CHAPTER 3

A Wading Component in the Origin of Hominin Bipedalism

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Abstract: For over 150 years the field of palaeo-anthropology has grappled with several problems of understanding human evolution, notably those explaining key differences between human beings and our most closely related species, the African great apes. The first difference to be explained, perhaps in terms of importance but certainly in terms of chronology, is our bipedality.

This chapter will review the models of hominin bipedal origins published to date, and categorize them, as was done by Rose [1], by the adaptive mechanism being suggested. In addition, it will propose a new evaluative framework against which each model may be assessed and compared. In this evaluation, published wading models appear to be among the strongest although they are among the least well reported in university-level text books, a discrepancy attributed here to their association with the so-called 'aquatic ape hypothesis' (AAH). Despite their apparent strengths, published wading models do nevertheless contain weaknesses. This chapter addresses a few of those weaknesses either theoretically or through studies, such as one obtaining new empirical data comparing the energy efficiency of different bipedal gaits in water. Furthermore, a series of falsifiable predictions of the wading hypothesis are made about the postcranial anatomy of australopithecines.

The chapter concludes by proposing a specific timescale and ecological niche where such wading behavior could have provided a stable evolutionary scenario in early hominins that is compatible with the fossil record and other models of human evolution.

Keywords: Bipedalism, hominin bipedal origins, wading.

CUTTING THROUGH THE TANGLED THICKET OF BIPEDALISM ORIGIN MODELS

To understand human evolution we need to be able to explain, in Darwinian terms, the key differences between us and the great apes and perhaps the most important of those is our bipedality. Despite a huge intellectual effort, spanning over 100 years, there is still no consensus among physical anthropologists as to which factors caused the remarkable divergence that led to one clade moving on land on two legs almost exclusively and the others, generally, on four. Students of anthropology today are consequently taught a very tentative picture about why only we, *Homo sapiens*, are obligate bipeds. This lack of consensus is indicative that, so far, either insufficient unequivocal evidence has been provided in favor of any particular idea on the matter to make it the generally accepted one, or that perhaps one of the ideas has been misunderstood.

There is a vast literature on the subject and most of it starts by stating the importance of understanding this problem. For example, the anthropologist Craig Stanford, in his book *Upright* makes the point: "The reason that upright posture and walking arose is the most fundamental question in human evolution [2]." So, considering the problem's importance, how have we progressed, since Darwin, in trying to solve it? Rose summed up the status quo in the early 1990s: "… despite a voluminous literature, our ignorance concerning bipedalization is almost complete" [1]. This situation doesn't appear to have improved during the last two decades.

Indeed the problem has recently been portrayed as being, if anything, even more uncertain than before. A special edition of the *Journal of Anatomy* in 2004, dedicated to the question of human bipedal origins, included a paper by Harcourt-Smith and Aiello which concluded: "In the light of the richness of recent findings in the hominin fossil

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record, it is important to ask the question of whether the evolution of bipedalism was a more complex affair than has previously been suggested" [3]. In 2007, another new idea made the front page of the journal *Science* with a model proposing that the ancestors of all great apes practiced "hand-assisted" arboreal bipedalism, as reported in orangutans [4]. The question as to why one lineage of great ape became an obligate biped, whilst the others did not, is avoided completely. Apparently, it was assumed that it was possibly just a matter of random genetic drift.

Kevin Hunt perhaps best summed up the situation when he recently gave a talk entitled *The tangled thicket of bipedalism origin hypotheses: Embarrassment of riches or just embarrassment?* [5]. This chapter will try to cut through this tangled thicket, categorize the various models that have been published, compare and evaluate them and then focus on one of them that appears to have been neglected for all the wrong reasons, the wading hypothesis.

CLASSIFICATION AND EVALUATION OF BIPEDAL ORIGINS HYPOTHESES

The literature discussing ideas on the origin of human bipedalism is so rich it might be helpful to begin by listing and classifying them. Here, the models will be structured according to an adaptation of Rose's [1] classification by suggested adaptive mechanism (Table **1**).

Clearly such classifications of models are a matter of opinion. It could easily be argued that some models should be placed under different or multiple categories. It should also be remembered that few proponents would claim absolute exclusivity for their model and most would concede that others probably played a part too.

It should also be noted that even the number of models listed here is open to interpretation. For example the differences between the three arboreal models (the 'hylobatian' or brachiator ancestor) model, the 'upwardly mobile'/vertical climbing hypothesis and the 'orangutan-like' hand assisted bipedalism model) are very minor and the 'wetland foraging' model, ascribed here to both Ellis [53] and Wrangham *et al.* [54] could easily be split into two separate ones.

Table 1: Published Bipedalism Models, Classified by Mode of Selection

Category	Subcategory	Code^a	Specific Idea	Original Proponent(s)
Forelimb pre-emption (Carrying)	Unspecified	1.0	General freeing of the hands	Darwin 1871 [6], Hooton 1945 [7]
	Food carriage	1.1.1	Carrying food back to gallery forest bases.	Hewes 1961 [8]
		1.1.2	Carrying and scavenging	Isaac 1978 [9]
		1.1.3	Migration-carrying hypotheses	Sinclair *et al.* 1986 [10]
		1.1.4	Male provisioning	Lovejoy 1981 [11]
	Infant carriage	1.2	Female driven infant carrying	Etkin 1954 [12], Iwamoto 1985 [13], Tanner 1981 [14]
	Tool/weapon throwing	1.3	Weapon throwing	Fifer 1987 [15], Dunsworth *et al.* 2003 [16].
	Tool carriage	1.4.1	Tool carriage	Bartholomew and Birdsell 1953 [17], Washburn 1960 [18], Marzke 1986 [19]
		1.4.2	Weapon wielding	Dart 1959 [20], Kortland 1980 [21]
Social behavior	Nuptial gifts	2.1	Nuptial gifts	Lovejoy 1981 [11], Parker 1987 [22]
	Aggression (interspecific)	2.2.1	Interspecific threat displays	Kortland 1980 [21]
	Threat display (intraspecific)	2.2.2	Intraspecific threat displays	Livingston 1962 [23], Wescott 1967 [24], Tanner 1981 [14], Jablonski and Chaplin 2004 [25]
	Evasion/Vigilance	2.3	Sentinel behavior (peering over the savannah)	Reynolds 1931 [26], Dart 1959 [20], Day 1977 [27], Ravey 1978 [28], Walter 2004 [29]

Table 1: cont....

	Sexual display	2.4	Phallic display directed at females	Tanner 1981 [14]
	A new ‘fashion’	2.5	Copied gimmick idea	Dawkins 2005 [30]
Feeding	Terrestrial Gathering	3.1.1	Seed eating	Jolly 1970 [31]
		3.1.2	Terrestrial squat feeding on the forest floor	Kingdon 2002 [32]
		3.1.3	Other gathering	Du Brul 1962 [33], Wrangham 1980 [34], Rose 1984 [35]
	Postural Feeding	3.2	Postural feeding hypothesis	Hunt 1994 [36]
	Arboreal Predation	3.3	Arboreal predation	Eickhoff 1988 [37]
	Terrestrial Predation/Scavenging	3.4.1	Stalking	Geist 1978 [38]
		3.4.2	Specific hunting	Cartmill 1974 [39], Carrier 1984 [40]
		3.4.3	General scavenging/hunting	Szalay 1975 [41], Merker 1984 [42], Shipman 1986 [43], Sinclair *et al.* 1986 [10]
Habitat compulsion	Wading	4.1.1	Coastal foraging	Hardy 1960 [44], Morgan 1972 [45], 1982 [46], 1991 [47], 1994 [48], 1997 [49]
		4.1.2	‘Aquarboreal’ model	Verhaegen *et al.* 2002 [50]
		4.1.3	Amphibische Generalistentheorie	Niemitz 2002 [51]
		4.1.4	River apes	Kuliukas 2002 [52]
		4.1.5	Wetland foraging	Ellis 1991 [53], Wrangham *et al.* 2009 [34, 54]
	Arboreal	4.2.1	Hylobatian (brachiator ancestor) model	Keith 1923 [55], Prost 1980 [56]
		4.2.2	‘Upwardly mobile’/vertical climbing hypothesis	Tuttle 1975 [57], 1981 [58]
		4.2.3	Orangutan-like hand assisted bipedalism	Thorpe *et al.* 2007 [4]
	Other	4.3	Variability selection hypothesis	Potts 1998 [59]
		4.2	Walking on snow or mud	Kholer 1959 [60]
Efficiency of Locomotion	Slow, long-distance walking	5.1	Slow, long-distance walking	Rodman and McHenry 1980 [61], Sockol *et al.* 2007 [62]
	Biomechanical inevitability	5.2	Biomechanical inevitability	Reynolds 1985 [63]
	Efficiency of moving from tree to tree.	5.3	Efficiency of moving from tree to tree	Pickford and Senut 2001 [64]
	Locomotor “de-coupling”	5.4	Locomotor de-coupling	Sylvester 2006 [65]
	Exaptation from ‘Endurance running’	5.5	Endurance running	Lieberman 2007 [66]
Selection for better Thermoregulation	Savannah sweat cooling	6	Thermoregulatory hypothesis	Wheeler 1984 [67]
Dietary Factors	Iodine deficiency and/or overly rich Calcium diet	7	Iodine deficiency	de la Marett 1936 [68]
Random Genetic Factors (Mutation/Drift)	Mutation in a key gene involved in vertebral development	8	‘Evo/devo’ mutation	Filler 2007 [69]
Combination of factors	Combination of factors	9	Multi-factorial	Napier 1964 [70], Sigmon 1971 [71], Rose 1984 [35], Day 1986 [72]

a: Refers to supplementary material.

REVIEW OF PUBLISHED HOMINID BIPEDALISM MODELS

What follows is a very brief description of known published bipedal origins models categorized according to the updated version of Rose's [1] classification in Table **1** above.

This chapter is supported by supplementary materials online, as indicated at the end of this chapter. This includes much fuller descriptions of the models about to be described here and the evaluative framework described later. It also provides details of a survey of how bipedalism models are reported in university level texts.

Forelimb Pre-Emption (Carrying) Models

The first adaptationist idea about bipedal origins was that it was to "free the hands". It was published by Charles Darwin, at a time when it was widely believed that the large brain (and also early aspects of human culture) preceded bipedality [6]. However, several variations on the theme have been published since the discovery of the Taung child corrected that view. These propose various ways in which increased use of the hands could have lead to increased bipedalism through positive feedback loops.

The carrying of food (usually meat) over long distances across open habitats back to 'bases' has been suggested [7, 8, 11], as has infant carriage [12-14] and both [10]. The original thinking of Darwin, and Dart, are probably more closely reflected in carrying models invoking the use of tools or weapons. Some [17-19] stress the carriage of tools, whereas others [20] stress the use of weapons, for example for throwing [15, 16]. One of the most oft-cited models is Owen Lovejoy's 'provisioning' hypothesis [11], which proposes a complex interaction of factors, including greater male provisioning of monogamously paired females, resulting in greater hominin bipedalism.

