to question its 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?

We have seen that bipedal wading is not so unusual a mode of locomotion in the *Hominoidae* after all. All of them have demonstrated that they are capable and prepared to move in this way when necessary. It would seem likely, therefore, that their ancestors were also capable of the same.

One of the predictions (the 'ideal' part of the 3rd) of the wading-origins model is that it should explain the features of the earliest bipeds such as *Australopithecus afarensis* better than the alternative theories. This section will now briefly review that contention.

If *A. afarensis* morphology is adequately explained in terms of its locomotory repertoire by existing models then the wading model would have nothing to contribute.

The section has 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.

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

Starting with the basics, the question must be asked: Was Lucy arboreal, terrestrial, a bit of both *or what?*

The debate thus far about the way *A. afarensis* moved (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. The discussion seems to attempt to place Lucy on a linear scale with totally erect human-like, bipedality at one end and a totally arboreal climbing repertoire

at the other. This essentially 'bi-modal' locomotory repertoire made sense because it naturally fitted the two substrates she was assumed to have moved in. She walked on the ground or climbed in the trees, the question was simply: 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).

They conclude that "Pre-bipedal locomotion is probably best characterised as a repertoire of terrestrial knuckle-walking, arboreal climbing and occasional suspensory activities, not unlike those observed in chimpanzees today".

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."

The issue of phylogeny is fundamental to this particular debate. It is possible that *A. afarensis* evolved from a knuckle walking ancestor, even though it no longer did so itself, in which case it could be argued that the traits were just "evolutionary baggage" from the past. However that argument might be seen as a little convenient to some. The same paper found that *A. africanus*, a putative descendant of *A. afarensis*, had lost those traits. If they were phylogenetically related and if the knuckle-walking traits were evolutionary baggage in *A. afarensis*, why did they then disappear in *A. africanus*? Baggage is baggage.

Furthermore, recent research has indicated that inferring phylogeny from skeletal structures is more unreliable than had been considered in the past (Gibbs, Collard & Wood 2000), adding further weight to the argument that the traits were functional, and others have highlighted the plasticity of bone during lifetimes. Oxnard (1983: p97) said “There is now every good reason for believing that most biological materials, especially bone, must be considered as anisotropic, poroelastic, materials.”

To conclude: The most parsimonious explanation for the knuckle-walking traits of *A. afarensis* has to be, simply, that *A. afarensis* was a *knuckle walker*.

This is indeed 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. It is claimed here that a clearer explanation has not, thus far, been suggested.

5.2 Predicting Lucy’s bipedal gait

Whether *A. afarensis* had two or three modes of locomotion nobody doubts that they were, at least in some way, bipedal.

The AL 288-1 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.

Not surprisingly too, there have been many excellent reviews of *A. afarensis* morphology. The reader is urged to refer to Aeillo & Dean (1999:Chs.14,19,20-21), which compares human, great ape and australopithecine bipedal morphology in a systematic and clear way.

Several elements of the post-cranial skeleton have been recognised as indicating her bipedality although, for brevity, only those concerned with the pelvis and femur (and not for instance vertebrae or feet) will be considered here.

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.” (p355).

This and other differences are reviewed by Aiello & Dean (1999:p451-453) where it was further observed that the *A. afarensis* pelvis further differs from the human condition “in their extreme width” not only at the iliac crests and at the acetabulae but also 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 specimens (a piece of proximal tibia and a distal femur) to be retrieved from Hadar in Ethiopia in 1973 were observed by Owen C. Lovejoy and diagnosed as have belonged to a hominid “that could walk upright.” He based the diagnosis on its clearly valgus knee, which indicated to him that not only was she bipedal, but that she exhibited an essentially human-like (erect) form.

Lovejoy added further weight to this view later when AL 288-1 was analysed a couple of years later, 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 view was the most logical interpretation especially after recent work (e.g. Patriaco 1981) had demonstrated, with myoelectric plots, the importance of the muscles involved with abduction in the human bipedal gait. Lovejoy consequently promoted an essentially human-like gait for *A. afarensis* even though its femuro-pelvic complex was quite different, morphologically.

Later, however, 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).

After studying displacements of centre of gravity. Tardieu proposed a “rope-walker” gait model for chimpanzees and early bipeds suggesting that their low centre of gravity meant that their “bipedal dynamic equilibrium was still precarious.”

Berge performed biomechanical studies on *A. afarensis* reconstructions based on two different (one ape-like and one human-like) gluteus muscle arrangements. She concluded (p271) “The present results lead to the conclusion that the bipedalism of *Australopithecus* must have differed from that of *Homo*. Not only did *Australopithecus* have less ability to maintain hip and knee extension during the walk, but also probably moved the pelvis and lower limb differently.” She characterised it as a “sort of waddling gait” with large rotatory movements of the pelvis and shoulders around the vertebral column.

And Abitbol (1994) cast serious doubt on the notion that *A. afarensis* walked in a fully-upright manner by challenging the way that her hip joints have been reconstructed in models to date, in particular the assumption that the hip joints “are aligned in a vertical plane” (p211). He concluded (p225) “one may justifiably wonder if Lucy’s erect posture might not reflect some characteristics of nonhuman-like bipedal posture and locomotion.”

Those in favour of a fully-upright mode were bolstered recently however when the BHBK hypothesis was countered 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. They conclude (1998 p 71) “It is thus difficult to envisage a selective pressure sufficient to bring about the undoubted bipedal adaptations of this species, if it habitually utilised ‘bent-hip-bent-knee’ bipedal walking.”

