A WADING COMPONENT IN THE ORIGIN OF HOMINID BIPEDALITY?

Ph.D. Thesis

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of Western Australia, Perth, Australia. It has not been submitted before for any degree or examination at any other University.

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Abstract

Fundamental to the understanding of human evolution are plausible solutions to questions surrounding why, uniquely among the primates, we habitually move bipedally almost totally without the aid of the upper limbs. However, despite about 150 years of intensive application of Darwinist theory by scientists of various genres, there remains little confidence or consensus in the field of palaeoanthropology about solutions to such questions.

This thesis (in Chapter 2) comprehensively reviews 42 models that have been published to provide potential solutions to these problems. Then, in Chapter 3, for the first time, an evaluative framework is proposed for models of bipedalism which is then used to assess and compare those described. This evaluative framework is essentially a “marking rubric” for which an on-line tool (see www.tinyurl.com/BipedalModels) is provided, which the reader may use to criticise the author’s assessment and substitute his or her own. Among the strongest models, according to this evaluation, are ones suggesting that a key driver of early hominid bipedalism was regular wading through shallow water. The author’s own wading model “River Apes … Coastal People” is briefly outlined in chapter 2 and evaluated in chapter 3, for the sake of completion, but the reader should refer to the later part of the thesis, namely chapters 5, 6 and 7, (specifically sections 7.2 and 7.3) for a detailed examination.

Chapter 4 examines, in detail, the wading hypothesis, which has hitherto received comparatively little attention from paleoanthropologists and human anatomists. The historical context of the wading hypothesis is described and it is proposed that its association with (in my opinion) the unfortunately labelled “aquatic ape hypothesis” accounts for why this idea has received less respect than it might have deserved. According to the evaluative framework described here, all models, including ones involving wading, have weaknesses and the rest of the thesis is an attempt to address some of them by testing various predictions of the wading hypothesis in order to arrive at a better wading model.

Two identified weakness of published wading models are addressed in Chapter 5, namely that they make few scientifically testable predictions and that they are somewhat contradicted by arguments of energy efficiency. One such prediction is that wading makes bipedalism less energetically costly in the earliest hominins still lacking the anatomical adaptations for bipedal efficiency of modern humans. The cost differential between optimal (i.e. fully upright, extended hip, extended knee, EHEK, human-like) and non-optimal gaits (i.e. Bent Hip Bent Knee, BHBK, chimp-like), according to this test, should be reduced in water. An empirical study from experiments on human subjects is reported, which found that the cost differential was indeed reduced from approximately 55% on dry land, to approximately 18% for a BHBK gait with 50^{o} knee flexion, at 0.6 m/s in water depth of approximately 1m. At greater depths, and/or using gaits with greater knee-flexion, the cost differential was reduced still further, or eliminated completely. This suggests that wading might well provide an optimal scenario for the earliest hominids to adopt bipedalism before they had evolved an anatomy to make it energetically efficient.

Another weakness of published wading models is addressed in Chapter 6. None of them offer any hard evidence from the fossil record of early hominin bipeds. This thesis reports a geometric morphometric study of the hominoid hip, comparing the shape of the australopithecine pelvis with extant great apes and humans. It tests the prediction that the shape differences between the australopithecine and human pelvis is consistent with adaptations for more efficient wading. Triangular sets of landmarks including hip muscle origin, the centre of rotation of the acetabulum, and a generated (fixed point) landmark modelling an insertion point on a fixed femur, were used to calculate the lever arm of the major muscle blocks involved with hip movement. For each specimen, each lever arm was expressed as a ratio of every other, yielding over 135,000 ratios in all. This data was then explored using a business analysis data summarising tool, the Pivot Table feature of Microsoft Excel. This allowed the production of succinct species summaries of broad lever arm groups, such as those pertaining to abduction compared to those pertaining to extension, or for rotation, compared to flexion. The pivot table feature is designed so that these broad summary data can be “drilled down” to get to ever increasing levels of detail, ultimately to the individual level arm ratio pairs. Although the scope of this study necessarily limited how “deep” this “drill through” process could be done, the method clearly shows promise for studies of this type in the future and produced results that were consistent with the prediction that australopithecine pelvic shape appears to be adapted to generating greater lever arms for abduction/adduction and rotation, as a ratio to extension/flexion than modern humans. This is what might be expected if regular wading was a part of their locomotor repertoire.

The thesis concludes, in chapter 7, by putting wading hypotheses of the origin of hominin bipedal origins in the broader context of waterside hypotheses of human evolution generally. An assessment of the mislabelled “aquatic ape hypothesis” is summarised and a new model of human evolution (called “River Apes… Coastal People”) is offered which draws upon the strengths of the still current mainstream “savannah-based” paradigm and those that propose many human traits that may have resulted from some selection from moving and procuring food from water. This hybridization of seemingly incompatible ideas is possible, it is argued, simply by scaling back the degree of selection for wading, swimming and diving being proposed, and acknowledging that even very slight levels of selection can, in evolutionary terms, rapidly overcome the effects of drift.

In Memory of Elaine Morgan

The main inspirer behind this work.

1920 - 2013

Acknowledgements

Many people have helped me to start this body of work and to build it up, from its earliest origins as an idea to follow on from a master's thesis at University College London, to the state it is now, 16 years later, and I must start by thanking as many of them as I can.

First and foremost, I want to thank my dear wife of 29 years, Lesley, without whom I'd be utterly lost. In the mid-late 1990s she put up with years of manic enthusiasm about these ideas when they were still new to my mind. She encouraged me to explore them fully by returning to academia, even though it involved effectively giving up on a potentially lucrative career in databases to take up a master's degree at University College London. She was totally supportive, even when it involved immigrating to Australia so that I could study it properly through a Ph.D. at the University of Western Australia. When things started to get frustrating, she was always there with a bright smile and never-ending optimism. After I'd essentially given up on the thesis, she never stopped (very gently) nagging me to put one last effort in and complete it. She never gave up on me, or the ideas in it.

Secondly, I must pay formal tribute to Elaine Morgan, my main inspirer for these ideas. She is the reason I resumed my fascination with human evolution and science. It is her overwhelming common sense that persuaded me that there might really be something in all of this and certainly that, until some serious science has been done, "more aquatic" ideas should not be dismissed lightly. I had the great privilege to meet Elaine on several occasions, the last of which was just a few weeks before her death in 2013. Every time I met her I never ceased to be impressed with her logic and rationality. She had a brilliant mind and people would be foolish to dismiss her.

I want to thank Charles Oxnard next. It was his team's brilliant, pioneering, computer analysis work on the shape of the australopithecine pelvis in the 1960s that first caught my eye whilst I was doing my Masters' at UCL and planted the seed for a potential idea to study for a PhD. It was Charles' presence at UWA that was the ultimate motivation for us to leave the UK and come to live in Perth. Although Charles was unfortunately not able to be my supervisor from the beginning of my time here, at least I managed to secure his guidance for a few years towards the end, after resuming my efforts to complete in 2012. I have always been impressed with Charles' immense knowledge and boyish enthusiasm and curiosity. You never leave a meeting with Charles feeling very clever, but you're always inspired to try to learn more.

Next I want to acknowledge the substantial work of my two formal supervisors from 2003 until I stopped working on my thesis in 2009.

Nick Milne always gave 100% support to me even if he was skeptical of the ideas behind the thesis. He taught me how to perform a 3D Geometric Morphometric analysis of skeletal samples and helped me enormously as I digitised hundreds of pelves and femora in several museums across Europe. His skeptical eye was invaluable in formulating experiments and studies to test some of these ideas and also in making sure their results were not overly interpreted.

Paul Fournier, conversely, *was always very enthusiastic* about the ideas behind the thesis, helped me design the wading experiments, and encouraged me to submit the paper reporting results of the wading study to the most reputable journals. Paul has a very critical eye in his proof-reading of text, and his enthusiasm is boundless.

There are many others who have helped along the way. Linc Schmitt, Head of Human Biology at the time, encouraged me to resume my work and complete. Dan Franklin and Ambika Flavel, whilst I was working with them at the Centre for Forensic Science, gave me the confidence to improve MorphDb's analysis features. Dan Franklin, Jens Hirschberg and Warren Mitchell, all completed their Ph.D. from the same section I worked from, and I'd like to thank them and all my peers in the department for their encouragement too. I must also thank the many people who volunteered their time to help me conduct my wading experiments and the kind and generous support of people at the Powell-Cotton Museum, Kent, The Natural History Museum, London and the Naturalis museum in Leiden, Holland, who gave me access to their precious skeletal samples.

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Last, but not least, I want to thank my son, Kęstutis Kuliukas, for building the on-line bipedalism model assessment tool (http://www.tinyurl.com/BipedalModels).

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CHAPTER ONE

A WADING COMPONENT IN THE ORIGIN OF HOMININ BIPEDALISM?

1. A WADING COMPONENT IN THE ORIGIN OF HOMININ BIPEDALISM?

1.1. Introduction

Fundamental to understanding human evolution are plausible solutions to questions surrounding why, uniquely among the primates, we habitually move bipedally almost totally without the aid of the upper limbs. However, despite almost 150 years of intensive application of Darwinist theory by scientists of various genres, there remains little confidence or consensus in the field of palaeoanthropology about solutions to such questions.

Before considering this peculiarly human problem, it is necessary to define a few specific terms used in this thesis and then place the topic of our bipedalism in the context of locomotion in the animal world and the thesis starts by discussing why the human form of bipedal locomotion is so peculiar compared to other forms of animal bipedalism.

Then, there follows a comprehensive review of the models that have been published to try to explain human bipedalism in an evolutionary context. In addition, it summarises and compares these ideas by proposing an evaluative framework of characteristics of good models of bipedalism against which all published models are then compared and ranked.
Among the strongest models, according to this evaluation, are ones suggesting that a key driver of early hominid bipedalism was regular wading through shallow water. The rest of the thesis then examines, in detail, the wading hypothesis, which hitherto has received comparatively little attention from paleoanthropologists and anatomists. The historical context of the wading hypothesis is discussed. It is proposed that its association with the unfortunately labelled ‘aquatic ape hypothesis’ accounts for why this idea has not been afforded as much time and respect as some others.

According to the evaluative framework, all models, including ones promoting wading, have weak aspects. The next two chapters of the thesis set out to address the weakest areas of the wading models and to test various predictions of it, some via empirical data through experiments on human subjects, or via geometric morphometric analysis of the hominoid hip, whilst other predictions are assessed by a thorough review of the literature.
The key goal of the thesis is to produce a model of human bipedalism that is the product of a detailed assessment of the pros and cons of all the previously published ideas and to provide new empirical evidence for that model. In the last chapter, the “River Apes… Coastal People” model is presented. In the opinion of this author, it fulfils the goal of the thesis. The model is included in the earlier evaluative framework for completion sake, but readers are encouraged to read the final chapter to learn more about it more first, if necessary. The model is placed into the context of other waterside hypotheses of human evolution and proposes further studies to test such ideas. The “River Apes… Coastal People” model is offered as a kind of “best of both worlds” of the still mainstream “savannah-based” paradigm and “more aquatic” ideas suggesting human evolution, in some ways,

resulted from selection from moving and procuring food from water. This hybridization of seemingly incompatible ideas is achieved simply by scaling back the degree of selection for wading, swimming and diving being proposed, and acknowledging that even very slight levels of selection can, in evolutionary terms, rapidly overcome the effects of drift.

1.2. Terms and abbreviations used

Throughout this thesis a few terms will be used which may mean different things to different authors. It may help to clarify some of them here.

“Aquatic Apes”

Desmond Morris first coined the term “**Aquatic Ape**” to describe the idea that some peculiar features of humans (including their bipedality) may be explained by an aquatic or semi-aquatic phase in their evolutionary past (Morris 1967 p 29). It is the somewhat controversial idea behind this thesis. It led to a whole series of books by playwright Elaine Morgan on the so-called “**Aquatic Ape Hypothesis**” (AAH) – also sometimes called the “**Aquatic Ape Theory**” (Morgan 1972, 1982, 1990, 1997).

It is the view of this author that this “aquatic ape hypothesis” was never sufficiently well defined, leaving each reader to interpret it in his/her own personal way and that this has been a big part of the cause of the controversy.

When the term is used in here, it is meant in a *sensu lato* (or broad, informal, popularly used) way. It will often be prefixed with “so-called” to make this clear.

In chapter 7, these ideas are discussed in detail and clearly defined. It is proposed that they be placed under a broad, umbrella term “**Waterside Hypotheses of Human Evolution**”. Under this umbrella, “the aquatic ape hypothesis” *sensu sricto* (or strict, formally defined) would be seen as the specific ideas of Hardy (1960) and Morgan (Morgan 1972, 1982, 1990, 1997) which is also sometimes called the “**U-turn hypothesis**” in a waterside context.

Arguments, and authors of arguments, that are skeptical of waterside hypotheses of human evolution, such as the so-called “aquatic ape hypothesis”, are informally termed “**aquaskeptics**” here. It is a neutral term and does not suggest the arguments are correct or otherwise. There are “proponents” of these ideas. “Aquaskeptics” are their opponents.

Types of bipedalism

Throughout these discussions various forms of bipedalism will be described. One of the key issues to be dealt with is how mandatory that bipedalism is as a means of locomotion. Clearly many animals, that usually move quadrupedally, are able to switch to a two-footed stance temporarily, and some are even able to move bipedally whilst doing so, even if they return to a four-footed stance rather quickly. This is termed “**facultative** bipedalism”, indicating its discretionary or optional nature.

Humans, by contrast, can move quadrupedally, if they choose to do so or of they are disabled in some way (e.g. by “disequilibrium syndrome”), but they normally move bipedally. Human bipedality is therefore, termed “**obligate** bipedalism.”

The key task here is to try to explain how facultative bipedalism, practiced by our earliest primate ancestors, evolved into the obligate bipedalism we exhibit today.

Another related concept is to describe the bipedal gaits of extant apes and early hominids when they did move bipedally. Modern humans have a series of anatomical adaptation which allow us to walk relatively efficiently, with an "**inverted pendulum**" (**straight legged**) gait. Here this is termed "**Extended Hip, Extended Knee**" (**EHEK**) or "**human-like**" to contrast it with the more typically "**ape-like**" "**Bent Hip, Bent Knee**" (**BHBK**) gait.

Hominid and Hominin

Any discussion of human evolution, requires terms to describe putative ancestors. Here, the use and '**hominid**' and '**hominin**' follow the principals described by Cameron and Groves (2004 p 61).

Use of the term "**hominid**" suggests that that its phylogenetic relationship to *Homo* is indeterminate. In other words, a hominid could be ancestral to orang-utans, gorillas, chimpanzees, humans, more than one, or none, of the above.

"**Hominin**" is used to describe an individual closely associated with the emergence of the human lineage. This is not to suggest that they were necessarily ancestors of humans, just that they shared a number of derived traits with humans.

In the context of this thesis, "homini**d** bipedalism" refers to a mode of locomotion that may or may not have been related to the form adopted by human ancestors. Conversely, the term "homini**n** bipedalism" refers to a mode of locomotion that *was* related to that adopted by our ancestors.

Refugia

In the context of this thesis, the term "**refugia**" is used to describe wooded habitats that have shrunk relative to their former size due to increased aridity. Most often they are associated with "**riparian zones"** closed to permanent or semi-permanent water courses and are termed "**gallery forests"**.

A key concept used in this thesis is the notion that as climates changed over evolutionary timescales, tropical rainforest habitats gradually changed into more open savannah grasslands, but retained thin strips of forest habitat close to those water courses that remained most of the time. These **gallery forest refugia** would be exposed to cyclical periods of wetter, as well as drier, climate as well as regular seasonal weather patterns which would have caused regular flooding.

1.3. Non-human bipedalism

The subject of this thesis is specifically the evolution of human bipedality but before starting to look at the peculiar form of locomotion of our species, a broader context is sought through a brief survey of other forms of bipedalism in non-human animals. The survey is structured as phylogenetic tree of the animal world.

Bipedal locomotion has evolved several times in land-dwelling vertebrates in forms both extinct and extant. The first four-limbed vertebrates and their descendants are termed "*Tetrapoda"*. Some exhibit forms of obligate bipedalism but none are like our own.

1.3.1 Non-mammalian examples

Reptilians

Extinct forms

The earliest evidence of a bipedal animal is *Eudibamus cursoris*. It was discovered in Germany and dated at approximately 290 Ma. (Berman et al. 2000), the fossil species adopted cursorial running bipedalism, employing a "parasagittal digitigrade posture" (one moving on its toes.)

Therapods ("Beast feet") are a major clade of the dinosaurs that are largely although not exclusively) considered to have moved bipedally. They lived in the Jurassic and Cretaceous eras (ca 200 – 65 Ma).

Extant forms

Extant lizards that sometimes adopt bipedalism for running include those of the genus *Basiliscus*, of Central America, which have been observed "running" bipedally on the surface of water.

Aves (Birds)

Almost all birds are bipedal when they are not flying. They contain a large clade, *Palaeognathae*, comprising ostriches, rheas, emus and cassowaries and kiwis, which are flightless, so they are obligate bipeds in a similarly strict sense as humans. Most of these are relatively large.

The vast majority of birds, however, do fly and spend much time in trees when they are not, providing an arboreal, rather than a terrestrial context for that behaviour.

Some groups of birds also spend much of their lives in water, either wading (bipedally, of course), swimming at the surface, or diving. One such group, the *speniscoformes* (penguins) have become so adapted to swimming that they too have lost their ability to fly.

1.3.2 Bipedalism in mammals

Macropoda

Macropods *(Macropodidae)* are a family of marsupial mammals (of the *Diprotodontia* order) comprising around 60 species. More commonly referred to as "Wallabies and Kangaroos", they are generally native to Australasia, New Guinea and nearby islands. They are characterised, primarily, by having a lengthened and narrowed hind foot (hence "*Macro*

Pod") and often a large, non-prehensile (not grabbing) tail which can act as a 3rd foot. (Novak 1999).

When needing to move rapidly, they exhibit a leaping style of locomotion, using only their hind limbs. This form of bipedal locomotion is at its most pronounced in the clade *Macropus* (kangaroos, wallaroos and several wallabies). It is generally believed that this form of locomotion is an adaptation to improve foraging distances, not as a means of escaping predators.

Kangaroos move pentapedally (using all four limbs and their tails) when moving slowly. They are also known to be adept swimmers.

Rodenta

Kangaroo rats and kangaroo mice (*Heteromyidae*), like Macropods, also have large hind limbs which appear to be adapted to a peculiar form of leaping bipedalism. They are native, mainly, to the southwestern regions of North America.

Studies have shown that bipedalism in these rodents allows them to move quicker (Djawdan & Garland 1988) leading to speculation that their bipedalism is an adaptation to help them escape predators.

Antelopes

A major Mammalian order is the *Artiodactyla* (the even-toed ungulates) which includes many large families (e.g. *Bovidae*), are all almost universally quadrupedal. However, some species have been known to exhibit facultative bipedalism from time to time, for example in the context of postural feeding. The gerenuk (*Litocranius walleri*), for example, are well known to stand on their hind legs to browse foliage from trees that they would not otherwise be able to access.

Carnivora

The order *Carnivora* is another diverse clade of mammals. As the name suggests, they are largely noted for their carnivorous lifestyle. They are split into two sub-orders, the feliformia (cat-like) and the caniforma (dog-like). Almost all species in Carnivora exclusively move quadrupedally but there are a couple of interesting isolated examples of bipedalism in each suborder.

Meerkat (*Suricata*)

One of the families of cat-like species is the *Herpestidae* (Mongooses) and within that clade is the genus *Suricata* (the meerkats.) Like most carnivores feeding mainly on insects but also other small animals such as lizards), meerkats move quadrupedally almost all the time. However they are noted for a peculiar type of sentinel behaviour where they adopt a bipedal posture and stand still whilst they seem to be on the look-out for predators, or prey.

Bears (*Ursidae*)

Amongst the dog-like (*caniformia*) carnivores are the bears. They are widely distributed across much of the world, except Africa. Bears also move almost exclusively quadrupedally but are known to adopt bipedal postures, and even use bipedal locomotion, from time to time. Scenarios include threat display and sentinel behaviour, such as looking out for prey. This has sometimes been observed in water, for example, when brown bears hunt salmon.

Bipedalism in primates

Humans, of course, are part of the Mammalian order called Primates, which comprises about 200 species. They are a diverse class of mammals with a few common themes and trends running through them, such as a propensity to arboreality (tree-living), increased sociality, and increased altriciality (greater care of fewer infants, rather than the reverse.) Most are arboreal, especially the smaller species. Small primates are able to move along the tops of branches by scrambling along quadrupedally on all fours). Larger primates naturally find this more difficult and their locomotor repertoire usually includes below-branch brachiation (branch swinging) and vertical trunk climbing. This size increase appears to provide a propensity to upright posture and bipedalism.

Lemuridae – sifakas

The lemurs, uniquely isolated in Madagascar for at least 20 Ma, have experienced an adaptive radiation there, allowing them to evolve into a variety of niches. Some have become larger species, some smaller.

The sifaka, has a body weight of 3 – 7 kg making them medium sized lemurs, large enough to adopt a vertical posture in trees. They appear to have evolved a locomotor specialism for leaping from tree to tree using their powerful hind limbs. Sifakas are also notable for their mode of locomotion on the ground, using bipedal leaping, throwing their arms above their heads for balance.

Ateles – spider monkey

As with the lemurs in Madagascar, a large group of Primates have evolved via an adaptive radiation in South America – the New World Monkeys (*Platyrrhini.*) One of the five families of New World Monkeys is the *Atelidae.* They contain some of the largest species of Primates living in South America.

The spider monkey (*Ateles geoffroyi*) is well known for its characteristic prehensile tail, which it can use to hold onto and swing from branches in trees. They are almost totally arboreal and are very adept climbers and brachiators, but are known to adopt a rather human-like form of bipedalism when on the ground. With their long tails held erect, they walk upright with bent hips and knees.

Hylobates – lesser apes, e.g. gibbon

Even larger, and more adept in trees, than spider monkeys are a family of tailless primates, called *Hylobates* or the lesser apes. They inhabit south East Asia and much of the Indonesian archipelago. They are certainly the most adept brachiators of all the primates.

Like the spider monkey, they rarely come down to the ground, but when they do they adopt a similarly bipedal posture and mode of locomotion. Their propensity to bipedal locomotion led some early anthropologists to suggest that human bipedalism evolved from such forms.

Great apes

The three major genera of great ape, *Pongo* (orang utan), *Gorilla* and *Pan* (chimpanzees and bonobos) are all relatively large compared to *Hylobates* and are consequently less adept at brachiation although *Pongo* spends much of its time moving in trees suspended below branches. Due to their large size, they have a propensity to upright posture when in trees, as their size precludes them from the smaller (horizontal) branches. Upright climbing is a major component in their locomotor repertoire and, according to Hunt (1994) postural feeding in trees is also strongly correlated with their occasional bipedalism.

On land, great apes are most likely to move quadrupedally. *Pongo* (orang utans) tend to move quadramously (on four hands), whilst chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and gorillas exhibit a peculiar form of quadrupedal locomotion called knuckle-walking. They have evolved various anatomical traits adaptive for this mode of locomotion, including thick knuckle pads analogous to the soles on our feet and bony protuberances which support the body weight without requiring muscular effort, in an analogous way to the human knee.

Apes have been observed moving bipedally whilst carrying things, although they can also do so tripodally (using three limbs), hold objects in their mouths (or in the case of infants) on their backs, whilst moving quadrupedally.

Another scenario where great apes are sometimes bipedal is during threat displays. In particular, gorillas are well known for their exhibitions of chest-beating. This has led some anthropologists to postulate that this factor may have been important on the evolution of human bipedalism. Finally, it should be noted that although the great apes are rarely seen moving through water, when observed doing so in depths around their waists, they appear almost obligated to move bipedally. (See section 7.2.2 for more on this.)

1.3.2 The uniqueness of hominin bipedalism

Even a perfunctory survey of forms of bipedal locomotion in other animals quickly leads to the conclusion that the human form is quite unique (after Skoyles 2006).

1. Humans engage in a variety of upright forms of locomotion (e.g. walking, running, sprinting, skipping, and dancing).
2. Human are obligate bipeds. Apart from a brief period in infancy, they do not normally engage in any form of quadrupedalism.
3. Humans walk with extended knees and hips in an upright posture with a vertical spine, arched in the lumbar region. Many other obligate forms have a very different body orientation, for example with horizontal or obliquely angled spines.
4. Humans use their upper limbs almost exclusively for functions not related to locomotion such as carrying, manipulation, throwing, and gesturing. This is in contrast to their lower limbs which are adapted to plantigrade walking.

The thesis will now turn to the subject of explaining this unusual form of locomotion in an evolutionary context, starting with a brief summary of the forthcoming chapters.

1.4. Thesis chapter overview

Chapter 2: Models of Hominin Bipedal Origins This chapter provides a review of 42 published ideas about the origins of hominin bipedalism. Following from Rose's (1991) classification, the models are grouped into nine categories according to the major mode of selection postulated: Forelimb pre-emption (carrying); social behaviour; feeding; habitat compulsion; locomotor efficiency; thermoregulation; dietary factors; random genetic drift and a combination of factors.

Chapter 3: A New Evaluative Framework – Chapter 3 provides an evaluative framework for comparing and assessing different models of hominin bipedalism. This takes the form of a kind of marking rubric, in the same way student essays and other pieces of academic work have been assessed for decades. 14 criteria are described which, it is argued, would be expected to be found in an ideal model. Using this framework, wading hypotheses are found to be relatively strong compared to others, especially considering their relative lack of popularity in university level texts. An on-line tool is provided allowing the reader to explore the reasoning behind the author's assessment and/or to substitute their own evaluations.

Chapter 4: History of the Wading Hypothesis – This chapter sets out to answer the question: If the evaluative framework found wading hypotheses relatively strong, why are they so unpopular in university level texts? The answer, it is suggested, lies in the idea's history and, in particular, its unfortunate association with the so-called "aquatic ape" hypothesis. The history of this idea is described along with the reaction to it from scientists, as can be deduced from the literature. The chapter finishes by summarising the idea's strengths and weaknesses. The weaknesses are then used to form the basis of the rest of the thesis which report a few new empirical studies which have set out to test some of the predictions made of the hypothesis.

Chapter 5: The Cost of 'Non-optimal' Human Gait in Water – One testable prediction of the wading hypothesis assumes that the gait of the earliest bipedal hominids would not be as energy-efficient as that of modern humans, and that such inefficiencies would be "buffered" whilst wading in water. This chapter, re-written from a paper published by the author in the journal Homo in 2009, sets out to answer one question relating to this: Under what scenarios could hominins have realistically walked with a BHBK gait? It describes a series of wading experiments, following Carey & Crompton's (2004) JHE paper showing that a BHBK was approximately 55% more costly than a fully upright gait in human subjects on a treadmill. The study confirmed their findings but added that the cost differential was significantly reduced in waist deep water and completely eliminated in chest deep water. It proposes that wading offers the perfect scenario for early (non-optimal terrestrial) hominid bipedalism.

Chapter 6: 3D Geometric Morphometric Study of the Hominoid Hip – A substantial 3D geometric morphometric study of the hominoid hip is described. This study, following on from Oxnard and colleagues' pioneering work in the 1970s, compares the pelvic and femoral skeletal anatomy of extant apes with key fossil hominins. It uses some novel techniques including semi-landmark traces of various linear shapes, particularly of the pelvis.

The *Australopithecus* pelvis is remarkably platypelloid, even compared to the human form which is itself more platypelloid than extant apes (Tague and Lovejoy 1986.) This chapter offers evidence consistent with a wading component explanation for this peculiarity. An analysis of the relative load arms of the different hip muscle groups showed that the australopithecine hip conferred some biomechanical advantage for abduction and adduction and rotation of the thigh, compared to extension and flexion, as might be expected if wading was a significant component of their locomotor repertoire.

Chapter 7: Waterside Speculations, Hypotheses and Potential Research This chapter acts as a summary and discussion of the whole thesis and ends by providing a set of testable predictions which could form the basis of some post-graduate research programs in the future. It puts the wading hypotheses in the context of waterside hypotheses of human evolution generally. A critical assessment of the mislabelled "aquatic ape hypothesis" is summarised and a waterside model of human evolution is offered which draws upon the strengths and answers criticisms of both the "more aquatic" ideas and mainstream "savannah-based" ones. This hybridization of seemingly incompatible ideas is done simply by scaling back the degree of selection for wading, swimming and diving being proposed. The "River Apes… Coastal People" model of human evolution is presented as the product of this thesis, including the best aspects of all the ideas evaluated here.