Models of Social Behavior

A number of ideas have been published positing a shift in social behavior as the driving force. These have been proposed to reduce both intra- 14, 23, 24] and inter- [20, 21, 26, 27, 29] specific conflicts, as a means of aiding sexual selection [14, 30], as well as including behaviors that overlap considerably with the carrying models [11].

The first 'behavioral' model to be proposed was one of vigilance or 'predator avoidance' [26]. Set in an open savannah ecological context ideas such as this propose that standing taller in grasslands would help individuals to detect prey and predators. These ideas often overlap with those promoting the use of tools and weapons [20].

Intraspecific competition has also been considered. Observations of gorilla threat displays inspired Frank Livingstone to postulate that threat displays might reduce intra group violence sufficiently to provide some selection [23]. It is a view championed today by Jablonski and Chaplin [25].

Sexual selection has also been suggested here, noting that a change to an upright posture could have been due to phallic display behaviors [14], or simply that it caught on as a kind of "fashion" [30].

Finally, there are also behavioral ideas which overlap with carrying models, notably the "nuptial gifts" idea of Parker [22] and the 'provisioning' hypothesis of Lovejoy [11] already mentioned.

Feeding Models

Another major category of models are those claiming that bipedalism developed to help food procurement. These ideas, again, often overlap with others. For example, models promoting terrestrial predation and/or scavenging as drivers of bipedalism [10, 38-40, 42, 43] are clearly complementary to (or even dependent on) food or tool/weapon carrying models. Some, on the other hand, stand on their own, independent of any assumption of travel or the need for tools such as Jolly's "seed eating" hypothesis [31], Kingdon's "Squat Feeding" hypothesis [32] and Hunt's "postural feeding" hypothesis [36]. Most assume that early hominins inhabited the fringes of woodland and more open grasslands and that bipedalism gave them some selective advantage to procure foods from such habitats, although specific arboreal contexts [37] and more aquatic ones have been suggested too. Hunt's ideas [36] are notable in that they are based on a long observational study of extant chimpanzees in the wild. Hunt found that the most common behavioral context for their (albeit quite rare, at around 3%) bipedalism was feeding from trees.

Habitat Compulsion

This category, not in Rose's classification, groups ideas proposing habitat as a compelling selective factor for increased bipedalism. Two habitats that clearly compel upright posture in apes are arboreal and aquatic ones but in addition two other habitat scenarios have been proposed.

Four wading scenarios have been published. The first is part of the controversial 'aquatic ape hypothesis' (AAH) of Hardy [44] and Morgan [45-49], postulating a specific "coastal" phase for early hominins. Niemitz's *Amphibische Generalistentheorie* [51] distances itself from the AAH hypothesis, but there is no doubt that he favors bipedal wading as a positive factor in the evolution of our bipedality. Verhaegen *et al.* [50] proposed that wading and climbing together were important factors. Finally, Ellis [53] proposed that wading would have been most plausible in wetland habitats. This is an idea which received significant backing recently from Wrangham and collaborators [54] in their study suggesting that wetted land plant tubers may have been key fallback foods in dry seasons for early hominins and that bipedal wading would have been a key locomotor strategy in their collection.

Arboreal scenarios also compel upright posture in large primates. Three ideas are grouped here, one from the early 20th century suggesting a brachiator-like ancestry [55] two from the 1970s and 1980s proposing a vertical climbing precursor [57, 58] and a recent one proposing a "hand-assisted" type of arboreal bipedalism [4].

Potts' 'variability selection' hypothesis [59] is also placed in this category as is the unverified claim by Rose [1] that Kohler suggested it was to do with walking in snow or mud [60].

Energy Efficiency of Locomotion

Another frequently mentioned model of bipedal origins is that promoting energy efficiency as a major factor, usually attributed to Rodman and McHenry [61]. The principle is simply that moving on two, extended legs, costs less energy than moving on four, more compliant (or flexed) limbs. The evidence that modern human anatomy is clearly adapted to an efficient striding gait strongly supports the notion. However, the model still raises questions, such as how the necessary anatomical adaptations could have evolved for reasons of energy efficiency from the beginning? One paper offering evidence as a possible solution to that question - that it simply evolved from variation in populations - was published by Sockol *et al.* [62], but, perhaps, more convincing answers can be found.

Three other ideas are also be grouped under this category. Those proposing that the evolution of human bipedalism was an almost inevitable trend in primate evolution [63], a similar idea that it involved locomotor "de-coupling" [65] and the new ideas of Lieberman promoting "endurance running" as a major factor in the evolution of human bipedalism [66].

Thermoregulation

Another frequently mentioned idea is Peter Wheeler's thermo-regulatory hypothesis [67]. The radical proposal is that upright posture evolved in order to expose more of the upper torso to cooling breezes above tall grasses in hot, dry savannah environments. Wheeler also suggests that an upright posture would also reduce the amount of the body's surface area exposed to UV rays around midday, compared to moving around quadrupedally.

Dietary Factors

Perhaps the most unusual idea [68] on hominid bipedal origins is that a shift in nutrients in the diet, especially the increased consumption of Iodine, was responsible for the evolution of bipedalism.

Random genetic Factors (Mutation/Drift)

Various evolutionary biologists have proposed that saltatory leaps in evolution have played a key role in the evolution of many lineages, including our own. Until recently, however, such proposals lacked hard evidence for plausible mechanisms that could account for such changes. It has now become increasingly well understood that mutations to genes involved in the developmental process can cause profound and immediate changes to the adult form. Aaron Filler's thesis [69] is that such mutations have been involved in several key stages in the evolution of Life on Earth, and notably one resulting in a profound change in the body form of our own lineage, giving us a distinct precondition for bipedalism. Perhaps more controversial is his view that evidence for the mutation can be seen already in the Miocene ape (20 Ma), Morotopithecus.

Combination of Factors

Few proponents of specific ideas of bipedal origins would claim exclusivity for their suggested model. They all leave room for other factors being involved, but some accommodate them more than others. The final category in this audit of published ideas of bipedalism models are those that deliberately avoid specifying a particular idea at all, but stress that it must have been a composite of several of them. Perhaps surprisingly, models such as this, proposing a specific combination of ideas are rarely mentioned in the text books surveyed here.

Probably the first such idea published was Napier's, based on the apparently generalized anatomy of newly discovered *Proconsul* [70]. This was followed by similar ideas from Sigmon based on the generalized locomotor repertoire of chimpanzees [71]. Accordingly, Day outlined three key selective pressures for the evolution of bipedalism, *i.e.*, improved food acquisition, improved predator avoidance, and, improved reproductive success, and he stressed that any model of bipedal origins had to account for all three [72]. Finally, the last word in this review is given to Michael Rose, the author of the most comprehensive review of bipedalism models to date, suggested that as the ancestor of humans must have had a much more sophisticated locomotor repertoire than we have today, it is likely that multiple factors must have driven their evolution [1].

HOW DO THE MODELS COMPARE?

A Review of Bipedalism Model Reporting in University-Level Texts

To get an idea of how popular (in terms of how frequently they are listed) these ideas are in texts presented to students of anthropology, a sample of 36 standard text books on human evolution was surveyed from science libraries from three major Perth (western Australia) universities to find out which models of bipedal origins are most often referred to.

The results, listed in Table **2**, show that the five categories of ideas on bipedal origins most likely to be presented to current university students are those proposing: carrying, food procurement, energy efficiency, social behavior, and thermoregulation. It should be noted that models under detailed examination in this chapter, i.e., the wading models, were among the least popular, but were still reported more often than the idea that no specific factor was responsible.

The bipedalism 'meta-analyses', surveyed here, were usually very short and always incomplete, although obviously space constraints were a limitation. Langdon's [73] is a rare exception, giving an adequate summary of most of the models listed. Perhaps a more serious criticism is that there appeared to be little justification for why the particular models chosen were included or why other might have been excluded from the discussion. It is suggested that a more rigorous approach can be found.

Table 2: Popularity of Bipedalism Models in 36 University Level Text Books

Rank	**Model Category**	**Popularity (%)**
1	Carrying	86
2	Food Procurement	69
3	Energy Efficiency	58
4	Social Behavior	50
5	Thermoregulatory	47
6	Non-wading habitat compulsion	25
7	Wading habitat compulsion	22
8	Combination	14
9	Dietary Effects	3

Since so little progress has been made towards achieving consensus on the causes of bipedalism, it might be expected that attempts to appraise and compare the existing hypotheses would be fairly common, and frequently updated. In practice such comparisons are virtually non-existent. The usual procedure is for proponents to put forward their own favored theory, which is compared with a few selected alternatives of the author's.

In the next section, it is argued for the first time, an evaluative framework is proposed for a more objective justification for selecting models of bipedal origins.

A Proposed Evaluative Framework

An evaluative framework is offered here, against which models of bipedal origins can be assessed and compared. The choice of criteria is inescapably subjective, but it is transparent, and may provide the incentive for others to re-examine them and offer improvements. It allows a more systematic and structured assessment of the strengths and weaknesses of the different models. It should be also noted that the formal assessment of written work, the very currency of academic achievement, is similarly based on such subjective opinions. There, the design of structured marking rubrics, to which multiple examiners subscribe to, followed by iterative methods of cross examination and feedback from peers, has stood the test of time. This remains today the most accepted method of assessing the presentation of complex ideas.

Fourteen criteria are identified which, I argue, characterize an optimal model of hominin bipedalism. For improved clarity, they have been divided into four subgroups.

Subgroup I. Darwinian

Increases Survival

In this context, one is looking for clear scenarios where adopting a bipedal, rather than quadrupedal, mode of locomotion, results in some distinct survival advantage. Although survival value may be realized in subtle ways, for example through kin selection, an immediate life or death scenario favoring bipedalism is judged stronger here.

Favors Reproduction

According to Darwinian theory, fitness is a combination of survivability and reproductive success. This second criteria assesses whether the model provides a robust case for improving reproductive success through increased bipedalism, for example, through increased sexual selection.

Is not Teleological

A key aspect of Darwinian thinking is that the selection for a particular trait must be present at each and every stage in its evolution. There is no ‘end goal’ in mind and so teleological factors must be discounted.

Subgroup II. Ecological

Offers Improved Food Acquisition

Food acquisition has been suggested as a key ‘pressure’ for the evolution of hominin bipedalism [72]. Models of bipedal origins providing clear advantage for food procurement using bipedal locomotion are judged stronger than those that do not.

Decreases Predation Vulnerability

Although this factor is closely tied to the first, survival value, it is treated as a separate category here because the question of predation has been such a specific key factor in much of the discussion in the literature on bipedal origins.

Explains why great Apes are not Bipedal

This criterion is similar to ‘not teleological’ but is more specific in that is asks whether the model in question includes an explanation as to why whatever factor is being proposed to have driven bipedalism in hominins did not also apply to the ancestors of the great apes.