Stern (1999:p567) replied to this by suggesting that his colleagues “never doubted that BHBK walking is more energetically costly” but that (p569) “the extra cost would have been small.” His last words on the matter were (p569) “It was only when life on the ground overwhelmed in selective importance any use of trees for feeding and escape, that the human ancestor was free to evolve the highly efficient mode of bipedalism with which we are personally familiar.”

The debate rages on today with no prospect of consensus in sight. A salvo from the trees, followed by a retort from the ground. Perhaps peace may be found by questioning their common assumption that the lifestyle of *A. afarensis* was not influenced by water.

Three positions on the bi-modal locomotor axis for *A. afarensis* are considered.

Terrestrial Human-Like Model

In the paper by Crompton *et al.* (1998), BHBK was suggested to have been energetically less efficient but this was based upon the unspoken assumption that her bipedality was *purely terrestrial*. Therefore no computer model was devised to test how BHBK would have performed in water. If they had, they might have come to a very different conclusion.

It would seem logical that, whilst wading, 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. This buoyancy could also explain the characteristically small, relative to body size, femoral head (Aiello & Dean 1999:p470-1) found in australopithecines which is normally interpreted as being correlated with the stress load resulting from body mass. Those volunteers who practiced BHBK for the waddling races in the swimming pool found it quite a comfortable, if unnatural, mode to adopt.

Their other main objection to BHBK, that it would have resulted in excessive heat generation, could also be easily countered if one assumed its bipedality was due to wading, 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 reasons 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.

Arboreal Model

The most extreme argument on the bi-modal terrestrial-arboreal axis, that *A. afarensis* did not spend much time on the ground at all and that its bipedality emerged from a purely arboreal niche does not make a clear distinction between the habitats of extant African apes such as *Pan* - the 6th (theoretical) test of the wading-origins model. If *A. afarensis* became bipedal in this habitat, why are chimpanzees not also bipedal today? Once again however, if her habitat is seen as being one where she practiced three modes of locomotion in three different substrates then one can clearly see why purely terrestrial/arboreal chimpanzees today would not be expected to be bipedal.

5.3 Sideways wading – Is it morphologically plausible?

This section began with the possibility that *A. afarensis* skeletal morphology might be so radically different from anything else yet found that perhaps Oxnard (1983:p329) had been right with his first (and most unlikely) explanation for it: That they had adopted “a totally new and unknown manner of locomotion which would be unique in its own right.”

Since then we have seen that a number of the controversies that surround the australopithecine locomotion debate might be solved if wading was considered as a possible mode for its bipedality. However none of this has, so far, gone any way to explaining its peculiar traits. Indeed earlier we saw how both extant apes and humans were able to wade satisfactorily without them.

The final part of this section proposes a potential functionality, based on a specialised mode of wading, which may explain them.

The 3rd prediction made of the wading-origins model was that any ape that became specialised to wading would optimise its wading method and in the human wading experiments we found a clear way how this might have been achieved. There was a clear correlation between speed (and drag) and submerged body profile in the water so, logically, through individual experimentation, cultural learning and/or natural selection a putative wading ancestor should adopt behaviours, and ultimately morphologies, that would minimise this profile.

The experiments which compared wading modes suggested that sideways wading, which resulted in a much smaller submerged profile, would theoretically be the fastest and most efficient if only human subjects could have propelled themselves sideways with sufficient force, which they evidently could not.

So we are left with an intriguing question: What evidence is there that *A. afarensis* was able to propel itself with sufficient force sideways to make this odd putative mode of locomotion a plausible one?

The muscles involved in such a sideways thrust are likely to be complex in humans and, of course, can never be known in extinct species of which only fossils remain. Those that took part in the sideways wading experiments in a swimming pool described the best way of doing

this, after a little trial and error, as a kind of “kicking out” action to push away with the rear leg and alternately “reaching out and pulling back” with the front one. Whatever the specifics of the movement, it would seem that a large part of the force needed to propel someone sideways would come from those muscles involved with the abduction (moving out laterally away from the medial line) and adduction (pulling back closer to the medial) of the femur from the pelvis.

The most promising approach, then, might appear to be to investigate the specific musculature and associated skeletal structures of human hip abduction and adduction. This could then be compared with the known morphological differences between *A. afarensis* and humans to see if any biomechanical inferences can be made relating to its ability to wade sideways.

Firstly there will be a brief description of the most significant muscles that arise from the iliac crest and their general role in humans. This is followed by a list of related morphological differences in *A. afarensis* pelvis and femur. Finally an attempt is made to infer the kind of limb movements that would be enhanced by these differences.

Aiello & Dean (1999:p410-413) describes the muscles and movements of the lower limb in humans.

The abductors are the Gluteus medius and Gluteus minimus.

Both arise from the iliac crest. The minimus lies underneath the medius and arises more from the centre of the iliac blade, towards the hip joint. (See Fig 22 below to clarify the relative positions of gluteus muscles in the great apes and humans. Taken from Aiello & Dean (1999:p414 after Sigmon (1974)))