1.5. Published work

A significant degree of this thesis has been previously published in the scientific literature. Chapters 2 – 4 are summarised in a chapter in an eBook (Kuliukas 2011a) and also in a paper (Kuliukas 2013). One of the critiques of the wading hypothesis (Langdon 1994) in chapter 4 is the subject of a whole chapter in the same book (Kuliukas 2011b) and a full review of various so-called "aquatic ape" ideas was published in the same volume (Kuliukas & Morgan 2001). The parts of chapter 4 that discuss evidence pertaining to the wading hypothesis formed part of my master's thesis at University College London (Kuliukas 2001) and was published in Nutrition & Health (Kuliukas 2002). Chapter 5 is a re-write of a paper published in Homo (Kuliukas 2009) and chapter 7 uses sections from that paper. Chapter 6 has not been published before.

List of published work:

Kuliukas, A.V. 2001. Bipedal Wading in Hominoidea past and present. Master's Thesis, UCL.

Kuliukas, A.V. 2002. Wading for Food: The Driving Force of the Evolution of Bipedalism? *Nutrition and Health* 16:267-289.

Kuliukas, A.V., Milne, N., Fournier, P. A. 2009. The relative cost of bent-hip bent-knee walking is reduced in water. *Homo* 60:479-488.

Kuliukas, A.V. 2011a. A Wading Component in the Origin of Hominin Bipedalism. In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2011b. Langdon’s Critique of the Aquatic Ape Hypothesis: It’s Final Refutation, or Just another Misunderstanding? In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V., Morgan, E. 2011. Aquatic scenarios in the thinking on human evolution: What are they and how do they compare? In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2013. Wading Hypotheses of the Origin of Human Bipedalism. Human Evolution 28 (3-4):213-236.

CHAPTER TWO

MODELS OF HOMININ BIPEDAL ORIGINS

2. MODELS OF HOMININ BIPEDAL ORIGINS

Reproduced and expanded upon from previously published papers…

Kuliukas, A.V. 2011a. A Wading Component in the Origin of Hominin Bipedalism. In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2013. Wading Hypotheses of the Origin of Human Bipedalism. Human Evolution 28 (3-4): 213-236.

Abstract

42 distinct published ideas on the origin of human bipedalism are described. A number of classifications are outlined before opting for a schema based on proposed mode of selection, modified from Rose (1991). The 42 models are grouped into 9 broad categories by this classification as they are discussed in some detail.

2.1. The bipedalism model "muddle"

Ever since Darwin's (1859, 1871) theory of evolution became generally accepted among anthropologists, an explanation for the phenomenon of human bipedality has been sought which is consistent with the idea of evolution through natural selection from ape-like origins. However, despite a huge intellectual effort, spanning almost 150 years, there is still no consensus among scientists as to which factors drove some apes to begin moving bipedally whilst leaving others, generally, not doing so, or, alternatively, what drove some apes to stop moving bipedally, whilst leaving others to continue doing so. Consequently, students of anthropology are still taught a very uncertain picture about why, today, only one primate species, *Homo sapiens,* is an obligate biped.

An estimate of the size of the literature on the subject can be obtained using a scientific search engine. "Web of Science" returned 409 papers in early-2016 to the search for "evolution human bipedalism" (and over 1,000 for "evolution human walking", although these are dwarfed by other searches, such as over 6,000 for "human language evolution"). Having no consensus is not necessarily a poor, or even an undesirable, situation, but it does indicate that, so far, insufficient unequivocal evidence has been provided in favour of any particular idea on the matter to make it the generally accepted one.

The importance of understanding bipedal origins, the most fundamental and probably earliest, hominin trait has not been underestimated over the years, and perhaps never less so than today. Darwin's much quoted observation is as good a place to start a thesis on bipedal origins as any: "Man could not have attained his present dominant position in the world without the use of his hands, which are so admirably adapted to the act of obedience to his will" Darwin (1871 p 52). It should be remembered, however, that Darwin gave primacy, in terms of importance, to the evolution of intellect: "Although the intellectual powers and social habits of man are of paramount importance to him, we must not underrate the importance of his bodily structure…" Darwin (1871 p 50).

Most of the hundreds of published items on bipedal origins in the scientific literature begin with a summary of such quotes (see, for example, Hewes 1961 p 687, Richmond et al. 2001 p 71) and I shall do so here too, but only from some works which are relatively new, and only in order to illustrate that the stated importance of this problem has not diminished.

Some of the most recent books published on the subject follow the same 'traditional' theme from their outset. In each, their authors have suggested that bipedalism is a key factor (or indeed, *the* key factor) to understand in understanding human evolution. Here are three recent examples:

The American Anthropologist Craig Stanford, in his book "Upright", makes the point quite clear: "The reason that upright posture and walking arose is the most fundamental question in human evolution." Stanford (2003 p xviii), and again "How we became bipedal is a chronicle of how we became human" Stanford (2003 p xx).

David Begun, considering the locomotor activity that was immediately precursive to hominin bipedalism, began his paper like this: "More than any other aspect of the morphology of fossil humans (hominins, or living humans and all fossil taxa more closely related to us than any other species), the postcranial characters that are associated with bipedalism represent the defining features of our lineage" (Begun, 2004 p 9).

The Swedish emeritus professor of archaeology, Bo Gräslund wrote, on the subject of how to define when, exactly, our ancestors became *people,* "I personally believe that anatomical features are a better way to trace an early 'humanity' that intellectual, social, cultural and moral criteria, which are all hard to define, perceive and date. A bipedal gait with all its implications seems more than enough to characterise the early humans." (Gräslund 2005 p 5).

It is clearly a very important aspect of human evolution to grasp, so how have we progressed in the 150 years since Darwin, in trying to understand it?

Rose (1991) summed up the status quo in the early 1990s in a nutshell: "The evolution of hominid bipedalism is recognised as a crucial element in the hominization process," he wrote. "However, despite a voluminous literature, our ignorance concerning bipedalization is almost complete." Rose (1991 p 38) quoting Day (1986), he continued "we really have no clear idea of what form of locomotion, in what creature, preceded or was immediately pre-adaptive for, upright posture and bipedal gait". This situation appears not to have improved in the decade that followed, indeed the problem has been portrayed as, if anything, even more uncertain now than before.

A special edition of the Journal of Anatomy in 2004, dedicated to the problem 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 record, it is important to ask the question of whether the evolution of bipedalism was a more complex affair than has previously been suggested" Harcourt-Smith & Aiello (2004 p 413).

Up until recently, most (but see Kleindeinst 1975 for a contrary view) published opinion assumed that the last common ancestor of humans and African great apes were mainly quadrupedal and that the adoption of bipedal locomotion was a phenomenon specifically of human ancestors. However, in the last few years this view appears to be shifting. Filler (2007) argued that bipedalism probably evolved, through a developmental mutation of the spinal column, much earlier – perhaps including *Morotopithecus*. Crompton et al. (2009) reported evidence supporting the view that a hand assisted, thin-branched arboreal kind of bipedalism, rather like that practiced by orang-utans, was the ancestral form and Lovejoy et al. (2009)'s report of the *Ardipithecus ramidus* hip promoted a similar view that the last common ancestor of all great apes probably was already somewhat bipedal in wooded contexts.

However interesting and important the *timing* and *phylogeny* of hominid bipedalism (and whether it happened just once or several times) may be, it does not help explain its behavioural *origins*. Even if the last common ancestor of all the great apes were already somewhat bipedal, it only raises at least two new questions: Firstly, because it only pushes the origin of bipedalism back in time, it poses: Why did *their* ancestors (of the common stock of the great apes themselves) start moving bipedally? And, secondly: Why did the ancestors of the great apes lose their bipedality, whilst our ancestors did not? If hominid bipedalism evolved more than once, it only multiplies these questions: So under which Darwinian scenarios of natural selection is this process most likely to have happened? And under which scenarios is some type of existing bipedalism likely to be lost?

That said, it is true that most of the published theoretical models that have been proposed to answer questions about bipedal origins since Darwin assume that bipedalism only evolved in our own lineage, and there are many of them. Anyone interested in the subject seems to have their own favourite. As Kingdon put it: “Speculations on the origins of bipedalism are often fascinating exhibitions of ingenuity – expressing above all, that this is a theatre for intellectual daring” Kingdon (2003 p 16). This claim was, incidentally, backed by two citations: one to Owen Lovejoy's ‘Provisioning Hypothesis (Lovejoy 1981) and the other to the Hardy/Morgan ‘Aquatic Ape Hypothesis’ (Hardy 1960). Several reviews of these models have been published over the years, including most recently, Kingdon's own (2003 p 16-17; 151-193, but see also Tuttle 1981; Rose 1991; Richmond et al. 2001).

Reviewers of bipedalism models have often attempted to classify them according to some criteria or other and the next section reviews a few of the classifications of bipedalism models that have been favoured in the literature over the years.

For a convenient, on-line summary of these models please go to www.tinyurl.com/BipedalModels.

2.2. Classification of bipedalism models

In his paper on ‘The Process of Bipedalization in Hominids’, Rose (1991) offered three types of classification: Firstly, by known types, secondly, according to the proposed agent of selection, and thirdly according to the mode of locomotion being proposed for the immediate precursor to the hominids. A fourth classification, by the author's approach, will be offered here too.

Rose set about his review in a systematic way and proposed that although “the study of hominid bipedalism necessarily becomes speculative … such speculations are useful if they are based on a critical utilization of indirect evidence, formulated within a general context of large hominoid relationships, and if they generate predictions that are testable against yet-to-be-found direct evidence” Rose (199 p 38). This is a point we shall do well to remember throughout all the speculations that follow.

Classification 1: By known forms.

Rose's (1991) first classification of bipedalism was to group different known forms by gait, body orientation and hind limb flexion/tail use:

	Bipedalism			
	Alternating Bipedal Striding		Saltatory Leaping	
	Horizontal Body	Vertical Body	Horizontal Body	Vertical Body
Hind limbs Flexed	Many Birds	Penguins		
Hind limbs Extended	Some Dinosaurs	Some primates, e.g. *Homo sapiens*		
Tail Used			Kangaroo	Some primates e.g. Galago
Tail Not used			Some rodents	Some primates e.g. Indri

Table 1 Bipedalism Classification by Known Forms

This approach is helpful in that it reminds us that bipedalism is far from a unique form of locomotion in the animal world and places the human form of that locomotion in some sort of broader context.

Having done this, Rose suggested that there were two questions to ask whilst looking at the specific problem of hominid bipedalism:

1) What was the primary agent of selection for early hominid bipedalism? And

2) In the immediate precursor to hominid bipedalism what was the dominant form in the locomotor repertoire?

He then went on to summarise the models according to the answer to these questions.

Classification 2: By agent of selection.

In this classification, Rose sought to group models of bipedal origins by the proposed agency of selection. Three of his original categories contain numerous well-known models and are easily recognisable: carrying models, those involving social behaviour and those involving feeding. The fourth was a 'catch-all' called "other" which constituted other agencies of selection which Rose simply could not list under the other three.

Rose's Original Classification According to Agent of Selection			
Forelimb pre-emption (Carrying)	Social Behaviour	Feeding	Other
Infant carriage Food carriage Tool carriage Tool/weapon throwing	Threat display Aggression Evasion Vigilance Sexual Display Nuptial Gifts	Arboreal Gathering Terrestrial Gathering Aquatic Gathering Arboreal Predation Terrestrial Predation Terrestrial Scavenging	Walking on snow or mud Iodine deficiency Biomechanical inevitability Overly rich Calcium diet Combination of factors

Table 2 Bipedalism Models according to agent of selection (from Rose 1991)

Here, this classification is updated and extended with some new ideas that have been published in the last 20 years.

I have kept Rose's three main categories: Carrying, Social Behaviour and Feeding and replaced his "catch all" "Others" with six new ones… "Habitat Compulsion", "Efficiency of Locomotion", "Thermoregulation", "Dietary Factors", "Genetic Factors" and "Combination of

Factors.” This, revised classification will be used to structure the review of bipedalism models discussed here later.

Classification of Bipedal Origins Models (Modified from Rose 1991)

Category	Subcategory	Code[a]	Specific Idea	Original Proponent(s)
Forelimb pre-emption (Carrying)	Unspecified	1.1	General freeing of the hands	Darwin 1871 [6], Hooton 1945 [7]
	Food carriage	1.2.1	Carrying food back to gallery forest bases	Hewes 1961 [8]
		1.2.2	Carrying and scavenging	Isaac 1978 [9]
		1.2.3	Migration-carrying hypotheses	Sinclair et al. 1986 [10]
		1.2.4	Male provisioning	Lovejoy 1981 [11]
	Infant carriage	1.3	Female driven infant carrying	Etkin 1954 [12], Iwamoto 1985 [13], Tanner 1981 [14]
	Tool/weapon throwing	1.4	Weapon throwing	Fifer 1987 [15], Dunsworth et al. 2003 [16].
	Tool carriage	1.5.1	Tool carriage	Bartholomew and Birdsell 1953 [17], Washburn 1960 [18], Marzke 1986 [19]
		1.5.2	Weapon wielding	Dart 1959 [20], Kortland 1980 [21]
Social behaviour	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 behaviour (peering over the savannah)	Reynolds 1931 [26], Dart 1959 [20], Day 1977 [27], Ravey 1978 [28], Walter 2004 [29]
	Sexual display	2.4	Phallic display directed at females	Tanner 1981 [14]
	A new ‘fashion’	2.5	Copied gimmick idea	Dawkins 2004 [30]
Feeding	Terrestrial Gathering	3.1.1	Seed eating	Jolly 1970 [31]
		3.1.2	Terrestrial squat feeding on the forest floor	Kingdon 2003 [32]
		3.1.3	Other gathering	Du Brul 1962 [33], Wrangham 1980 [34], Rose 1985 [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], 1990 [47], 1997 [49]
		4.1.2	‘Aquarboreal’ model	Verhaegen et al. 2002 [50]

Classification of Bipedal Origins Models (Modified from Rose 1991)				
Category	Subcategory	Code^a	Specific Idea	Original Proponent(s)
		4.1.3	Amphibische Generalistentheorie	Niemitz 2000, 2002, 2004, 2006, 2007, 2010 [51]
		4.1.4	River apes	Kuliukas 2011 [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	Orang-utan-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	Khöler 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]
Genetic Factors (Mutation/Drift)	Mutation in a key gene involved in vertebral development	8.1	'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]

Table 3 Bipedalism Models, Classified by Mode of Selection (after Rose 1991)

Classification 3: By proposed precursor locomotor behaviour

Rose's discussion suggests that the hypothetical 'protohominid' that was the immediate precursor to hominin bipedalism probably adopted the typical primate pattern of having a locomotor repertoire which comprised several different types of movement (e.g. Climbing, quadrupedalism, brachiation and some bipedalism) and that in early hominid bipeds (e.g. *Australopithecus*) bipedalism would have begun to dominate as the major type of locomotion. This transition is postulated because, clearly, the human locomotor repertoire is almost completely dominated by the one single, bipedal, activity. (Rose 1991 p 39-41). This said, the third classification Rose offered was one based on the *primary* mode of locomotion that was proposed to act as an immediate precursor to the advent of hominid bipedalism.

Rose's original model classification according to suggested precursor to hominid bipedalism			
Habitat	Locomotion Type	Proposed Precursor	Proponents
Arboreal	Suspensory	Brachiating 'troglodytean'	Keith 1923; Gregory 1927; Cant 1986.
		'Hylobatean'	Morton 1926; Tuttle 1975.
		'Orangutanean'	Stern 1975; Fleagle 1976, Thorpe et al. (2007).
		Postural suspension	Hunt 1994.
	Other	Plantigrade quadrupedalism	Straus 1949; Straus 1963.
		Climbing 'troglodytean'	Prost 1980; Fleagle et al. 1981; Stern and Susman 1981; Ishida et al. 1984, 1985.
		Semibrachiation	Napier 1964.
		Tarsian Climbing	Wood Jones 1929.
Terrestrial	Quadrupedal	Chimp knuckle-walking	Washburn 1967; Washburn and McCown 1972; Lovejoy 1981.
		Gorilla knuckle-walking	Elliot Smith 1924.
		Plantigrade quadrupedalism	Delmas 1972; Hotton et al. 1984.
	Other	Sitting	Wrangham 1980.
		Shuffling	Jolly 1970.
		Squatting	Kingdon 2004
Aquatic		Wading/Swimming	Hardy 1960; Morgan 1982; Verhaegen 1987.

Table 4 Published Bipedalism Models, by Precursor (from Rose 1991).

The problem with this approach is that there is nothing at all in the fossil record that is unequivocal evidence of any taxa that preceded *Pan* and/or *Homo*. It could be argued that this same lack of evidence hinders the previous classification, that by adaptive benefit, just as much. However, at least with that classification other forms of evidence, such as the behaviour of extant apes, come to bare.

Classification 4: According to the author's approach

Several other authors (Isaac 1978 p 240) have also categorised proposed models of hominid bipedalism according to the approach of the author. Isaac put it this way…

> *"It has become fashionable for all kinds of research workers to present models intended to elucidate the process by which early hominids became differentiated. To mention but a few: Lancaster (1967) wrote from the stance of primate studies; Fox (1967) tackled the questions from the viewpoint of a social anthropologist; Reynolds (1966 and 1968) used chimpanzees studies as a basis; and Jolly (1970) offered a very specific seed-eating model inspired by patterns in comparative anatomy and by his interpretation of the development of masticatory mechanism. More or less comprehensive models have been put forward by human biologists such as Washburn (1960, 1965, 1968b); Campbell (1966) and Pilbeam (1972)." Isaac (1978 p 240-241)*

To this list, a few more approaches might be added. Darwin's original ground-breaking approach might be classified as one of "anthropocentric logic", in that it was based on a largely Victorian viewpoint of man's evolving to eminence in the animal kingdom through his intellect and industry. In the post-war years other approaches might be seen in a similar, but less positive light: Some very much based on the rather dark image that man was evolved from ‘Killer Apes’ (Ardrey 1961). Others were more positive, e.g. Lovejoy’s (1981) model, which was based on more altruistic motives (at least those involving pair bonding). Several authors (Vrba 1985) have looked at the problem from the point of view of the paleoecological record and proposed ways of life that early hominids might have been able to survive in the early Pliocene.

Another approach has been that of looking at the question from a human biological perspective. It asks: What does our anatomy ‘speak of’ in terms of locomotor adaptation? The answer, according to some (Rodman & McHenry 1980), is efficient long distance locomotion, or endurance running (Lieberman 2007). Others (Wheeler 1991), suggest that thermoregulation, through sweat cooling, appears to have been a major driver of our anatomy.

One of the most potentially promising approaches is that of Kevin Hunt (1994), by studying primate behaviour. Based on the premise that “contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism” (Hunt 1994 p 183) wild chimpanzees were studied to determine which behavioural contexts were most likely to induce facultative bipedalism.

Finally, one of the latest novel approaches to this problem has been that of computer modelling. Crompton et al. (1998) are others who have recently used computer modelling to estimate the likely modes of locomotion of the earliest bipeds and used this as evidence to support other models. Of course, on that point, it should be remembered that most authors have used more than one approach in putting forward their ideas on the subject.

Classification according to Approaches of the Author			
Extrapolating Backwards from Today		Analysing Evidence from the Past	
Anthopocentric	Primatological	Palaeoecological	Fossil Anatomical
Darwinian – industrial Dart/Ardrey – violence Washburn Pilbeam, Campbell Lovejoy – Provisioning Rodman & McHenry Wheeler	Hunt – Contexts of bipedalism Jolly – Baboons Tuttle – Apes Reynolds Fox Lancaster Thorpe et al	Isaacs Vrba	Crompton et al

Table 5 Classification according to Author's Approach

2.3. Review of published models

What follows is a comprehensive review of all known published bipedal origins models categorised, for convenience, according to an updated version of Rose's (1991) classification, according to the proposed factors of selection. Each model is summarised and perceived strengths and weaknesses are documented.

For the sake of brevity, models are grouped under broad headings and subheadings and treated accordingly. Aspects of individual models are only described where they are significantly different from others.

2.3.1 Upper limb pre-emption (carrying) models

General notion

Original Proponent(s): Darwin 1871 p 50-54

Mnemonic: "Freeing of the hands"

Perhaps the first adaptationist idea published on bipedal origins was to "free the hands" (Darwin 1871 p 52), when it was widely believed that the large brain (and also early aspects of human culture) preceded bipedality. Fossil evidence of small-brained bipedal hominids, which began to emerge early in the 20th century, (Dart 1925) corrected this view.

When fore limb function of primates is compared to that of most quadrupedal animals, their utility for carrying and manipulation is marked. In humans this trend has continued, through our commitment to bipedal posture and locomotion, to the point that our hands now appear to have been 'freed' to carry things.

This has some evolutionary advantages that would have clearly benefited hominin ancestors. Hands 'freed' of the burden of locomotion (carrying body weight, as in quadrupedal terrestrial animals, or climbing as in arboreal) allowed "their delicate use" (Darwin 1971 p 52) to be put to more intellectual utility.

Two arms are able to carry greater loads whilst moving bipedally than would be the case whilst moving quadrupedally or, as is often seen in the case of African apes, tripodally (Hewes 1961). The better use of weapons, such as stones, spears and clubs, which was conferred onto bipeds, would have made them better able to defend themselves (Dart 1959).

One compelling factor in carrying models is that they provide a rather elegant feedback loop: Increased carrying would favour greater bipedalism which, in turn, would allow still more carrying. However, feedback models have also been criticised in their difficulty to discriminate between cause and effect as they promote scenarios that both result *in* and result *from* more bipedalism **(**Jolly 1970 p 5).

A few additional problems with carrying models have been articulated:

Firstly, compared to other primates, it has been argued (Gräslund 2005 p 66) that it is not so much that bipedalism has 'freed' the hands, as much as it has 'enslaved the feet'. Chimpanzees, for example, are well known to manipulate objects such as food with all four limbs, whilst sitting down, and are able to carry things with their hind limbs, whilst climbing trees.

Secondly, extant apes have rarely been observed using their forearms for carrying items whilst moving bipedally. In Hunt's (1994 p 185) study, carrying (specifically of infants) amounted to only 1% of the already relatively rare (around 3% of time) bipedal behaviour. Apes are as often observed carrying things with their teeth, their hind limbs or tripodally (Hewes 1961).

Thirdly, more recently, Watson et al. (2008) published findings showing that asymmetric carrying significantly reduced locomotor efficiency and therefore, unless the behaviour of carrying infants was itself an adaptive response to strong selection pressure, it was unlikely to have been a precursor to the evolution of hominid bipedalism.

The idea of the benefit of freeing the hands has persisted, however, and several more specific models have been proposed, varying in complexity, the main sex involved and the actual use to which the hands were employed. Some of these will now be described. It should be noted that most of these specific models are mutually compatible and often overlap considerably.

Variations on the theme

Four subcategories of carrying models are briefly reviewed in this section: Food carriage, Tool Carriage, Weapon Wielding/Throwing and Infant Carriage (Rose 1991).

Food carriage

Original Proponent(s): Hewes 1961; Isaac 1978; Lovejoy 1981; Sinclair et al. 1986.

This broad idea proposes that hominin ancestors underwent a phase in their evolution when it became more critical to be able to carry food from one location to another (and usually over further distances) than it did for the ancestors of the great apes. The postulated reason offered for the increased distance is usually environmental change, specifically an opening up of the wooded habitat into more open savannah, where early hominids lived. Gallery forests have been suggested as potential habitats for this early need for carrying (Hewes 1961, Isaac 1978) as have open plains, literally whilst following herds of ungulate migrating species (Sinclair et al. 1986).

Various types of food have been proposed, although meat is perhaps the most popular candidate (Hewes 1961, Isaac 1978, Sinclair et al. 1986) usually by means of scavenging rather than hunting.

The evidence cited in favour of these models includes extant primate behaviour (Hewes 1964) and from evidence of cut-marks and stone tools in the fossil record (Isaac 1978).

Lovejoy's evidence is based on comparisons with other orders such as canids and aves (Lovejoy 1981 p 345) as well as fossil evidence which he takes as being indicative of monogamy amongst australopithecines.

Carrying food as a model for early adopters of bipedalism has a problem, however: It makes already terrestrially vulnerable hominids even more vulnerable to attack from predators.

Specific models in this category will now be discussed in more detail.

Food transport and the origin of hominid bipedalism.

One of the first papers written specifically about the idea that human bipedality had evolved largely as an adaptation to carrying food was written by Gordon Hewes in the early 1960s. His thesis is perhaps best articulated by this paragraph:

> *Stated simply, our problem is this: why did certain quadrupedal Primates already capable like other Primates of sporadic bipedalism, become habitual*

> *bipeds? … Our suggested answer, to be elaborated below, is: because the effective use of a new food resource required its transport over considerable distances, and only by bipedal locomotion, by freeing the arms and hands for carrying, could achieve maximal transport efficiency. Obviously we are dealing with a time before the invention of pack-straps and side-saddles – cultural solutions to animal transport which permit even hoofed quadrupeds to carry loads for long distances. Hewes (1961 p 689)*

Hewes reviews the early (pre 1960) literature about bipedal origin hypotheses but generally favours a model which specifically postulates carrying bulk food items (rather than infants, tools or weapons) 'long distances' as the only factor which could have driven this change in locomotion. There is no doubt about which kind of food he is referring to, meat (p697), but then offers some debate about how this meat might have been procured. Hewes appears to be quite set against the notion that early bipeds were hunters and argues against weapon carrying models, thus favouring a distinct scavenging model (p698).

Later in the paper when postulating a habitat where this could have feasibly occurred, he suggests the gallery forest. He writes "Changes in habitat are amongst the prime movers of biological evolution. Contemporary paleoanthropological opinion places the transition to hominid status in tropical park-savannah lands, where narrow forest environments extend along river courses, flanked by grassy plains (Washburn and Howell 1960 p 37)" Hewes (1961 p 700).

In a second paper, in 1964, Hewes carried the idea a little further and backed it up with some new empirical evidence from four independent reports of wild and semi-feral bipedal food carrying apes and monkeys from the Congo, Tanganyika, Japan and a Puerto Rican monkey colony. On the basis of these findings, Hewes backed away, slightly, from the notion that it was meat-eating that was necessarily the object of carriage and, interestingly in the context of this work, appeared quite compelled by the idea that moving through water might have also been a factor. Hewes wrote:

"Hardy's hypothesis of an "aquatic past" for man was doubtless extreme, but some of his notions seem less improbable in the light of Kawai's remarkable report [of Japanese macaques adopting bipedalism partly for carrying objects and partly for moving in the shallows]. In many parts of southeast Asia, macaques have taken up a beachcombing existence: I am not aware of any reports of bipedal locomotion to an unusual degree amongst these littoral primates, but perhaps previous observers did not pay sufficient attention to the matter." Hewes (1964 p 418).

Carcass carrying back to gallery forest bases.

Glyn Isaac (1978) published a paper suggesting that bipedalism evolved largely through the scavenging of carcasses on the savannah. The idea was that it became necessary to carry relatively large pieces of meat back to the home base which required the use of forearms to carry the food and therefore precluded them for use in locomotion, thus driving the adoption of bipedalism.

His model goes further than merely explaining the adoption of bipedalism…

"I suggest therefore that one conveniently divide the continuum of human evolution into two phases. Probably the first involved shifts in the basic systems of locomotion and subsistence, plus two new ingredients - tools and food sharing. This led to a pattern of adaptation which in hindsight we see as proto-human, but which is probably better termed 'early hominid', since it was probably a nonhuman system that was effective in its own right." Isaac (1978 p 244).

And…

"It is widely believed that the process involved extensive feedback amongst the several subsystems, thus: hunting facilitated food-sharing since meat was more readily carried than any other common food stuff; missiles, weapons and tools facilitated the killing and butchering of larger and larger animals; bipedalism facilitated weapon use, the carrying of food for sharing, and long range mobility; gathered vegetable foods remained as a staple and as an insurance policy against failure in the hunt, so that division of labour (and pair bonding?) gave stability to the system; bags and baskets facilitated food-sharing and division of labour etc." Isaac (1978 p 245).

Isaacs makes the point that he did not see this process as necessarily driven by any particular change in climate (Isaac 1978 p 245) although he makes extensive references to the savannah and gallery forest habitats which would have protruded into them. For example, he writes “it can thus be argued that savannah *sensu lato* constituted a vacant ecological niche for an animal of the hominoid grade, capable of basing its subsistence on a combination of hunting and foraging.” (p240) and “…hominids, whilst colonizing the savannah, may have preferred to keep their home bases in strips of woodland that extended out into more open country” (p239.)

Some paleontological evidence is offered in favour of this model:

“Most of the early sites at Olduwai and the two excavated sites at the Lower Member of the Koobi Fora Formation consist of coincident patches of stone artefacts and scatters of broken bones. The conclusion seems inescapable that the same hominids who made the artefacts concentrated the bone. It also seems virtually certain that the bone was the residue discarded after the consumption of meat.” Isaac (1978 p 235). However this can be criticised as being too late to be significant. The earliest evidence of stone tool assemblages is dated much more recently than the earliest fossil evidence for bipedalism (AL 288-1, Johanson 1974) and this disparity has become even greater since Isaac’s paper was published.

Migration-carrying hypothesis

In a short letter to Nature, Sinclair et al. (1986 p 307) suggested a new and rather ingenious-sounding idea on bipedal origins: That specifically long-distance on-foot scavenging, alongside existing herds of ungulate migrating species, was the key driver.