Fits with Examples of Behavior Visible in Extant Apes

It has been suggested [36] that contexts of bipedalism in extant apes may give clues as to factors which led to the evolution of hominin bipedalism. This criterion judges models on this basis.

Applies to Both Sexes

This criterion simply asserts that a model which promotes bipedality in only one gender is weaker than a model that promotes bipedality in both.

Subgroup III. Palaeontological

Fits known Palaeo-Ecological Record

This criterion evaluates each model according to how well it fits the currently known palaeo-ecological record of the earliest bipedal hominids.

Explains Anatomical Traits of Early Hominids

This criterion assesses how well the model explains the differences in the postcranial anatomies of the earliest hominin bipeds. For example, the australopithecine pelvis is quite different from our own. The model is judged favorably if it offers a plausible explanation for such differences.

Provides Plausible Precursor to both Human Bipedalism and Knuckle-Walking

This evaluation specifically sets out to assess whether the model's concept of the precursor to hominin bipedalism is also a good candidate for chimpanzee and gorilla knuckle-walking.

Subgroup IV. Epistemological

Has Extended Explanatory Power

This evaluation assesses whether the model goes further than just attempting to explain hominin bipedal origins. Ideally, the model should also parsimoniously explain other aspects of human evolution.

Is Complementary with other Models

There is a wide variety of ideas which have been suggested to explain the origins of hominid bipedalism. So diverse are the ideas that it has often been suggested that several, if not all, of them must have been working in concert. The specific question of model compatibility, however, seems not to have been systematically considered in the literature to date. Here, a model is judged better the more compatible it is with others.

Is Falsifiable, or at Least Testable

This criterion evaluates any attempt of the proponent to make falsifiable predictions of their model, or at least subject it to some kind of objective testing.

Applying the Evaluative Framework

To complete the theoretical half of this chapter, three questions will be posed and possible answers discussed:

1. Based on this evaluation, which models were rated best and why?
2. Is there a discrepancy between this and the most popular models promoted in the literature?
3. How might such a discrepancy be explained?

Which Models were Rated Best?

The evaluative framework described here, generally ranked postural feeding models and wading models the best, with energy efficiency and intraspecific threat displays also ranked highly (Table **3**).

Table 3: Assessment of Published Models of Hominin Bipedal Origins.

Rank	**Group**	**Name**	**Code**[a]	**Result (%)**
1	Habitat compulsion / Wading	River apes	s4.1.4	87
2	Habitat compulsion / Wading	Aquarboreal model	s4.1.2	85
3	Habitat compulsion / Wading	Wetland foraging	s4.1.5	83
4	Habitat compulsion / Wading	Amphibische Generalistentheorie	s4.1.3	79
5	Feeding / Postural feeding	Postural feeding hypothesis	s3.2.1	77
6	Habitat compulsion / Wading	Coastal foraging	s4.1.1	72
7	Locomotor efficiency / Moving from tree to tree	Efficiency of moving from tree to tree	s5.3.1	65
8	Habitat compulsion / Arboreal	Orangutan-like hand assisted bipedalism	s4.4.3	65
9	Habitat compulsion / Arboreal	Arboreal "upwardly mobile" hypothesis	s4.4.2	65
10	Carrying / Weapon throwing	Weapon throwing	s1.4.1	62
11	Habitat compulsion / Arboreal	Descent from arboreal hylobatian locomotion	s4.4.1	61
12	Feeding / Terrestrial gathering	Terrestrial squat feeding on the forest floor	s3.1.2	59
13	Carrying / Tool carriage	Tool carriage	s1.5.1	59
14	Carrying / Tool carriage	Weapon wielding	s1.5.2	59
15	Behavior / Threat display (Intraspecific)	Intraspecific threat displays	s2.3.1	58
16	Carrying / Food carriage	Carrying and scavenging	s1.2.2	58
17	Carrying / Unspecified	General freeing of the hands	s1.1.1	57
18	Behavior / Aggression (interspecific)	Threat displays directed at other species	s2.2.1	57
19	Feeding / Terrestrial predation	General scavenging/hunting	s3.4.3	56
20	Carrying / Food carriage	Carrying food back to gallery forest bases	s1.2.1	56
21	Feeding / Terrestrial predation	Stalking	s3.4.1	55
22	Feeding / Arboral predation	Arboreal predation	s3.3.1	55
23	Locomotor efficiency / Locomotor de-coupling	Locomotor de-coupling	s5.4.1	54
24	Feeding / Terrestrial gathering	Other gathering	s3.1.3	54
25	Habitat compulsion / Variability selection	Variability selection hypothesis	s4.3.1	54
26	Carrying / Food carriage	Migration-carrying hypotheses	s1.2.3	53
27	Combination / Combination of factors	Multi-factorial	s9.1.1	53
28	Carrying / Food carriage	Male provisioning	s1.2.4	52
29	Genetic / Mutation in vertebral development	'evo/ devo' mutation	s8.1.1	52
30	Feeding / Terrestrial predation	Specific hunting	s3.4.2	52
31	Locomotor efficiency / Walking	Slow, long-distance walking	s5.1.1	51
32	Feeding / Terrestrial gathering	Seed eating	s3.1.1	50
33	Thermoregulation	Thermoregulatory hypothesis	s6.1.1	49
34	Carrying / Infant carriage	Female driven infant carrying	s1.3.1	49
35	Locomotor efficiency / Endurance running	Endurance running	s5.5.1	48
36	Locomotor efficiency / Biomechanical inevitability	Biomechanical inevitability	s5.2.1	47
37	Behavior / Nuptual gifts	Nuptial gifts	s2.1.1	47
38	Behavior / Evasion/Vigilance	Sentinel behavior	s2.4.1	44
39	Behavior / A new "fashion"	Copied gimmick Idea	s2.6.1	43
40	Habitat Compulsion / Walking in snow/mud	Walking on snow or mud	s4.2.1	40
41	Behavior / Sexual display	Phallic display directed at females	s2.5.1	40
42	Dietary factors / Iodine deficiency	Iodine deficiency	s7.1.1	22

a: Refers to supplementary material.

What follows here is a summary of this author's assessments for each of the models, organized by the evaluative framework. Detailed justifications of these assessments are not provided in this text due to space constraints but can also be accessed online, *via* pages for each model.

A tentative, 'SIMPLE' ranking of models is offered by totalling the number of marks (just three levels: 9 for *good*, 5 for *fair* and 0 for *poor*) accrued for each criterion. At the end of the section these marks are totalled and an overall score generated as a percentage. The 'SIMPLE' assessment does not attempt to give any weighting to different criteria.

Darwinian

Increases Survival

Most models were rated fair or good, with most of the carrying and wading models being assessed best. It should be noted that whereas in the 'simple' assessment, wading models were rated the same (*i.e.*, good) as many others, wading models were rated higher than others in the 'detailed' assessment (see supplementary materials), as they uniquely offer the strongest and most immediate survival benefit, *i.e.*, the ability to continue breathing. About 10% of models, such as 'phallic display', 'copied gimmick', 'iodine deficiency' and the 'neutral mutation idea', were designated as being poor in this category, because they do not offer any positive selection advantage.

Favors Sexual Selection

Behavioral models were mainly rated 'good' here as they promote realistic scenarios for preferential mate selection based on upright posture and movement. Most were regarded as fair.

Is not Teleological

Here, models were divided fairly evenly into three assessment groups. Generally speaking, habitat compulsion models were judged good, and carrying models were judged poor as it could be just as easily be argued that carrying was a result of bipedalism, rather than the cause of it.

Ecological

Offers Improved Food Acquisition

Generally those models postulating feeding or carrying food as a mode of selection were rated good, and those that proposed social behavioral models were ranked poor.

Decreases Predation Vulnerability

Those models postulating weapon carrying or habitats where predation was either unlikely of avoidable were rated good on this criterion. Those postulating food or infant carriage or suggesting relatively slow locomotion across vulnerable habitats, were rated poor.

Explains why Great Apes are not Bipedal

Habitat compulsion models postulating arboreal factors were generally rated poor as they simply beg the question: if humans are bipedal due to their arboreal past, why are no other primates obligate bipeds too? Wading compulsion models were rated good because they explain this very simply: our ancestors moved through water more than theirs.

Fits with Examples of Behavior Visible in Extant Apes

Hunt's observational evidence of postural feeding in extant apes is taken as a benchmark here. Although bipedalism was only observed about 3% of the time, about 80% of those instances were in the context of postural feeding which, it is argued, is very compelling evidence for his 'postural feeding' model [36]. Models that can provide similar evidence were rated good, those that cannot were rated poor.

Applies to both Sexes

Almost all models assessed were found to propose factors that applied equally to both sexes, however about one in four did not. The models rated as poor were those that proposed sexual selection or behaviors that have largely been seen as male-dominated, such as hunting or threat displays. Female-dominated carrying [14] was also rated poorly by this evaluation.

Palaeontological

Fits known Palaeo-Ecological Record

This criterion acted to discriminate against those models that promote a purely savannah-based paradigm, as in the past twenty years hominid finds have repeatedly urged a reassessment towards relatively wet and wooded habitats.

Four models were rated *poor* because of explicitly referring to the savannah as a driver of bipedalism: the 'thermoregulatory' hypothesis [67], the 'endurance running' model [66] the 'seed eating' hypothesis [31] and the 'migration-scavenging' idea [10]. Proponents of all of these models either implicitly or explicitly state an assumption that hominin bipedalism evolved in the ecological context of open plains, something that appears increasingly less plausible today.

Hardy's 'more aquatic' hypothesis [44] which specifically promoted a coastal niche for the origin of hominid bipedalism, was also rated poor as there is, as yet, only limited evidence associating early hominids with coastal niches.

Most of the models were rated *fair* as they are either non-committal about the palaeohabitat proposed or else they are ambiguous about it. One in four models were rated as *good* because they propose habitats that are either explicitly wet and forested, or else propose habitats that are variable or marginal such as gallery forest.

Explains Anatomical Traits of Early Hominids

Most models of hominin bipedalism do not give a great deal of attention to the anatomical differences between early hominins and modern humans and fewer still allude to those differences to justify their proposed model. All models were ranked fair in this regard, then, apart from five which did, at least, propose a mechanism that might help explain why australopithecines were different. Kingdon's 'squat feeding' discussion [32] was one of the few that seriously considers the anomalies of the australopithecine hip and tried to provide an explanation for them in the context of his model. The 'endurance running' of Lieberman [66] and the 'throwing' ideas of Dunnsworth [16] also did at least allude to differences between our bipedality and theirs. The 'iodine deficiency' idea [68] was included merely because cretinism is associated with short legged, small brained pathologies.

Provides Plausible Precursor to both Human Bipedalism and Knuckle-Walking

Unfortunately, as almost all the models failed to describe what they saw as the precursive form of locomotion before hominin bipedalism, they had to be rated fair. None of the models reviewed here were explicit in describing a form of locomotion that was incompatible with extant ape knuckle walking and so none could be rated poor.