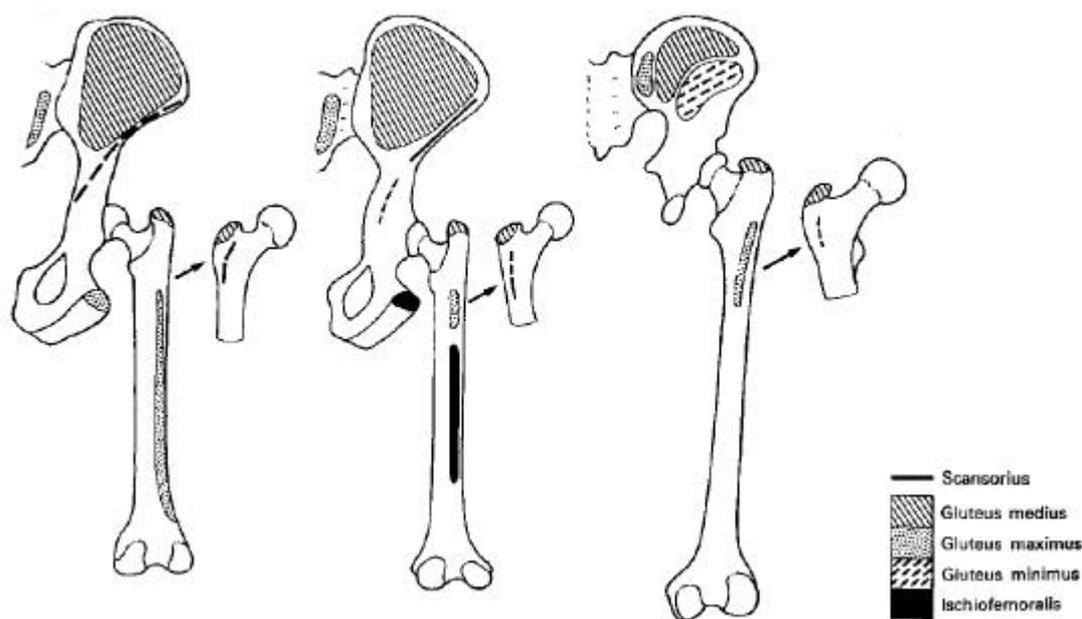


Figure 22 Pelvis and femur of Pan/Gorilla (left), Pongo (centre) and Homo (right)

Both insert onto the femur, the gluteus minimus more posteriorly and the gluteus medius more anteriorly.

“The position of these muscles over the lateral side of the hip joint and their function as abductors and stabilizers of the pelvis are unique features of human bipedal locomotion.”

Aeillo & Dean (1999:p413)

The Gluteus minimus and medius that are therefore likely to be the ones primarily concerned lifting the leading leg away and forward from the body and kicking out, and back, the rear leg in sideways wading.

There are five adductor muscles. The largest, Adductor magnus, arises from the ischial tuberosity and the ischiopubic ramus. It inserts on the femur along the linea aspera. Four of the others (pectineus, adductor brevis, adductor longus) fan out from the pelvis in similar ways and insert at points along the length of the femur. One, however, the gracilis inserts onto the tibia.

Applying basic lever theory to the biomechanics involved with hip abduction (for example) makes it clear that the efficiency of the force acting on the femur is related to the distance of from the hip socket from the insertion point onto the bone and the distance from the hip socket to the feet. (See fig 23 below)

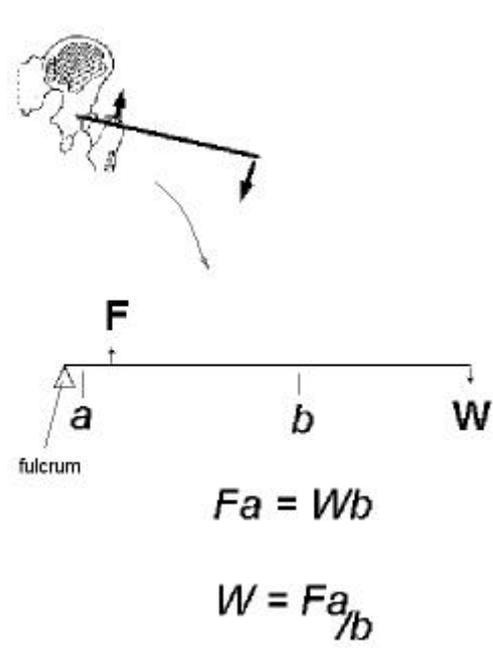


Figure 23 Suggested, simplified biomechanics of hip abduction in sideways wading in humans.

(F = Force of abduction from gluteus minimus and/or gluteus medius muscles.

W = Work required for propulsive sideways kick. a = Femoral neck length, b = Leg length)

To be able to propel itself sideways with greater wading force (W) than humans *A. afarensis* should have any of the following morphological differences:

- An increased pulling force, *F*, applied to the greater trochanter.
- An increase in femoral neck length, *a* (the biomechanical neck length as defined by Lovejoy, 1975).
- A decreased leg length, *b*.

Any combination of these would be predicted to improve the power and/or efficiency of the thrust of hip abduction but *A. afarensis* would appear to have all three.

According to Aiello & Dean (1999:p470) biomechanical neck length in australopithecines is long in comparison to humans and African apes (p461). However they say that this is more pronounced in the later, more robust australopithecines than in the earlier ones, such as AL 288-1 which are “closer to the modern human mean.” Berge (1994:p261) just describes the femoral neck as “very long.”

A. afarensis has been noted for their short limb length. Berge (1994:p261) describes “a very short femur” in AL 288-1 and recent studies (e.g. Kramer and Eck 2000) have even suggested that this might have been adaptive for slow, short-distant walking.

It is impossible to deduce anything about the thrust of Lucy’s gluteal muscles but a more prominently flared iliac blade from which they arose would seem to be consistent with the hypothesis that they were stronger.

According to Aiello & Dean’s summary of Lovejoy’s interpretation of the pelvis (1999:p451) “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 hip joint.”

Adduction forces could be treated similarly and would be increased if :

- The muscles described were more powerful,
- Leg length decreased or
- The distance between the acetabulum and the points of insertion on the ischiopubic ramus was increased.