The idea is rather theoretical, being based on the assumption that there was an "unfulfilled niche" for any mammalian scavenger that would be able to combine long-distance locomotor efficiency with carrying. Like most carrying models, it is open to criticisms of being teleological and also increases the risk of predation.

They suggest several arguments in favour of this hypothesis.

From an ecological point of view they suggest that this was an “unfulfilled niche for a mammalian scavenger” and that any species that could combine long-distant efficiency with the ability to carry their young along with them would be at a distinct selective advantage. This niche would offer an abundant and constant supply of carcasses (“at least 1 carcass per 20 km 2 per day” p370) much more than non-migratory systems.

They support this hypothesis by citing two species of vulture, which follow the migrating ungulates, which are considerably more numerous than sedentary species. They suggest that bipedalism was "a necessary adaptation" (p307) to exploit this food supply because it relied upon carrying of infants and efficient long distant walking. Mammal predators and scavengers, they suggest, do not follow migrations "because their young are slow growing and cannot travel with the adults." (p307) This hypothesis, it is argued, helps to explain the early adoption of stone tools by early *Homo*, as carcasses would require fairly rapid butchering and "avoid competition with other stronger mammal predators" (p308.)

However their paper appears to have a number of weaknesses:
Firstly, there is a distinct paucity in consideration of other ideas. They suggest (p307) that "the current explanation" was Isaac's (1978). But it is unlikely that, since Darwin, there has never been one explanation that has won primacy, and certainly not in 1986. Isaac's chapter in 'Early Hominids of Africa' (1978) was not the only view on bipedal origins published in that volume. Later, they suggest that "The Alternative hypothesis" is that "bipedal hominids were plant gatherers in a savannah home range" (p308). The use of this term is unfortunate, as they are not proposing their hypothesis against any null, but suggesting it is the only real alternative to their own. Their characterisation of Isaac's idea as being about 'plant carriers' is also unfortunate, because his (much more thorough) paper made it clear that he also saw early hominids as scavengers of carcasses. Much of the evidence he gave in support of this was the use of stone tools and that even very small flakes chipped off stones could be very useful in dismembering carcasses (Isaac 1978 p 234)
Models relying on early meat-eating as drivers appear to be contradicted by evidence which suggests that the earliest bipeds were not actually meat eaters (see, for example Andrews 1981) and certainly not hunters. It is difficult to imagine how butchering a carcass and carrying it alongside the migrating herd would "avoid" competition with big savannah predators, as they suggest (p307). The smell of exposed meat would no doubt attract a great deal of attention. Indeed their model has nothing to say at all about how the migrating hominids would avoid becoming prey themselves. Compared to the ungulates next to them, they'd be relatively slow and vulnerable, especially the mothers with infants under arm, and whose presence forms a major part of this hypothesis. Furthermore, the authors' claim that infant carrying would be the key differential to encourage bipedalism appears tenuous. Carrying infants is easier for a quadrupedal primate, as the infant can simply climb on the mother's back. Adopting bipedalism for this reason would seem to be counter-intuitive. Although humans are undoubtedly efficient long-distant walkers today – due mainly to a rather specialised anatomy – it is not clear if the earliest bipeds could have been much more efficient from the beginning – before those specialised traits had evolved.

Male provisioning

A more habitat-neutral carrying model is Lovejoy's (1981, 1988, 1993) "provisioning hypothesis" which asserts that in order for female hominids to maximise their reproductive potential, one of their few options was to enlist a resource that few other primates use, the utilisation of a male food provider.

Unlike Hewes and Isaacs, Lovejoy suggests that the food would comprise eggs, small amphibians and reptiles, nuts and fatty fruits as possible food sources rather than animal carcasses (pers. comm. 2003).

Lovejoy's thesis is based upon the observation that there seems to be a trend in human evolution towards ever greater 'k selection' (i.e. socio-sexual systems which maximise reproductive success by greater parental investment in the young and longer maturation times, inter-birth intervals, pregnancies and life expectancies) away from the typical primate pattern which is more 'r selected' (i.e. systems geared towards maximising reproductive success by reducing the parental investment, maturation times, inter-birth intervals and lengths of pregnancies.) Furthermore, he postulates that as relatively slow reproducing apes were being out-competed by faster reproducing old world monkeys in the Pliocene, that both inter-birth interval reduction and increased survivorship must have been achieved in successful hominid clades (p344).

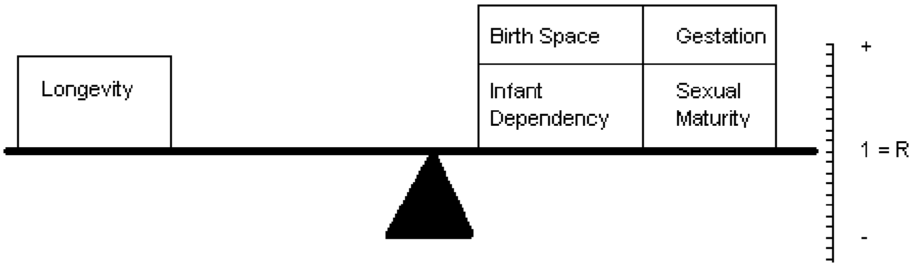

Figure 1 Life History Balance (After Lovejoy 1981 p 343)

His argument about bipedalism is that by gathering and collecting food items for their female partners, male hominids would be better able to improve their kin selection. Unlike Hewes and Isaacs, Lovejoy suggests that the food would comprise eggs, small amphibians and reptiles, nuts and fatty fruits as possible food sources rather than animal carcasses (pers. Comm. 2003.) Lovejoy asserts that in order for female hominids to maximise their reproductive potential, one option was to enlist a resource that few other primates use, but that is commonly used in other orders (e.g. canids and aves p345) – that is the utilisation of a male food provider. Following on from this is the logic that bipedal locomotion would maximise the transportation of such food items. The model assumes that sexual pairing was already prevalent at this time and Lovejoy is quite explicit, although speculative, in proposing that early bipedal hominids such as *Australopithecus afarensis* were basically monogamous (p345).

However, the reliance of the provisioning model on monogamy is problematic as there is little evidence in the fossil record for it. Indeed the consensus view of *A. afarensis* has been that it exhibited a fairly large degree of sexual dimorphism indicating, if anything, a very different sexual social system (see, e.g. McHenry 1991). Analysis of sex ratio evidence suggests that australopithecine male-female numbers were unequal, another counter indicator of monogamy (Reno et al. 2003). Carrying food as a model for early adopters of bipedalism has another general problem, however: It makes already terrestrially vulnerable hominids even more vulnerable to attack from predators. If walking alone through open woodland is dangerous, how much more dangerous would it be to do so with both arms loaded with food items?

The strength of the model is that it is quite elegant in explaining several strands of human evolution at the same time, namely bipedality, increased monogamy and altriciality. It also satisfyingly fits the evidence that an early radiation of apes, apparent in the Miocene, was superseded by another radiation of old world monkeys.

Critique of Lovejoy's "k selection" principle.

Lovejoy does make a sophisticated case for selection on the basis of the resulting increased survivability from this shift in locomotion. In addition to the increased food procurement proposed by the division of labour resulting from monogamous pair bonding, he suggests that better mothering skills, e.g. resulting in fewer infant deaths from falling out of trees (p 343), as a consequence of safer carrying, would result in better reproductive success compared to old world monkeys, which were more 'r selected'. Substituting known life history data from old world monkeys, apes and humans into the formula below, Lovejoy (1981 p 344) was able to demonstrate that with annual survivability figures of 98% or more, the typically human 'k' selection becomes advantageous over the typically 'r selected' old world monkey pattern in terms of reproductive success.

$$RV = \frac{1}{\beta}\left[l(s) \int_{s}^{MLP} l(x)dx \right]$$

Where…

RV = reproductive value,

β = inter-birth interval

MLP = maximum life potential

s = age at sexual maturity

l(x) = survivorship at age x

l(s) = survivorship at sexual maturity

Annual Survivability	OWM	Apes	Humans
	MLP = 20	MLP = 40	MLP = 60
	SM = 4	SM = 10	SM = 15
	IBI = 2	IBI = 3	IBI = 2.5
0.90	17	4	2
0.92	23	7	4
0.94	31	13	9
0.96	42	25	24
0.98	58	50	64

Figure 2 Survivability Figures (After Lovejoy 1981 p 343)

However, Lovejoy appears to overlook a couple of key factors which would alter the results of this table significantly.

- The human menopause was not considered. Lovejoy's equation assumed that females potentially could continue to give birth at the same inter-birth interval until the age of 60. If realistic figures for menopause were used instead, survivability levels even closer to 1.0 would be needed to give *Homo* the same advantage.
- The mothering ability was not offered as a factor in the 1981 paper. Lovejoy reports that even in apes the success of raising a first infant is much worse than later infants. The presence of elder females around, especially grandmothers who have passed into the menopause, would be likely to give humans an edge in this area over other species. Perhaps this was the main point Lovejoy should have been making.

Generally, even accepting the basic argument that a more 'k selected' species would be able to out-compete the old world monkeys, it is not clear that the provisioning model provides that selection, either through improved mothering (infant carrying) or through paternal provisioning. In terms of the survivability Lovejoy's thesis relies upon, it seems unlikely that bipedal carrying of small infants is any safer, for a terrestrial primate, than quadrupedal clinging.

Infant carriage

Original Proponent: Tanner (1981)

Etkins (1954 p 136) discusses the potential social behaviour of early hominids, assuming that they had a division of labour along the lines of 'man the hunter' 'woman the gatherer'. Like Lovejoy, he assumes that pair bonding would have been the natural result of such scenarios. "The central feature of the social behaviour of the 'hunter' anthropoid therefore, must be an integration of the male into the monogamous family unit in which he is the primary hunter." Etkin (1953 p 137) Tanner (1981), also argued that sexual selection would have favoured "males who sometimes shared food" (p164) but, unlike Lovejoy, added that female bipedality would also have been strongly selected for, both for gathering plants and carrying infants.

Although Rose (1991) categorised Tanner's thinking on bipedal origins under the heading "Infant Carriage", her book argues for a far more sophisticated cluster of factors than that being involved in the process of early human evolution.

She argues that "transitional hominids", as she regularly calls them, would have found many benefits of increased upright posture and bipedal gait, including food carriage, threat displays against potential predators and even sexual displays in males directed at females. Throughout her work, Tanner (1981) is clear in making a stronger case for the role of women in human evolution than many others (mostly men) did before her. A big part of this, of course, would naturally include infant carriage and this is perhaps why Rose decided to classify her contribution in this way.

For example, Tanner (1981 p 164), argued that sexual selection would have favoured "males who sometimes shared food" but, unlike Lovejoy, added that female bipedality would also have been strongly selected for, both for gathering plants and carrying infants.

Other than this, much of her thinking appears to be based upon many of the same assumptions of aridity driving early humans into more open habitats.

For example, she wrote: “As the population was able to increasingly utilize forest fringes and areas away from forests, gathering for offspring became necessary. Food, though plentiful, was less readily accessible, required tool use to obtain in many instances, was acquired in areas where the hominids were more vulnerable, often not immediately visible, and was more widely dispersed.” Tanner (1981 p 145)

Clearly, her views could just as easily have been placed under the ‘threat display’ category: “Predators now posed a problem for this diurnal omnivorous primate, which was now obtaining a large proportion of its food in the relatively open African savannah where predator pressure was high. Their upright posture and developing bipedal locomotor pattern meant that the transitional hominids were more visible to predators. The hominid pattern of dealing with predators was basically one of intelligent avoidance supplemented by intimidation. For the transitional population defence consisted, first of all, in being able to see predators better because of walking upright. Transitional hominids, when displaying bipedally, would appear large, their arms could be waved while they vocalised, and sticks and rocks could be thrown. As intimidation this would be quite effective.” Tanner (1981 p 150-151)

Sinclair et al. (1986) also suggested infant carriage as a factor in the adoption of hominid bipedalism in their migration hypothesis.

Weapon wielding / throwing

Original proponent: Dart 1925.

Although the earliest recorded thinking in favour of weapon wielding was from Darwin (1871), Raymond Dart and Robert Ardrey were the most notable proponents of this specific aspect of forelimb pre-emption as a driver of hominid bipedalism.

As early as 1925, when describing the Taung Child, Dart alluded to his thinking behind the switch to bipedalism evidenced by an anteriorly placed foramen magnum: “Bipedal animals, their hands were assuming a higher evolutionary role not only as delicate tactual examining organs which were adding copiously to the animal's knowledge of its physical environment, but also as instruments of the growing intelligence in carrying out more elaborate, purposeful and skilled movements and as organs of offence and defence” Dart (1925 p 197).

Later, he articulated this point more clearly: “The terrestrial human precursors, who adopted bipedal in preference to quadrupedal postural habits, were forced simultaneously to rely upon their hands instead of fangs for assault and repulse. The inevitable result of the absence of long tearing canines and shearing premolars (or the presence of stubbed canines and grinding premolars) in the advanced anthropoid is aggressive hands.” Dart (1949 p 1).

A rather very specific form of a throwing model was espoused by Fifer (1987) who argued that the development of a specific defence mechanism, namely throwing stones, resulted in such modifications to the postcranial skeleton, musculature as well as CNS, that hominid bipedalism resulted.

The basis of the model was Darwin’s (1871) ‘freeing of the hands’ idea but Fifer went further in suggesting cause, rather than effect (Fifer 1987 p 136).

The bulk of his argument promotes stone-throwing mainly in terms of biomechanical overlap with human bipedalism as there is a paucity of hard evidence in the fossil record either for or against the hypothesis.

Fifer argues that there are a number of anomalies in the anatomy of humans, if one assumes they evolved purely as a result of an adaptation for walking, and claims that throwing explains the anomalies better.

The ‘anomalies’ listed were as follows:

- The lower limbs in humans are relatively massive, compared to mammals more specialised in cursorial forms of locomotion, such as horses;
- Humans have relatively long and mobile waists, unlike quadrupeds and other bipedal animals such as the ostrich;
- The well-developed gluteus maximus muscles play, it is argued, “little or no part” Fifer (1987 p 141) in general walking gait;
- The structure of the foot, it is claimed, has more internal mobility than it would need purely in the role of locomotion;
- The short lever arm of the extensor muscles of the leg, Fifer claims, is another anomaly. The lever arms of extensors of the lower limbs are rather small, indicating a shift of emphasis from ‘power’ to ‘speed’ and yet, humans are clearly not very fast compared to the sort of predators they may have encountered on open grassland habitats in East Africa;
- Finally, the orthodox ‘energy-saving’ explanation for man’s knee-locking mechanism, it is claimed, is countered by the fact that other muscles are needed to hold the knee joint in position.

The “weapon throwing” idea was updated by a paper by Bingham (1999), suggesting that throwing might have provided a mechanism for "coalition enforcement" in human ancestors, and has received recent support from Dunsworth et al. (2003).

Tool/Weapon carriage

Selected proponents: Haeckel 1900; Carter 1953; Hill 1954; Etkin 1954; Shapiro 1956; Washburn 1960.

The importance of tool making in human evolution has long been recognised as a significant measure of ‘progress’ from the fossil and archaeological record.

The degree of sophistication of stone tools found associated with hominids has been seen as a key indicator of this and, therefore, tool carriage has been viewed as a key motivating factor for our bipedalism.

Bartholomew and Birdsell (1953) suggest that the real advantage of freeing of the hands was in using tools: “Only man has his locomotion essentially unimpeded whilst carrying or using a tool” (p 482).

Etkins (1954 p 136) discusses the potential social behaviour of early hominids, assuming that they had a division of labour along the lines of ‘man the hunter’ and ‘woman the gatherer’. After having considered, and rejected, various other ideas prevailing at the time which in his view did not sufficiently explain why humans, but not apes, would have evolved their ability to retain and promote culture, he describes a thesis that, like Lovejoy, assumes that pair bonding would have been the natural result of such scenarios. “The central feature of the social behaviour of the ‘hunter’ anthropoid therefore, must be an integration of the male into the monogamous family unit in which he is the primary hunter” Etkin (1953 p 137). Washburn (1960 p 69) and Hockett (1960 p 96) made similar arguments.

These models were specifically criticised by Jolly (1970). He wrote

> *“if the theory of artefactual determinism is to be applied consistently, regular tool and weapon-making has to be extended back into the Miocene, and also attributed to* Hominoidea *other than the direct ancestor of the Hominidae…*
>
> *… This is eminently likely, but is no explanation for anterior dental reduction since the chimpanzee has relatively the largest canines and incisors of any pongid, much larger than those of the gorilla, which has never been observed to use artefacts in the Wild. To explain hominid dental reduction on these grounds, therefore we presumably have to postulate that the basal hominids were much more dependent upon artefacts than the chimpanzee, without any obvious explanation of why this should be so.*
>
> *One would also expect signs of regular tool making to appear in the fossil record at least as early as the first signs of dental reduction, rather than twelve million years later. The more artefactually sophisticated the wild chimpanzee is shown to be, of course, the weaker the logic of the tool/weapon determinant theory becomes, rather than the other way about, as its proponents seem to feel.” Jolly (1970 p 7)*

Weapon wielding

A more specific (and violent) variant of this model was first proposed by Raymond Dart. The concept is basically that intra and/or inter specific violence lead to the adoption of bipedality through increased weapon wielding.

In his original paper describing the Taung Child in 1925, Dart alluded to his thinking behind the switch to bipedalism he found evidenced by the more anteriorly placed foramen magnum: “Bipedal animals, their hands were assuming a higher evolutionary role not only as delicate tactual examining organs which were adding copiously to the animal's knowledge of its physical environment, but also as instruments of the growing intelligence in carrying out more elaborate, purposeful and skilled movements and as organs of offence and defence” Dart (1925 p 197). Later, he articulated this point more clearly: “The terrestrial human precursors, who adopted bipedal in preference to quadrupedal postural habits, were forced simultaneously to rely upon their hands instead of fangs for assault and repulse. The inevitable result of the absence of long tearing canines and shearing premolars (or the presence of stubbed canines and grinding premolars) in the advanced anthropoid is aggressive hands.” Dart (1949 p 1).

The strengths of the model may be characterised as:

- Using weapons often does require bipedal posture. “Jabbing with sticks or hurling stones would be most effective from a standing position” (Hewes 1961 p 694).
- One of the key problems with adopting human-like bipedalism, particularly in open habitats, is that it would appear to put the individual under far greater vulnerability from predation. The strength of these kinds of bipedalism models is that they not only offer a very strong counter argument to that increased threat, they

simultaneously suggest that carrying weapons itself would have favoured the adoption of bipedalism itself.

- One of the five key trends in the process of hominisation, as described by Lovejoy (1981) is dental reduction. Observers like Dart point out that the reduction in canine teeth, which appears to be an early feature of hominins, is also suggestive that some alternative method of combat would have evolved to take its place.

But the idea also has several weaknesses:

- The archaeological evidence suggests that tool use, such as those that might have been used as weapons, came at much later stage (ca 2.6 Ma) of human evolution than the onset of bipedalism (at least 6 Ma). (Hewes 1961 p 695). Although this does not disprove that the earliest bipeds were not using weapons that were not made of stone (e.g. clubs from branches or bones) it certainly is not a point in its favour.
- The argument that early bipedal hominins were effective hunters is questioned by Hewes on the basis that even 'primitive' hunter-gatherer societies today, equipped with much better weapons and with several million years of natural selection for better bipedalism behind them, still find it troublesome to hunt down big game. He summarises this: "A long preparatory phase is indicated, in which pre-hominid bipeds might have been meat and marrow eaters, but seldom actual hunters." (Hewes 1961 p 695).
- Weapon use could clearly have been very beneficial to early bipeds, but here is another example where cause and effect are difficult to discriminate between. It seems unlikely that danger from predators could have resulted in the adoption of a brand new form of locomotion to allow carrying weapons which would be very difficult to carry in early anatomical forms.

It is interesting to speculate how much of the 'killer ape' ideas of Dart (1959) and Ardrey (1961) resulted from reflections after the horrors of two recent world wars. Certainly they did leave an awesome legacy in Europe with tens of millions of deaths resulting directly from armed combat.

2.3.2 Models citing aspects of social behaviour

General

The second of Rose's categories, around which a number of variations on the theme are based, is the one that posits some kind of shift in social behaviour as a driver. These social behaviours, as we shall see, include those which are proposed to reduce either *intra-specific* or *inter-specific* (or both) conflicts as well as behaviours that appear to overlap considerably with the carrying models. Washburn (1960), for example, suggested that it was man's ability to use and make tools that drove the change in locomotion and Dart (1949; 1959) specifically argued that it was for the use of weapons that standing upright would provide a visual advantage to survey the surroundings (1959 p 223). These ideas imply both carrying and social behaviour as key drivers for the adoption of bipedalism.

Livingston (1962) suggested a specific behavioural causal factor: That ape-like threat postures, by reducing the number of physically costly, and possibly injurious, attacks, would have provided a selective advantage for early adopters of regular upright movement.

In our classification seven such models are discussed here: Threat display, Aggression, Evasion, Vigilance, Sexual Display, A new ‘fashion’ and Nuptial Gifts. However, for brevity, a number of them have been grouped together.

Variations on the theme

Nuptial gifts (Lovejoy 1981; Parker 1987)

One behavioural model, based on sexual selection, which overlap considerably with one of the carrying models already discussed is the idea that females selecting males for their carrying of “nuptial gifts” was a major factor in the adoption of bipedalism. Specifically it proposes that male ability to carry large amounts of food to relatively sessile females would have been sexually selected for and this would be favoured by greater bipedality.

Among the proponents of this kind of idea is Owen Lovejoy in the ‘Provisioning hypothesis’ (discussed in the last section.) Here we will focus on Parker’s similar ideas which were more specific to the sexual selection argument.

Parker described a model for “rapid evolution of bipedal locomotion as a male adaptation for nuptial feeding of females” (Parker 1987 p 235).

His sexual selection model for the origin of hominid bipedal locomotion may be summarized thus:

If australopithecines (and *A. afarensis* specifically) were ancestral to humans, and if there was a significant degree of sexual dimorphism in the behavioural roles of the genders, such that, males would have done more “wandering” for food than females, the assumption is that our ancestors were socially pre-adapted for greater male provisioning.

Parker suggests that, at around the time of the ape-human divergence, some of that ancestral stock began living in more arid habitats, where food procurement was more difficult. From this he postulates that it is likely that male hominids did proportionately more of that difficult procurement than females and would have used this to attempt to gain more sexual access to females. Equally, females would have selected males more on the basis of how much high energy, difficult to procure, foods they could provide.

There is clearly a degree of overlap between Parker’s model and others. For example, like Lovejoy, it assumes that male provisioning was a key factor.

“Bipedal carrying and presentation of nuptial gifts would allow them to accurately assess the size of the male and the size of the gift …” Parker (1987 p 243). And like Tanner and others, it assumes penile display could also have been important too: “…, bipedal locomotion would also allow females' to assess the size and tumescence of the male's genitals.” Parker (1987 p 244). However, importantly, Parker himself distances his own model from that of Lovejoy’s on the grounds that it does not assume monogamous pairs.

Inter/Intra specific threat display/aggression

Original Proponent(s): Inter-specific: Kortland 1980; Intra-specific: Livingston 1962, Wescott 1967; Later backed by Jablonski and Chaplin (1993)

Inter-Specific Displays

Kortland (1980) published a short paper describing a study where thorny branches were successfully used to deter lions from getting access to bait. It was argued that the use of such branches could have been a significant factor in the evolution of hominin bipedalism considering their small size and vulnerability in savannah contexts.

Intra-Specific Displays

A behaviour in apes that has been popularly associated with a change to upright posture is the kind of social display adopted by gorillas when performing their characteristic chest beating. It was this sort of observation that first led Frank Livingston to publish, in the journal American Anthropologist, a model…

> *"… to reconstruct the transition from ape to man along the lines of the mountain gorilla. The fact that they sometimes stand up to beat their chests and charge bipedally is seen as a model for which the earliest carnivorous hominids began moving" Livingston (1962 p 301).*

He suggested that it was at the edge of woodland and more open habitats where the increase in this sort of behaviour was likely to have occurred.

Livingston referred to such hominids as "edge-specific - or at least an edge preferring - species", although this assumption seems to be based only upon the presence of mountain gorillas, away from the tropical rain forests.

Livingston's main point is this: Upright threat postures which 'free' the arms to act as weapons, or as threatening devices would be "remarkably pre-adapted to the carnivorous, bipedal, open grassland ecological niche which the early hominids appear to have occupied" (Livingston 1962 p 304). His argument ends with speculation that reductions in normal food supply on the edges of shrinking woodland might have driven such hominoids to adopt such charging displays in order to begin to procure food through a carnivorous life style.

Later, in a brief letter to the same journal, Roger Wescott supported this view. He wrote:

> *"… early hominid reactions [to extra-specific threats] must have frequently been agonistic. Part of this agonistic response undoubtedly consisted of two-legged standing or running, probably accompanied by fist shaking or arm-waving, and possibly involving the seizing and brandishing of sticks and stones." Wescott (1967 p 738)*

Guthrie (1970) and Simons (1972) also supported the idea as did Tanner in 1981. She wrote "standing and walking bipedally would also contribute to the effectiveness of defensive displays, as observed for chimpanzees. Transitional hominids, when displaying bipedally, would appear large, their arms could be waved while they vocalised, and sticks and rocks could be thrown. As intimidation this would be quite effective." Tanner (1981 p 151)

More recently, the idea has been championed most seriously by Jablonski and Chaplin. By examining ecological transformations in the 'late-middle' and late Miocene of East Africa, Jablonski & Chaplin proposed that bipedal threat display-appeasement behaviours (i.e. "stationary bipedal displays, bipedal charges and bipedal mock fights and deference to these behaviours," Jablonski & Chaplin 1993 p 272) are important in understanding the origin of habitual terrestrial bipedalism.

They supported their argument by constructing an elaborate phylogenetic case that the common ancestor of *Pan/Gorilla/Homo* exhibited bipedal displays (Jablonski & Chaplin 1993 p 266-270). In support, behavioural field observations of *Pan troglodytes, Pan paniscus, Gorilla gorilla* and even *Homo sapiens,* were cited, where bipedal social displays are important, to indicate that it was therefore parsimonious to assume the last common ancestor also performed bipedal displays (Jablonski & Chaplin 1993 p 271).

Their main argument is that "climatic deterioration of the late middle and late Miocene led to the gradual fragmentation of the forests of equatorial Africa and the fragmentation of the ranges of several species of ancestral hominoids. In the most marginal habitat of all evolved the ancestor of the Hominidae." Jablonski and Chaplin (1993 p 272-273).

According to the authors, the resulting habitats would have had food and water resources which were sparsely distributed and this would have led to larger ranges being covered by their early hominid inhabitants. From this, "increased competition for resources probably ensued," (Jablonski and Chaplin 1993 p 273) and this competition would have led to greater adoption of bipedal displays. The authors "suggest that bipedal displays and increased deference to them were the behaviours essential to the success of pre-hominids in this environment in that they allowed for the relatively peaceful resolution of intra-group conflicts, including those over scarce resources" (Jablonski and Chaplin 1993 p 273).

Their argument also contains elements of the "fashion" model favoured by Dawkins (2004, see section later) as they suggest that perhaps occasionally bipedal displays won an argument, without a fight, purely "by dint of their sheer novelty" (Jablonski and Chaplin 1993 p 274) and that this could have been followed by greater mating success in those that had performed them.

The authors further speculate that female inter-group migrations would, having resulted from the off-spring of such encounters, act to spread the behaviour and associated traits across the wider population. And, that once this behaviour reached a critical mass, other benefits of bipedalism, cited here as alternative models in its origin, would have naturally resulted, further reinforcing the behavioural switch.

Jablonski & Chaplin recently added further support to this hypothesis with a chapter evaluating three theories of bipedal origins.

In that work they concluded:

> *"The results of this study suggest that two of the most strongly favoured hypotheses for the evolution of habitual bipedalism, the food carrying hypothesis of Lovejoy (1981) and the arboreal feeding hypothesis of Hunt (1994, 1996) are untenable because they are not compatible with the anatomical evidence of the fossil record and because they propose activities that are extremely costly in terms of energy expenditure." Jablonski and Chaplin (2004 p 290-291).*

Evasion and vigilance models

Original Proponent(s): Reynolds 1931 (Evasion); Dart 1959 p 223; Day 1977; Ravey 1978 (Vigilance).

Mnemonic: "Meerkat peering" (Also referred to as "sentinel behaviour" and "the tower hypothesis").

Predator avoidance is another major idea around which models regarding bipedal origins have been proposed. Rose originally separated this into two separate groups: 'Evasion' and 'Vigilance' but here they will be treated as one.

Reynolds (1931) was the first to articulate this idea in the literature and Washburn (1960) suggested that it was man's ability to use and make tools that drove the change in locomotion and Dart (1949; 1959) specifically argued that it was for the use of weapons that standing upright would provide a visual advantage to survey the surroundings (1959 p 223). The more recent literature from proponents of this idea turns out to be rather thin, apparently comprising of just two very short pieces: one attributed to a transcribed lecture by Day (1977) and another, a letter to the journal Science a year later.