Four published models were rated good because they either elaborated on the precursive form or proposed a last common ancestor that was already somewhat bipedal and so would be compatible with both human bipedalism and forms of extant ape locomotion. These were the 'aquarboreal' (climbing-wading) model [50], Filler's 'evo/devo' mutation idea [15], Kingdon's 'squat feeding' [32] and the 'hand-assisted arboreal bipedalism' idea of Thorpe et al. [4].

It should be noted here that there is growing support for the idea that the last common ancestor (LCA) of humans and great apes was in some way bipedal, and that chimpanzees and gorillas both independently (and perhaps orangutans too) lost that bipedalism. Models that were flexible enough to take this possibility into account were rated higher here than those that assumed a knuckle-walking LCA.

Epistemological

Has Extended Explanatory Power

Five models promoting purely arboreal factors were rated poor here, as they offer little in terms of a novel scenario that could account for other aspects of human evolution. Most models were rated fair, but four were rated good. These included very different ideas to promote bipedalism but all shared a willingness to explain more than this. The 'infant carrying' idea, for example, also promoted increased altruism and tool use as ways of accounting for increased intelligence in 'transitional' hominids. Lovejoy's 'provisioning' model [11], also explains a whole set of ape-human differences. Wheeler's thermoregulatory hypothesis [67] also explains hair loss and the adoption of sweat cooling. And the so-called AAH, associated with most of the wading models, accounts for this and other aspects of human evolution too [44].

Is Complimentary with other Models

As we have seen, there is a wide variety of ideas which have been suggested to explain the origins of hominid bipedalism. So diverse are the ideas that it has often been suggested that several, if not all, of them must have been working in concert. The specific question of model compatibility, however, seems not to have been systematically considered in the literature to date. The different models were cross-tabulated to consider if they were complimentary, compatible or contradictory. The results are presented in a matrix showing supportive and contradictory models (see Supplementary Materials: Compatibility.html). Carrying models, generally, are rather incompatible to arboreal ones. This is clearly because models which postulate carrying objects with the forearms are likely to be rather incompatible with models which suggest the forearms were used for climbing trees.

Is Falsifiable, or at Least Testable

This evaluation was by far the worst overall assessment of the models with almost half of models rated poor. This is because much of the literature on of hominin bipedal origins is largely speculative and is not investigated in a scientific way. Clearly, hypotheses of palaeontology, as in all historical (versus empirical) sciences, do not lend themselves to falsification in the Popperian sense, but they should at least make predictions that are testable and be constructed in a way that allows them to be compared and evaluated with other competing models. Only two models were rated good here: Jablonski and Chaplin's latest promotion of their 'threat display' idea, which included a reasonable argument to reject several competing hypotheses before promoting their own. The only other model rated this way was Filler's [69] genetic mutation hypothesis, simply because it proposes an explanation that may, over the course of time, prove to be invalid. His model is therefore the only one yet proposed that appears to be readily falsifiable.

Summary

This meta-analysis of published models of human bipedalism, like those before it, is essentially based on the subjective opinion of the author. What is new here is that it covers the models in more detail (at least online) and it offers a way of evaluating and comparing them. The evaluative framework and individual assessments given are openly submitted for public scrutiny so that they may be criticized and improved upon.

There are a number of ways in which the evaluative framework itself might be criticized. 'Predator avoidance' may, for example, be subsumed into 'survival value'. Similarly, 'Not teleological', 'explains why apes are not bipedal' and 'proposes precursive locomotion that overlaps human bipedalism and knuckle-walking' might be condensed into two, or even a single, criterion. Other reviewers might prefer to remove a few criteria altogether or give greater priority to others. They might also prefer to judge each criterion with more degrees of freedom than I have here in this 'simple' assessment.

Is there a Discrepancy Between this and the Most Popular Models Promoted in the Literature?

Having set a cautious tone, the key finding from the point of view of this chapter was that wading models were all much higher rated than their popularity in university level texts would have predicted. Wading models were the 7th (out of 9) most popular category in the text books, but were ranked 1st here. Arboreal models, too, were rated higher here (2nd) than their popularity in the texts (6th). Carrying and behavioral models, according to this evaluation, conversely, were found to be over-represented in the text books.

How Might such a Discrepancy be Explained?

One possible explanation for such discrepancies could be that text books surveyed were often published before some of the models being assessed. Filler's 'evo/devo' mutation idea [69], for example, was only published in 2007, later than all but three of the text books surveyed. However, the least popular ideas in the texts, *i.e.*, the arboreal and wading models, are almost a hundred and fifty years old, respectively, older than any of the texts.

WHAT ABOUT WADING?

It is the remarkable discrepancy between the popularity of the wading model in university-level text books and their strength that is really the main focus of the rest of this chapter. Clearly, for the models to be evaluated in a way that would rank them according to their popularity in the texts would require drastic changes, either to the evaluation framework itself or the assessments of wading models, or both.

The Wading Controversy

The evaluative framework proposed in this chapter identifies wading models among the best despite their lack of popularity in university-level texts. It is suggested here that this discrepancy is most simply explained by the wading model's unfortunate association with the so-called AAH and the negative reception to that idea by the field of anthropology.

One example (out of several) illustrating anthropologists' negativity to the AAH from the literature will suffice. A book review by Crompton [74] criticized reported observations of bipedality in bonobos in the context of 'aquatic foraging' [75]. Myers-Thompson's chapter was just one of twenty monographs about behavioral diversity in *Pan* reported in Boesch *et al.* [76] but Crompton selected her observations as being particularly noteworthy. He wrote: "The 'aquatic hypothesis' of Sir Alister Hardy is quite popular among chimpanzee fieldworkers although evidence offered in support of this 'theory' is hardly earth shattering: one paper notes that fully 24% of locomotion in water is bipedal!" [74]. Such criticism appears to have been anticipated, as Myers Thompson urged that "caution must be exercised when drawing any inferences from these findings" [75] although neither she, nor any of the other authors, mentioned, or even alluded to, the hypothesis Crompton was referring to. It does seem odd that perhaps the highest level of bipedality yet reported from studies of wild great apes (Myers Thompson did not actually specify exactly how much of the report bipedality was actually in water) should illicit such apparent controversy and indicates that the risk of associating one's work too closely with the AAH is an unbearable one.

How was the Wading Hypothesis Rejected?

At this point some discussion about what the AAH actually is might have been useful. Part of that discussion, it is argued, would involve asking questions such as "Was the AAH rejected?" and "If, so, how?", but for reasons of brevity, such a discussion has been removed from this text and is available as Supplementary Material. A more relevant question for this chapter to consider is specifically if and how the wading hypothesis was rejected.

Whether or not the so-called AAH, as a whole, has been rejected, it is necessary to consider how a significant part of that hypothesis, the wading hypothesis of bipedal origins, was evaluated in that literature and whether this in itself also constitutes a rejection.

Two papers, both published in Roede *et al.* [77], specifically considered, and rejected, the wading idea. One reported a set of experiments conducted to compare the relative efficiency of wading "up to the arm pits" [78] with walking on land and, hardly surprisingly, found that moving, at around 0.7 m/s, was between four and five times more costly. The wading hypothesis was rejected on that basis even though, at lower speeds, the differential reported was around 20%. This study did not consider movement in shallower water, the possibility of different gaits other than the normal fully upright one might have been used, or the proposition that hominids may have been compelled to move through water through seasonal flooding of gallery forest habitats, rather than by choice.

The 'epistemological' critique of waterside hypotheses by Preuschoft and Preuschoft [79] rejected what they termed a "marsh-wading" hypothesis, apparently on the basis of the lack of convergence between early bipedal hominids and wading birds. As they put it: "adaptation to wading will inevitably produce short femora and long tibiae" [79]. However, one should remember that early hominids probably had complex locomotor repertoires including a fair degree of arboreality [80] and were thus likely to have evolved compromise anatomies [1] which would have provided selective pressure against this.

In considering the 'bipedal origins' component of the AAH, Langdon [81] only considered one argument of many in favor of it from its main proponent: Morgan [46] suggested that peculiar human conditions such as hernias and varicose veins, which appear to have resulted from a switch to bipedalism, may have been less problematic, and hence more understandable, if this bipedalism had first been practiced in the context of wading. Langdon did not challenge that assertion, even by stating the obvious retort that such uniquely human conditions may be simply due to extended ageing. Instead he complained that "authors who wish to recite the many disadvantages of bipedalism commonly do so by comparing humans to medium-sized terrestrial quadrupedal mammals" [81]. His argument included no criticisms of the wading idea at all but instead advocated vertical climber/brachiationist ideas, such as those recently promoted [4], which are, in any case, quite compatible with some wading models [50]. In a table, listing traits which have been argued to support the AAH, Langdon simply noted: "Bipedalism - not typical of aquatic animals" [81]. This superficial treatment does no justice to Morgan's work, which includes eight chapters on bipedal origins in five books, and of which two Australian anthropologists recently noted has "reached a sophistication that simply demands to be taken seriously" [82]. It is outside the scope of this paper to evaluate other aspects of Langdon's critique, but many of the other 'aquatic traits' he considered were treated even more superficially in what was, basically, a 'straw man' portrayal of its main arguments. It should also be documented that Morgan's attempted reply to Langdon was rejected [83].

The papers outlined above appear to be the only three published that offer specific objections to the wading hypothesis of hominid bipedal origins. Other, more general, critiques of the so-called AAH deal with it, either by promoting alternative models of bipedalism [84-86], reminding us that bipedalism is not typical of aquatic mammals [87], or by ignoring it completely [88-92].

Whatever one might think about waterside hypotheses of human evolution generally, published criticisms of their important wading component do appear to be comparatively weak. It is therefore argued that no justification for a dismissal of the wading hypothesis should be made, purely on the assumption that the so-called AAH has been rejected.

The Wading Hypothesis: Strengths and Weaknesses

It is argued here that the wading hypothesis is a strong model of hominin bipedal origins which has been given less serious consideration by anthropologists than it deserves simply because of its association with the (rightly, or wrongly) discredited AAH. What little attention it has received in the literature could hardly be considered a serious rejection. In this section, its strengths and, more importantly, its weaknesses will be outlined.

Strengths

There were several criteria where wading models, generally, were judged better than others and none of them were judged 'poor'.

Increases Survival

No other published model can offer such a clear-cut and decisive theoretical survival advantage for bipedalism over quadrupedalism. In waist to chest deep water bipedalism places the head well above the surface allowing the individual to breathe.

Is not Teleological

As all great apes have been observed switching to bipedalism in waist deep water, it cannot be claimed that this model is anthropomorphic. It proposes a very Darwinian scenario that would encourage bipedalism from the outset and continues to do so even in modern human forms.

Improves Food Acquisition

Four of the published wading models specify food procurement as the motivation for increased wading and shallow water niches are known to be very productive in terms of biomass.