The analysis can largely be repeated from that of the abductor muscles. But in addition Berge (1994:p267) notes that “it appears that the australopithecine adductor musculature must have been more powerful than that of humans” because of longer lever arms. (See fig 24)

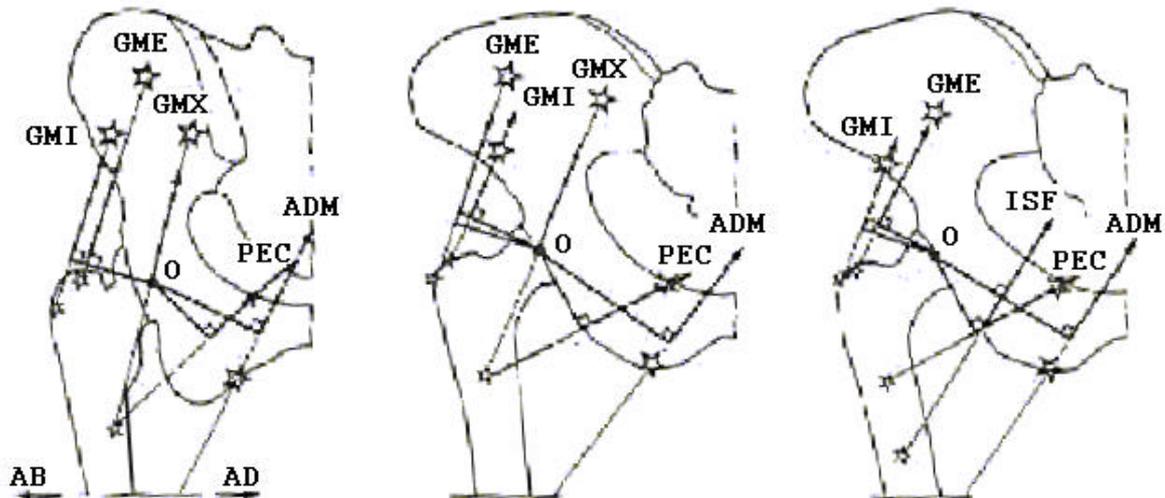


Figure 24 Abduction-adduction of australopithecine thigh by action of the gluteal and adductor muscles. The pelvises are oriented in the frontal plane. Left is Homo (female pygmy), Centre is human-like *A. afarensis* reconstruction and right is ape-like reconstruction. (From Berge 1994: p268) GMI – Gluteus minimus; GME – Gluteus medius; GMX – gluteus maximus; ISF – ischiofemoralis; ADM – Adductor maximus; PEC – pectineus.

There is one more aspect of *A. afarensis* skeletal morphology which would be consistent with sideways wading model. A number of workers (e.g. Berge 1994:p261, Aiello & Dean 1999:p452, Rak 1991) have commented on the platypelloid (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.

Rak (1991) explains the wide pelvis as an adaptation to reduce the vertical displacement of the centre of mass during terrestrial walking which, he argues (p286-7) “increases the vertical component of the ground reaction force, an increase that implies a less efficient forward progression, since more energy is expended to cover a given distance” and “the cyclic falling

of the centre of mass causes an increase in joint reaction force and thus affects the joints and their physiology.”

He contends that the ancestral pre-bipedal hominoid essentially had a choice of two ways of solving this problem - either to widen the hips as did *A. Afarensis* or to lengthen the legs as did the ancestors of *Homo*. This is an ingenious idea but it is one that is, again, based upon the assumption that water was not a factor.

Rak (1991:p285) compared the pelves of *A. afarensis* with *Homo* by superimposing one image on another. He scaled the image of AL 288-1 so that they were the same height dorso-ventrally in order to emphasis Lucy’s relatively wide pelvis. This has become the traditional interpretation of *A. afarensis* morphology. However the diagram, and perhaps that view of her pelvis in general, is a little misleading because it requires scaling to make Lucy’s pelvis wider than it actually is.

If one ignores scaling and measures the pelvis itself one finds that it is not so much that her pelvis was wide laterally but that it was *shallow dorso-ventrally*. In fig. 25 (below) a photograph of pelves 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.