Day's lecture 'Locomotor Adaptation in Man' itself only mentioned the idea briefly: "The lifting of the head high above the ground permits the long view, of clear value in open country, and the sense of smell lessens in importance." Day (1977 p 150).

Ravey's (1978) short letter in the journal Science also articulated the view that, for a relatively short hominid, upright posture could be adaptive for predator detection in open habitats as an "early warning system."

The idea is logical if one assumes that early bipedal hominids lived in rather open habitats where vigilance from predators was an activity of high importance, then being upright is likely to have some selective advantage. However, at least two major counter-arguments have been made to this idea. Firstly, some authors have made the obvious counter-point that whereas being upright might indeed enable a hominid, out in open grassland, to see its potential adversaries (and potential prey) better, it will certainly make it more visible to them. For example Tanner (1981 p 150) noted that "Predators now [in her speculation that australopithecines had moved to more open, savannah habitats] posed a problem for this diurnal omnivorous primate, which was now obtaining a large proportion of its food in the relatively open African savannah where predator pressure was high. Their upright posture and developing bipedal locomotor pattern meant that the transitional hominids were more visible to predators." Secondly, a number of workers have expressed skepticism that a sporadic behaviour like a threat display or even wielding a club would become the habitual mode of locomotion. For example, Stanford asked "why is it important to be permanently upright? Standing upright for just a few seconds would achieve the same results," Stanford (1999 p 45). Others have cited evidence that no other species, living in open habitats, have adopted bipedalism as an evolutionary strategy for this reason. Hewes (1961 p 695), for example, suggests that "it is curious, however, that the [vigilance] advantages of bipedalism have not led to a more widespread adoption of this habit among both predators and their prey in grassland environments." This is a point that could be echoed against almost every model of hominid bipedal origins but, it would seem that in this case, the answer to that particular quandary is simply that when it comes to escaping a predator, four legs is better than two. Also, if early hominins evolved in more closed woodland it is difficult to see how this model might work at all.

Phallic display

Original Proponent(s): Tanner 1981

One major difference between the genus *Pan* and *Homo* resulting directly from the way they generally move is the relative visibility of the sexual organs. In chimpanzees and bonobos, females in oestrus are easily identifiable by their tumescence, or exaggerated sexual swellings whereas in women any analogous, or any other visible signs of sexual receptiveness, are notable only by their absence.

On the other hand, whereas male genitalia in *Pan* are usually obscured from view, whilst moving quadrupedally, a bipedal naked man has to take deliberate action if he wants to conceal his sexual organs from being displayed.

That there is a clear difference between the orientation of the sexual organs in male and females in Hominoidea, directly dependent on their posture, upright or otherwise, is not in any doubt. The issue here is one of cause and effect: Was this difference in sexual display a causal factor in the adoption of hominid bipedalism, or merely an unavoidable consequence?

Tanner is one adherent to the view that might have been the former, through some kind of sexual selection. She wrote:

> *"Much of the selection pressure engendered by the female choice of sexual partners was directed toward male social and communication behaviour, reinforcing the potential and capacity for sociability, social learning, and intelligence. Sexual selection also increased the contribution of genes from males who exhibited frequent bipedalism. A male's contribution to the gene pool necessitated his keeping up with the gathering females as they covered large expanses searching for food.*
>
> *Further, obvious visual cues such as a bipedal male's erect penis could have attracted female attention and action. [Even more directly, in the above context, sexual selection may have contributed to growth in the size of the male's penises. Homo sapiens males are quite well endowed] Such an image might appear amusing and improbable, but let us remember that these ancient forebears living in the warm African savannahs had not yet invented clothing. As the female hormonal cycle and ovulation came to contribute less to timing of her arousal, it is not illogical that visual cues could become increasingly significant. If so, sexual selection for bipedalism would be yet another instance of natural and sexual selection together advancing the species adaptation farther along the same path for both females and males." Tanner (1981 p 165-166)*

A 'trend' or 'fashion' (Dawkins 2004)

Original Proponent(s): Dawkins 2004

Another idea, related to sexual selection, regarding bipedal origins which can also be broadly classified under the heading 'social factors' is that which suggests that bipedalism was practiced by some hominids for reasons that are not really important, but once it was observed, others copied it and consequently it 'took off' as a kind of fashion.

The chief proponent of this idea is Richard Dawkins who, in his rather famous work 'The Selfish Gene' proposed another level of natural selection on top of that taken for granted at the level of the gene – the 'meme', or memory selection unit.

The meme concept has been embraced by many workers in anthropology and several books have been written based on them (Blackmore 2000), although others have argued that it may have been taken too literally. However, as a concept they would appear to be quite useful in describing cultural artefacts that can get passed on from one person to another. Languages and many other cultural elements, not necessarily human, seem to fit into the model quite nicely and, according to Dawkins, behavioural changes might do also. Dawkins has applied his memetic notion to the problem of hominid bipedal origins and suggested that, perhaps, it could have just started, originally, as some kind of 'fashion'. He expounds this idea, perhaps better than elsewhere, in his popular book 'The Ancestors Tale.'

> *"Sexual selection, and its power to drive evolution in non-utilitarian arbitrary directions, is the first ingredient in my theory of the evolution of bipedality. The second is the tendency to imitate. The English language even has a verb, to ape, meaning to copy, although I am not sure how apt it is. Among all the apes, human are champion copyists, but chimpanzees do it too, and there is no reason to think the australopithecines did not. The third ingredient is the widespread habit among apes generally of rising onto the hind legs, including during sexual and aggressive displays.*
>
> *Putting all these ingredients together, my suggestion for the origin of human bipedality is this. Our ancestors, like other apes, walked on all fours when not up in trees, but reared up on their hind legs from time to time, perhaps in something like a rain dance, or to pick fruits off low branches, or to move from one squat-feeding position to another, or to wade across rivers, or to show off their penises, or for any combination of reasons just as modern apes and monkeys do. Then – this is the crucial additional suggestion I'm making – something unusual happened in one of those ape species, the one from which we are descended. A fashion for walking bipedally arose, and it arose suddenly and capriciously as fashions do. It was a gimmick." Dawkins (2004 p 227).*
>
> *The idea is peculiarly bereft of any survival advantage and relies purely on the speculation that such a 'gimmick' might confer some advantage in terms of sexual selection. Such speculation is not testable, and as it is neutral with respect to the environment, the fossil record cannot be used to refute or support it.*

2.3.3 Postural feeding models

General

Most of the postural feeding models assume early hominins, inhabited the fringes of woodland and more open grasslands although Eickhoff (1988) suggested it was in a specifically arboreal context and some considered the possible effect of moving through water. Any such 'aquatic' models will be discussed later in a section of their own.

Here, several non-wading models of bipedal origins based on feeding will be reviewed.

The authors of these models usually start by making the point that as food procurement is a most important aspect of animal life, it must be a strong candidate amongst factors responsible for the shift in locomotion we are seeking to explain.

There is quite a variety in the types of food that have been suggested were key in driving this change in behaviour and in the actual type of behaviour it is suggested this kind of feeding induced. Several of the models propose postural adaptations resulting from food gathering that, although quite unlike human bipedalism, could have been natural pre-cursors for it. For example, Hunt (1994) suggested that bipedal *posture* resulted from the feeding of food from low branches, but this did not include a large locomotor component. Jolly (1970) and, later, Kingdon (2003) proposed sitting on haunches or squat-feeding, respectively, as necessary pre-cursors to upright hominin bipedalism. Geist (1978) proposes stalking prey.

Most of these models therefore require two phases in the evolution of hominid bipedalism: an early phase in which a change of habitat caused a divergence between human and ape ancestors in terms of posture, and then a secondary stage where the resulting greater tendency for bipedalism was then specifically selected for, for other reasons.

This is both a strength and a weakness in this group of models. Although they do provide plausible scenarios for forms of posture and early forms of locomotion that, although not human-like, may well have preceded them, it remains largely speculation to suggest that a relatively passive feeding behaviour might transform into a general shift in locomotion.

Wrangham (1980) and Rose (1981) support these ideas by suggesting that it would be more efficient to maintain an upright posture whilst shuffling from tree to tree, than to repeatedly shift from bipedalism to quadrupedalism and back again, a view backed up recently by some theoretical modelling (Sylvester and Kramer 2008). However the biggest criticism remains that the behaviour they espouse actually has, little to do with locomotion. Jolly (1970) and Kingdon (2003) do not even necessarily propose an upright posture whilst Hunt's (1994) definition of bipedalism included any posture resulting in greater than 50% of the body weight being borne on the hind limbs, which included many incidents of arboreal posture whilst stretching for food in trees.

Variations on the theme

Seed eating

Original Proponent(s): Jolly 1970

The Seed-Eaters: A New Model of Hominoid Differentiation Based on a Baboon Analogy (Jolly 1970)

One of the most cited papers in palaeoanthropology is Clifford Jolly's 'Seed-eating hypothesis'. Jolly began his thesis by attacking those models which, in his view, did not give satisfactory causal factors for the origin of hominid bipedalism and only offered arguments which would reinforce the behaviour once started. These 'feedback models,' as he referred to them, promote scenarios that both result in and result from more bipedalism. For example, carrying models suggest scenarios that would both encourage more bipedalism and result from more bipedalism. He criticises the circularity of these models which, he claims, renders them unable to explain their own beginnings: "In fact the more closely the elements of the hominid complex are shown to interlock, the more difficult it becomes to say what was responsible for setting the feedback spiral in motion, and for accumulating the elements in the cycle in the first place." Jolly (1970 p 5).

Specifically, Jolly critiques two main groups of models of hominin divergence, especially those broadly grouped under ‘hunting’ or ‘tool/weapon use’ and then the threat posture model proposed by Livingston (1962) and Wescott (1967). Many of his criticisms surround the question of whether dental reduction would logically follow from increased tool use and the contradictions in the evidence used to support that view. This extract is typical:

If the theory of artefactual determinism is to be applied consistently, regular tool and weapon-making has to be extended back into the Miocene, and also attributed to Hominoidea other than the direct ancestor of the *Hominidae*, whether one considers this to be *Ramapithecus*, *Oreopithecus*, or neither. Simons and Pilbeam (1965) regards *Ramapithecus* is as too early to be a tool-maker, but they suggest that it was a regular tool-user, like the savannah chimpanzee (Goodhall I964; Kortlandt 1967) This is eminently likely, but is no explanation for anterior dental reduction since the chimpanzee has relatively the largest canines and incisors of any pongid, much larger than those of the gorilla, which has never been observed to use artefacts in the Wild. To explain hominid dental reduction on these grounds, therefore we presumably have to postulate that the basal hominids were much more dependent upon artefacts than the chimpanzee, without any obvious explanation of why this should be so. One would also expect signs of regular tool making to appear in the fossil record at least as early as the first signs of dental reduction, rather than twelve million years later. The more artefactually sophisticated the wild chimpanzee is shown to be, of course, the weaker the logic of the tool/weapon determinant theory becomes, rather than the other way about, as its proponents seem to feel (Jolly 1970 p 7)

Jolly’s earlier criticism of ‘feedback models’ is also invoked to counter this kind of model, noting that “… the more proficient a hunter the non-bipedal, large-canined, large-incisored chimpanzee is found to be, the less plausible it becomes to attribute the origin of converse hominid traits to hunting” (Jolly 1970 p 8).

On the threat display idea, Jolly makes two objections. The first one “… that it is illogical to invoke the behaviour of living apes to explain the origin of something that they themselves have not developed; if upright display leads to habitual bipedalism, why are gorillas still walking on their knuckles?” (Jolly 1970 p 9), could be countered by an argument suggesting that the ancestors of the living apes have just not performed this behaviour sufficiently to have caused them to follow the same pathway as our ancestors.

The second “… if hominid bipedalism were initially used solely in display, why should they have taken to standing erect between episodes? Even if we grant that the savannah is more predator-ridden than the forest (a view often stated but seldom substantiated, even for the recent, let alone the Tertiary), it is difficult to believe that attacks were so frequent as to make defensive display a way of life” (Jolly 1970 p 9), appears to be more difficult to counter. Jolly’s point about ‘feedback models’ is apt, and it is easy to see how some benefits of bipedalism could get confused with potential causal factors. It is a type of thinking that has been labelled Lamarckism, where beneficial behaviour (if practiced enough in one generation) is proposed to be passed onto the future generations through unspecified means. Darwinism, on the other hand, requires that this behaviour be translated into the currency of benefit in terms of selection of the genes responsible for whatever traits favour that behaviour. It would seem however that such beneficial behaviours are likely to incur greater selective fitness upon the individual, thus serving the genes which made them possible and therefore rendering them compatible with Darwinism after all. This would make Jolly's criticism of them less valid. Indeed one of the criteria proposed for an ideal bipedal model proposed here is that it should confer benefit throughout its evolution and not just as an 'end result'. This usually invokes a high degree of positive feedback in the model.

Having criticised Jolly's initial objections of some of the common aspects of other models, we may now turn to his own ideas specifically. The evidential basis of them is a systematic comparison between two species of baboon; one more adapted to open habitats than the other, and how the differences are mirrored in comparisons between hominids and chimpanzees. In a nutshell, his basic argument is that *Theropithecus* are more adapted to open habitats and 'seed eating' than *Papio*. Before looking at his findings in detail it is worth pointing out that there is already a difficulty here because Jolly does not make it clear as to which species of *Papio* he is referring to. He merely writes "Table 1 summarises characters by which either early Pleistocene Hominidae differ from *Pan*, or *Theropithecus* from *Papio* and *Mandrillus*, listed without regard to their function interrelationships or significance, (Jolly 1970 p 9.) Indeed, later in the paper he uses one such *Papio* species (*P. hamadryas*) along with *Theropithecus* as examples of savannah-woodland species.

According to Rowe (1996) there are eight species of baboons and their habitats and diets are described as in the table below.

Species	Habitat	Diet
Papio hamadryas anubis (Olive Baboon)	Semi desert, thorn scrub, savannah, woodland, gallery and rain forest up to 4500m. Water must be available.	Fruits, seeds, tubers, leaves, flowers and animal prey including invertebrates, reptiles, birds and mammals.
Papio hamadryas cyncephalus (Yellow Baboon)	Thorn scrub, savannah, woodland, gallery forest up to 1000m. Water must be nearby.	Fruit, seeds, leaves, flowers, roots, tubers, bulbs, animal prey (invertebrates, reptiles, amphibians, birds and mammals). A total of 180 plant species are eaten.
Papio hamadryas hamadryas (Hamadryas Baboon)	Arid semi desert and savannah woodland, up to 2600m.	Grass seeds, roots, tubers, leaves, flowers and animal prey including invertebrates (termites) and small vertebrates. Hamadryas baboons may raid crops and garbage dumps.
Papio hamadryas papio (Guinea Baboon)	Evergreen gallery and woodland savannah. Guinea baboons avoid tall grass.	Fruit, seeds, flowers, and animal prey, including mammals. These baboons will raid crops.

Papio hamadryas ursinus (Chacma baboon)	Woodland, grassland, acacia scrub, and semi desert habitats including small hills (kopjes), seaside cliffs and mountains up to 2980m. Water must be nearby.	Fruit, seeds, leaves, flowers, and animal prey, including reptiles, birds and mammals. Baboons living near the sea eat crabs, mussels and limpets. Chacma baboons raid farms and beg food from tourists.
Mandrillus leucophaeus (Drill)	Gallery, lowland rain forest to montane forest. Drills have never been observed outside forest boundaries.	Fruit, seeds, roots, fungus, small vertebrates, insects.
Mandrillus sphinx (Mandrill)	Primary and secondary dense rain forest, as well as gallery and coastal forests. The savannah is used only rarely.	Fruit and seeds 92%, bark, leaves, stems, pith of plants, palm nuts, and animal prey including ants, termites, dung beetles, spiders, tortoises, duikers, birds, mice, frogs.
Theropithecus gelada (Gelada).	Montane grassland with no tall trees, only at altitudes of 1400-4400m	Grass 90%, seeds, leaves, bulbs, animal prey (insects, mammals.) Crops are raided.

Table 6 Baboon species and habitats (after Rowe 1996)

It should be noted that, according to these reports, the diets of all of these species include seeds (although these reports suggest that geladas rely on them more) and so it is reasonable that Jolly's premise should be at least questioned. It is likely (Oxnard, personal comment) that Jolly was referring to *P. anubis* in his list but even if that is assumed, there would not appear to be as large a distinction in habitat between the species as Jolly implies. Even assuming his premise is correct, there are still other criticisms that can be made of his approach. Below is a subsection of his table which listed characters where hominids and *Pan* differed (A) compared to where *Theropithecus* and *Papio* differed. Here only behavioural and postcranial structures are shown as they are the ones most relevant to this study.

Character	A	B	C	D
1. Behavior				
a, Open-country habitat, not forest or woodland.	X	X		
b, Trees rarely or never climbed when feeding.	X	X		
c, One male breeding unit.	X	X		
d, Foraging mainly in sitting position.	?	X		
e, Small daily range.	?	X		
f, More regular use of artifacts in agonistic situations.	X		X	
g, Regular use of stone cutting-tools.	X		X	
h, Most food collected by index-pollex precision grip.				
2. Postcranial structure				
a, Hand more adept. Opposability index higher.	X	X		
b. Index finger abbreviated.	?	X		
c. Hallux short and weak.		X		X
d. Hallux relatively non-abductible.	X	X		
e. Foot double-arched.	X		X	
f. Phalanges of pedal digits 2-5 shorter.	(X)	X		
g. Ilium short and reflexed.	X		X	
h. Sacro iliac articulation extensive.	X		X	
i. Anterior-inferior iliac spine strong.	X		X	
j. Ischium without flaring tuberosities.	X		X	
k. Accessory sitting pads (fat deposits on buttocks) present.	(X)	(X)		
l. Femur short compared with humerus.	?	X		
m. Distal end femur indicates straight-knee ‘locking’	X		X	
n. Epigamic hair about face and neck strongly dimorphic	(X)	(X)		
o. Female epigamic features pectoral as well as perineal.	(X)	(X)		

Table 7 Behavioural differences between Species investigated by Jolly

A) refers to traits distinguishing hominins from *Pan* and other great apes. B), characters distinguishing from *Papio* and *Mandrillus*.(C) features of the hominid complex not seen in *Theropithecus*. (D) Features of *Theropithecus* not seen in Hominidae.

One criticism that can be made is that the list of characters chosen for comparison is apparently arbitrary. Jolly finds 22 out of 48 character sets which show parallelisms but one is tempted to ask how many character sets could have been listed that would have shown far fewer. He suggests that “This hypothesis can be tested by checking the elements of the complexes for cross-occurrence in *Papio* & *Pan*. If the high number of common characters were simply due to chance, rather than to parallelism, we should not expect significantly fewer of the Hominid characters to appear in *Papio* (as opposed to *Theropithecus*), or significantly fewer of the *Theropithecus* complex characters to occur in *Pan*.” (Jolly 1970 p 12) But this argument appears flawed because the list of characters selected for each comparison (hominid with *Theropithecus* or *Papio* with *Pan*) is still itself not a random sample. On top of this, some of the parallels Jolly reports can also be questioned. For example, hominids, like *Theropithecus*, are reported as having moved to more open habitats. On this, Jolly writes: “Of these, only one certain one appears in the behaviour category, largely because of the impossibility of observing the behaviour of fossil forms.

Inferences of behaviour from structure are, of course, not permissible at this stage of analysis. The single common character is the basic one of true open-country habitat, inferred largely from the death-assemblages in which early *Theropithecus* and Hominidae are found, as well as the habitat of *T. gelada* (Jolly 1970 p 12). This is far from certain, however. Hominids are not proved as having lived in open habitats merely because their fossil sites share faunal assemblages that include species adapted to such niches, any more than they are indicated as being semi-aquatic merely because crocodilians and hippopotami are present. There is also a body of evidence which suggests that early hominid actually lived in relatively wet and wooded, as opposed to arid and open, habitats (See, for example WoldeGabriel et al. 2001 and Trauth et al. 2005).

There do appear, nevertheless, to be a few interesting parallels which give his model some weight. It is beyond the scope of this study to consider cranial features in too much detail but a major aspect of Jolly's argument does follow from some parallels in this area. Canine reduction along with molar increase is a phenomenon of hominid-ape divergence in need of an explanation and Jolly may well have stumbled across an interesting parallel in baboons. If early hominids did begin to procure a greater percentage of their food from seeds, it is logical that dental reorganisation would proceed along the lines Jolly suggests. And, if seed eating became a major part of the diet, it is further likely that a large primate would procure much of this whilst sitting down. As Jolly puts it: "thus, truncal erectness is more habitual than in any non-bipedal catarrhine, and the mastoid process becomes explicable." (Jolly 1970 p 13). Whilst this is hardly bipedalism it does, at least, place them in a more upright posture, in a terrestrial setting, more often. This is an idea favoured, as we shall see, by another author, John Kingdon.

The rest of Jolly's paper outlines a two phase model of hominid-ape divergence which suggests that a seed-eating first phase came before a later, meat-eating, phase. It is proposed that the seed-eating phase resulted in a kind of stable evolutionary platform that existed for several million years, characterised by some early form of bipedalism. It is claimed that this accounts for several evidential aspects of the fossil record, again mainly concerning the large disparity between the appearance of evidence for dental reduction and the appearance of the use of stone tools in the fossil record.

Jolly makes a strong case that something other than meat-eating through increased tool use probably accounts for dental reduction in early hominids, and possibly a number of other ape-hominid differences (e.g. sexual differences in hair covering). However, when it comes to an explanation for a shift towards bipedalism, there is a distinct paucity of specific arguments for why putative ancestors that moved into grassy habitats generally, or a seed eating lifestyle specifically, would have switched to this form of locomotion. Indeed, Jolly makes several points himself which increase one's skepticism about this. For example: "Most of the postcranial elements of the hominid complex are absent in *Theropithecus*, being related to upright bipedalism (Clark 1964)" (Jolly 1970 p 13). And: "In *Theropithecus*, this behavioural trait (and its associated adaptive features) are superimposed upon a thorough ongoing, cercopithecoid quadrupedalism, producing a locomotor repertoire in which the animal abandons' bipedal' bottom-shuffling for quadrupedal locomotion when it moves fast, or for more than a few paces" (Jolly 1970 p 18-19.)

However, undeterred, Jolly manages to convince himself that despite this, it was the increased truncal erectness from "sitting while foraging (hands free)" (Jolly 1970 p 20) in open habitats that was the essential missing ingredient to bipedal origins. “This combination of heritage and adaptation may have been the elusive determinant of terrestrial bipedalism, a gait that is inherently 'unlikely', and which would thus have begun as a gelada-like shuffle. Locomotion of any kind is infrequent during gelada-like foraging, so that (unlike hunting!) it is an ideal apprenticeship for an adapting biped” (Jolly 1970 p 19). So, when it comes to postulating a model to explain bipedal origins, the closest Jolly comes is to provide a scenario for more truncal erectness. It might be suggested that, as it is assumed that hominids evolved from large climbing apes, we already had that.

Jolly’s own arguments against other models can easily be directed against his. Of the tool-weapon holding idea, for example, Jolly suggests: “The objection to this notion is again that is illogical to invoke the behaviour of living apes to explain the origin of something that they themselves have not developed; 'if upright display leads to habitual bipedalism, why are gorillas still walking on their knuckles?” (Jolly 1970 p 9). One might ask if seed-eating lead to bipedalism, why are gelada baboons amongst the most committed quadrupeds?

One interesting point Jolly makes, as evidence for a grassy habitat being a key factor, is that many early hominid habitats are associated with edaphic grasslands, prone to flooding. This view seems to have been strengthened by subsequent fossil discoveries which increasingly appear to place early hominids in gallery forest habitats which are both close to grasslands and yet relatively wet and wooded at the same time. It was the shift in climate, Jolly points out, towards a generally arid but seasonally wet zone east of the rift valley that specifically promoted the savannah grassland habitat as a climax ecosystem. This is an aspect we shall return to in other models.

Postural feeding

Original Proponent(s): Hunt 1994

A model with far better evidence (from extant great apes) is the postural feeding model, first proposed by Hunt (1994), and then revised in subsequent papers (Hunt 1996, 1998).

Based on over 700 hours of observation of wild chimpanzees at Gombe in Tanzania, it was found that the behavioural context most likely (almost 80% of recorded instances) to result in bipedalism was postural feeding. It should be noted, however, that these bipedal incidents were themselves relatively rare, comprising only about 3% of all observations recorded in the chimpanzees.

A major premise of this model is that “contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism” (Hunt 1994 p 183). If this assumption is correct then the plausibility of models of hominid bipedalism might be quantitatively measured by the degree of bipedalism exhibited in analogous behavioural scenarios to those being proposed as drivers for the evolution of bipedalism.

In a later paper, Hunt (1998) reported his findings even more fully and also placed greater stress on other feeding models as a basis for his, notably the original views of Jolly (1970), the revised form of this in Jolly & Plog (1987), Tuttle (1981), Rose (1991) and Wrangham (1980). Hunt pointed out that as primate time budgets are dominated by feeding behaviours it is likely that such behaviours would have been important in whatever factors led to a change in posture and mode of locomotion, in addition to other early anatomical changes signalling ape-human divergence, such as dental reduction and encephalisation.

Hunt’s studies showed that almost half of the recorded arboreal bipedal feeding activity was in relatively small, forest edge, small fruit-bearing trees (Hunt 1998 p 404). These findings led him to promote the hypothesis that increased postural feeding in some groups of hominin could have begun the evolutionary trajectory towards obligate bipedalism. Specifically, Hunt suggests that this kind of behaviour would be most favoured in habitats where tree size and density was reduced, perhaps in ecotones bordering on savannah grassland and woodland and the types of trees being foraged were ones bearing small-diameter fruit.

Unfortunately, the vast majority (>90%) of the incidents of bipedalism reported by Hunt were postural and/or supported by the upper limbs. Almost none were purely for locomotion and unsupported.

It could be argued that it might have been more useful to look for even rarer behavioural contexts of bipedalism, but where that bipedalism is unsupported and actually used during locomotion. If such behavioural contexts were found, Hunt’s premise that behavioural contexts that illicit bipedalism could offer clues as to the evolutionary pressure involving early hominid bipeds might be more illuminatingly applied.

Squat feeding

Original Proponent(s): Kingdon 2003

Kingdon (2003) introduced a novel idea in this area by suggesting “squat feeding” in ‘ground apes’ (a term derived from the recently labelled paleospecies *Ardipithecus ramidus*, lit. “stem ground ape,” inhabiting riparian habitats adjacent to rivers east of the rift valley, flowing into the Indian ocean (See, e.g. Wolde-Gabriel et al. 2003).

Kingdon explained the postulated habitat this way: “One challenge for species adapting to new or different habitats has been the repetitive drying out and retreat of extensive forest into a network of narrow galleries and riverine strips. During the Plio-Pleistocene, this tended to coincide with each global glaciation and gave a special importance to rivers as focal areas or refuges. With the return of humid climates, forests could expand from their riverine cores and swallow up the intervening country.” (Kingdon 2003 p 11).

Kingdon’s hypothesis is quite unique in that it offers a rather simple explanation for the peculiar postcranial anatomy in general, and the shape of the pelvis in particular, of early hominin bipeds such as *Australopithecus afarensis*. He promotes several aspects which may have helped in this squatting behaviour, for example long iliac wings, sacral compression, and more orthograde head orientation (Kingdon 2003 p 128). He argues that ‘squat-feeding’ is a natural precursive form locomotion to human-like bipedalism and backs this up with some convincing paleoecological and paleogeographical arguments. His observation that African forest species tend to have closely related non-forest cousins, placed in an East African gallery forest zone, led him to suggest that this is “…what might have been so odd about the east to trigger the development of such an aberrant ape” (Kingdon 2003 p 121). The implication of these factors, according to Kingdon, is that hominin ancestors living there would have to spend more time on the ground foraging for foods and be smarter at dealing with the more complex environment.

Overall the main point he makes is the assumption that ‘squat-feeding’ was an essential pre-requisite for a re-organisation of the upper body which was, itself, a pre-requisite to bipedalism.

Arboreal predation

Original Proponent(s): Eickhoff 1988

Another very different idea on the postural feeding theme was published by Eickhoff (1988). She suggested that arboreal predation was the likely precursive mode of locomotion for early hominid bipeds, suggesting that it might have evolved several times in arboreal apes “well before the Middle Miocene” (Eickhoff 1988 p 486).

It is proposed that early higher primates lived in the canopy of rain forest with an ecosystem with extremely dense vegetation serving a large enough community of primates for some to have specialised into a larger, more carnivorous role. The postulated “sit-and-wait predator” (Eickhoff 1988 p 487) type, it is suggested, would have gained selective advantage from skeleto-muscular ‘redesign’ allowing for greater efficiency whilst maintaining upright posture during waiting phases.