Explains why other Great Apes are not Bipedal

Wading models suggest that the most important factor in human-ape locomotor divergence was the level of exposure to moving through water. This is a very simple and clear-cut reason to explain why some great apes become more bipedal than others.

Provides Plausible Precursor to both Human Bipedalism and Knuckle-Walking

It can be argued that bipedal wading, as a pattern of locomotion, is an ideal precursor to both human striding bipedalism and chimp/gorilla knuckle-walking.

Provides Extended Explanatory Power

Most of the published wading models explain bipedalism as just one of a suite of unique human traits that resulted from greater selection from moving through water.

Weaknesses

There were also some criteria where at least one of the published wading models was judged poor.

Analogous Behavior does not Exist in Extant Apes

The wading model, in its original formulation [44] lacked good evidence in extant apes for wading. However, other formulations published since, have started to correct this weakness by alluding to examples of proboscis monkeys [48] and baboons in the Okavango delta [54].

Provides no Explanation for Anomalies in Hominins

Very few published models of human bipedal origins take the trouble to consider the post-cranial anatomy of australopithecines and other putative hominin ancestors and the published wading models are no exception. Indeed, Verhaegen *et al.* suggest that *Australopithecus* might be closer relatives rather of gorillas and/or chimpanzees than of humans, and are therefore irrelevant to the evolution of the genus *Homo* and consequently to AAH in its strict sense (see also Chapters **4** and **6**, and references [9-11] in Chapter **6**).

Does not Fit the Palaeo-Ecological Record

Hardy's original proposed timescale and coastal habitat [44] is incompatible with the fossil record for early hominin bipedalism that has emerged since. However, other published models promoting wading as a factor of human evolution have largely addressed this weakness [50, 51]. See also the chapter on possible aquatic scenarios (see Chapter **6**).

Is not Compatible with Other Models

Hardy's model [44] is largely incompatible with other ideas of human evolution as are two other wading models. Niemitz suggests that hominins may not have "come down from the trees" [51] and Verhaegen *et al.* doubt about the importance of australopithecines in human evolution [50].

Does not make Falsifiable Predictions

One of the most common criticisms against the AAH and its subhypotheses is that proponents have not demonstrated good scientific methods such as expressing the hypotheses in terms of verifiable, if not falsifiable, predictions.

Can these Weaknesses be Improved Upon?

Although it is argued that the strength of published wading models generally outweighs their weaknesses, it is clear that they could all still be improved upon. So, in remaining part of this chapter, five improvements are suggested. Empirical data in support of analogous behavior in extant apes is offered. A review of the palaeohabitats associated with early hominins is given and a wading model is promoted which, it is argued, is entirely compatible with mainstream views of human evolution. Empirical data is provided which shows compatibility between the wading model and energy efficiency models of human evolution. Finally, a research program is proposed, including a set of falsifiable predictions about the biomechanics of the australopithecine pelvis and what it might tell us about their relative performance in gaits conducive to efficient wading bipedalism.

WADING BIPEDALISM IN GREAT APES

As one wading model was rated *poor* in providing examples of such behavior in extant apes, a short literature review of documented examples is offered and a brief pilot study of the locomotor behavior of captive bonobos is reported. It should be noted that both Ellis [53] and Morgan [47, 49] did correct this weakness to a large degree in their published work by providing good examples of bipedal wading in proboscis monkeys and other large primates, including apes.

Anecdotal Evidence for Bipedal Locomotion in Great Apes

If one considers how most large terrestrial mammals move from land into shallow water, it is clear that almost all of them continue to move quadrupedally as the depth of water rises, until they begin to swim. Notable exceptions are the great apes and large primates. Although they are all known to almost always move quadrupedally on dry land and may continue to do so in very shallow water, there is growing anecdotal evidence that they all switch to bipedalism in deeper water.

Orangutan (Pongo)

There is little documentary evidence of the movement of orangutans in shallow water, but a growing amount of photographic evidence suggests that when they do so they wade bipedally. An authority on the species, Birutė Galdikas, wrote: “Orang-utans have surprisingly little fear of water” [93]. Galdikas [94] includes a sequence of photographs of an orangutan wading through a swamp.

Gorilla (Gorilla)

Gorillas were rarely linked with water in the literature until recently. Doran and McNeilage, reviewing the ecology and behavior of the least studied subspecies, western lowland gorillas, wrote: “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” [95]. The paper is illustrated with a photograph of a bipedally wading adult male (see also Chapter **4**, Fig. **3**).

Observations of ‘spectacular splash displays’ in male silver backs were reported soon after [96]. Although much of the film evidence of this behavior indicated quadrupedal wading in very shallow water, gorillas often switched to bipedal locomotion when the need arose. Parnell noted thirteen incidents of bipedal wading in several weeks of observation. He informed me: “When crossing any expanse of open water too wide to bridge by reaching and clinging to swamp vegetation and dragging oneself cross, in water over about two feet deep, most adult gorillas waded bipedally. Water up to approximately 100-150 cm deep has been crossed in this way.” [97].

This peculiar switching from quadrupedalism on land or in very shallow water, to bipedal locomotion in deeper water was graphically illustrated in western lowland gorillas by a recent paper that received much attention because it reported the first case of tool making and use in gorillas [98]. However, the context that the tool (a specially prepared stick) was used for, as a depth gauge, seems to have passed without comment.

Chimpanzee (Pan Troglodytes)

Chimpanzees at a sanctuary in the Conkouati reserve lagoon have been observed for several years. The chimpanzees are placed on 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. Karlovski described what typically happens when a boat arrives: “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.” [99]. Perhaps most striking is the video evidence shown in the BBC documentary “The life of mammals”. Several chimpanzees are shown wading bipedally in water at the same time at various depths (from knee to waist deep), some carrying infants as they did so [100].

Bonobo (Pan paniscus)

Bonobos are the least studied of the 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. The Myers Thompson study referred to earlier, in particular, reported 24% bipedality in bonobos largely in the context of aquatic foraging [75].

Study of Locomotor Preference in Captive Bonobos

A short pilot study for my master's thesis was conducted at the Planckendael wildlife park, Mechelen, near Brussels, Belgium in 2001. The study set out to test the hypothesis that in water extant apes should exhibit a greater tendency to bipedalism than on dry land. Its findings are reported here because, nine years later, it still appears to be the only study which has set out to systematically test this hypothesis.

Methods

Detailed materials and methods are described elsewhere [101] and available as Supplementary Material (Msc.PDF). Suffice it to say that the methodology used was largely based upon Hunt's much more extensive study of wild chimpanzees [36]. The main difference was that, whereas Hunt was looking for the behavioral contexts in which bouts of bipedalism occur, this study looked for differences in substrate, and its effect on their likelihood to move bipedally. Two observation techniques were used. Focal studies, where one animal was followed continually for half an hour at a time. Second, an hour's worth of observations were also recorded of isolated, real or anticipated instances of contextual wading behavior.

It is well known at Planckendael that visitors often throw food items to bonobos, despite it being strongly discouraged. Often these pieces of food fall short of their intended destination and, instead, drop into the water which surrounds it. When this happens, the bonobos simply wade in and claim it. Sufficient instances were recorded to allow a frame by frame analysis. Bipedalism was classed as supported or unsupported, depending on whether the forearms were used to support the body.

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 (Fig. **1**, left).
>
> *Partly in water*, where at least one part of the body was touching dry ground (Fig. **1**, right).

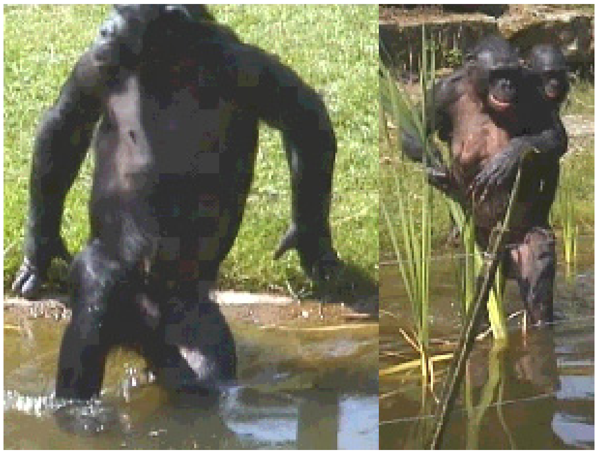

Figure 1: Kidogo (left) is showing supported bipedalism 'partly in water'. Hermien (right) is showing unsupported bipedalism totally in water'.

Results

As expected, analysis of focal study data showed that bonobos prefer the terrestrial substrate (72.6%), with arboreality taking up almost all the other time (27.0%). Only 0.4% of time (38 seconds) was spent in contact with water. The contextual data and focal data together were used to determine the levels of bipedality in different substrates.

Although only 37 seconds was spent in water in total, almost 92% of this time was spent in an upright posture (Fig. **2**).

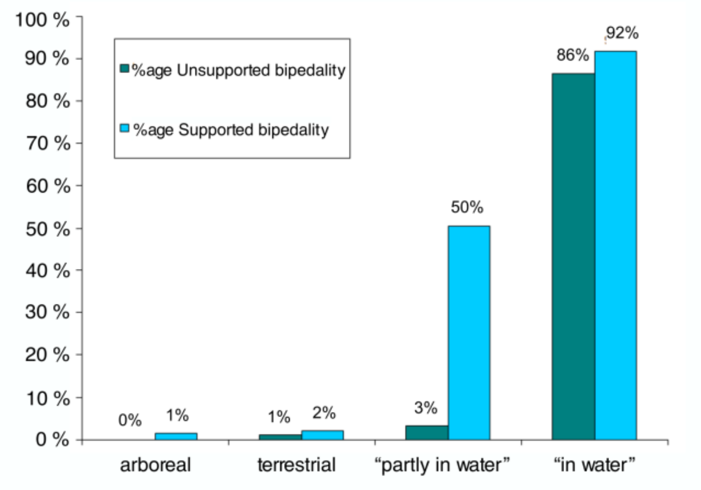

Figure 2: Degree (time) of bipedality in different substrates.

Of the time bonobos spent in water with no contact at all with dry land, over 86% was spent in an unsupported bipedal posture. 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. A short video clip of a typical wading bout is available in the supplementary materials online (bonobo_wading.wmv).

Discussion

The bonobos observed at Planckendael spent very little time in water. However, whenever they did, they showed a remarkable tendency to switch from quadrupedalism on land, to bipedalism in water. Therefore, the prediction, which this study set out to test, was 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. **3** shows, if the water was deeper than 0.5 m (about 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).