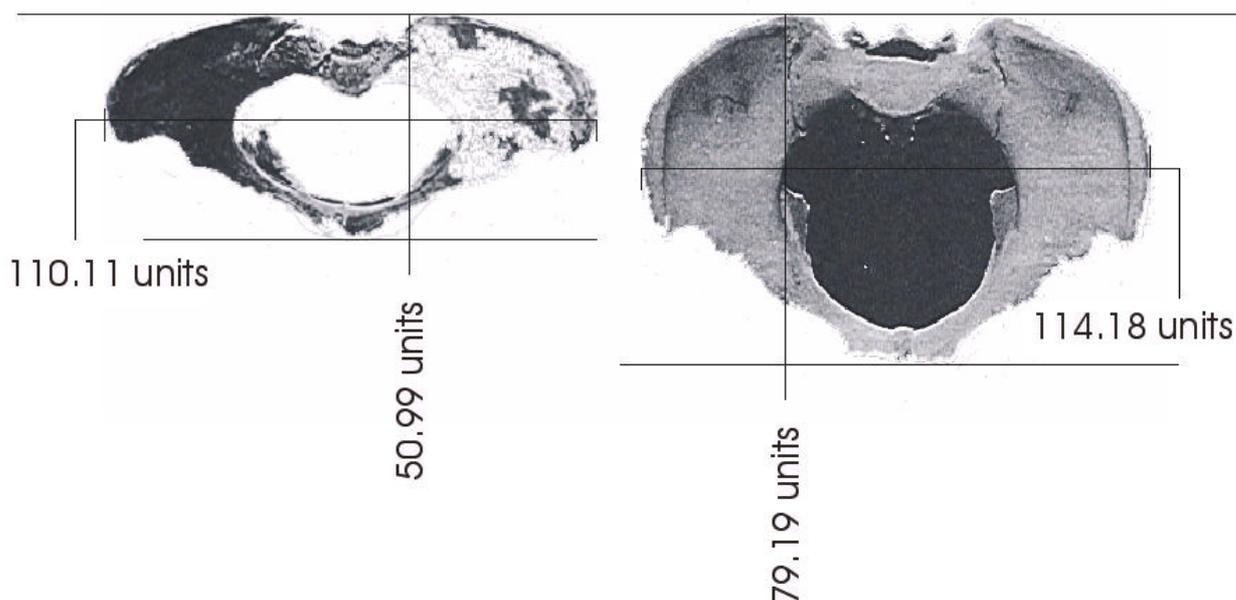


Figure 25 Pelvis of AL 288-1 compared with Human.

(Images from Abitbol 1992:p226 Measured Using CorelDraw 8)

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 wider than Lucy's but was more than 50% deeper dorso-ventrally. The platypelloid shape of the *A. afarensis* pelvis might be its most remarkable feature.

Inferring the external body shape from the skeletal is not a precise science but this data would imply that the bodies of *A. afarensis* were platypelloid at the hip and presumably also lower abdomen. Rak (1991:p285) agreed with this point indirectly by arguing against the concept – put forward by McHenry 1986, Tague & Lovejoy 1986 and Lovejoy 1988 - that Lucy's wide

false pelvis was explained by the need for a biped to accommodate the abdominal viscera. Rak argued basically that the reduced anterior-posterior distance would reduce the capacity of the abdomen.

As the human experiments showed in the previous section, submerged body profile is significantly reduced when wading sideways and therefore, it would be logical that any ape specialising in such a niche might evolve a lower body shape that reduces this profile still further.

After consulting general body proportions from Zihlman (1978), AL 288 estimated stature from Aiello & Dean (1999 p 264) and AL 288-1 femur length from Zihlman (1978 p 89) it was decided that the Planckendael bonobo Hermien were similar enough in size and shape (frontally at least) to AL 288-1 to use her profile for a very simple comparison with humans.

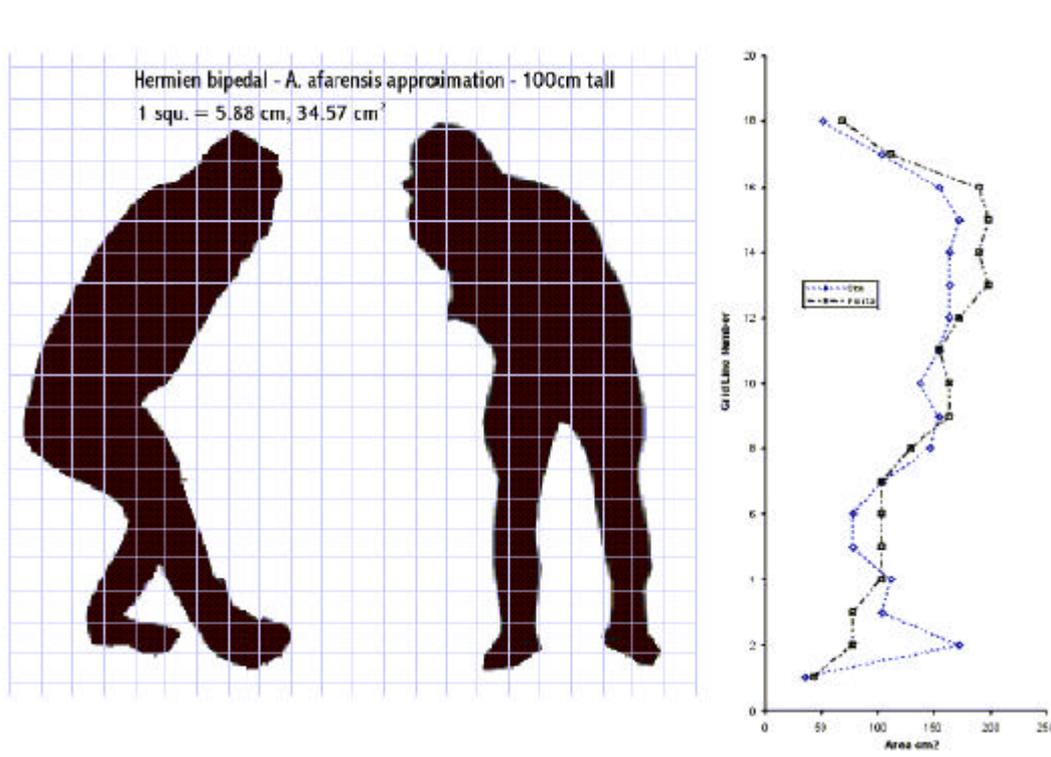


Figure 26 Bonobo comparison of frontal and sideways profiles
 Arms were removed from the plot to simulate a live wading event.

Notice here that her sideways profile is hardly smaller (about 5% less) than her frontal profile. This is partly due, no doubt, to the imperfection in the frontal and sideways postures. Neither were as accurate as for the human images. It would seem, however, that bonobo sideways profile is rounder than that of humans.

It is predicted that, *A. afarensis* would differ significantly in this regard from *P. paniscus*. Perhaps their frontal submerged body area plot would be wider but their sideways profile is likely to be far less, (probably about half) evidenced largely by her platypelloid pelvis with its width ratio of over 2:1.

A plot of submerged frontal body profile against water depth shows that bonobos, due to their more 'squatting' posture, have a greater profile in shallower depths than humans indicating that *A. afarensis* might incur greater drag costs when wading frontally even than humans.