Eickhoff postulates that the precursive form of locomotion to bipedalism was “upright quadrupedalism” allowing apes to travel along “canopy highways” providing both substrates and superstrates in the form of branches, and that once populations of these apes had spread out of Africa to Asia and Europe, an abandonment of the ancestral, arboreal, niche led to a radiation into a variety of new niches, including terrestrial bipedalism.

Woodland stalking

Original Proponent(s): Geist 1978

The fact that human bipedalism is relatively slow and vulnerable compared to most terrestrial animals has not prevented hunting models from being constructed which are based on other characteristics of human bipedalism which can be construed in a more favourable light.

The stalking model of Geist (1978) is one such idea. It's premise is the observation that the human foot is very well adapted to stalking behaviours, as it provides very sensitive tactile feedback allowing, it is claimed, a would-be hominin hunter to creep up within grabbing distance of prey without being noticed, before stunning it with hand-held rocks.

Geist put it this way: "Far from having been reduced to the function of locomotion, our feet have evolved into instruments of silent approach to permit the capture of a prey unaware of the hunter" (Geist 1978 p 252).

Merker (1984) supported the stalking model and, importantly, offered to help answer one of the biggest question marks against it: Namely how is it proposed that prey would not have seen stalk-hunting hominids approaching? His suggestion is that upright posture is ideally suited for this in the context of wooded habitats. Although this somewhat contradicts Geist's writings – who is quite clear that such hunting phases happened away from wooded habitats – it may help, if one suggests that stalk-hunting might have been practiced around wooded water courses, such as gallery forests.

Endurance running

Original Proponent(s): Carrier 1984

Carrier (1984) offered others arguments for terrestrial predation based on observations surrounding human locomotor efficiency. Noting that typical cursorial quadrupeds are at least twice as efficient (oxygen consumed per unit mass per distance travelled). Carrier reminded us that another parameter of locomotion, in addition to speed and efficiency, is endurance. And it is in this area that humans, appear to have rather an edge over other types of mammals. Citing mainly anecdotal evidence of hunting behaviours of indigenous people from four different continents, a good case was made that humans are actually able to out-run many species specifically by exhibiting greater stamina, in the long run. From here, Carrier suggests that this ability was due to several anatomical and physiological traits in the hominid line that could have evolved as adaptations for this kind of life style, for example our glabrous (near naked) bodies which have allowed us to sweat independently of breathing rhythms. This has allowed us, argues Carrier, rather uniquely in mammals, to avoid over heating whilst running long distances, particularly in high temperatures. Furthermore, being bipedal, these respiratory cycles have also been 'de-coupled' from rigid gait patterns inherent in quadrupeds. Namely, we have the ability to breath more rapidly, out of synchrony with the strides we are taking whilst running, whereas quadrupeds are forced to take breaths only during hind limb propulsion phases.

The proposal is that these traits would allow humans, almost uniquely, to exploit a diurnal (and specifically during a midday time zone) hunting niche which allowed them to run down prey that, although being much faster over short distances, were susceptible to overheating during prolonged periods of exertion. Even big cats on the savannah could not compete with humans in this regard, it is claimed, and it is argued that this endurance running niche would explain not only the evolution of the striding bipedalism of modern humans but also the evolution of our loss of body hair too.

The "endurance running" (ER) hypothesis recently received strong support from Lieberman et al. (2006). The paper's main finding was to show that the human gluteus maximus plays a more important role in running than walking. Electromyographic data indicated that the gluteus maximus mostly has low levels of activity during level and uphill walking, but increases substantially in activity and alters its timing with respect to speed during running. They state that evidence for when the gluteus maximus became enlarged in human evolution is equivocal, but suggest that the muscle's minimal role in walking supports the hypothesis that enlargement of the gluteus maximus was likely to have been important in the evolution of hominid running capabilities.

Contradictory new studies

In 2012, a study challenging the long-established idea that human striding bipedalism was more efficient than quadrupedalism was published. Halsey & White (2012) argue that when a proper comparative analysis of the cost of animal locomotion is done, taking into account their phylogenetic history, there is no evidence from metabolic data that humans, or *A. afarensis*, have/had a reduced energy cost of pedestrian locomotion compared to other mammals in general. This is also supported by Rubenson et al. (2007)

Scavenging

Original Proponent(s): Szalay (1975), Shipman (1986).

Szalay (1975), contrary to Jolly (1970), argues that selective pressures for bipedalism are most like those providing greater energy efficiency, at a premium for a species who obtained a significant amount of their food from hunting and scavenging rather than from feeding off seeds. As Szalay puts it: "The hominid locomotor mechanism is drastically transformed in the common ancestor of both gracile and robust lineages to cover large distances, yet a shuffling, haunch-sitting ape, bent on picking tiny seeds from the grasses all around, requires relatively little territory to cover. In fact the locomotor requirements would certainly favour staying close to the ground where the food grows, rather than undergoing the drastic change involved in bipedalism" (Szalay 1975 p 426).

Shipman (1986) was offered by Rose (1991) as an example of an argument in favour of scavenging. However his paper, from the outset, makes it clear that the timescale considered for a scavenging life scale is as recent as 2 – 1.7 Ma. This is far too late, of course, to have acted as a factor in hominid bipedal origins unless the proposed selective pressure discussed has its behavioural roots much earlier. The paper is therefore considered here on this assumption alone.

Shipman (1986) basically attempts to determine if the evidence suggests that bovid faunal remains associated with Olduwai hominids were killed as a result of hunting or scavenging. He concludes that although there was evidence that some animals showed signs of being killed as a result of a more modern hunting technique, most appear to have bone scarring symptomatic of scavenging.

This was offered as evidence that scavenging, not hunting was the likely main causal factor for the process of hominization and its characteristic bipedalism.

The energy costs of scavenging, based largely on known figures from modern humans, is estimated and the biomass of meat which could have feasibly been scavenged is estimated from the faunal remains of the Olduvai site, taking account of competition from other scavengers and predators, also estimated from the faunal remains. On this basis Shipman suggests that “all tests of predictions of the scavenging hypothesis given here are fulfilled by a generous margin. It is concluded that the scavenging hypothesis is not refuted and is worthy of additional investigation” Shipman (1986 p 37).

2.3.4 Models invoking habitat compulsion

General notion

This category was not included in Rose’s (1991) survey but I have added it here to group together a set of ideas that suggest there was some specific factor, resulting merely from the habitat in which the hominid population lived, which provided a selective pressure for greater bipedalism.

Several of the models listed under this heading have already been dealt with elsewhere, to some degree. For those, only aspects of the model specifically pertaining to habitat compulsion will be discussed here. Three major habitat types have been suggested for this role: trees, certain types of terrestrial habitat and shallow water.

Variations on the theme

Kieth’s Hylobatian model

Probably the earliest publication of ideas pertaining to bipedalism originating merely though some form of improvement in efficiency or as a kind of biomechanical inevitability, was that by Sir Arthur Keith in the early part of the last century (1923), when he noted that gibbons (*Hylobates*) and some new world monkeys such as spider monkeys (*Ateles*) were particularly prone to bipedal locomotion on the ground. These species are highly specialised arborealists and their main locomotor repertoire is best described as brachiation (swinging).

They rarely move on the ground but when they do so they are usually bipedal. This led Keith to propose his “hylobatian” model for early human evolution – basically that humans had branched off quite early from a brachiating form of ape. This idea gradually fell out of favour throughout the last century as more evidence became available (particularly molecular evidence) showing that humans are much more closely related to the great African apes, *Pan* and *Gorilla*.

‘Biomechanical inevitability’ (Reynolds 1985)

“Stresses on the Limbs of Quadrupedal Primates” Reynolds (1985)

The view that bipedalism is almost a logical conclusion of a trend towards increasingly orthograde posture in the primates is a difficult one to place in any classification. I have placed it here because it appears to invoke, like Keith’s hylobatian model, the notion that our upright posture and bipedal form of locomotion did not require any special adaptive explanation.

Reynolds’ paper in the *American Journal of Physical Anthropology* gave detailed evidence showing that primates, even when quadrupedal, bare a larger percentage of their body weight through their hind limbs than is the norm amongst mammals. The basic argument is that where animals use their upper limbs for other actions than quadrupedal weight bearing locomotion, they are likely to take more of their body weight on the lower limbs and that this trend would ultimately favour the evolution of bipedalism.

Reynolds argued that whereas non-hominoid primates typically possess narrow thoraces and laterally positioned scapulae, which have glenoid fossae that face largely ventrally, hominoids have relatively broad flat thoraces and dorsally placed scapulae with glenoid fossae that face more cranially and laterally. Consequently, vertically directed forces on the forelimbs of hominoids during quadrupedalism have a large component that shears across the gleno-humeral joint Reynolds (1985).

His study captured force plate data for the ground reaction forces during quadrupedal locomotion of eight primates, from five species, to estimate the distribution of the support of the body weight in order to test the hypothesis that those primates with more dorsally orientated scapulae should decrease the forces on their forelimbs during quadrupedal locomotion.

The data presented (Reynolds 1985 p 357) did not support this hypothesis but it was shown that primates generally do support most of their body weight on their hind limbs than do typical cursorial mammals. Of the species tested, *Ateles* showed the greatest hind limb support at around 70-72% with *Pan* at around 54%-56%, both increasing with higher speeds of locomotion. It was found that there was significant variation in the weight supported by the forelimbs and proposed that this variation correlated with the locomotor adaptations of the primate, be it brachiation or vertical climbing

Reynolds' conclusion that "the occurrence of bipedalism in primates represents the extreme expression of the tendency in primates to reduce the compressive forces on their forelimbs" (Reynolds 1985 p 351) was characterised by Rose (1991 p 41) as 'biomechanical inevitability' although Reynolds never used that term himself.

One of the strongest points argued was that "t[T]he stability of a joint is maintained by congruence of the articulating surfaces, strength of the joint capsule, and muscles spanning the joint. Mobility is obtained via laxity of the capsule and lack of congruence of the articulating surfaces. Thus mobility is generally obtained at the expense of strength and stability. Consequently, the forelimb joints of primates are likely to be less stable than those of most other mammals." (Reynolds 1985 p 359).

As primates, particularly large ones, have evolved the ability for various degrees of vertical climbing and brachiation, it is clear that this evolutionary trend must have reduced the stability of the forearms when used in 'standard' cursorial quadrupedalism.

Trends do seem to be identifiable, also, within those primates which are quadramanous climbers. "The rank order of these stresses suggests a source of variation. Hylobatids are bipedal; spider monkeys support 70% of their weight on their hind limbs when quadrupedal; common chimpanzees support roughly 55% of their weight on their hind limbs and also decrease the stresses on their forelimbs by other means at higher speeds, and the limited data on orang-utans indicate that they support approximately 50% of their weight on their hind limbs." (Reynolds 1985 p 360)

However, the main hypothesis of the study, that primates with more dorsally orientated scapulae should show this trend more, was not actually borne out by his data.

If one is postulating the evolution of hominin bipedalism as 'biomechanical inevitability' as does Rose (1991), then this view is not supported by the findings here either, as the taxon closest to humans, *Pan*, was found to be significantly less bipedal than Hylobatids and *Ateles*. Data from *Pongo* and *Gorilla*, not part of this study, would contradict that proposed trend even more as *Pongo* (more distant) are more bipedal than *Pan*, whereas *Gorilla* (less distant) is less bipedal.

Reynolds' paper strongly supports the assertion that the high mobility of the upper arm, which must have evolved in both old world and new world monkeys, is a strong factor in predisposing some primates to move with more of their body weight on their hind limbs. Although this does strongly imply that arboreality was a necessary prerequisite to hominin bipedalism, it seems insufficient to explain it alone, as only Hylobatidae and *Homo* amongst the primates could be said to exhibit bipedalism whereas our closest relatives, *Pan* and *Gorilla*, rarely do.

Arboreality and brachiation

Most models of hominid bipedal origins are based on the assumption that whatever caused it must have happened on an evolutionary trajectory towards a more terrestrial life from a more arboreal one.

Some models of hominin bipedal origins have emphasised this arboreal past more than others and there is good comparative evidence among arboreal primates to support them as well as in the fossil record.

Several species, e.g. the sifaka (*Propithecus diadema*) most gibbons (*Hylobates*) and the spider monkey (*Ateles geoffroyi*), have been observed to move almost exclusively bipedally on the ground in various, non-human, gaits (Fleagle, 1988) and climbing and brachiation has long been associated with the upright predisposition that bipedalism requires.

Tuttle (1969) and Stern and Susman (1983) have repeatedly argued that certain traits of the australopithecines provide evidence for quite extensive arboreality. This evidence suggests that brachiation (under-branch swinging) or vertical climbing, in primates that were relatively large, was an essential pre-requisite for hominid bipedality. The idea was perhaps initially promoted by Keith (1923) in his Hylobatian (i.e. gibbon-like) model of hominid bipedal origins but has been supported by several authorities since. Prost (1980), for example, compared the detailed locomotor limb patterns of human and chimpanzee walking and climbing using the globographic convention of Albert, Strasser, Grassmann, and Dempster (cited in Prost 1974). This method allows limb displacements during typical locomotor patterns, recorded cinematographically, to be measured, represented and thus compared. It was concluded that "field patterns of human and ape bipedalism are so different that it is doubted whether the nonhuman type could ever have been a precursor of the human type" (Prost 1980 p 175). Prost however did find an overlap in limb patterns in human bipedalism and chimpanzee vertical climbing.

Senut (2003) backs the vertical climbing idea by reviewing hominids from the early Miocene (*Proconsul heseloni*) onwards. She suggests that most of them, including *Orrorin tugenensis*, were arboreal and probably 'vertical climbers'.

Brachiation and vertical climbing are not the only forms of locomotion which have been cited as potential vehicles to get apes to begin moving bipedally. In 2007 another idea was added to the list (Thorpe et al. 2007) published their findings which basically suggest that moving about on "slender, springy supports" (O'Higgins and Elton 2007 p 1292) provided by the thinner branches of trees was the specific extra factor that caused apes to adopt the form of arboreal bipedalism which was the precursor to the human form. One distinguishing feature of their model is their support of the idea (Verhaegen et al. 2002; Niemitz 2000, 2002, 2004, 2006, 2007, 2010; Wrangham 2005; Filler 2007) that this form of locomotion was the precursor not just to hominin bipedalism but also to African ape knuckle-walking and the quadramanous climbing practiced by orang-utan, on whose locomotor behaviour the study was based. They cite the recent fossil evidence of *Sahelanthropus* and *Orrorin*, both showing some indications of upright posture, to support this claim.

Walking on snow and mud (Khöler 1959)

One of the oddest-sounding models in Rose's (1991) table is one which appears to suggest that walking on snow and mud was a factor being proposed in the evolution of hominid bipedalism. However Khöler's only reference to anything remotely related to this idea was a report that amongst the chimpanzees he studied "upright walking (without brachial support) takes place when the hands are full, when the ground is wet and cold, or when the animals are excited in various ways" (Khöler 1959 p 313). It would appear that this observation would have to be interpreted in a grossly exaggerated way, if one was to take it seriously as a potential model for hominin bipedal origins and it is not my intention to do so here.

Wading models

Due to the special consideration given to wading models in this thesis, they are dealt with on their own at the end of this section.

2.3.5 Improved efficiency of locomotion

Taylor and Rowntree (1973) argued against citing energy efficiency as a potential driver for the evolution of hominid bipedalism. Their comparison of the energy expenditure during quadrupedal and bipedal locomotion in four young trained primates (two capuchin monkeys and two chimpanzees) revealed that there was almost no difference between them. They concluded: "It is clear, although somewhat unexpected, that a number of primates expend the same amount of energy whether they move on two or four legs. Thus the cost or efficiency of bipedal versus quadrupedal locomotion should not be used in arguments weighing the relative advantages and disadvantages that bipedal locomotion conferred on man." (Taylor and Rowntree 1973 p 187).

Rodman & McHenry (1980) re-interpreted Taylor & Rowntree's (1973) work and came up with very different conclusions. Although at running speeds humans were found to be much less (about half as) efficient that a general quadruped, at slower walking speeds they turn out to be slightly more efficient (Taylor et al. 1970). Furthermore, Taylor & Rowntree (1973) had found that common chimpanzees and capuchin monkeys used more oxygen (148% and 132%, respectively) than would be predicted by this relationship and that there was no significant energetic difference, in those species, between the cost of moving bipedally and quadrupedally. Rodman & McHenry thus argued from this that human bipedalism sometimes has an energetic advantage compared to hominoid quadrupedalism and that "there was no energetic rubicon for an early hominid to cross."

The model is based on two assumptions: That the earliest bipedal apes were rather chimp-like and certainly quadrupedal on the ground, and that they started moving bipedally, thereby gaining in energy efficiency immediately, without any significant rubicon to cross.

The ‘quadrupedal last common ancestor’ assumption has long been held due to arguments based more upon parsimony (three out of four of the Hominoidea families are quadrupedal) than fossil evidence, which is all but non-existent. It is an assumption that appears much less likely today than it did in 1980 after recent new fossil finds and data from molecular evidence (more on this later).

The ‘no energetic rubicon’ assumption also has a major difficulty: If it really involves no extra effort for extant African apes to move bipedally on the ground rather than quadrupedally, as the Taylor & Rowntree (1973) data suggests, then one would predict that they’d do so around 50% of the time, or at least that it would be a more significant part of their locomotor repertoire than studies have shown. Hunt (1994), remember only found 2-3% bipedality in extant chimpanzees and almost none of that was during unsupported locomotion.

Other studies since Taylor & Rowntree (1973) have cast doubts on the assumption that there is no cost differential between quadrupedal and bipedal locomotion in primates (e.g. Rodman & McHenry 1980).

There is another problem: If the last common ancestor was a terrestrial quadruped, and if one (hominid) lineage since that ancestor became bipedal because it was more energetically efficient to do so, why not the other lineages too? One suggested solution to that problem was offered by Isbell & Young (1996), who suggested that the different evolutionary strategies resulted because hominins had larger group sizes than the ancestors of *Pan* & *Gorilla*.

Sockol et al. (2007) gave long overdue evidential support to Rodman & McHenry’s paper. They studied a group of five adult chimpanzees which was a significant improvement over the two juvenile chimps and capuchins Taylor & Rowntree studied. Their data clearly supported Rodman & McHenry’s (1980) assertion that chimpanzee locomotion is relatively inefficient as compared to modern human bipedalism at slow, walking speeds.

Significantly, however, their results included evidence which offered an explanation as to how energy efficiency might have still acted as an adaptive drive to the early adoption of bipedalism, even before any anatomical adaptations for it had evolved. One individual out of their group of five chimpanzees, had limb dimensions and gait characteristics that appeared slightly more human like. This individual was significantly more efficient than its peers. The authors submitted that such variation in a natural population of early hominids may have been sufficient for some to have begun to adopt bipedalism randomly and selection for energy efficiency naturally occurred from there.

In summary, although the energetic efficiency model does seem irresistible as a means for modern human bipedalism to have become optimised, it is far from clear that it answers questions about how hominid bipedality began in the first place. The evidence on which the model is based is mainly from perfect (treadmill) conditions. It is not at all clear that such a slight energetic advantage would favour bipedalism in the less optimal walking conditions early hominids might have encountered. For example Zamparo et al. 1992 found that the cost of walking on dry sand was 2.5 times as high as on concrete and Pandolf et al. (1976) found that the cost of walking in deep snow was up to 5 times as high as that on a treadmill. It is interesting to speculate as to whether slow human bipedality still provides an energetic advantage in such situations, or indeed if there are any conditions in which quadrupedalism may be energetically favourable.

Locomotor de-coupling (Sylvester 2006)

A sophisticated and updated form of one of the original ideas on bipedal origins, the Hylobatian (gibbon-like) theory of Keith (1923), was published in 2006 by Adam Sylvester. Although it overlaps significantly with the hylobatian model, I have classified it here under the energy efficiency category here because Sylvester's thesis (the “Locomotor de-coupling” hypothesis) is based on human biomechanics much more than comparative anatomy with gibbons. His theoretical argument is basically that certain combinations of weight bearing and flexibility in the upper limb are likely to pre-dispose some primate forms to greater degrees of bipedal locomotion. The selective pressure that produced bipedalism was the need for effective suspensory and terrestrial movement, a feature important to suspensory behaviours.

His paper reviews various ideas on bipedal origins before picking out two questions that he regards as pivotal:

1) What might have been part of the daily locomotor repertoire of early hominins and their relative capacities for different locomotor adaptations? And

2) What were the selective pressures that caused hominin bipedalism to evolve?

For the later, Sylvester lists out some of the ideas under review here and then sets out his objective:

“The purpose of this paper is to explore a possible increase in fitness resulting from the relaxation of the selective pressure for shoulder stability, which would have accompanied the adoption of bipedalism” (Sylvester 2006 p 582.)

He defines the hypothesis:

“The DH (Decoupling Hypothesis) posits that hominin bipedalism is an adaptation that reduces the selective pressure for shoulder stability so that hominins could simultaneously achieve highly effective terrestrial and suspensory behaviours, a combination not accessible to quadrupeds because of a trade-off in shoulder stability and mobility. Negative effects on fitness related to changes in hind limb morphology are not included in the models, but are discussed.” (Sylvester 2006 p 582.)

‘Locomotor decoupling’ is where a complex locomotor repertoire becomes split into two or more components. Sylvester provides a few good examples in evolution where it has occurred in the past such as the evolution of avian bird flight and argues that the evolution of human bipedalism is such an example, where a previously complex locomotor repertoire has decoupled into a dependence on bipedalism with a mobile shoulder.

Basically, Sylvester sets out a theoretical case that primate shoulder traits include conflicting selection pressures for mobility and stability and that bipedalism would reduce the selection on traits requiring stability. The study was purely theoretical, using a computer simulation, but he proposed that a baboon-like model where open terrestrial locomotion interspersed with regular arboreality might provide the right kind of mix to select for shoulders with human levels of mobility and reduced stability due to increased bipedality. However, whereas baboons tend to move in trees above branch, apes (due to their relatively large size) tend to move below branch. Sylvester tests this through computer simulations of habitats and provides some falsifiable predictions about primate locomotion and human evolution.

Some of the strengths of Sylvester's idea are that it is not teleological, that it provides a plausible precursor to human walking and knuckle walking and that it attempts to provide some falsifiable predictions. But its main weakness is that it is purely theoretical and does not provide any concrete idea which helps hominin survival value, improved food acquirement etc.

2.3.6 Wheeler's thermoregulatory model

In a series of papers in the late 1980s and early 1990s, Peter Wheeler developed a new and radical idea on hominid bipedal origins – that a major factor in its adoption was a thermoregulatory advantage in hot, grassy environments.

"The evolution of bipedality and loss of functional body hair in hominoids" Wheeler 1984

Wheeler's first paper demonstrated that an upright posture provides distinct thermoregulatory advantages for a biped over a quadruped in open, equatorial habitats. Specifically, he argued, they would be subject to significantly less direct solar radiation whilst standing in an upright posture at around noon (where the amount of body surface exposed to the sun may be as low as 7%) and also that their upper bodies, being placed higher up away from the ground, would be subject to stronger convective air currents helping them to keep cool though evaporative sweat cooling. Most of his conclusions were drawn from measurements of body profiles in the frontal and vertical planes and estimating similar body profiles in australopithecines.

Most savannah-adapted mammals, Wheeler reminds us, tend to have an advanced set of features, including the 'carotid rete', to prevent their brain from overheating. As humans lack these features, some other mechanism for cooling the brain would be required if our ancestors had also evolved there. Wheeler's hypothesis is that the upright posture offered by bipedalism may have been a significant part of another such mechanism. Using two small scale models of a putative hominid ancestors, one positioned in a quadrupedal posture and the other bipedal, Wheeler photographed the models from a range of angles corresponding to position of the sun. His results showed that the bipedal posture significantly reduced the amount of body surface exposed to the sun's rays, particularly around noon.

“The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling” (Wheeler 1991).

The arguments were developed mathematically in a later paper where Wheeler also tested his hypotheses using models placed in various grassy situations. He showed (Wheeler 1991 p 111) that a hominid which stood 1.25m tall when bipedal would gain an advantage, in terms of convective cooling, over the quadrupedal form, when standing in vegetation up to 1m tall. The same findings showed, however, that if the vegetation was taller than 1.25m then there would be no advantage at all.

To summarise, Wheeler’s thesis was that bipedalism conferred distinct thermoregulatory advantages over quadrupedalism for hominids living in open, grassy environments typical in the African savannah. However, the model is contradicted by growing evidence that the paleohabitats of the earliest bipeds appear to have been predominantly wooded and not open grasslands. (Cerling 1992; WoldeGabriel et al. 2001). This is damaging to Wheeler’s thermoregulatory hypothesis, because it is simply not workable in habitats that would offer shade from the sun and shield the hominids from breezes – both assumed in his model.

Another criticism of the model is that there is very little evidence of any animal, other than proverbial mad dogs and Englishmen, leaving the shade in the hottest part of the day in equatorial zones. To postulate that hominids would have done so in order to gain an advantage in foraging time against competitors, seems rather fanciful and seems to generate more questions than it answers. For example: What benefit does an upright posture give a hominid, in terms of thermoregulation, when the sun is lower in the sky? And: If thermoregulation was achieved by sweat cooling, from where did these hominids replenish the water that would have been lost in this way? Assuming, as this model seems to, that early hominids always lived within close proximity to permanent fresh water supplies appears to defeat the premise on which the model is based: water-side vegetation, even grasses, are usually much taller than 1.25m.

2.3.7 Dietary factors

Perhaps the most unusual idea on hominid bipedal origins was advanced in a book by de la Marett (1936a), which was greeted with a fair amount of criticism from Zuckerman (see de la Marett 1936b for a reply). Its central theme was that environmental factors, especially those influencing nutrients such as iodine, were responsible for major shifts in the attributes of populations and, consequently, the evolutionary history of many species, including *Homo sapiens.*

It is postulated that the immediate ancestors of the hominid line were brachiating apes, whose hind limbs had reduced in size and function rather like in Hylobates, and that some of these apes found themselves in elevations above “the hitherto unbroken carpet of forest with which it was formerly covered.” (de la Marett 1936a p 127) in habitats that were severely Iodine deficient.

This Iodine deficiency, according to the book’s argument, was the basis of many alterations of hominid phenotype, due mainly to mutation. In the case of mode of locomotion, the already hypertrophic forearms, it is claimed, were more vulnerable to this kind of mutation which resulted in them basically not being used at all, thereby forcing a change to bipedalism.

There is good evidence that Iodine levels are significantly depleted in mountainous areas but, as de la Marett admits, there is no real evidence to suggest that such a mineral deficiency could result in such peculiar, limb specific, deformations as to convert a brachiating ape into a bipedal one.

2.3.8 Genetic factors or lack of negative selection

Rose’s (1991) classification (according to factors of proposed selection) contains a number of groups of models which all set out to provide a plausible scenario where positive selection for bipedal posture and locomotion would have encouraged it’s adoption. The inherent assumption in all of them is that the starting point was some other form of locomotion, i.e. not bipedalism, usually some form of quadrupedalism.

There remains, however, the distinct possibility that some form of bipedalism actually preceded ape-human divergence and that it represents the ancestral state. Such models clearly should not be precluded from this review but, in such scenarios, how should one represent their suggested selective pressure for bipedalism?

It is proposed here that such models propose that the selection pressure for bipedalism was either neutral or that some negative selection pressure applied to lineages other than our own which directly or indirectly led them to ‘revert’ to the mammalian norm: quadrupedalism.

Three models of bipedal origins are discussed here which broadly fit under this category.

Vertebral development gene mutation theory (Filler 2007)

Various (Klein 1999) evolutionary biologists have proposed that distinct leaps (as opposed to strict gradualism) have played a key role in the evolution of many lineages, including our own.

Until recently, however, such proposals lacked any hard evidence as to plausible mechanisms that could account for such changes.

It has become increasingly well understood that mutations to genes involved in the developmental process can cause profound and immediate changes to the adult form. A whole field of biology, studying the evolution of development (or 'evo-devo' for short) has emerged mapping out specific mechanisms where alterations to development processes can create new and novel structures from existing genetic structures. One worker who has drawn upon these ideas in the area of the origin of hominin bipedalism is Aaron Filler.

Filler (2007) argues that mutations to the development process have clearly been involved in several key stages in the evolution of life on earth, notably those resulting in profound changes in body form. For example, Filler argues that the divergence between protostomes and deuterostomes was very unlikely to have occurred in small incremental changes of a fraction of a degree at a time, but rather simply due to a mutation in a genetic switch that caused the orientation of a larval form of an early invertebrate to switch 180º in one generation.

Along similar lines, Filler's thesis on bipedal origins is that the very orientation of the lateral spinal processes in the vertebrae appears to have switched very suddenly from the ancestral, cercopithecoid, form to something quite different in the Hominoidea. Fossil evidence from *Morotopithecus* is offered to suggest that this switch probably occurred very early, easily predating not only *Pan-Homo*, and divergence but also the much earlier *Pongo* divergence too (although not that of Hylobates).