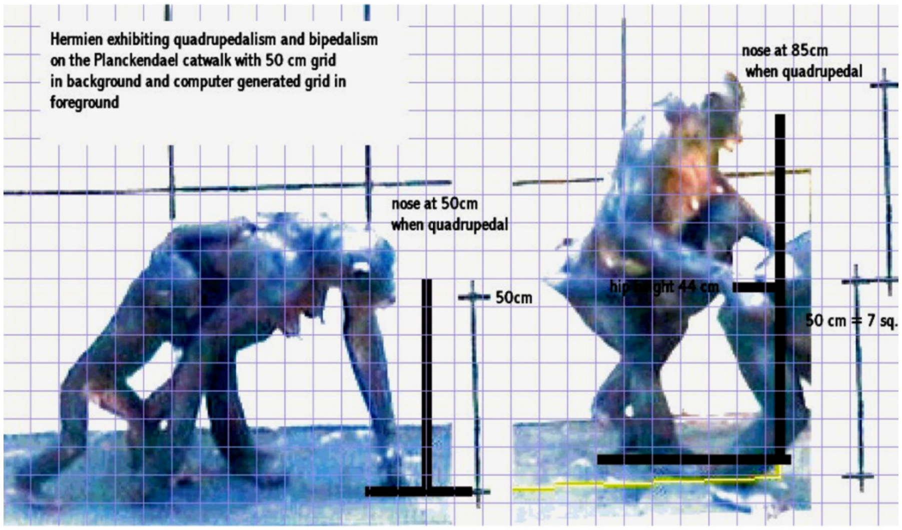

Figure 3: Same individual in quadrupedal and bipedal modes. In the background is the 'cat-walk' at Planckendael with 50 cm squares.

This study can be criticized for the fact that the apes were observed for only a very short time, only 38 seconds of which was in contact with water. However, an interview with a long-term researcher at Planckendael [102] indicated that this kind of behavior was typical. Also, it should also be noted that even in over 700 hours of study, Hunt made even fewer observations of several behavioral contexts of bipedalism than this [36].

Extant ape Wading Conclusions

The literature about bipedal wading in extant apes is still very sparse. However, what little evidence there is clearly indicates that even great apes that prefer not to go into the water, are prepared to do so if necessary. Equally clear is their distinct tendency to switch from quadrupedal locomotion to bipedalism when doing so.

At least two objections may be made to the notion that there may be some unique evolutionary trend in the hominoid clade to switch to bipedalism whilst wading in shallow water. First, bipedality has also been observed in bears (*e.g.*, *Ursus arctos horribilis*) in shallow water [103]. However, these observations are rarely of locomotion. Mostly, their bipedality is purely postural and momentary (*e.g.*, when looking for salmon) or as a threat display to other bears. Second, some primates, *e.g.*, *Macaca fuscata* [104], and even great apes, *e.g.*, *Pan paniscus* [105], have also been observed moving quadrupedally in shallow water. However, anecdotes of primate quadrupedalism in water are always in very shallow depths and usually in the context where the animal was foraging for food just below the surface. Even humans would have to get down on their haunches, or hands and knees, in order to do this.

Although Hardy's original wading model did not report any evidence of extant ape wading bipedalism and so was rated *poor* by this evaluation, it would seem that this was merely because it was published long before primatologists had observed extant apes enough to witness such behavior. On closer examination, this would appear to be one of the strongest criteria for the wading models.

PALAEO-ECOLOGICAL ARGUMENTS FOR THE WADING HYPOTHESIS

Another factor where some published wading models were rated *poor* was in terms of offering supporting evidence from the fossil record. To address this weakness, a brief review of the palaeo-ecological sites associated with the earliest bipedal hominins is offered. It should be noted that most proponents [48-53] of wading ideas have addressed this weakness before, to varying degrees.

Every fossil gives a reliable location for where its one previous owner died, a good estimate of when it lived and, possibly, a fairly good idea of the palaeoclimate and palaeo-ecology of its habitat. However, the oft-repeated principle that 'absence of evidence is not evidence of absence' teaches us that the hypothesis that wading played a key role in the lives of early hominin bipeds is not open to any reasonable falsification through this evidence. What is presented here, then, is simply some more supporting evidence for the hypothesis that early hominins lived in habitats where regular wading was possible.

Taphonomic Bias

The anticipated objection of taphonomic bias in this evidence should be addressed straight away. Clearly, although death close to water courses doesn't necessarily suggest a more aquatic lifestyle, it would be a grotesque distortion to argue that it provided evidence against it. The matter at hand is simply the question as to whether such habitats may have provided sufficient selective pressure to favor increased levels of bipedality.

The faunal assemblages found alongside hominins have usually been taken as reliable indicators of the palaeohabitats in which they lived but these are usually equivocal as they usually contain species indicative of more than one micro-habitat. One point about taphonomic bias that is often overlooked is simply the difference in numbers of fossils attributed to human and extant great ape ancestors. Literally thousands of fossils have been found attributed to humans, with over 400 to just one palaeospecies [106], whereas a handful at most has been assigned to the ancestors chimpanzees or gorillas.

It could be argued that this remarkable discrepancy might be explained because wooded habitats are less conducive to fossilization, or that palaeontologists just have not been looking in the right places to find fossils of our cousins, but this has the appearance of special pleading. Another explanation is that, perhaps, many of these fossil hominins have been incorrectly assigned. However, even if australopithecines and earlier hominins were excluded, it would still leave hundreds of other fossils that seem certain to have been correctly assigned.

A more parsimonious explanation, it is argued, is simply that more of our ancestors were fossilized than those of chimps and gorillas, simply because ours lived in places where this was more likely to happen, *i.e.*, by the water's edge.The only hard evidence we have for actual bipedal locomotion in our ancestors are footprints. Although the evidence from Laetoli is often cited as evidence of purely terrestrial bipedalism [107], it should be noted that such prints could not have formed unless the ground was wet and muddy, and perhaps even flooded. Another, less well known fossil footprint site in Koobi Fora provides unequivocal evidence of wading at 1.5-1.6 Ma [108].

Review of some Hominid Palaeo-Habitats

What follows is a brief review of some of the palaeohabitats of the earliest putative hominin bipeds. This is a selective list, illustrating that many of the palaeohabitats of early hominins were likely to have been conducive to wading. It is not implied here that there are not other palaeohabitats where wading could not have been practiced. Palaeohabitats dated later than the earliest members of *Homo*, ca ~ 2.6 Ma, are not included, as it is argued that they can have had little bearing on the origins of hominin bipedalism. See Table **4** for a summary.

Dryopithecus brancoi

This early-Miocene ape (20-5 Ma) (and others) are included, even though some may doubt their importance in human evolution specifically, because several models of bipedal origins reported here now assume that whatever caused it, happened very early [69]. There are four known species of dryopithecine apes, which inhabited what is now southern central and Eastern Europe, at the time that the Mediterranean and Tethys seas separated Europe from Africa.

Oreopithecus bambolii

The "cookie monster" is a controversial ape that has sometimes been referred to as a "swamp ape" [32: 130]. It is remarkable in that it does have a number of unique characteristics (*e.g.*, a vertebral 'wedging pattern' indicative of some kind of lumbar lordosis, and an australopithecine-like pelvis [110]) that appear to imply a somewhat bipedal form of locomotion or at least posture. This has led to it being placed in a variety of genera. As Cameron put it, *Oreopithecus* has, over the years, been considered an early hominin, a fossil monkey, and everything in between [109].

Whatever the local palaeohabitats were of these Miocene apes, (and there are many) it is worth considering how, from such a stock, emerged the lineage of apes leading to *Hylobates* and *Pongo* to the East, and *Gorilla*, *Pan* and *Homo* to the South, without some kind of interaction with the ever changing coastline of the Tethys/Mediterranean seas at the time.

Sahelanthropus tchadensis

The findings of *Sahelanthropus*, TM 266 or 'Toumaï Man', were published in 2002. It is a great ape that is considered by some [111] to have been somewhat bipedal due, largely, to the anterior position of the foramen magnum. Unfortunately, no postcranial remains have yet been found to further support this idea.

From the point of view of this chapter, the most striking aspect of the finding was the palaeohabitat, which was located inside the outer most known margins of palaeo-Lake Chad. The bed in which TM 266 was found was called the anthracotheriid unit (AU), due the large number of this semi-aquatic species (thought to be an extinct relative of the hippopotamus) found alongside it [112: 154]. Arboreal and open habitat species were found in the unit too.

Orrorin tugenensis

Orrorin, or 'Millenium Man' was found before 'Toumaï Man', but is dated around one million years later. It represents another early hominin fossil with bipedal traits [64, 113] that was found in the palaeo-ecological context of a river and lake.

Ardipithecus ramidus

Before the discovery of Orrorin, this was the oldest putative hominin biped and it regained prominence when a major set of papers was published in a special edition of the journal Science in 2009 [114]. The key message from those papers was the re-assignment of the early ancestral home of human ancestors away from open plains and back into woodland. It would appear that this finding has put the final nail in the coffin of the 'savannah theory', but a clear narrative as to an alternative has not yet emerged.

Australopithecus afarensis

The most complete hypodigm of the early bipeds with over 400 specimen attached to it [106], is for *A. afarensis*. See Table **4** for a selection of sites where *A. afarensis* was found. The Laetoli site is included as an example of one which is not associated with waterside habitats.

Kenyanthropus platyops

Kenyanthropus was assigned to another genus because it contained a mosaic of contradictory features that made it hard to place in existing genera. Table **4** shows the site where *K. platyops* was found.

Later palaeohabitats

Although hominin palaeohabitats later than ca 2.6 Ma are not listed here, it should be noted that Wrangham *et al.* [54] list 25 such sites, for their association with waterside habitats conducive for the procurement of underground storage organs as fallback foods in times of aridity. Part of their argument is that the procurement of such foods through bipedal wading could have been a factor in the origin of hominin bipedalism.

Palaeohabitat Conclusions

Hardy's original coastal wading idea has largely been discredited by the fossil record that has emerged since, and so was rated *poor* by this evaluation. There appear to be a number of reasons for this. First, it is possible that Hardy's emphasis on coastal habitats was simply wrong. Fresh water habitats, inland, might offer alternative scenarios for wading that are more compatible with the fossil record. Second, it could be that as coastal habitats are not conducive to fossilization, exposed as they are to severe erosion, no such evidence of the early coastal hominins Hardy proposed will ever be found. Finally, it is possible that some sort of bipedalism in apes evolved much earlier even than Hardy had anticipated.

The balance of evidence reported here associates many of the earliest bipedal hominids with habitats conducive to wading. Once again, on closer inspection, a criterion that might have appeared at first to be a weakness for wading models has turned out to be another strength.