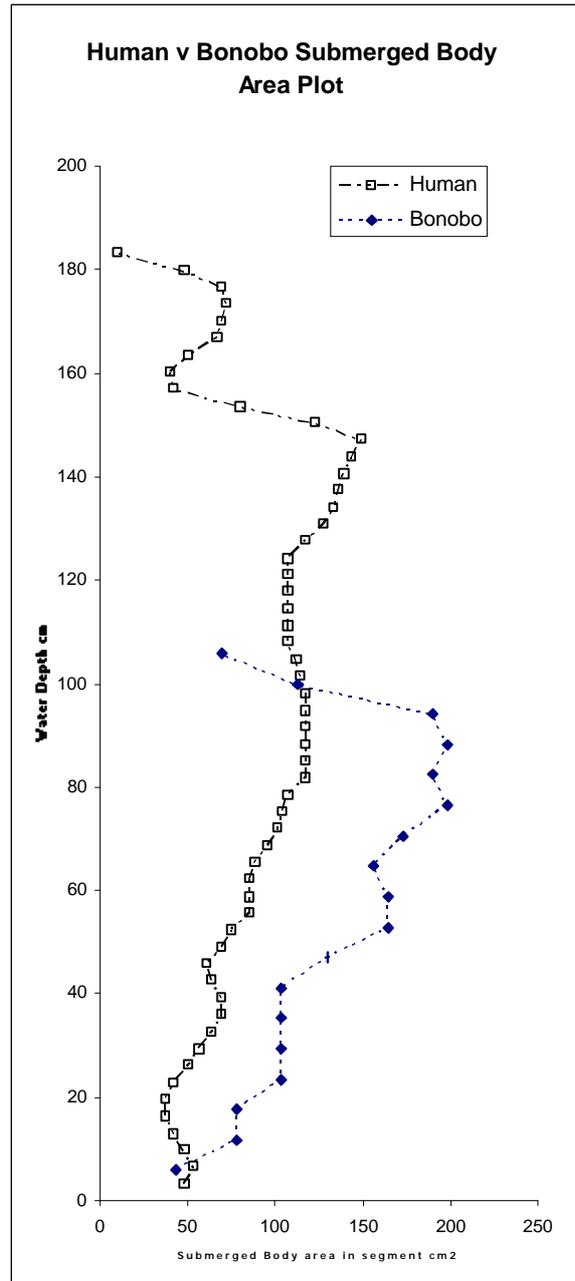


Figure 27 A comparative profile plot of *H. sapiens* and *P. paniscus*

Unfortunately it was not possible to race bonobos in Amersham multi-pool but one peculiar incident was reported by the field worker Maarten De Rouck at Planckendael, which might give a clue as to how they might have performed if they could have been induced to do so.

He described an incident he observed recently 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 speculate about whether this behaviour has been reported elsewhere and, if so, about its functional significance.

Any suggestions about how *A. afarensis* might have performed in this experiment are even more 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*.

5.4 Conclusions

In this section several controversies and arguments that have arisen in interpreting the fossils of *A. afarensis* 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 relaxed.

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. This might seem a little fanciful at first but it is the logical conclusion of this line of enquiry. It is consistent with the fossil record and, it is suggested here, provides a clearer more parsimonious explanation of its morphology than any of the alternatives.

Therefore it is argued here that the 3rd prediction of the wading-origins model has been met by this test and much more fully than could have been anticipated.

Considering that *A. afarensis* fossils have been studied by so many experienced and respected paleoanthropologists, one is hesitant to question the assumptions they have based their work on for so long. The temptation is very much, instead, to follow in their footsteps. However, when one finds a plausible alternative assumption that seems to have been dismissed without being researched first, scientific curiosity insists that the possibility be explored.

Such an assumption appears to have been made about the habitat and lifestyle of the earliest hominids. The view that their time was spent only in trees or on dry land seems to have become *de rigueur* whilst the possibility that they were adapted to a water-side habitat has, as far as one can judge from published texts, simply been dismissed, although it is not clear on what basis this rejection has been made. We have seen that apes are at their most predictably bipedal when wading in waist deep water and it is clear that habitats where periodic wading could have evolved are common throughout the world both today and in the past.

6. 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 sufficient evidence can be extracted from what fragments are found to infer that they were predominantly bipedal then the other data could still be more than enough to refute the 4th prediction of wading origins model. All that would be needed was to demonstrate that the earliest bipeds lived in habitats where wading could not have been practiced.

6.1 Paleo-habitat of the earliest bipeds

According to Klein (1999 : p 161) the three earliest bipedal hominids were *Ardipithecus ramidus* (5.0 - 4.3 mya), *Australopithecus anamensis* (4.2 – 3.9 mya) and *Australopithecus afarensis* (3.9 – 3.0 mya.) Since then a much older putative hominid *Orrorin tugenensis* (6.0 mya) has been found and, more recently, one not so old: *Kenyanthropus platyops* (3.5 mya) (Leakey *et al.* 2001.)

The limestone cave sites associated with *Australopithecus africanus* and later species are dated at 3 mya or less. Consequently they have not been included in this review because, as they appear quite late in the evolution of bipedalism, they cannot provide a significant objection to the assertion that water was a significant causative factor in its early adoption.

Another putative biped *Oreopithecus* is also not included because it has not been associated with the *Hominoidae*. It should be noted, however, that *Oreopithecus* is perhaps the earliest evidence of a bipedal primate and has been strongly associated with an island (Moyà-Solà *et al.* 1999:p316) habitat. If bipedalism emerged once due to adaptive pressures from a water-side habitat it might have happened again.