Filler argues that upright posture and locomotion probably evolved quite by chance and that as little negative selection worked against it, it eventually became fixed in the population of all great apes.

The difficulty of why only humans became obligate bipeds and the great apes, generally, 'reverted' to the mammalian norm of quadrupedalism is not addressed very clearly but Filler argues that it was likely to be due to habitat, the humans have greater need for carrying objects than the apes.

2.3.9 Combinatory models

General notion

Several models of bipedal origins have, as their central theme, the idea that it was a mixture of locomotor requirements or a temporal mix of habitats that, acting together, drove it (Napier, 1964; Sigmon 1971; Day 1986; Rose 1991). These are briefly reviewed here. It should be remembered that very few, if any, of the models reviewed here propose an entirely exclusive scenario for the origin of hominin bipedality but those discussed here deliberately propose that a combination of factors was necessary.

Variations on the theme

Napier (1964) used an anatomical analysis of *Proconsul* as a basis for considering the precursive form of locomotion to hominid bipedalism. His conclusion was largely that their forearms were used as extant 'semi-brachiators' do today, particularly those among the New World monkeys and that truncal erectness was also part of the precursive form of locomotion. Generally, Napier rejects arguments that the immediate predecessor to the earliest hominid bipeds were in any way specialised. "… O[o]ne must look for the antecedent stage of hominid bipedalism not among the fully specialised brachiators, (as is, of course, now almost generally agreed) nor among specialised quadrupeds adapted to ground-living life, but among agile forms that employed their forelimbs in suspending the body and their hind limbs in supporting and propelling it in such a manner as to promote mobility of the hips without incurring the specialisations associated with extreme prehensility of the feet" (Napier 1964 p 685). Furthermore whatever factors drove a move to bipedalism, Napier argues that they were not singular. "It seems unlikely that any single factor was responsible for such a dramatic change in behaviour" (Napier 1964 p 687). The idea is that by a slow, incremental process, unspecialised apes, pre-adapted to upright posture and movement through a climbing ancestry, gradually adopted more bipedalism for a variety of reasons.

Becky Sigmon (1971) came to similar conclusions based on an analysis of four different extant chimpanzee behaviour studies. Her conclusions were quite clear: "Thus the nature of the habitat occupied by the four groups of chimpanzees reported in the above studies appears to have been a major factor in determining the amount of bipedal behaviour that was observed. A semi-open environment, as in Goodall's and Kortland's studies, appears to be a stimulus for increased use of bipedal locomotion, while a dense rain forest environment, as in Nissen's and Reynolds' and Reynolds' study, does little to encourage a two-legged gait" (Sigmon 1971 p 56). As chimpanzees were reported to exhibit bipedalism in several behavioural contexts it is unlikely that a single specific behaviour should be proposed as the major preadaptation for erect bipedalism. It is this aspect of Sigmon's thesis that qualifies her under the category 'combination of factors'. As she puts it, bipedalism might be expected to be used "whenever it improves the chances of survival of the animal" (Sigmon 1971 p 59). Her thesis is therefore that a change from closed to more open habitats caused various behavioural behaviours to be practiced more and that this translated, eventually, into selection for anatomical traits that made that bipedalism more efficient.

Day (1986) outlined three key pressures for the evolution of bipedalism: Improved food acquisition; improved predator avoidance; and, improved reproductive success. He then reviewed the published work in the literature that shed light on which specific factors may have worked in these three areas and appeared to support almost all of them. Specifically, in terms of food acquisition, he cited carrying ideas (Hewes 1961), the importance of woodland and vertical climbing in primates (Napier 1964), positional behaviour in food acquisition (Ripley 1979; Prost 1965; Rose 1984) and models surrounding the scavenging of food (Shipman 1983, 1984). In favour of predator avoidance, Day cited, without strong support, Kortland's (1980) suggestion that the use of thorny bushes could have been used to keep large predators at bay but argued that "upright stance and tree climbing ability both combine to increase the visual horizon for early warning of danger so that an early retreat to a safe place becomes a viable strategy" (Day 1986 p 189). Finally, Day cites Lovejoy's (1981) provisioning model in support of his claim that reproductive success would have been enhanced by bipedalism. In conclusion he wrote "I believe the pressures for the evolution of upright stance and bipedal gait can be explained in terms of improved survival advantage through enhanced food acquisition (new options in positional behaviour, food carriage and hunting), predator avoidance (running and climbing, early warning of danger and freed hands for threat displays and defence) and improved reproductive success (two freed hands for safer infant carriage and for nursing at pectoral mammae in the light of a prolonged infant dependency)" (Day 1986 p 190).

Another paper emphasising a composite solution to the problem of causation in hominid bipedalism is the much cited one by Rose (1991). Rose categorises bipedalism in several ways, as described earlier in this chapter, before going on to the main theme of his paper, which is that humans are rather unusual, amongst the primates, in having only one specific mode of locomotion which is adopted almost all the time. This peculiar state of affairs is contrasted with all other most primates, which have locomotor repertoires comprising several key modes, such as brachiation, climbing and some form of quadrupedalism, and several other minor modes. We are reminded that even modes of locomotion that are very rarely adopted may still be very important to the survival of the individual and that the overall anatomy of any primate is therefore likely to be formed by a set of traits which is, in effect, a compromise between optimal configurations for each competing mode of locomotion in the overall repertoire, including configurations that may be rarely used. Rose suggests that the australopithecines were unlikely to have been obligate bipeds, as are modern humans, but more like the typical primate pattern. He proposes however that they would have a locomotor repertoire which, perhaps, contained a much greater proportion of bipedalism than most apes. Like Sigmon (1971) and Day (1986) before him, Rose suggests that as primates exhibit facultative bipedalism in several normal, and often important, situations it is merely a question of finding a scenario whereby the importance and/or frequency of such occurrences might be amplified rather than trying to identify which of the many proposed factors might have been the *exclusive* key to the problem. Unfortunately, a clear linkage between his postulated gradual move towards more open habitats and the need for greater bipedalism is not made. In particular, no argument is attempted to explain why other primates which have made this move to more open habitats did not similarly become bipeds. Such an argument is required because, as Rose should know having studied them extensively, species of *Papio* are among the most open-living primates and, crucially in this debate, they are also amongst the most committed terrestrial quadrupeds. (*Papio anubis* were observed to spend 0.9% of their time in two-legged posture and almost never moved bipedally. 99.5% of their walking was done quadrupedally Rose 1977 p 66).

2.3.10 Wading models

As the subject of this thesis is the wading hypothesis, previously published ideas on these models are discussed last and in more detail than those covered previously.

The three models reviewed in this section all invoke moving through shallow water as a major factor in the adoption of bipedalism. As noted above, I have categorised them under the heading 'models invoking habitat compulsion', although the first (Hardy 1960) was categorised by Rose (1991) under 'postural feeding'. The choice was fairly arbitrary and I have listed it here merely because since Rose (1991), two other significant papers have been published both supporting wading models in a slightly different (and not specifically a feeding-related) context. All three versions of this hypothesis draw, primarily, on the notion that shallow water has a tendency to illicit upright posture and bipedal gait in large primates, especially apes.

“Aquatile” hypothesis (Westenhöfer 1942)

The first publication of the idea that wading in shallow water may have been a factor in the evolution of human bipedalism appears to be contained in a book called “Der Eigenweg des Menchen” (“The path of man”) by the German anatomist, Max Westenhöfer (1942).

It is a comprehensive and ambitious tome of which starts by summarising the history of ideas about human evolution and speciation from the time of the ancient Greeks through to Haeckel and Dollo.

The section postulating a possible “aquatic mode” in human evolution is relatively short (just over 2 pages out of 388, approximately 800 words) and so it is included here in full. This translation was first published in Roede et al. (1991 p 6-8) by Elaine Morgan (1991).

> *“The hypothetical aquatic life?*
>
> *The postulation of an aquatic mode of life during an early stage of human evolution is a tenable hypothesis, for which further inquiry may produce additional supporting evidence.*
>
> *The shape of the human foot, broadening towards the front, could indicate a paludine habitat, especially when we note the observations Of Mr O. Abel in his Palaeobiology (Stuttgart, 1912, pp. 229—30) where he discusses the secondary plantigradism of certain fossilised bog animals, for instance, Mesodon and Coryphodon, whose footprint shows a remarkable similarity to that of humans. For such a mammal, moreover, a move to an aquatic environment would mean that powerful teeth would become unnecessary due to the relative softness of the available food resources.*
>
> *The fact that man lacks hair — but probably was hairy at some earlier stage — suggests an analogy with the relative absence of hair in water mammals (whale, sea-cow, hippopotamus), especially since so far there is no other plausible explanation. Another indication is the subcutaneous layer of fat in humans; its capacity for expansion appears to predate human civilisation. The so-called Venus statuettes, back to the Stone Age, support this assumption. The hitherto unsolved problem concerning pigmentation in humans may be related to this problem; rather than loss of pigment in the white races, there may have been increased pigmentation in coloured ones, corresponding. In his latest book on the Significance of the Ear Muscle, Mr Henneberg also proposes an aquatic mode of life in the primate. He assumes that this ancestral hominid featured a contractile form of the ear muscle, with the anthelix (tragus and antitragus) differing in shape from that of Homo, and that this original form was subsequently lost during the transition to life on land. It is still easily possible to reproduce the original form in children by artificial means, and the original feature has in fact been observed in one living newborn baby. In his famous work Physiology of Movement (Philadelphia, 19491, Duchenne shows that electrical stimulation of the tragus and antitragus muscles in human beings is capable of closing the entrance of the ear, which is why he calls the two muscles 'constrictor conchae sup. and inf.'*
>
> *Man shares with the water mammals the regression of the olfactory organ, the bulbus and lobus olfactorlus which, according to A. Kappera and Count*

> *Haller, is connected with a certain development in the conformation of the brain, not found in the macrosomatic animals.*
>
> *As further evidence of an earlier aquatic way of living for man, one could also point to the existence of mucous glands in small benign tumours in the skin of man's back which the Prague pathologist Schickel has investigated and which, in the absence of any other possible explanation, with reference to fish and frogs, he has called atavistic. Such mucous glands have survived as the normal condition in the hippopotamus as a physiological adaptation to its aquatic environment, while in humans they appear under pathological conditions about which little is understood.*
>
> *To this can be added the not particularly rare web-like skin formation on the hand and toes (seen also in Potamogale, the otter shrew), and the direction of the body hair towards the elbow on the lower arm in human beings and anthropoids, as well as in other apes and quadrupeds. The usual explanation, that the direction of the hairs functions as protection against rain when the arms are placed over the head, is too naive to be correct. Apart from the fact that the head does not even get covered, the water then would be conducted forward from the elbow between the hairs of the upper arm and thereby directly to the skin of the armpit and chest, which would hardly be advantageous. Even if this direction of the hairs were peculiar to man, I would see it as not insignificant support for my aquatic hypothesis, since such a direction of the hairs on the lower arm during swimming (stretching the arms forward) would have been useful. This summary should not be concluded without some reference to the ideas of the anthropologist, G. L. Sera, in Naples. He takes the view that the form and development of the Adam's apple, the shortness of the outer auditory passage, the form of the musculus glutaeocruralis (m. tenuisaimus), some characteristics of the female genitals, the formation of the kidneys, the form and development of the nasal cartilage, and the form of the ear muscle may constitute evidence of a possible aquatic phase in the evolution of the platyrrine New World primates. And finally, I would point out that man's way of mating is also the standard method among water mammals such as beavers, cetaceans and sirenians.*
>
> *The aquatic theory remains an open question. But such hypotheses, which at first sound so improbable, should at least serve as a stimulus to further research, on the principle that a good detective follows up the least promising clues as well as those which seem to point to a simple solution.” Westenhöfer (1942 p 310-312).*

Thus Westenhöfer made a number of observations about unique aspects of human anatomy that appear unusual in the context of Primates but seem to echo some peculiar similarities with aquatic mammals.

This was a way of looking at the human form that was definitely unusual but it would be one that was repeated, we are told independently, by Sir Alister Hardy and then by Welsh playwright, Elaine Morgan and others.

Aquatic gathering: 'Was Man more aquatic in the past?' (Hardy 1960, Morgan 1972, 1982, 1990, 1991, 1993, 1997, 2008)

Mnemonic: 'Wading Hypothesis'

Perhaps one of the most controversial ideas on bipedal origins was that brought to the debate by Sir Alister Hardy in 1960 and subsequently developed by Elaine Morgan (For a detailed discussion of this controversy see section 2.4).

His idea was that humans had diverged from the great apes mainly through a phase of greater adaptation to moving through water including shallow coastal waters where, it was speculated, bipedalism would have evolved as a behavioural consequence of foraging for food (Hardy 1960).

Hardy described his foraging scenario this way:

> *"My thesis is that a branch of this primitive ape-stock was forced by competition from life in the trees to feed on the sea-shores and to hunt for food, shell fish, sea-urchins etc., in the shallow waters off the coast.*
>
> *I imagine him wading, at first perhaps still crouching almost on all fours groping about in the water, digging for shell fish, but becoming gradually more adept at swimming. Then, in time, I see him becoming more and more of an aquatic animal going farther out from the shore: I see him diving for shell fish, prising out worms, burrowing crabs and bivalves from the sands at the bottom of shallow seas, and breaking open sea-urchins, and then, with increasing skill, capturing fish with his hands" Hardy (1960 p 642).*

At the time of publication Hardy appeared to be unaware of any reported observations of bipedal wading in extant apes and so his arguments promoting this scenario were purely theoretical and speculative.

Hardy's argument continued:

> *"It seems indeed possible that his mastery of the erect posture arose by such toddling but performed in the water, like children at the seaside. Wading about, at first paddling and toddling along the shores in the shallows, hunting for shellfish. Man gradually went farther and farther into deeper water, swimming for a time, but having at intervals to rest - resting with his feet on the bottom and his head out of the surface: in fact, standing erect with the water supporting his weight.*
>
> *He would have to raise his head out of the water to feed: with his hands full of spoil he could do so better standing than floating It seems to me likely that Man learnt to stand erect first in the water and then, as his balance improved, he found he became better equipped for standing up on the shore when he came out, and indeed also for running. He would naturally have to return to the beach to sleep and to get water to drink: actually I imagine him to have spent at least half his time on the land." (Hardy 1960 p 644)*

Hardy's contribution to the literature on this subject was relatively small and the idea appeared to be heading for complete obscurity when it was seized upon by a successful

Welsh television playwright, Elaine Morgan, who stumbled across a positive reference to it in Desmond Morris' "The Naked Ape" (Morris, 1967).

Her deliberately provocative and controversial book "The Descent of Woman" (Morgan, 1972), published 100 years after Darwin's "Descent of Man", had two main themes. The first was to try to critique what she perceived (largely from the work of Robert Ardrey and Desmond Morris) as a very imbalanced, largely male dominated, view of the evolution of mankind. She mocked the well-established, savannah-based "Man the Mighty Hunter" view of our evolution, and offered a radically different idea in its place. The second aim of the book was to promote that idea: Hardy's "aquatic ape" hypothesis. The idea that wading might help to explain our bipedality was only briefly mentioned in that first book but her later volumes increasingly focused on it.

Morgan wrote a full chapter on bipedalism in her 1990 book, where she evaluated the wading idea against two others, labelled 'the savannah theory' and the 'neoteny theory'. The former is the 'traditional' view that humans evolved due to a change in habitat from woodland to open grassland, the latter is a view picked up from Gould (1977) suggesting that many aspects of ape-human divergence may be explained merely by a shift to more infant-like forms in the adult. Gould had noted that all apes are born with a more upright posture and with the foramen magnum anteriorly orientated as in humans. Only in apes, does the foremen magnum gradually migrate dorsally as more quadrupedalism is practiced. Morgan argued that this was more of a proximate explanation than an ultimate one. It failed to explain 'why' early hominids may have begun to move bipedally in the first place (Morgan 1990 p 64).

Her 1994 book, 'Scars of Evolution', expanded her theorising on bipedalism to two chapters. The first outlined a list of problems for bipedalism, such as much of the body's weight being transferred through the spine, an increased risk of physical damage through tripping up and falling over and a requirement to 're-engineer' the circulation to pump blood down to the feet and back up again, as well as to the brain. The second chapter listed explanations for the phenomenon as proposed in the literature. Among the theories of bipedal origins reviewed is one she labels "the water theory". Using film footage of the proboscis monkey as her primary source of evidence she described their reasons for adopting bipedalism in stark, simple terms: "Inundation of the habitat is their incentive for bipedalism. For proboscis monkeys crossing a stretch of water a couple of feet deep, walking upright offers only one single advantage, but it is an offer they cannot refuse. It enables them to breathe, whereas if they walked on four legs, their heads would be under water." (Morgan 1990 p 46)

The selective advantage of this, she argued, is much more immediate and straightforward than alternative 'savannah scenarios' where the costs, described earlier, would be greater and the benefits far fewer. "In the aquatic scenario the position is reversed." She wrote. "Walking erect in flooded terrain was less an option than a necessity. The behavioural reward - being able to walk and breathe at the same time - was instantly available. And most of the disadvantages of bipedalism were cancelled out. Erect posture imposes no strain on the spine under conditions of head-out immersion in water … In water, walking on two legs incurs no more danger of tripping over and crashing to the ground than walking on four… Water thus seems to be the only element in which bipedalism for the beginner may have been at the same compulsory and relatively free of unwelcome physical consequences" (Morgan 1990 p 47-48).

The rest of the second chapter argues against one of the main criticisms of the idea, namely that primates in general, and apes in particular, are usually averse to moving in water. Her counter-argument, to suggest that “the apes stayed where they were and the sea came in to them” (Morgan 1990 p 48), was based on geological findings that the Danakil depression became inundated by sea around 4 million years ago and that this could well have isolated, on newly formed islands, groups of early hominids living in high ground forest. She ends by offering the example of *Oreopithecus bambolii,* an ape some have considered to be a hominid ancestor, as a possible example of convergent evolution. The evidence does indicate that this species was isolated on a Mediterranean island when sea levels rose there, that it has traits indicating a kind of bipedalism and that it inhabited swampy habitats (Azzaroli et al. 1986).

Morgan’s next book on human evolution was published in 1997 which included four short chapters on the problem of bipedal origins. The first considered possible precursive forms of locomotion in hominid ancestors and in particular the ‘Hylobatian hypothesis’, which suggests that early bipedal hominids were brachiators and so, like many extant brachiators, they would have practiced bipedalism when on the ground. Morgan reports the consensus in the paleoanthropological literature that our ancestors did not evolve from chimp/gorilla-like knuckle-walkers and suggests “they simply climbed down [from the trees] and stood up” (Morgan 1997 p 42). The next three chapters then attempt to answer the question posed: ‘why?’ In the first, Morgan primarily addresses the ‘Energy efficiency’ model proposed by Rodman & McHenry and concludes that even though humans might well be 45% more efficient at slow walking than chimpanzees this is largely because we are anatomically specialised for bipedalism whereas they are not. As she puts it “the only thing wrong with it is that it has fallen into what Lewin called the ‘teleological trap’” [assuming that the final resulting condition was a major causal factor of its evolution] (Morgan 1997 p 50). In the next chapter, Morgan briefly reviews the diversity of views on bipedal origins by summarising six of them. She ends by noting that “it has been argued that with all the wealth of possible explanations to choose from, the last thing we need is yet another hypothesis” Morgan (1997 p 61), and yet, another hypothesis is exactly what she alludes to in the fourth chapter: ‘The Wading Ape?’

Her first point in the chapter is to remind readers that the paleo-environment of perhaps the best known early hominid bipeds, at Hadar, was decidedly wet and wooded and clearly prone to flooding. She wrote “There must have been times in such areas when Lucy’s ancestors were unwilling to forego the food supplies still visible on the branches of the partly submerged trees. Seeking to exploit them would have placed them in the one situation where an ape, still largely arboreal, would be obligatorily bipedal as soon as it descended to ground level” (Morgan 1997 p 63-64).

Furthermore, in contrast to the energy efficiency model she notes that “if we postulate that bipedalism arose as a consequence of wading behaviour, we are in no danger of falling into the teological trap. For an anthropoid ape in three feet of water, the motive for walking upright – however clumsily and laboriously – does not lie in some advantage that might accrue to its descendants. It is immediate and individual and, indeed indispensable. The advantage is that it allows the animal to go on breathing, whereas if it walked on four legs its nostrils would be under water” (Morgan 1997 p 64).

The simplicity of this argument ignores the fact that almost all quadrupedal mammals do not attempt to walk quadrupedally with their nostrils under water, but begin to swim. However, this only adds strength to the argument: Only apes and other large primates appear to switch from quadrupedal walking to bipedalism before attempting to swim, a rather unique trait that might will offer clues as to its origin in our lineage.

Morgan finishes her discussion of bipedal origins by giving examples of bipedalism proboscis monkeys (*Nasalis larvatus*), chimpanzees (*Pan troglodytes*) and *Gorilla*, suggesting that it is in the behavioural context of wading where they are most likely to move bipedally.

The main problem with Hardy's original idea, and Morgan's early support of it, is the lack of evidence for a coastal phase in early human evolution. In 1960 Hardy could have been forgiven for speculating that such a phase accounted for the perceived 'gap' in the fossil record (at the time) between *Proconsul* and australopithecines as coastal sites are notoriously poor at producing fossils. However, since then, increasing evidence has emerged for early bipedal hominids, each one filling in more of the 'fossil gap' and each one geographically distant from coastal habitats, thus making Hardy's coastal foraging idea seem increasingly unlikely.

Morgan followed this line in her first books too. Talking about scenarios as to why apes might have started to move in water in 1990, she suggested that the "sea came in to them" (Morgan 1990 p 48). At least this was backed up with some solid geological evidence for inundation in the north east rift valley, very close geographically to the sites most famously associated with *Australopithecus afarensis*. However, in her last book, Morgan is very clear and persuasive in promoting the inland, wet and wooded paleohabitats of Hadar as equally compelling environments where early hominids could have begun an evolutionary trajectory towards obligate bipedalism. Indeed, it was the overwhelming common sense of her writing in that fourth book that inspired me to return to academia to pursue this line of study.

The "Amphibische Generalistentheorie" Niemitz (2000, 2002, 2004, 2007, 2010)

Undoubtedly, the most significant contribution to the academic literature specifically about the contribution of wading in the evolution of human bipedalism is the work of the German anatomist and human evolutionary biologist, Carsten Niemitz. Starting in 2000, Niemitz has published one book and five scientific papers on the idea, which he has called the "Amphibische Generalistentheorie" (The Generalist Amphibian Theory).

Niemitz theory stresses a distinct demarcation between the wading idea and the so-called "aquatic ape hypothesis", contra to the opinion of this author, and so this model deserves more attention than others. All the arguments Niemitz published in the English-language are reviewed in full here – both the pro-wading ideas and those contra-"AAH" (see section 4.1.1.2 for that). The publications in German are summarised more briefly.

A theory on the evolution of human bipedalism - Die Amphibische Generalistentheorie (Niemitz 2000)

In May 2000 Niemitz first presented his ideas on this subject to a symposium on "Evolutionary Transformations and Mass Extinctions" at the Natural History Museum, Humboldt University in Berlin. The abstract of the presentation makes some general points about the uniqueness of human bipedalism before, assuring the reader that “There are a number of reasons why the Aquatic Ape Theory is obsolete. More and new arguments will be presented here.” (Niemitz 2000 p 48). The reason for this statement, odd in the context of what preceded it, immediately becomes clear with the sentence that follows: Niemitz adds “But long legs are an excellent adaptation for wading - much more than for fast running, since even small galloping monkeys are faster than running *Homo*.” (Niemitz 2000 p 48). And so, the foundation is carefully laid for the Amphibische Generalistentheorie which, one can only presume, was spoken about at greater length in the talk.

A theory on the evolution of the habitual orthograde human bipedalism - The "Amphibische Generalistentheorie" Niemitz (2002).

This talk was followed by a comprehensive paper on the subject two years later which promoted wading in shallow water as a key driver of hominid bipedalism. Like the ideas of Westenhöfer (1942), Hardy (1960), Morgan (1972, 1990, 1991, 1994, 1997) and Verhaegen et al. (2002), “The Amphibian Generalist Theory … suggests that bipedalism began in a wooded habitat … not far from a shore where our early ancestor, along with its arboreal habits, walked and waded in shallow water finding rich food with little investment” (Niemitz 2010). Food procurement from ponds and small pools is stressed in Niemitz (2004) too. “All kinds of wooded shores yield good food, almost independent of any season” (Niemitz 2015.) After a review of 14 major model types of bipedal origins, Niemitz begins to outline and evaluate his theory that of “an amphibious locomotor generalist as an ancestor of *Homo* - The ‘Amphibische Generalistentheorie’” (Niemitz 2002 p 11).

The argument begins along the lines of Rose (1991) suggesting that humans, rather uniquely amongst primates, have a single mode of locomotion in their repertoire but Niemitz makes the point that although this is undoubtedly true, humans also are unique in their ability “without special training” to undertake a diverse array of locomotor tasks: walking 30km in one day, sprint 150m, jog over 1500m, climb up a tall tree, jump, after a run up, over a 3m wide ditch, dive to a depth of 2m to retrieve an object from the bottom and swim ‘fast’ for 200m. Niemitz claims that this combination of tasks could not be done by any other mammal, let alone any non-human primate. As he puts it “In spite of the apparent specialization for bipedal posture and locomotion, humans are amazing postural and locomotor generalists” (Niemitz 2002 p 11).

Niemitz argues that this generalist capability suggests that the precursive form of locomotion could not have been highly specialised. Then, as with Reynolds (1983), Niemitz suggest that the primate trend, because of their arboreality, is hind limb dominance. This, clearly, is an important precondition for the later evolution of human bipedality. After some consideration of the evolution of the human hand and general body and limb proportions, Niemitz begins to consider the rather controversial idea that “we never came down from the trees” (Niemitz 2002 p 22). It is a surprising view, considering his emphasis on forest habitats in hominid evolution but it is supported with good comparative evidence from various primate groups showing that generally larger species are less arboreal. A clarification should also be added that “never came down from trees” does not equate to “never went up trees to escape predators.” Niemitz is not suggesting that human ancestors were not capable of climbing trees.

In a key statement, Niemitz supports Martin's (1990) statement about primate evolution: "For the reasons given here, I agree only partially with the following quote: 'The ancestral simians were presumably still essentially arboreal in habitats', but I fully agree, when Martin continues: '... But there is increasing evidence that Old World Monkeys at least underwent a shift to more terrestrial habits that has left its mark on all modern representatives of this group (see: Andrews and Aiello 1984)' " Niemitz (2002 p 26) and then spells out his assumption that the immediate precursor to human bipedalism "… never came down from the trees. They merely stayed where they were anyway – i.e. on the ground." (Niemitz 2002 p 26), although it is conceded that they retained some ability to climb trees for food and for safety from predators.

The second half of his paper begins with an impressive catalogue of reports of wading, swimming and/or food procurement from aquatic or semi-aquatic sources in at least 21 primate species. It summarised: "These episodes clearly reflect that there is a much closer relationship between quite a number of primate species and life near the shore or even in the water than has been realised. In one way or another, these > 35 primate species have close relationships with water (see also below). If we include man (for reasons, see below), we have to list about 40 species. As we have seen, this also refers to our closest relatives" Niemitz (2002 p 39).

Next, attention is turned to geological and paleoanthropological findings. Niemitz cites several fossil sites of early hominids, such as *Ardipithecus ramidus, Australopithecus afarensis* and *A. anamensis* which are associated with permanent water courses. Additionally, some evidence is provided indicating an association between human ancestors and waterside niches from the time of *Homo erectus* and later, (even including data about recent fish imports from some countries and about holiday makers' preferences for seaside locations). This later evidence is clearly much too late to have any bearing on the evolution of human bipedalism.

Then Niemitz returns to perhaps his most interesting observations, those pertaining to how human functional anatomy may be related to an amphibious life style. Some human-ape differences which have been used as explanatory vehicles by the so-called "aquatic ape hypothesis" are given primacy in the early part of that discussion. In Niemitz's words, "they will suffice to show that several of the main pillars of the theoretical building do not carry the theoretical construction" (Niemitz 2002 p 47), which I take to mean that Niemitz thinks these four characteristics do not indicate an adaptation to a fully aquatic (i.e. involving significant swimming/diving) niche. On the contrary, he cites the four traits: descended larynx (due to longer necks, and longer necks are adaptive to wading), ventro-ventro copulation (a result of bipedalism), an insulating fat layer (mainly, Niemitz claims, in the lower part of the body) and bipedalism (wading) as being better explained by what he terms his "Amphibische Generalistentheorie" (or 'general amphibious theory'), in other words by bipedal wading.

He writes "Summing up, almost all characters that have been used to lend support to the aquatic ape theory can be shown to be insignificant" Niemitz (2002 p 48).