Table 4: Summary of Early Hominin Palaeohabitats

Genus/Species	Time (Ma)	Site	Palaeohabitat/Faunal Notes
Dryopithecus	*11 - 9*	Rudabanya, Hungary	Dark forest swamp located close to the gigantic Panonian Lake [109]. Woodland species such as the ape *Anapithecus.*
Oreopithecus	ca 8	Monte Bamboli, Tuscany, Italy	Lowland mixed forest [109]. Large quantities of aquatic seed plants, algae and ferns indicate that the lowland region was poorly drained… lignite fossil deposits further indicate swampy conditions [109].
Sahelanthropus	6-7	AU (Anthrocotheriid Unit), Lake Chad, Chad (Africa)	Within the margins of the outer most extended range of palaeo-Lake Chad [112]. Anthracotheriidae, Hippopotimidae present as well as mammals from arboreal and open habitats [112].
Orrorin	5.6-6.3	Tugen Hills (Lukeino Formation)	Fluvial and shallow lacustrine deposits [64]. Open woodland" or "Denser strands of trees in the vicinity, possibly fringing the lake margin and streams that drained into the lake [64].
Ardipithecus ramidus	5.0-5.6	Lothagam, Baringo and Tabarin	Lacustrine (lake) sediments and fluvial (river) deposits [115].

Table 4: cont....

	4.4	Middle Awash (Aramis)	Low-relief aggrading floodplain [114]. Faunal assemblages indicate mainly woodland habitats but included several Hippopotimidae [114].
Australopithecus afarensis	3.46 - 3.86	Laetoli, Tanzania	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" [107]. Closed to medium density woodland [116].
	3.4-3.2	Dikika, Middle Awash, Ethiopia	River dominated deltaic system. The abundance of freshwater gastropods, fishes (mostly catfish), hippopotamids, crocodiles and giant tortoises, associated with the hominin corroborates the interpretation of a mesic deltaic environment, with nearby permanent water [117].
	3.2-3.3	West Turkana (Lower Lomekwi)	Fluvial unit overlain by lacustrine deposits. Lakeshore or river floodplain [107].
	3.18-3.2	Hadar, Middle Awash, Ethiopia.	Sediments accumulated from streams in a basin periodically flooded by a lake [115]. Lakeshore or river floodplain [107]. Evidence of lake with marshes in the early part of this member, but this changes to flood plains and deltas later.
Kenyanthropus	3.3-3.5	West Turkana (Kataboi)	Fluvial unit overlain by lacustrine deposits. Lakeshore or river floodplain. Relatively well watered and vegetated. More vegetated and wetter than Hadar [107].

ENERGY EFFICIENCY OF WADING

The third criterion, where some wading models were rated *poor*, is their compatibility with other models published. It might be argued that this is a difficult one to improve upon but at the end of this section I will show how adding a wading component helps practically all of other models. First, a specific aspect of wading is selected for further investigation, which would, at first, appear to be very contradictory to other models of human bipedal origins, the question of energy efficiency.

The Compatibility Issue

One of the very few scientific investigations undertaken to test the wading hypothesis [78] found the cost of bipedal wading to be about four times greater than walking on dry land at the same speeds. The authors used these finding to reject the wading hypothesis. This would appear to suggest that the wading hypothesis is very contradictory to the energy efficiency model of Rodman and McHenry [61], to say the least.

However, one must remember the protocol of these experiments placed volunteers in water "up to their arm pits." It is hardly surprising that, in such depths, wading would incur far greater energetic costs than moving on dry land. Shallower water was not considered, and neither was the question whether moving through water might have been a favorable environment for early, non-human, forms of bipedalism.

In 2004, a paper, published in the *Journal of Human Evolution* [118], reported that the cost of an ape-like 'bent-hip, bent-knee' (BHBK) gait to be about 55% more than a fully upright (FU) gait in humans whilst walking on a treadmill. The authors concluded from these findings that early bipedal hominin must also have walked with a FU gait and not, as has often been proposed by some, [80, 119, 120] with a relatively inefficient BHBK gait. This supports the authors' wider view that hominin bipedal origins was much older than had been previously thought, stretching back to the LCA with *Pongo*, evidenced by the orangutan propensity to extended hind-limb, hand assisted bipedalism in trees [4].

It seemed to me that Carey and Crompton's [118] assumption that australopithecines must have moved on land, as evidenced by their exclusive use of the rather optimal substrate for walking, the treadmill, should be challenged.

I wanted to know what affect moving through water would have on the relative efficiency of different gaits.

A series of experiments were designed to test the hypothesis that moving through water should remove or reduce the cost differential between moving with an optimal (*i.e.*, FU) gait and one that is non-optimal (*i.e.*, BHBK).

Wading and the Energy Efficiency of Bipedalism Methods

The full details of the experimental protocol, the volunteers who helped and ethics approval obtained can be found elsewhere [121] but suffice it to say here that a group of healthy volunteers were asked to perform a set of wading and walking experiments in or on the side of a swimming pool during which their exhaled respiratory gases were captured. From this, the energetic cost of locomotion could be calculated for different permutations of depth, speed and knee flexion.

Results

In agreement with Carey and Crompton [118], it was found that the cost of a BHBK gait with 50º knee flexion (BHBK) at 0.3 m/s was approximately 57% higher ($p < 0.05$) than an FUp gait on land (Fig. **4a**). However, when similar experiments were conducted in chest deep water, also at 0.3 m/s, there was no significant difference in the gross energetic cost of locomotion between FUp and BHBK gaits, ($p = 0.631$, Fig. **4a**.) In waist deep (0.96 m) water and at higher speeds (0.5-0.6 m/s), the difference in energetic cost between the two gaits was approximately 18% ($p < 0.001$; Fig. **4b**).

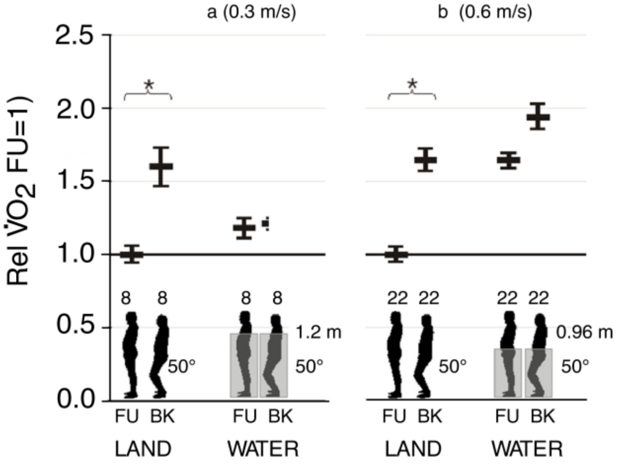

Figure 4: Relative cost of walking with fully upright (FU) and bent knee-bent hip with 50° knee flexion (BK) gaits on **a)** land *versus* chest-deep water (1.2 m depth) at 0.3 m/s, measured for 8 individuals, or **b)** land *versus* waist-deep water (0.96 m depth) at 0.5-0.6 m/s, measured for 22 individuals. All results for each panel are expressed as means ± S.E.M. relative to the cost of the FU gait on land. Asterisks indicates statistically significant difference at $p<0.05$ from [121].

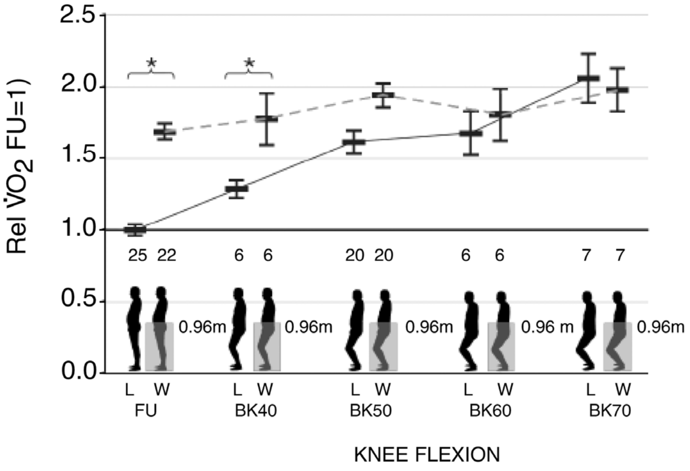

Figure 5: Relative cost of walking with fully upright (FU) gait *versus* with bent knee-bent hip (BK) gait with varying knee flexion (40-70 °), on land (solid line) *versus* waist-deep water (0.96 m) at 0.6 m/s (dotted line). All results are expressed as means ± S.E.M., relative to the cost of the FU gait on land. Asterisks indicates statistically significant difference at $p < 0.05$ from [121].

As knee flexion increased, there was a greater difference between the cost of FUp and BHBK walking on land, but this effect was diminished in water ($p < 0.001$; Fig. **5**). It was also found that it was about 73% more costly to move with an FUp gait in water than on land, but that this difference gradually diminished as knee flexion increased. Walking with a knee flexion of 60° or more was actually found to be just as costly (no significant difference) in water as on land, and a linear regression analysis clearly predicts that there are some knee flexions and depth permutations where it would be less costly to wade in water than walk on dry land.

Conclusions

The findings of this study were consistent with the hypothesis that moving through water should eliminate or reduce the energetic cost differential between moving with an optimal (FU) gait and an inefficient (BHBK) gait. This suggests not only that shallow water is a medium through which early hominids may have practiced 'non-optimal', BHBK, bipedal gaits without incurring prohibitively high energetic costs, but that such environments with smooth depth gradients, are places where such gaits could have evolved into FU gaits, more optimal for efficient terrestrial bipedalism.

Therefore it is argued that wading models are not contradictory to those promoting energy efficiency at all, but are actually complimentary to them because they provide a plausible means for the process to start in the first place.

Wading is Complimentary to other Models of Hominid Bipedality

It is argued, in fact, that most of the ideas of hominin bipedal origins could be enhanced by an additional component of bipedal wading through shallow water. For example, models promoting forelimb pre-emption are certainly not contradicted by any putative bipedal wading locomotion. Shallow water is a medium that could only be expected to encourage the use of forelimbs for carrying, no matter what the proposed object being carried might be. Indeed, objects that are heavy on land, such as carcasses, usually have some inherent buoyancy that would make them easier to carry in water. It is difficult to imagine a place more critical for a hominid mother to carry an infant bipedally than in waist deep water.

Similarly, models promoting aspects of social display are also not mutually exclusive to wading behavior. Actually, some of the models proposing the use of threat displays and aggression are directly supported by evidence of such behavior, for example by gorillas in swamps of the Congo [95, 96]. Those that promote evasion and vigilance as an adaptive pressure for upright posture [20, 27, 28] may note that wading away from dry land into shallow water might deter some would-be savannah predators, although clearly the threat of aquatic predators, such as crocodiles, would be a strong counter-pressure on occasion. Other models promoting sexual display [14], or a new 'fashion' [30], similarly, are hardly contradicted by the possibility of movement through water.

It could be argued that feeding models are, for the most part, bolstered by adding a wading component. Hunt's postural feeding model [36], for example, is only strengthened by assuming that the habitats, where upright foraging feeding behavior from small bushes, were seasonally flooded. Bipedal wading would allow access to a significant amount of food that would otherwise be rendered inaccessible. Although most feeding models propose some kind of terrestrial gathering, scavenging or hunting [10, 31, 33-35, 38, 40-43], many of them suggest that gallery forest habitats, close to regular supplies of water, would have been ideal places, either to procure the food or to take it to, as a base. Again, assuming seasonal flooding occurred in such habitats makes these models mutually compatible with the wading idea.