In the following sections the sites in which hundreds (Klein 1999: p180) of hominid fossils have been found are reviewed.

6.2.1 *Orrorin tugenensis*

The recent discovery of *Orrorin Tugenensis* from the Lukeino formation in Kenya at the end of 2000 (Senut & Pickford 2001) is the 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. In fact before December 2000 most authorities were firming up on the idea that the mrca of *Pan/Homo* lived around 5.5 mya. If anything the tendency was to make the date even more recent. A paper by Baird *et al.*(2000), for instance, quoted three separate sources, including Takahata & Satta (1997), that had calculated the date as recent as 4.5 mya. Very few (e.g. (Kleindienst (1975), Goodman (1982: 260), Gribbin & Cherfas (1983), Hasegawa *et al.*(1985) and Edelstein (1987)) in the field have predicted that the mrca was already bipedal and that *Pan* and/or *Gorilla* had since reverted to quadrupedalism.

It is true that dates based upon the molecular clock had always been calculated with the usual confidence limits and so it would be reasonable to suggest that the date of last common ancestor had always been more blurred than some had assumed. Aeillo & Collard (2001) reminded us of this when they were the first to publish a specific reaction to the finding in March 2001. They state that “*Orrorin*’s age falls within the molecularly determined range of the last common ancestor between humans and the African apes (8- 5 million years ago.)” They do not “seriously question” the accuracy of the age of the fossils but they do have doubts about the claim of Senut *et al.* that *Orrorin* was bipedal suggesting that it is “based on detailed aspects of the anatomy of the upper part of the thigh bone that are open to alternative explanations.” They also cast doubts about the legitimacy of placing *Orrorin* as ancestral to

Homo (via a novel intermediary genus *Praeanthropus*.) So, for the time being at least, the exact status of *Orrorin tugenensis* is still in some doubt.

Table 5 Orrorin tugenensis site

Site	Site	Ecology	Age (mya)
Tugen Hills (Lukeino Formation)	“fluvial and shallow lacustrine deposits” Pickford & Senut (2001: p145)	“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

6.2.2 *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 6 Ardipithecus ramidus sites

Site	Site	Ecology	Age (mya)
Middle Awash (Aramis)	Lacustrine silts	“Relatively Wooded” Klein (1999:p185)	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

6.2.3 *Australopithecus anamensis*

According to Klein (1999:p177) *A. anamensis* is “the second oldest hominid species and the oldest for which bipedalism has been conclusively shown.” The fossil sites where it has been identified are shown in the table below from (p188).

Table 7 *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

6.2.4 *Australopithecus afarensis*

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

Table 8 *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 <i>et al.</i> (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:p309)	3.2 – 3.18
Hadar (Sidi Hakoma)	AL 417	“medium to open density woodland” or “riparian” Reed (1997: p308)	3.4 – 3.2
Middle Awash (Belohd elie) 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 <i>et al.</i> (2001 p 439) Reed (1997:p307) “closed to medium density woodland”	3.86 – 3.46
Feje	Fluviolacustrine (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:p310)	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:p310)	“mostly closed woodland with riverine forest and edaphic grasslands.” “Other habitat reconstructions include a riverine forest and... a wooded savannah and forest.” Reed (1997:p310)	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:p309)	2.68 – 3.32
West Turkana (Lower Lomekwii)	Fluvial unit overlain by lacustrine deposits.	“Lakeshore or river floodplain.” Leakey <i>et al.</i> (2001 p 439)	3.3 – 3.2 (p 181)

6.2.5 *Kenyanthropus platyops*

The most recent new hominid find. This table shows the sites where *K. platyops* has been identified. Data from Leakey *et al.* (2001.)

Table 9 *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:p440) "more vegetated and wetter than Hadar"	3.3 – 3.5

6.3 *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:p292). 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 (not covered here because of their relatively late dates) and Laetoli.

The Laetoli site offers a significant rebuttal to the wading-origins of bipedalism theory. At 3.86 – 3.46 m.y. the site provides an example of where fairly early bipedal hominids lived. The only response to this would be to suggest that the inhabitants of Laetoli could have been descendants of wading apes that were forced, perhaps through competition, to inhabit a more arid habitat.

The fact that the sites of the very earliest bipeds, especially of *Orrorin* and *Ardipithecus*, were predominantly “wet and wooded” is consistent with the 4th prediction of the wading-origins model.

7. 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. Nine predictions about the wading-origins model were made and four were tested by empirical studies and via researching the published literature. The others have been evaluated generally throughout the paper or will be in this conclusion.

This study especially sought pieces of evidence that might disprove the hypothesis.

From the point of view of comparative animal behaviour it could be argued that there are very few species adapted to water-side habitats that ever adopt a bipedal form of locomotion (a notable exception, perhaps, is the proboscis monkey). Nearly all go straight from quadrupedalism to swimming as the water gets deeper. Furthermore this study found data from *Pan* and *Homo* to suggest that there is a significant overlap in depths of water where quadrupedalism and swimming would both be possible.

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. The significant threat from water-living predators, such as crocodiles, also adds to the implausibility of the idea.

However, if one looks at the comparative evidence with a cladistic eye one would have to give a higher weighting to the water-side behaviour in *Hominoidae* than in other genera. Here the evidence is unequivocally that great apes tend to wade bipedally in water rather than

swim. Although they clearly prefer not to get their feet wet at all, each species of great ape has been seen to be more than prepared to go into water when the need arises.