Niemitz appears to be making a distinction between what he has classified as 'swimming and diving' adaptations (those cited by 'AAH' proponents) and 'wading' adaptations (those promoted by the 'Amphibische Generalistentheorie). This is a false dichotomy in my opinion, as the wading hypothesis of hominid bipedal origins is one of the most compelling arguments made by Hardy (1960), Morgan (1972, 1990, 1994, 1997) and Verhaegen et al. (2002).

In my opinion it unfortunate that Niemitz sought the need to distance himself from the so-called 'AAH', but having done so he proceeded to construct a theoretical framework for wading in the evolution of human bipedalism based on an analysis of human long-leggedness. His argument starts by suggesting that long-legged bipeds are very rare and most often found in wading birds and suggests four main selective advantages that would also arise form long leggedness in a hominin that regularly waded.

Increasing leg length is likely to reduce the drag on the body whilst moving through most depths of water as it raises more of the torso above the surface. This also will lead to a reduction in buoyancy which would have the effect of increasing ground reaction forces, allowing the hominid to propel itself with greater force. In deeper water, having longer legs would increase the depth threshold at which a hominid would have to beginning swimming. This is likely to have selective advantage in reducing the risk of drowning. Having longer legs are more advantageous for wading than for swimming. This would have acted as a kind of negative feedback loop on increasing the degree of aquatic adaptation.

Niemitz suggests that the limb segment lengths of humans appear to be a compromise for wading, climbing and terrestrial locomotion: "This combination of characters (1. long hind limbs, 2. middle sized plantigrade foot and 3. hind limb muscles with not very long distal tendons) makes an excellent, optimised wader. At the same time, this human anatomy is a compromise that makes a perfect walker and a good long distance runner, but a less good sprinter." Niemitz (2002:54) The argument is continued by suggesting that energetic disadvantages that are likely to be incurred by early hominid bipeds are compensated for by buoyancy in wading situations.

Niemitz concedes that such adaptive benefits in favour of upright posture and bipedal gait as may be expected in wading situations were unlikely to have resulted from only infrequent, short bursts of wading behaviour. He therefore proposes that "a truly amphibious stage seems quite probable" (Niemitz 2002 p 55), a view that turns out to be very close to that originally proposed by Hardy (1960).

He summarises his argument by suggesting that "w[W]ading proved to be energetically a very rewarding way of foraging, especially for high quality animal protein. This was probably of decisive importance for the survival of some of our ancestors in - possibly seasonal - periods of scantiness of food outside the water (cf. chapter 3.2). An ecological and locomotor generalist (opportunist) type of wading non-human primate is, at a certain stage of our evolution, a very probable ancestor to *Homo*, while the likelihood of being a descendant of a specialised type of primate is genetically very improbable." Niemitz (2002 p 57)

The paper ends…

"While other mammals have enlarged and optimised their front limbs upon entering the water, the main reason for our bipedality on the hind limbs is, ultimately, the position of the centre of mass in the bodies of primates, while the second is our increased demand for animal protein. Third, there is a development changing the landscape with increasing savannah areas. Fourth, our ancestors could make use of this scenario best, or only by changing strata and habitats, using, fifth, the gallery forest in a climbing fashion, the water in a bipedally wading manner and, finally, the savannah as the only habitual orthograde bipedal walker" Niemitz (2002 p 57).

Theorem of ubiquitous scarcity of energy (Niemitz 2002, 2004)

As an "excursus" to his main thesis, Niemitz discusses the role of energy and food acquisition in hominid evolution in what he calls the "theorem of ubiquitous scarcity of energy". Although not specifically a wading-related idea (having much in common, it seems, with Malthus' (1872) "Theory of Population") it is included here for completeness.

The argument begins with the statement that, "the ultimate motor of evolution is the latent and unavoidable scarcity of energy" (Niemitz 2002 p 8), whilst accepting that there are occasions where energy is abundant, (such as in a fruiting season). The point is thus made that all species adapt to their environment, in its ecological niche, with its specific amount of energy available.

However, Niemitz argues, that all species suffer, to a certain extent, from a scarcity of energy because as soon as there is more energy available to them than is needed to maintain a stable population size the species will use this energy in order to intensify their reproduction. Once this happens, of course, greater competition starts. The argument is then that the species will begin to evolve new strategies to use this energy faster or more .efficiently and will do so until a new balance is quickly (in evolutionary terms – perhaps a few hundred generations) found.

Das Geheimnis Des Aufrechten Gangs - Unsere Evolution Verlief Anders (2004)

Niemitz's presentation (2000) and paper (2002) was followed by a 256 page book, in German (2004), expanding greatly on the subject of the evolution of human upright posture and bipedalism and the "Amphibische Generalistentheorie" for a more general audience.

The first two chapters reviewed 16 previously published ideas. See the section on meta-analyses for more detail on this section.

Niemitz's "Theory of ubiquitous energy shortage" is outlined in the next chapter (see previous section) before one of the main points of the "Amphibische Generalistentheorie" is outlined over three chapters – the argument our ancestors were locomotor and ecological generalists and did not simply "come down from the trees" and out onto the open savannah.

The next chapter "water and water use from the beginning" provides a comprehensive survey of evidence of extant primates behaviour in water and following that, "The history of shore settlement", makes the point that humans too, have long been associated with waterside environments. The next chapter then looks at landscape preferences of modern humans and speculates that our love of water may have evolutionary roots.

The penultimate chapter ("Not out of the water") ensures a distancing from the so-called "AAH" by criticising it. See section 4.1.1.2 for more on this.

The final chapter offers more arguments for wading, and not swimming, being key factors in the evolution of human bipedalism. In a key section entitled “Natural selection for the optimal wading Primate” Niemitz (2004 p 215) poses two questions that should be asked about a putative wading ancestor:

Which body proportions might provide positive selection pressure to a quadrupedal primate that moved by wading bipedally? And…

What evidence is there that such proportions have likely evolved for such reasons in humans?

Niemitz offers several ideas supporting the notion that longer legs are a likely body proportion change in such a putative ancestors. Firstly, improving the angle one can look down into the water to detect food and dangers. Secondly, that longer legs offer less drag in water than the abdomen. Niemitz also argues that having longer legs counteracts the effect of buoyancy allowing a quicker exit from the water if one needed to escape from aquatic predators and allows one to detect the bottom earlier and safer if one had to swim.

Niemitz end his book by arguing that adding a wading perspective to previously published arguments and idea into a new synthesis, and by including a synopsis of the paleontological, anatomical, physiological, the comparative primatological and human ethological findings, a stable theoretical framework for the evolution of upright human has been possible.

Indications for an evolutionary correlation of human upright posture and an ecological niche on the shore (Niemitz 2006)

Niemitz published a second paper reinforcing his arguments in 2006. Its ten pages repeat the main arguments of the Amphibische Generalistentheorie, emphasising the paleontological evidence of early hominin sites which show evidence for an affinity to shore habitats.

The paper focuses on three main arguments for a shore dwelling scenario for human ancestors.

The first argument is one of landscape preference. Niemitz cites several cross-cultural studies which have shown that humans appear to have a preference for watery landscapes.

Niemitz cites evidence of 6 or 7 water-borne parasites associated exclusively with human beings and suggests that their co-evolution must have been multi-million year phenomenon.

A new angle is offered, where the Barbie doll is offered as a cross-cultural phenomenon indicative of a selective advantage to long-leggedness in women and (as “Ken”, the male version also has longer legs than the usual real-life form) men.

The question is posed that if muscles and body height in men are seen as indicators of evolutionary selective fitness, what might the evolutionary benefit be, specifically, of long legs? Niemitz postulates that a long leggedness in a wading ancestry would have brought about a number of advantages, which were covered before.

On similar lines, Niemitz suggests that the complicated phenomenon of varicose veins in humans might also be better explained if our ancestors had regularly waded.

The paper concludes that various problems concerning the evolution of the hominid bipedality are overcome if one considers shore habitats of African gallery forests.

Unstable and slow (“Labil und langsam” Niemitz 2007)

In 2007 Niemitz published another paper on the theme in the German natural sciences journal *Naturwissenschaftliche Rundschau*. The paper's title is a statement of a couple of the big problems with human bipedalism – its instability and lack of speed - compared to the quadrupedal locomotion of most animals. The purpose of the paper, then, is to suggest that none of the previous theories published to explain human bipedality offer scenarios with sufficiently strong selection pressure to overcome these, and other, problems and to argue that wading, alone, does so.

Niemitz backs this up with several lines of evidence.

Firstly, it is argued that many extant primates exploit shore and shallow water habitats and that when they move through shallow water they tend to stand up on their hind limbs and move bipedally.

Palaeontological evidence is also offered, as Niemitz points out the close association with the paleohabitats of early hominid fossil sites with swamps and other permanent water courses.

Then, differing from his other papers, Niemitz gives an argument from the point of view of nutrition. The polyunsaturated omega 3 fatty acid DHA is essential for brain growth and is rich in fish, the eggs of sea birds and shellfish. Another angle offered is that water-borne parasites have a very close relationship with humans which indicates that their co-evolution is very likely to have taken place in a shore dwelling context. Another physiologically-based argument offered is that common human problems associated with standing upright, such as dizziness and varicose veins are aided in water which acts rather like a "support stocking".

Niemitz argues that wading offers selection for bipedalism, and longer legs to do so, in several ways, such as reducing drag in water, allowing a better view of submerged items such as food and to allow safer movement in deeper water.

The paper ends with findings presented from surveys of the kinds of landscapes people prefer. It is noted that according to their data, in general, people prefer watery landscapes.

The evolution of the upright posture and gait - a review and a new synthesis (Niemitz 2010)

Niemitz's most recent English-language publication on the origin of human bipedality was his 2010 paper in the journal Naturwissenschaften, where he reviews 14 models of bipedal origins, including and of course paying particular attention to his own "Amphibische Generalistentheorie" or "Shore dweller hypothesis".

In eight pages, Niemitz updates the arguments for his idea that the human clade evolved from "an ecologically nonspecialized ancestor that was opportunistic in its feeding habits" (Niemitz 2010 p 250).

In comparison to the other models reviewed, it is postulated that wading behaviour provides several advantages:

- Shores are relatively food-rich.
- It can be collected reliably and consistently throughout the year.
- Water provides significant hydrostatic support.
- Water may provide sufficient buoyancy and viscosity to prevent an individual hominid (in "transitional phase") from falling.

To support his argument that humans evolved from nonspecialised ancestors, Niemitz shows evidence of the non-specific dentition in humans and compares it with similar dentition in the macaque, in contrast to the gorilla and orang-utan, which have relatively specialised teeth.

Niemitz then argues that the growing fossil evidence indicates that the "quadrupedal-bipedal" transition "took place in the huge areas of patchwork forest between the west and east coast of Africa with many thousand kilometres of shore lines along streams, lakes, and rivers" (Niemitz 2010 p 251).

Two of the earliest pieces of fossil evidence of hominid bipedalism are implicated with waterside habitats, Niemitz suggests. To support this he cites Senut (2004 p 377) that *Orrorin tugenensis* "inhabited a forested environment on the fringe of a lake margin" and Brunet et al. (2004) about *Sahelanthropus tchadensis* "The fauna comprises vertebrates that are aquatic (fish, turtles, crocodiles) and amphibious (anthracotheriids, hippopotamids) but also species adapted to the gallery and islet forests (monkeys), wooded savanna (proboscideans, giraffids, suids, etc.) and grassland (bovids, tridactyl equids)".

Next, Niemitz updates his survey of Old World monkeys (Niemitz 2002 p 24-25), collating data from Rowe (1996), Macdonald's New Encyclopaedia of Mammals (2001) as well as a number of further references, to show that 49 out of 108 were labelled as, at least occasional, swamp, mangrove, or shore dwellers, etc. and that many of them have been reported to wade bipedally when observed in water.

This locomotor response to moving in water is addressed next. "In most cases, a monkey or ape assumes an upright bipedal posture as soon as it ventures into the shallow water." Niemitz then makes perhaps the most significant point about the wading hypothesis when he states: "In contrast to all other hypotheses discussed above, wading behaviour, as proposed here, is the only behavioural pattern in which a primate is not only stimulated to stand up or to make one or two steps (e.g., harvesting food; see above). When foraging in the water, the monkey or ape is forced not only to stand up but to walk." (Niemitz 2010 p 253).

It is argued that regular wading in shallow water may have acted as an agent of selection for longer legs, and interestingly that simply being taller in the water would allow submerged items such as food to be more visible (Niemitz 2010 Fig 6 p 257). "Hence, it seems likely that, in wading ancestors, after many generations, longer legs were selected for until they became so long that they gradually lost their suitability for fast quadrupedal locomotion." (Niemitz 2010 p 256).

The issue of dangers (including that from aquatic predators) from shallow water is then specifically addressed next. Niemitz suggests that there is "a much greater spectrum of predator species on dry land than in the shallow water of streams and ponds" and that extant Primates have been seen to be "extremely vigilant on the African shores." (Niemitz 2010 p 257)

Another piece of evidence is offered, relating to the close human association with water borne parasites in Africa. Niemitz cites the claim of (Aspöck and Walochnik 2007) that such parasites as *Plasmodium vivax, Plasmodium ovale, Plasmodium falciparum, Schistosoma haematobium, Dracunculus medinensis, Brugia timori, Onchocera volvulus* and *Wucheria bancrofti* "…must have had a long common evolution with hominids" and "Almost all anthropostenoxic (Homo-specific, CN) parasites, the presence of which is bound to water, originate from Africa–i.e. from that part of the earth, where the process of hominisation began and where the upright gait evolved."

Next, Niemitz claims that "it seems of great significance that humans show anatomical adaptations, unique among primates, to insulate their lower body and legs" (Niemitz 2010 p 257), however the evidence cited to back this up is rather disappointing: a set of four thermographic images of a baboon, a bonobo and two human beings showing more heat being radiated from the lower limbs of the non-human primates than humans (Niemitz 2010 Fig. 7 p 258.) The section on the "Amphibische Generalistentheorie" ends with a section on "habitat preference" which, following on from Niemitz (2002), appears to support the idea that the humans predilection for water may be evidence of a shore dwelling past.

See section 3.2 ("Meta-analyses…") for more details on the models reviewed and section 4.1 ("Literature critical of the AAH") for more on Niemitz's included criticisms of the "Aquatic Ape Hypothesis".

'Aquarborealism' (Verhaegen et al. 2002)

Following the Hardy/Morgan idea and problems inherent in it, other proponents of the so-called 'aquatic ape' hypothesis have arrived at models of bipedal origins which are more consistent with the fossil record and timescale as we currently understand it. Perhaps the best example of this thinking is that described in Verhaegen et al. (2000) "Aquarboreal Ancestors".

The authors of this model take a quite different view to the timing of the so-called 'aquatic phase', placing it both earlier and later than that postulated by Hardy and Morgan.

According to Verhaegen et al. (2000) all great apes evolved from a last common ancestor that was already fairly well adapted to moving through water. It is important not to misinterpret this as being an "aquatic ape" or even a 'semi-aquatic' one. The term coined (originally by Marcel Williams 1998) to describe this life-style is "aquarboreal" (or climbing-wading), suggesting that they were adept both at climbing trees as well as moving through swamps and inundated terrain, rather like proboscis monkeys are today. Much of this bipedalism, clearly, would have been associated with wading through relatively shallow water for food. According to this model *Pan*, *Gorilla* and *Homo* diverged from this common starting point. *Gorilla* and, especially, *Pan* became more adapted to dry ground – and hence reverted to quadrupedalism - whereas, according to the authors, *Homo* became still more aquatically adapted having migrated to the coasts where their life style included a significant amount of swimming and diving. Important for Verhaegen et al, in this later stage, is the evolution of the 'linear build' associated with modern humans, which is proposed to have evolved as an adaptation to more streamlined swimming and diving, rather than as a result of more efficient bipedalism. Indeed they argue that modern human obligate bipedalism would not have evolved without this swimming and diving 'exaptation'.

Although the 'aquatic' part of this model is supported by very few professional physical anthropologists, the idea that the last common ancestor of all three great apes was already somewhat bipedal has almost become *de rigeur* over the last few years. Recent fossil finds and studies of molecular data have increasingly brought into question the long held assumption that the evolution of bipedalism occurred only on the hominin line. The finding of *Sahelanthropus tchadensis*, at 7 million years, is perhaps the strongest evidence to support this part of the model of Verhaegen et al.

A more significant problem with the Verhaegen et al. model though is the idea that human 'linear build' resulted from an adaptation to swimming and diving as a precursor and necessary pre-requisite to modern human bipedalism, rather than being a consequence of it. The thinking is strongly based on examples of convergent evolution, using the same sorts of analogies (e.g. blubber in marine mammals) as first proposed by Hardy (1960). For example, the bipedalism and linear build of the penguin has been cited as an example of convergence with that of humans and the fact that other birds are bipedal but not linear is offered as evidence that 'linear build' most likely evolved as a swimming/diving adaptation. However this sort of thinking seems to ignore the observation that, mostly, evolution creates diversity. Examples of convergence are common but they are still very much the exception rather than the rule. Human bipedalism obviously had a very different evolutionary history to that of the birds. Hard evidence that human bipedalism is much more efficient when fully upright, as compared to that moving with a bent hip, bent knee gait (e.g. Carey & Crompton 2005; Kuliukas et al. 2009,) provides a much more parsimonious reason why 'linear build' would have resulted once our ancestors began moving bipedally on land and the lack of analogous examples through convergence does not, in any way, damage this explanation. Finally there is a distinct paucity of evidence placing early *Homo* along coasts and even *Homo erect*us, cited by the authors as evidence of a much more aquatic (e.g. diving) hominid, has much more fossil evidence indicating it lived in-land rather than on coasts. More recently, the authors have published papers arguing that 'heavy boned' traits (e.g. pachyostosis) of *Homo erectus* is evidence of adaptation to diving, as another example of convergent evolution – this time with *Sirenia* (the manatees and dugongs).

In conclusion, although Verhaegen et al. follow some arguments of convergent evolution (e.g. linear build like penguins, heavy bones like manatees) that this author strongly disagrees with, the wading components of their model does, at least answer some of the objections to the Hardy/Morgan model – particularly in terms of timescale, and may therefore be considered to include a few improvements on their wading hypothesis.

Wrangham et al.'s shallow water fall-back foods and wading

Wrangham et al. (2009) published a paper promoting the use of wetland refugia, analogous to the modern day Okavango Delta, as key habitats in early human evolution, and even suggested that the act of moving bipedally through shallow water may have "promoted adaptations for habitual bipedality" in early hominins. They noted that underground storage organs (USOs) have been proposed as critical fall-back foods for early hominins in savannah habitats, and suggested that aquatic habitats could have been a useful source for hominins as shallow aquatic habitats tend to offer high plant growth rates, high USO densities, and relatively continuous USO availability throughout the year. Their study focuses on ecological questions about human evolution but did differ from most "traditional" savannah-based models of hominin origins in one key aspect: they proposed that access to aquatic habitats was a necessary condition for survival in broader savannah-based macro-habitat contexts (Wrangham et al. 2009).

2.3.10 Summary

This chapter has reviewed all the best known models about the evolution of hominin bipedalism published in the literature to date. It has provided some discussion as to their strengths and weaknesses but no attempt has been made to assess them. This will be addressed in the next chapter though a structured evaluative framework.

CHAPTER THREE

A NEW EVALUATIVE FRAMEWORK

3. A NEW EVALUATIVE FRAMEWORK

Reproduced and expanded upon from previously published papers…

Kuliukas, A.V. 2011a. A Wading Component in the Origin of Hominin Bipedalism. In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2013. Wading Hypotheses of the Origin of Human Bipedalism. Human Evolution 28 (3-4):213-236.

Abstract

Most papers about hominid bipedal origins start with a selective review of other previously published models. Few have attempted a comprehensive meta-analysis of them, and none have attempted to objectively assess and compare them.

Here, an evaluative framework, akin to a student essay's marking rubric, is offered for critical review. It is used by the author to evaluate and compare the 42 published models described in the previous chapter. 14 criteria are identified, organised into four main categories: Darwinian, Ecological, Paleontological and Epistemological.

A brief survey of the bipedalism models described in university-level textbooks is reported, which showed that models based on carrying, feeding, energy efficiency, social behaviour and thermoregulation were by far the most commonly discussed and that wading models were rarely mentioned.

In contrast, the evaluative framework described here found that wading models were among the strongest of the 42 models described.

The author's detailed assessments are published on the web through an open on-line tool (http://www.tinyurl.com/BipedalModels) for anyone to read, criticise and substitute with the reader's.

3.1. Introduction

In the previous chapter, 42 published models of hominin bipedal origins were reviewed and classified according to the mode of selection proposed. With so many differing potential explanations on offer, an obvious list of follow up questions might start with "which models are seen as the strongest?" and "why?"

This chapter attempts to provide some answers to these questions by reviewing the literature for any meta-analyses that have been done, by conducting a survey of university-level texts on human evolution and, most significantly for this thesis, by offering a new evaluative framework to assess and compare bipedalism models.

It needs to be stressed, from the start, that it is well understood that this is a largely subjective matter. Obviously, authorities will have different opinions about the relative merits of the ideas discussed here, and how they may or may not be assessed. It is absolutely not my intention to pretend that this chapter provides an authoritative assessment of which models of bipedalism are better than others, but merely to report my own opinions on the matter after a thorough scholarly review, and to uniquely demonstrate that these opinions have been arrived at through a methodology that is clearly defined, objective, rigorous and is itself open to criticism.

For a summary of these evaluations, and an on-line tool to enter your own, please go to www.tinyurl.com/BipedalModels.

3.2. How to assess models?

The problem of explaining hominid bipedal origins in a Darwinian context is at least 150 years old and has produced quite a voluminous literature. It is therefore perhaps surprising that little of the peer reviewed matter on the subject has focused on assessing and comparing the various published ideas. This section starts with a review of known previous meta analyses on this subject.

Meta-analyses in the peer-reviewed scientific literature

Although most of the hundreds of publications in the scientific literature about hominin bipedal origins begin with some sort of discussion of other models, very few of them could be described as offering a rigorous meta-analysis on the subject.

In this section a brief review is given of seven publications that offer a significant review of other models. Most of these do so as an introduction to the problem before offering a specific model of their own for consideration, but only their analysis of other models will be considered here.

Reviewed Meta-analyses				
Year	Paper	Description	Models Listed	*Approx. Words*
1962	Du Brul, E. The General Phenomenon of Bipedalism. American Zoologist 2 p 205-208.	Brief analysis of major types of bipedalism in animals: lizards, humans and birds. Promotes feeding models for bipedal origins.	*2*	*650*
1979	Zihlman, A., Brunker, L. Hominid Bipedalism: Then and Now. Yearbook of Physical Anthropology 22 p 132-162.	A review of different published investigations into the putative mode of locomotion of australopithecines and whether they were closer to apes or humans in their bipedality.	10	*900*
1986	Day, M. (1986). Bipedalism: Pressures, Origins and Modes. In: Wood, Bernard; Martin, Lawrence; Andrews, Peter (eds.). Major topics in primate and human evolution. Cambridge University Press (New York)	Paper discussing the adaptive pressures (aspects we're concerned with here), origins (precursive hominoid forms of the last common ancestor of apes and humans, and modes (anatomical postcranial differences between australopithecines and early *Homo*.)	9	*650*
1991	Rose, M. (1991). The Process of Bipedalization in Hominids. In "Origine(s) de la bipedalie chez les hominides" CNRS	*A classic review of ideas on bipedal origins. 20 models are listed and classified but no evaluation or comparison attempted.*	*20*	*1,300*
2002	Niemitz, C. (2002) A Theory on the Evolution of the Habitual Orthograde Human Bipedalism - The "Amphibische Generalistentheorie". Anthropologischer Anzeiger.	*A paper promoting an 'amphibian general theory' giving a fairly thorough review of earlier models.*	*16*	*3,700*
2003	Kingdon, J. (2003). Lowly Origin. Princeton University Press (Woodstock)	*A textbook dedicated to hominin bipedal origins generally, and Kingdon's promotion of his 'ground ape' squatting model for its evolution. A book of 400 pages but only ten of which were spent reviewing other models.*	*15*	*4,000*
2004	Niemitz, C. (2004) *Das Geheimnis des aufrechten Gangs. Unsere Evolution verlief anders.*	*A book discussing the evolution of the human upright posture and gait. Includes two chapters discussing 17 models in 24 pages.*	*17*	*8,000*
2004	*Jablonski, N., Chaplin, G.* (2004). *Becoming Bipedal: How do theories of bipedalization stand up to anatomical scrutiny? In: Anapol, Fred C; German, Rebecca Z; Jablonski, Nina G (eds.), (2004). Shaping Primate Evolution. Cambridge (Cambridge)*	*A detailed comparison of three models (Carrying food, postural feeding and threat display) from the standpoint of australopithecine postcranial anatomy. Most of the other published models are listed and categorised.*	*22*	*3,000*
2005	*Langdon, J. H.* (2005) The Human Strategy.	*Textbook on physical anthropology containing a chapter (9) on bipedalism where the models are reviewed in about 5 pages.*	*11*	*3,300*
2010	*Niemitz (2010). The evolution of the upright posture and gait—a review and a new synthesis*	*An updated review of bipedalism models based on the notion that savannah models are now somewhat outdated.*	*14*	*9,600*

Table 8 Reviewed Meta-Analyses

Meta-analysis review

The earliest discussion of models of bipedalism found for this review was by Du Brul (1962). It only compared factors favouring the evolution of bipedalism in hominids with other orders, such as lizards and birds. The only model of hominid bipedalism cited was his own feeding hypothesis (Du Brul 1958.)

The next, “Hominid Bipedalism: Then and Now” (Zihlman and Brunker 1979) paper analyses the behavioural and anatomical characteristics of ape and human post-crania with regard to locomotion and includes the australopithecine post-cranial anatomy in order to infer how human-like bipedalism may have evolved. Most of the paper subsequently provides a review of anatomy and behaviour of extant and extinct forms. However, a substantial part reviews the literature about the australopithecine anatomy in order to demonstrate that the consensus is of the view that it was significantly different from our own. They report that most papers used terms such as “transitional”, “intermediate”, “not fully human”, “distinctive” or “unique” (Zihlman and Brunker 1979 p 148) to describe early hominid locomotor anatomy and behaviour. None of the papers were reviewed in terms of modes of selection proposed to have caused the anatomical and behavioural shifts and therefore it is unlikely their paper influenced opinion about that subject.

Day’s (1986) paper “Bipedalism: Pressures, Origins and Modes” attributes three factors as being key in the origin of hominin bipedalism: Improved food acquisition; Improved predator avoidance and Improved reproductive success and he then identifies various models that offer strong arguments in favour of such selection pressures. No single hypothesis is favoured, rather nine different ones are suggested as being important in the process.

The 1991 CNRS publication “Origine(s) de la bipedie chez les hominides” contains several good discussions and includes one of the most cited papers on bipedal origins, Rose’s (1991) paper, “The Process of Bipedalization in Hominids”, which was used as the basis for classifying bipedalism models in the previous chapter of this thesis. As I discussed then, Rose (1991) offers a number of ways of classifying models of hominid bipedal origins and lists 20 such published models under a classification based on ‘agency of selection’ and 14 under a classification based on putative precursive forms of locomotion. Six models overlap both classifications, according to the published authors cited by Rose (1991 p 41-42) under both classifications, but only Hunt’s (1994) postural feeding hypothesis and the aquatic gathering models of Hardy (1960), Morgan (1982) and Verhaegen (1985) are exclusively cited as models under both classifications. Although Rose reports about 28 different published ideas on hominid bipedal origins, no attempt is made to evaluate them or rank them.

Kingdon’s 2003 treatise on bipedal origins, ‘Lowly Origins’ ran to some 400 pages. It included a section reviewing previously published models, listing 14 in addition to the one he promoted in his book, squat feeding. The review itself is relatively sparse, however, being completed in less than ten pages (Kingdon 2003 p 15-23) and little of it actually goes into any detail about the other models. Four alternative ideas are singled out for more elaboration than the others. Three are negatively criticised: Dawkins’ ‘behavioural meme’ idea, Rodman & McHenry’s energy efficiency model and Chapman & Jablonski’s ‘threat display’ ideas, whereas Jolly’s (1970) ‘seed eating hypothesis’ is warmly promoted possibly because it complements Kingdon’s own squat feeding hypothesis. Only one of the many forms of the carrying model are assessed. The rest of the review, as well as Kingdon’s book as a whole, covers and promotes the squat feeding hypothesis described on p47 of this thesis.

Jablonski and Chapman’s (2004) paper “How do theories of bipedalization stand up to anatomical scrutiny?” included introductory passages, which include a comprehensive list of 22 different ideas cited in 50 different publications, are promising and the authors set out a reasonable methodology to evaluate the models in terms of how they are supported by the postcranial anatomy of the australopithecines, rather like my own 14 criteria described below. However, the paper is disappointing because it only really evaluates three theories: the carrying idea, Hunt's (1994) postural feeding model, and their own 'threat display' proposal. The carrying and feeding models are rejected on the basis that they would require the putative hominin to adopt an upright posture for a large amount of time, which would be costly in terms of energy. It was argued that their own model, postulating only transitory bursts of bipedal activity, would not suffer from this problem. Most of the other twenty models they listed were mentioned only by name and no other was analysed in the same level of detail. To be fair, such a detailed examination of so many other models would have certainly been lengthy and the authors did evaluate the energy efficiency model and the thermoregulatory model in a similar way elsewhere.