Furthermore, aquatic foraging itself, as originally suggested [44], provides a powerful incentive for bipedalism, as long as the habitat was food rich with relatively sessile foods such as aquatic plants, shell fish and/or molluscs and the waters were relatively shallow.

The thermoregulatory model [67, 86] is perhaps the one most strongly complimented by an additional wading component of all. Clearly, the quickest and most efficient way of cooling down for equatorial hominid would simply be to go for a dip. Even wading in very shallow water would allow water to be scooped up and splashed over the upper torso to augment body cooling and delay and/or reduce the requirement for sweating. One should also recall that Wheeler's model relies heavily on the proximity of hominids to reliable supplies of fresh water as it is dependent upon sweat cooling.

Finally, as has been shown here, even the purely terrestrial efficiency model of hominin bipedalism [61] need not necessarily be contradicted by a wading component, as the energy efficiency model includes an inherent problem that wading might resolve: How did the regular practice of the bipedal locomotion begin, even before the anatomy evolved to make it efficient?

PROPOSED STUDY: A BIO-MECHANICAL AND MORPHO-METRIC ANALYSIS OF THE EARLY HOMININ HIP WITH RESPECT TO WADING

Australopithecine Anatomical Anomalies for Bipedalism

There are two other perceived weaknesses of most wading models (and practically all other models of bipedal origins, for that matter). First, the epistemological criticism [79] that proponents make no falsifiable predictions and so do not subscribe to proper scientific methodology, and second, that they make no attempt to account for anomalies of the australopithecine pelvis. This section attempts to address both of these weaknesses by making a series of falsifiable predictions about features of the australopithecine pelvis and a structured research program that could test them.

The anatomy of the australopithecine pelvis, when contrasted with that of extant great apes (Fig. **6**), clearly indicates that it moved bipedally as indicated by many well known features.

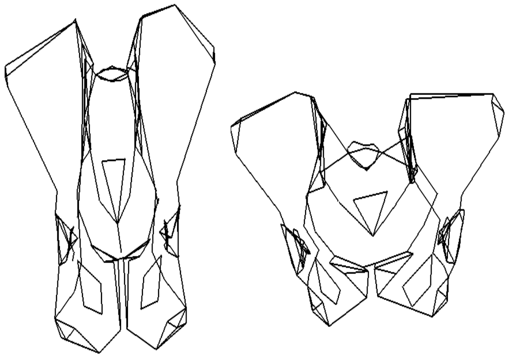

Figure 6: *Pan/Gorilla* generalized pelvic morphology, shown as a wireframe of connected analogous landmarks, compared with AL 288-1 (*A. afarensis* 'Lucy') in the same frontal plane after a Procustes analysis with Morphologika [122].

For example, the pelvis is relatively short in the longitudinal axis (craniocaudally). The vertebral body on the sacrum is much closer to the acetabulae providing greater stability for upright weight bearing. The lunate surface of the acetabulum itself indicates weight bearing from the cranial direction, whereas in the great apes it is generally orientated more dorsally, indicating a more quadrupedal posture.

The iliac blades are orientated more laterally, indicating greater capacity for abduction of the gluteal muscles, important in supporting the body weight when only a single limb is on the ground during walking.

On the other hand, if australopithecines walked exactly like we do, their pelvic morphology seems to contain a few anomalies (Fig. **7**).

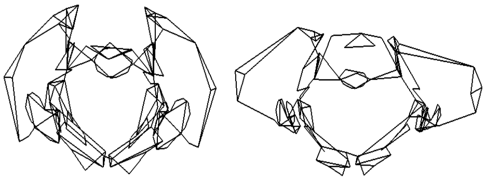

Figure 7: Modern human generalized pelvic morphology compared with AL 288-1 in the same transverse plane after Procustes analysis with Morphologika [122].

For example, the pelvis is very platypelloid (broad pelvis). Its lateral:anterio-posterior diameter ratio is about 80% larger than that of humans. The ischial rami are more laterally orientated, indicating significantly different biomechanics to our own. Although the iliac arches are more laterally flared than extant great apes, they are still more dorsally aligned than ours. There has been some dispute about what these bipedal 'anomalies' might tell us about the way australopithecines walked. It has been argued, for example, that a BHBK 'waddling' gait would have been too energetically costly to have been used [123], whereas others have countered that a FU human like gait would, for this anatomy, have been too unstable [119].

The idea that australopithecines may have been subjected to sufficient selection from wading to have affected their pelvic morphology does not seem to have been considered anywhere. Perhaps such an idea can be expressed in the form of an hypothesis that is open to some form of testing.

Hypothesis

The major morphological differences between the australopithecine pelvis and the modern human pelvis are explicable in terms of adaptations for efficient wading in australopithecines.

This hypothesis is clearly not falsifiable in the Popperian sense, but a number of falsifiable predictions can be constructed around it, and a program of research designed to test them.

Falsifiable predictions:

1. Individuals with wider hips (greater lateral:anterior-posterio ratio) will wade more efficiently through waist deep water if there is a greater component of lateral motion in the their gait. In other words, individuals with platypelloid hips will find it easier to move with a twisting (side-to-side) gait or a sideways gait, than a fully frontal (normal) gait.
2. The movements involved in twisting or sideways gaits include significant contributions from the rotators, abductors and adductors of the hip.
3. The biomechanical load arms of these muscle groups, as predicted from a biomechanical analysis of the australopithecine hip, will be greater than those of the human form, when differences in body size are taken into consideration.
4. Computer simulations of australopithecines moving in water will show their combination of a more platypelloid pelvis and musculature with greater load arms for rotation, abduction and adduction made them able to wade through shallow water, with twisting (side-to-side) or sideways gaits, more efficiently than models of humans, or extant great apes.

Proposed research program to test the hypothesis. Most of the predictions made by the hypothesis above could easily be tested with a reasonably simple research program, suitable for a Ph.D. candidate.

Wading experiments. First, volunteers could be recruited who have extremes of the Lat:AP ratio. As some humans are known to have relatively platypelloid pelves [124], there should be sufficient variation to test the effects of this shape difference and gait on wading efficiency. To create greater variation, experimental apparatus could be designed which artificially increase the physical width of an individual's hip. The apparatus should allow the hip width to be varied (perhaps by fitting silica gel bags of varying sizes into bathing shorts designed with a long side-pocket.) This way, the same individual could wade through the water with the apparatus set to their own (natural) hip width as a control, one that more approximated the australopithecines', and one that was intermediate. An experimental protocol could be devised where volunteers waded through waist deep water using three different gaits: normal human walking, a twisting side-to-side gait and one that was sideways. Data could then be collected to see if there is any correlation between hip shape and gait in terms of energetic cost.

EMG studies. Second, an EMG-based gait analysis of small sample of these volunteers could be performed to determine exactly which muscles are involved, and at what times in the gait cycle, for wading with a twisting, side-to-side gait and with a sideways gait in waist deep water.

Morphometric/biomechanical studies. Third, a morphometric analysis of the australopithecine hip could be conducted to estimate the load arms of the muscle groups identified in the second phase above. These figures could be compared with those for modern humans.

Computer simulations of drag through water. Finally, fluid dynamics computer simulation software could be used to generate a model of a wading hominin. By varying the shape of the pelvis and the biomechanical force of the muscle groups between australopithecine-like forms and human forms, it should be possible to determine whether the australopithecine form gives an advantage in terms of drag reduction and biomechanics to wading over the human form.

CONCLUSIONS

It could be argued that human bipedal origins is a problem that is long overdue a generally accepted solution. Some [5] have argued that the response to the problem has become a tangled thicket. I argue here that, contrary to current popular belief, there is potentially a rather simple solution, if only we allow ourselves to look at the problem rationally, perform a little selective pruning, and look at an unpopular idea without prejudice.

The literature is rich with ideas on the issue but critical thinking about them is sparse. There are many reviews of previously published idea but few that could be called a meta analysis in the proper sense and there are none that attempt an objective comparison and assessment of their relative merits. The evaluative framework proposed here has been designed to be built upon and developed to allow models of bipedalism to be critically compared.

From this evaluative framework and a thorough review of the literature, I think it is clear that wading models of human bipedal origins have been grossly underrated due to their association with the mislabelled ‘AAH’. Re-labelling them “wading hypotheses” under the umbrella of “waterside hypotheses of human evolution” might help anthropologists move beyond their reluctance to seriously consider these ideas.

The wading hypothesis, as published to date, have few perceived weaknesses, but some of them were addressed here: Anecdotal evidence from the field studies and observations of captive apes show a remarkable propensity to switch to bipedalism when moving in shallow water. A literature review of the palaeo-ecological record of hominin fossil sites revealed that, contrary to popular belief, the fossil record is largely supportive of, and certainly not contradictory to, the wading hypothesis. A wading study found that the energy cost differential between optimal and non-optimal gaits is reduced in water, suggesting that this would make an ideal environment for transient forms of bipedalism to have existed in evolutionary stable scenarios. It was argued that adding a wading component helps practically all the other models of bipedal origins and is complementary to most, even the energetic efficiency model. Finally, a hypothesis and a series of falsifiable predictions was made about the wading hypothesis in relation to australopithecine pelvic anatomy, answering the oft-repeated criticism that waterside proponents are not exponents of the scientific method.

ACKNOWLEDGEMENTS

So many have helped me over the years I want to select just four people here for special mention. First, the great work of my son, Kęstas, who built the Bipedalism Model Evaluator Web Pages. Second, my fantastic wife, Lesley, who has stood by me despite my unbearable mood swings. Third, the underappreciated work of Derek Ellis, which reminds us of the massive potential importance of wetlands in human evolution.

Finally, and most of all, I’d like to acknowledge the indefatigable Elaine Morgan and her amazing 40 year contribution to our understanding of human evolution. That she is, even today, still almost totally unappreciated in anthropology is, I think, a scandal of Piltdown proportions. Although the conception of the wading idea must ultimately be credited to Alister Hardy, it was Elaine Morgan who did more than anyone to flesh it out, and promote it, to the point where it can be viewed as a serious hypothesis. She has been my ‘main inspirer’ these last 15 years.

SUPPLEMENTARY MATERIALS

The supplementary files that can be found online at
http://www.riverapes.com/Papers/Wading%20Paper/Supporting%20Files/ are listed below.

File	Description
Table_S1.xls	University text book survey of bipedalism models - books surveyed.
Table_S2.xls	Details of bipedalism models reported in university text books.
MSc.pdf	Algis Kuliukas' Master's thesis. Details of extant bonobo study.
Bonobo_Wading.wmv	Short video clip of a typical bonobo wading bout.
Model_Evaluator.html	Interactive evaluative framework to assess models of hominin bipedalism. The Model_Evaluator_Files contains all the supporting files it needs.
Compatibility.xls	Excel tool to help derive evaluations for their 'compatibility'.

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