It is not difficult to conceive of scenarios where ancestral apes might have been forced to do so, either chronically or just regularly. Natural selection theory teaches us what would happen in such a scenario. If a young adolescent ape was forced to wade across a stretch of water bipedally even just once a week before it reached sexual maturity, it would still represent hundreds of wading events, each yielding an opportunity for selective pressure to eliminate the traits that hindered orthograde posture and bipedality. In this model the actual percentage time in water need not be high and the threat of predation would significantly increase the adaptive pressure required. The model provides selective pressure towards bipedality at all stages, reduces the energetic costs and provides a clear survival benefit. It applies equally to both sexes and not only explains why *Pan* and *gorilla* are not bipedal, it uniquely may also explain why they knuckle-walk, if one were to assume that they too evolved from wading ancestors.

There are many habitats that would provide such opportunities for these selective pressures to work. Hardy (1960) originally envisioned a coastal habitat. La Lumiere (1981) and Morgan (1990) refined this by suggesting it was the flooding of ancestral forests leaving island niches. Verhaegen & Puech. (2000) have proposed coastal mangrove swamps. Or perhaps (as in the opinion of the author) it was in gallery forests that surrounded rivers and lakes. This habitat is arguably more consistent with the fossil record and could even work in arid zones, as forestation inevitably shrinks closer to water sources as the climate becomes drier. Perhaps it was a combination of all of them.

Another piece of evidence against the wading-origin theory comes from the point of view of the fossil record. The *A. africanus* sites of southern Africa have been specifically associated

with habitats where water was not present. This is also true of the Laetoli site in Tanzania. These provide strong evidence that the early hominids that lived there were not influenced by water.

However these sites are in the minority and are relatively recent. Laetoli is the only paleohabitat predating 3 million years ago where lakes, rivers and streams have not been shown to have been part of the landscape. Generally, the earlier the site, the wetter it appears to have been. The conclusion has to be that there is actually no evidence from the fossil record that refutes the hypothesis that bipedalism first arose in habitats conducive to wading.

These were the only serious objections to the wading-origins model that were found other than the overwhelming conclusion that it was not even worth looking at *because if it were, someone else would have already done so*. Charles Oxnard (1983:p323) wrote “but though numbers may prevail in democratic institutions, in academia and in science they do not. One fact that controverts an hypothesis is more powerful than a thousand that support it.”

It was the objective of this study to find one fact that indicated that wading could not have played a part in the origins of human bipedalism, but it failed to do so. Instead it only found more and more evidence that supported it.

Perhaps other workers, who are more skilled and scientifically minded, may find the evidence that indicates that bipedalism could not have originated from apes that waded. But in order to do so they would have to take the possibility far more seriously than has hitherto been the case. Before the hypothesis is dismissed, it has to be properly investigated. Scientific objectivity demands it.

8. Call for further studies

This thesis has highlighted, as much as anything, how much work has still to be done in this area.

Observational studies of ape wading

There is clearly much more to be done with wading behaviour of extant apes. The study carried out on captive bonobos could easily be repeated for much longer periods, with different species, in the wild as well as in captivity.

Human wading experiments

The wading experiments carried out in the variable depth pool were carried out with a very small group of volunteers. It would be useful to repeat them with larger numbers and with a bigger range of sizes and shapes.

With a bigger and more impersonal group (i.e. not close friends) detailed body measurements could be more comfortably made to test the relationship between body shape and wading speeds and methods.

BHBK was not specifically looked at in this study. Adult volunteers that performed the waddling races did use it but it was not investigated in any more detail than that. It would be interesting to see if BHBK could be maintained over long distances, as that is one of the objections that Crompton *et al.*(1998) have made against it, assuming a terrestrial substrate. Oxygen consumption could also be measured using different wading techniques.

This study hardly scratched the surface of the theory of fluid mechanics. With more time several enhancements could be made and much more detailed results could be obtained: Estimates for the drag co-efficients of different parts of the body; The effect of hydrostatic

buoyancy on getting a grip on the surface to push against; The difference in getting a firm grip between sideways wading and frontal wading.

These experiments only looked at speed. There is an equivalent amount of work waiting to be done looking at energy consumption and temperature.

Wading habitats

Another angle that was not covered here was studying the plausibility of wading in real life niches. It is one thing to demonstrate that wading was faster in a pristine swimming pool but would that also be true in a slimy mangrove swamp, teething with wild life? It would be interesting to compare different habitats such as rivers, lakes, coastal and estuaries for water depths and variation to consider if such a habitat would be conducive to wading.

The fossil record

This study only provided a review of the literature for *Australopithecus afarensis*. A renewed look at the original fossils with sideways wading in mind could be useful. For example, if *A. afarensis* did adopt a sideways mode of wading one might expect to find asymmetries in the fossil record. It would be predicted that an individual would habitually adapt a left or right sided mode for wading and consequently one or other Calcaneus (Heel bone) might be expected to differ slightly in its morphology.

It would be useful to investigate whether the later robust *Australopithecines* showed any clues of this putative mode of locomotion and a further, more thorough investigation of the paleo-habitats of the early bipeds could be carried out to ascertain more precisely what kind of wading niches might have been present.

Biomechanical studies

One would think that the amazing computer models of Crompton *et al.* (1998) and others could easily be enhanced to include a wading model to further test some of these ideas, in particular sideways wading.

It was not possible, in the rather short time for this project, to attempt to predict the speeds that *A. afarensis* might achieve in similar water depths but it should be possible to get a good estimate even from this data.

Having done that, assuming we could estimate the propulsive force for sideways wading from the various biomechanical models that have been devised for AL 288-1, and assuming a fairly accurate estimate could be made of her sideways body profile, it would be possible to predict the speed of Lucy wading sideways. I bet the results would be astonishing!

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