A textbook on physical anthropology by John Langdon included a chapter (9) on Bipedalism with a 5 page section which reviewed 11 "historical speculations concerning the origin of bipedalism" as an historical narrative about the "imaginations of generations of anthropologists" and "how we have looked at ourselves" (Langdon 2005 p 121).

The author who appears to have written most about the published ideas on the evolution of human bipedalism is Carsten Niemitz. His first major paper promoting his "Amphibische Generalistentheorie" (Niemitz 2002), reviewed 15 other models, taking up over 3,700 words in about eight pages. The three models receiving most attention were Wheeler's Thermoregulatory hypothesis (approx. 22%), Rodman & McHenry's Energy Efficiency model (10%) and Lovejoy's provisioning hypothesis (6%).

This review was expanded upon in his book "Das Geheimnis des aufrechten Gangs. Unsere Evolution verlief anders" (Niemitz 2004). Two chapters were dedicated to reviewing the same models he discussed in his first paper, albeit in more detail, with one addition: the throwing hypothesis. The thermoregulation hypothesis was covered most, taking up approximately a quarter of all the discussion. Lovejoy's "Provisioning" model and the "energy efficiency" models were covered next most.

The most recent meta-analysis covered here is "The evolution of the upright posture and gait - a review and a new synthesis" Niemitz (2010). The whole paper was organised around a review of 14 models including his own. There was a change in the models reviewed based on the claim that "savannah scenarios" had largely been discredited in exchange for forest-based ones. Four new ideas were included that were not covered in his earlier reviews (Niemitz 2002, 2004): "The Throwing Hypothesis", "The Orthograde Scrambling Hypothesis", "The Decoupling Hypothesis" and "The Disequilibrium Syndrome Hypothesis". "Carrying Food" and "Carrying Food in combination with Social Structure" (Lovejoy's Provisioning Hypothesis) were merged into "Carrying Food and Provisioning". "Long legs and Bipedal Velocity", "Sexual Display", "Bipedalism and Energy" and "Migrations" were simply omitted as was "Evolution of Bipedalism in the Forest". So, altogether from 2002 until 2010, including his own, Niemitz has published his thoughts on at least twenty models in all.

Summary

A number of conclusions can be made from this review of meta analyses on models of hominid bipedal origins.

- Even the most comprehensive reviews are of relatively shallow depth considering the volume of literature on the subject generally. Of the 40+ models reviewed in chapter 2 (some 28,000 words in about 60 pages) only Jablonski & Chaplin (2004) and Niemitz (2002, 2004, 2010) cover more than half of them and only Niemitz (2004, 2010) spends more than ten pages doing so.
- Those papers that do analyse other models of bipedalism usually do so as a preamble to promoting their own idea.
- None attempt to rank, rate or objectively compare other models.

Survey of university-level texts

In this section, a survey of 36 undergraduate and graduate level university texts (published up to and including 2009) concerning human evolution is undertaken to determine which models of human bipedalism are most popular among the texts drawn on to teach undergraduates. No attempt is made here to evaluate if each model is presented favourably or otherwise or even to quantify how much space is given to each idea.

Textbooks were selected for this review by searching the internet for suggested reading lists for undergraduate/postgraduate taught anthropology courses from universities in English-speaking countries around the world.

Often the author classified ideas on bipedal origins, or hominin evolution generally, in ways that were quite different from those of Rose (1991) used here. In such situations I attempted to identify individual paragraphs describing the models listed by Rose and attributed them accordingly.

Sample of University Texts on Human Evolution		
No	Year	Texts reviewed, in order of publication date
1	1955	La Barre, W. The human animal. University of Chicago Press (Chicago)
2	1961	Lasker, G W. The Evolution of Man.
3	1963	Washburn, S (Ed.) Classification and Human Evolution. Aldine de gruyter (Chicago)
4	1967	Korn, N & Thompson F (Eds.) Human Evolution: Readings in Physical Anthropology. Holt, Reinhart and Winston. (New York)
5	1971	Young, J. An introduction to the study of man. Clarendon Press (Oxford)
6	1973	Buettner-Janusch, J. Physical Anthropology: A Perspective. Wiley (New York)
7	1980	Wolpoff, M. Palaeoanthropology (1st Ed). Knopf (New York)
8	1987	Lambert, D. The Cambridge Guide to Prehistoric Man. Cambridge University Press. (Cambridge).
9	1992	Jones, S., Martin, R. D., Pilbeam, D., Bunney, S. (Eds.) The Cambridge Encyclopaedia of Human Evolution. Cambridge University Press (Cambridge)
10	1995	Tudge, C. The Day Before Yesterday. Pimlico (London)
11	1996	Stringer, C. & McKie, R. African Exodus. Henry Holt & Co. (New York)
12	1997	Conroy, G. C. Reconstructing Human Origins. Norton (New York)
13		Howells, W. Getting Here. Compass Press (Washington)
14		Bradshaw. Human Evolution: A Neurological Perspective. Psychology Press. (Sussex)
15	1998	Lewin, R. Principles of Human Evolution: A Core Textbook (3r Ed.). Blackwell Science (Massachusetts)
16		Tattersall, I. Becoming human. Harcourt Brace & Co (New York)
17	1999	Klein, R. G. The Human Career (Human Biological and Cultural Origins). University of Chicago (London)
18		Lewin, R. Human Evolution - An illustrated introduction (4th Ed.) Blackwell Science (Cambridge)
19		Deacon & Deacon. Human Beginnings in South Africa. David Phillips (Cape Town)
20		Wolpoff, M. Palaeoanthropology (2nd Ed.) McGraw-Hill (Boston)
21	2000	Boyd, R. & Silk, J. B. How Humans Evolved. Norton (New York)
22		Ehrlich. Human Natures. Island Press (Washington)
23	2003	Kingdon, J. Lowly Origins. Princeton University Press (Woodstock)
24	2004	Lewin, R., Foley, R. Principles of Human Evolution: A Core Textbook (2nd Ed.) Blackwell Science (Oxford)
25		Dunbar, R. The Human Story. A New History of mankind's evolution. Faber and Faber (London)
26	2005	Langdon, J. The Human Strategy. Oxford University Press (Oxford).
27		Rice, P. C. & Moloney, N.. Biological Anthropology and Pre-History. Prentice Hall (New Jersey)
28		Gräslund, Bo. Early Humans and their World. Routledge (New York)
29		Palmer, Douglas. Seven Million Years. Orion Books (London)
30	2006	Campbell, B., Loy, J., Cruz-Uribe, K. (Eds.), Humankind Emerging (9th Ed.) Pearson (Boston)
31		Relethford, J. The Human Species (6th Ed.) McGraw-Hill (New York)
32		Gibbons, A. The First Human. Doubleday. (USA)
33		Ciochon & Fleagle (Eds.) The Human Evolution Source Book (2nd Ed.) Pearson (Boston)
34	2008	Lewin, R. Human Evolution - An illustrated introduction (5th Ed.) Blackwell Science (Oxford)
35	2009	Stanford, C., Allen, J. S., Anton, S. C. Biological Anthropology (2nd Ed.) Pearson (Boston)
36		Boyd & Silk. How Humans Evolved. Norton (New York)

Table 9 Sample of University Texts on Human Evolution

This review showed a wide variation in the number of models covered, the amount of discussion afforded to the subject as a whole and as to which individual models (if any) were favoured over others. In general, the model in question is described in a few sentences followed by an argument or two either in favour of it, or against it. The results of this brief survey are listed in Table 10.

They 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 behaviour, and thermoregulation. It should be noted that models under detailed examination in this thesis, i.e., the wading models, were among the least popular, but were still reported more often than the idea that no single factor was responsible.

Model	Text Book No (See text)																																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	N	%age
	1955	**1961**	**1967**		**1971**	**1973**	**1980**	**1987**	**1992**		**1995**	**1996**	**1997**		**1998**		**1999**				**2000**		**2003**	**2004**		**2005**				**2006**				**2008**	**2009**		N	%age
01 / Carrying: Unspecified		○				○	○		○	○	○		○		○		○	○	○		○	○	○	○		○	○							○			18	50%
01.1.1 / Carrying: Food back to gallery forest bases (Hewes 1961)			○		○				○			○								○		○				○	○					○					9	25%
01.1.2 / Carrying: Male Provisioning (Lovejoy 1981)							○		○			○		○	○		○	○				○	○	○		○		○		○	○	○	○	○	○		18	50%
01.1.3 / Carrying: Migration-carrying hypothesis (Sinclair 1986)															○		○							○										○			4	11%
01.2 / Carrying: Female driven infant carrying (Zihlman & Tanner 1981)									○			○			○		○		○	○			○	○			○	○				○		○			12	33%
01.3.3 / Carrying: Weapon wielding (Dart 1949/ Kortland 1980)							○				○							○				○				○											5	14%
01.4 / Carrying: Tool carriage (Bartholemew & Birdsell 1953)				○	○		○	○	○		○	○		○				○		○		○				○	○	○		○	○						16	44%
FORELIMB-PREHENSION (CARRYING)		●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●		●	●	●		●	●	●	●	●	●		**31**	**86%**
02.2.1 / Behavioural: Threat displays directed at other species (Kortland 1980)																				○																	1	3%
02.2.2 / Behavioural: Threat Display (Wescott 1967, Jablonski/Chapman 1990)												○			○		○					○	○	○		○				○				○			9	25%
02.3.1 / Behavioural: Vigilence (Dart 1925, Ravey 1978)					○			○					○	○	○		○		○	○			○	○		○	○	○		○	○			○			16	44%
02.4 / Behavioural: Phallic Display directed at females (Tanner 1981)																			○				○														2	6%
02.5 / Behavioural: Copied Gimmick Idea (Dawkins 2005)																							○														1	3%
SOCIAL BEHAVIOUR					●			●				●	●	●	●		●		●	●		●	●	●		●	●	●		●	●			●			**18**	**50%**
03 / Postural Feeding (Unspecified)	○									○	○			○												○	○		○				○		○		9	25%
03.1.1 / Postural Feeding: Seed-eating (Jolly 1970)							○		○			○			○		○	○				○	○	○		○								○			11	31%
03.1.2 / Postural Feeding: Terrestrial squat feeding on the forest floor (Kingdon 2003)																														○							1	3%
03.2 / Postural Feeding: From small bushes (Hunt 1994)									○			○		○	○		○		○		○	○		○		○		○						○		○	13	36%
03.4 / Postural Feeding: Specifically hunting (Cartmill /Carrier 1974)				○													○																	○			3	8%
FEEDING	●			●			●		●	●	●	●		●	●		●	●	●		●	●	●	●		●	●	●	●	●			●	●	●	●	**25**	**69%**
04.1 / Wading: Aquarboreal model (Verhaegen 2000)																							○							○							2	6%
04.1 / Wading: Coastal foraging model (Hardy, 1960)								○															○			○		○				○					5	14%
04.3 / Habitat Variability Selection Model (Potts 1998)	○															○														○							3	8%
HABITAT COMPULSION (WADING)	●							●								●							●			●		●		●		●					**8**	**22%**
04.3 / Habitat Variability Selection Model (Potts 1998)	○																																				1	3%
04.2.1 / Hylobatian Theory (Keith 1912)			○			○			○					○									○			○											5	14%
04.2.2 / Arboreal: "Upwardly Mobile" hypothesis. (Tuttle 1977)							○											○				○	○			○											5	14%
HABITAT COMPULSION (NON-WADING)			●			●	●		●					●				●				●	●			●											**9**	**25%**
05.1 / Energetic Efficiency (Rodman & McHenry 1980)									○			○	○	○	○		○			○	○		○	○		○	○			○	○			○	○	○	17	47%
05.2 / Biomechanical Inevitability: (Reynolds 1925)	○																																				1	3%
05.4 / Endurance Running (Leibermann 2006)													○													○											2	6%
05.3 / Efficiency of moving from tree to tree				○																					○			○							○		4	11%
LOCOMOTOR EFFICIENCY	●			●					●			●	●	●	●		●			●	●		●	●	●	●	●	●		●	●			●	●	●	**21**	**58%**
06 / Thermoregulatory hypothesis. (Wheeler, 1984)										○	○		○	○	○				○	○	○	○	○	○		○	○			○	○				○	○	17	47%
THERMOREGULATION										●	●		●	●	●				●	●	●	●	●	●		●	●			●	●				●	●	**17**	**47%**
07 / Dietary: Iodine deficiency (de la Marett 1936)	○																																				1	3%
DIETARY FACTORS	●																																				**1**	**3%**
09.1.1 / Combination: (Day 1971)												○																									1	3%
09.1.2 / Combination: (Napier 1964)					○																		○														2	6%
09.2 / Combination: Locomotor reprtoire (Rose 1991)																						○								○							2	6%
COMBINATION OF FACTORS					●							●										●	●							●							**5**	**14%**

The bipedalism ‘meta-analyses’, surveyed here, were usually short and incomplete, although obviously space constraints were a limitation. Langdon (2005) 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>
<tr><th colspan="3">Popularity of Bipedalism Models in University Level Text Books</th></tr>
<tr><th>Rank</th><th>Model Popularity</th><th>% age popularity</th></tr>
<tr><td>1</td><td>Carrying</td><td>86%</td></tr>
<tr><td>2</td><td>Feeding</td><td>69%</td></tr>
<tr><td>3</td><td>Energy Efficiency</td><td>58%</td></tr>
<tr><td>4</td><td>Social Behaviour</td><td>50%</td></tr>
<tr><td>5</td><td>Thermoregulatory</td><td>47%</td></tr>
<tr><td>6</td><td>Non-wading habitat compulsion</td><td>25%</td></tr>
<tr><td>7</td><td>Wading habitat compulsion</td><td>22%</td></tr>
<tr><td>8</td><td>Combination</td><td>14%</td></tr>
<tr><td>9</td><td>Dietary</td><td>3%</td></tr>
</table>

Table 11 Popularity of Bipedalism Models in University Level Text Books

How have bipedalism models been rated before?

This review of meta-analyses of models of the origin of hominin bipedalism in the scientific literature at large and university textbooks specifically reveals an absence of any systematic methodology for evaluating and comparing them. Clearly, the choice of models for inclusion in the discussion, the amount of prominence given to them and the degree of support afforded to each of them is largely a matter of opinion of the authors or editors of the texts. The process is usually done with little or no guidance offered to the reader as to understanding on what basis the decisions were made.

More often than not, it is apparent that the author wants to promote his/her own preferred model, and thus whatever ‘meta-analysis’ is given at the beginning of the piece is done to set the scene, so that the arguments presented later make even more impact.

This is an accusation that may also cross the mind of any reviewer of this thesis, as it so clearly states a preference for wading models, and indeed it is a difficult accusation to contradict. So, as a pre-emptive response to any anticipated criticism of bias, I have tried to lay out, as openly as possible, my reasons for favouring wading models by describing a comprehensive evaluative framework (see next section) so that critical reviewers will be able to identify where they think any biases may lie and react accordingly. I dare suggest that such openness has rarely been evident in previous pieces on hominid bipedal origins.

The need for an open evaluative framework

Amongst the considerable literature on hominid bipedal origins very few papers have attempted to perform a meta-analysis of other models and as far as I know, none has ever deliberately set out to evaluate and rank them.

Such a treatment may be useful to attempt to identify those models which are the strongest, or at least to determine patterns of strengths and weaknesses among them. Perhaps weaknesses in the strongest models may be found which could be remedied, thus allowing some models to be bolstered sufficiently for them to gain the sort of consensus that has been lacking in this field for so long.

This is the broad aim of the rest of this chapter. It is recognised from the outset that such an endeavour is likely to be subject to personal opinion and risks accusations of bias. To counter such criticisms, a methodology will be employed which has stood the test of time in academia.

Critical assessment of written work is the currency by which academic progress is measured. Every school pupil and undergraduate student understands that their level of scholarly accomplishment will be measured by assessments of their written work. And anyone given the task of making such assessments knows that although such measurement is apparently subjective, every attempt is made to maximise the objectivity of the process through a variety of checks and balances.

Evaluating a piece of written work, such as a student’s essay, is a difficult task by anyone’s standards, but it can be made easier and more rigorous with the use of a marking scheme or rubric. Basically, one sets out to define what one might reasonably expect of a ‘perfect’ or ‘ideal’ answer to the essay question and then a series of marks are allocated to each part of that answer. Then, irrespective of how many essays there are to mark, or even how many assessors are doing the marking, one at least has a clear guide against which to evaluate the essay. If there are multiple examiners, variation will exist within them in terms of their leniency for error and opinion but even here, these problems can be minimised by some essays being marked by second examiners so that marks may be scaled up or down accordingly.

Here, I have attempted to create what is, effectively, a marking rubric for models of hominid bipedalism which I then use to assess all the models published so far. Although I will be doing all the marking myself, justification for all my marks will be given so that other assessors may criticise my work and may arrive at their own.

In order to reduce the amount of subjectivity involved here to a minimum, I have made no attempt to weight any criteria according to some ranking of perceived importance, even though undoubtedly some such weighting is warranted (and may be applied through the provided on-line tool www.tinyurl.com/BipedalModels). Therefore, each model of bipedalism is marked very simply, against each of the evaluative criteria, as poor (0 marks), fair (1 mark), or good (2 marks).

There can never be complete agreement among readers of this thesis about either the evaluative framework itself or the resulting marks given to each model, but I am confident that such an approach is justified and worthwhile in trying to objectively assess the various models of bipedalism under review.

The basic strategy of the whole thesis is to use this evaluative framework to identify those models that are highest rated and to find weaknesses in them so that they might be improved upon. I have used this methodology to come up with what I regard as an ‘ideal’ model, which I have labelled the “River Apes… Coastal People’ model. As this model has been designed to score highly by this evaluative framework, it should be no surprise to the reader that, in the assessments that follow, my own model tends to score highest.

The model itself is outlined in detail in the last chapter (See section 7.4). Readers should jump to that section at any point in the thesis if they want to read about the model in detail.

3.3. An "optimal" model?

In this section an attempt is made to provide an evaluative framework against which models of bipedalism may be judged and compared. The purpose here is to list a set of attributes which, it is suggested, most reviewers will be able to agree with. Some attributes will be seen as more important than others but no attempt will be made here to give relative weightings to them.

Fourteen characteristics are listed and discussed below which, I argue, are important components of strong models of hominid bipedal origins.

For convenience, the criteria are grouped into four categories, labelled: Darwinian, Ecological, Paleontological and Epistemological.

The first examines the model in terms of classic Darwinian theory, and how well it promotes survivability and sexual selection in the putative hominin. The model is also tested here for being teleological ('goal orientated') as Darwinian theory dictates that each adaptation should be beneficial for the current generation and not future potential generations.

Ecological considerations evaluate the model in terms of food procurement, predator avoidance and plausible ecological scenarios for the ape-human split.

Models are also assessed for paleoecological criteria which assess how well they fit the paleoecological record and the differences between the fossil record of the earliest hominids and modern humans.

Finally, each model is evaluated epistemologically in order to assess whether it has been reported in a scientific (and testable) manner, whether it may also explain other aspects of human evolution and how compatible it is with other models.

A. Darwinian

Darwinian theory asserts that traits evolve from a combination of survivability and sexual selection. Both are vital factors. If an individual does not survive to a reproductive age, its genes cannot be passed on. Equally, no matter how well adapted an individual is to its environment and no matter how long it may survive as an individual, it must reproduce for those adaptive traits to be inherited.

It may be argued, therefore, that of all the evaluative criteria listed here, survivability and favouring sexual selection are the most important. A third factor "not teleological" is listed under this 'Darwinian' heading because it is also a key aspect of Darwinian theory that every adaptation must be of benefit to individuals currently and not to benefit some future 'design goal'.

A.1. Survival value

The model should provide plausible selection for bipedalism.

Darwinian models of bipedal origins are expected to suggest a distinct survival advantage for moving bipedally, rather than quadrupedally. Many authors have alluded to this in their work. For example Day asked "what survival advantages could have been conferred on a primate by its assumption of upright posture and bipedal gait?" Day (1986 p 188) in his review of models of bipedalism in his paper "Bipedalism: Pressures, Origins and Modes" Day (1986).

Selection can act directly, in a crude way, as a consequence of the individual's immediate locomotor behaviour, or in a more subtle way, later, through kin selection, on the offspring of individuals practising slightly more bipedalism. Population genetics teaches us that even very slightly positive selection for a particular allele can still result in fixation within a relatively short period of time. (see, e.g. Li and Graur 1991.) However, it is tentatively suggested here that the more 'immediate' and clear cut the selective advantage proposed, the better.

A.2. Favours sexual selection

It is in accordance with basic evolutionary theory that fitness is a combination of both fecundity and survivability. Whatever theory is put forward to explain the evolution of bipedal locomotion should be cognisant of both factors. Ideally it should offer scenarios where the attraction of the opposite sex is possibly enhanced, but certainly not reduced, by the adoption of bipedalism.

If the model favours selection by one sex rather than the other it should, ideally, justify that by providing good reasons for that imbalance.

A.3. Not teleological

The model should describe intermediate steps between the precursive locomotor mode suggested and human-like bipedalism that are, themselves, plausible and advantageous in their own right. One important aspect of Darwinian theory is the gradual nature of natural selection, which occurs slowly from variability in populations. In evolutionary timescales, the switch from quadrupedalism to bipedalism may well have been fairly rapid, but at the level of the living generation, it would still probably have been relatively slow and across many tiny increments. However, for a contrary (more punctuated or mutation-driven) view to this see Filler (2007).

Good models of bipedal origins should, therefore, offer a plausible selective advantage at each intermediate stage in the evolutionary process and avoid the anthropocentric notion that bipedalism was somehow 'inevitable', or 'our destiny'.

They should offer some behavioural characteristic that was practiced first before morphological adaptations followed (Napier 1964 p 687), or, ideally, the model should offer some kind of positive feedback loop suggesting that any increase in bipedalism practiced by one generation, is likely to favour more bipedalism in subsequent generations.

B. Ecological

B.1. Offers improved food acquisition

The model should offer a means for food acquisition to be improved, or at least not hindered. In Day's (1986) paper "Bipedalism: Pressures, Origins and Modes" he listed improved food acquisition first in his assumed "pressures."

As we have seen, a whole category of bipedalism models are based on the assumption that improving food procurement was a key driver for the adoption of bipedalism. Such models will be favourably judged according to this criterion.

B.2. Accounts for predation vulnerability

The model should have good answers to predation vulnerability questions.

One of the first problems to consider about the human mode of locomotion compared to that of most primates surround questions like: 'Why did our ancestors abandon the relative safety of the trees for a terrestrial existence?" and "Once they did, why adopt a relatively slow, and therefore vulnerable, mode of locomotion?" Therefore it is important that whatever the model of bipedalism, it should offer some good answers to these sorts of questions.

Models that increase the risk of predation or, at least, do not offer plausible defences would be seen as weaker on this point than ones that reduce the risk and/or provide means of escape, deterrence or some weaponry to fight.

B.3. Explains why great apes are not bipedal

Good models, in addition to giving a strong account as to why humans became obligate bipeds, should also go to the trouble to explain why extant apes, *Pan/Gorilla,* did not do so.

In this regard, it is worth remembering that although most specialists until recently, at least, still seemed to assume that the last common ancestor of *Gorilla, Pan* and *Homo* was essentially a quadruped, or at least did not practice very much bipedalism, this is no longer a consensus position. Some authors, such as Kleindienst (1975) have long argued for a more orthograde last common ancestor and in recent years evidence seems to be growing for that view. (Thorpe et al. 2007; Filler 2007.)

The possibility that *Homo* and the African great apes evolved from a common ancestor which was, to some degree at least, already partly bipedal adds another twist to this characteristic and, if anything, makes it even more important.

A good model explaining the adoption of bipedalism in the *Homo* lineage should take into account these subtleties and provide good evidence to back up whatever assumptions they make about the primary precursive mode of locomotion, and why it changed in some lineages, but not in others. Ideally, it should work whether the last common ancestor was predominantly quadruped or bipedal.

B.4. Examples of behaviour visible in extant apes

Homo sapiens is cladistically placed well within the Hominoidea (i.e. being more closely related to *Pan* than *Pan* is to *Gorilla* or *Pongo*). On that basis, it is reasonable to argue that examples of the bipedal behaviour being proposed as drivers in early hominid evolution may be exhibited as vestiges in extant apes. It has been claimed that "contexts that elicit bipedalism in extant apes may provide evidence of the selective pressures that led to hominid bipedalism" Hunt (1994 p 183), and strong evidence of this must be considered favourably when assessing any proposed model.

Extant apes clearly cannot be seen as exactly analogous to the species that existed in the Miocene from which both humans and African great apes evolved, but it is equally clear that they are the closest analogues available for study today. It is therefore proposed that whatever the model of bipedalism, it should ideally have some behavioural context that can be demonstrated, however rarely, ideally in extant great apes, or at least in some other large primate.

It is perhaps worth pointing out that this factor is probably even more important if the model assumes the last common ancestor or all the great apes was already partly bipedal, rather than a unique characteristic that evolved only on the hominid lineage from essentially quadrupedal ancestors.

B.5. Applies to both sexes

Many of the models reviewed here apply to one sex or another, quite exclusively (Dart 1959; Lovejoy 1981; Kortland 1980; Tanner 1981.) It is not suggested here that such models can be discounted on that basis but that, all other things being equal, a model that applies equally to both sexes would be seen as favourable to one that only applies to one or the other, as men and women both adopt obligate bipedalism equally well.

This point has been made by some proponents of bipedal models, including Jablonski and Chapman (1993) whose own ideas largely favour male threat displays.

C. Paleontological

C.1. Fits known paleoecological record

As argued by several proponents (Jablonski and Chaplin 1993), good models of bipedal origins should draw upon support from the fossil record and, in particular, make sense in terms of the known palaeoecological record for early hominids. Our knowledge and understanding of the ecology of the habitats of early bipeds is improving all the time. It is suggested that better models of bipedal origins should make more sense, in terms of the current paradigm of reconstructed paleohabitats, than poorer ones.

C.2. Explains anatomical anomalies of early hominids

We do not know if the fossil assemblages that have been taxonomically labelled 'australopithecines' are ancestral to *Homo,* or *Pan,* or both, or neither. However, their chronological and geographical placement, as well as the cluster of anatomical features they possess, make them acutely relevant to the debate on hominid bipedal origins. They certainly are in the hominid 'grade' if not our exact 'clade'.

Therefore, as the best estimate we have as to what an early bipedal ancestor to *Homo* might have looked like, a very positive point in favour of any model of bipedal origins would be if the bipedalism model also took some account for the traits in australopithecines that are different to both humans and apes. Ideally, it should have a compelling explanation for the locomotor anatomy differences that distinguish australopithecines from humans in terms of the putative early form of that switch to bipedalism.

C.3. Proposed precursive locomotion overlaps human bipedalism.

A model may assume that some particular form of locomotion was practiced immediately before hominid bipedalism, or in an early or intermediate form of it. If so, it is argued that this form of locomotion should significantly overlap with both human bipedalism and also with chimpanzee and gorilla knuckle-walking.

Ideally, models should propose forms of posture and/or locomotion which, although not exactly matching either human bipedalism or chimpanzee knuckle-walking, should act as a plausible precursor to both. Any adaptations that might be expected to favour that form of locomotion should also favour human-like bipedalism, as a form of exaptation.

D. Epistemological

D.1. Extended explanatory power

Good models should have explanatory power about human evolution beyond bipedal origins. Bipedal locomotion is only one major ape-human difference. Ideally, a good model explaining this trait should also account for other differences, or at least offer good reasons why, if it does not do so. According to the principle of parsimony, if a particular model, which explains hominid bipedal origins, can also explain other traits, it would be seen as stronger than an alternative which requires multiple models to explain the same set of traits.

On this point, however, care must be taken. It has to be remembered that the evolution of bipedalism in the hominin lineage clearly did precede divergences evidenced in other anatomical traits (such as encephalisation). Therefore, there is a danger of any model of bipedalism over-extending itself in trying to explain other traits which may have followed it. Ideally, the model should be sophisticated enough to cope with these points of chronology and have explanatory power beyond bipedalism without invoking any special pleading.

D.2. Complementary to other models

Science does not work on democratic principles. As Oxnard (1983 p 323) put it, "one fact that controverts an hypothesis is more powerful than a thousand that support it." However, in a highly speculative field such as this, common sense tells us that it is most unlikely that any single model of bipedal origins is likely to be *absolutely right* at the expense of every other, which therefore would be rendered *absolutely wrong*. Appeals for exclusivity in this area, it is suggested, are not positive indicators of a good model. Many, quite brilliant, people have spent most of their careers thinking about this problem and it is argued that whatever actually happened is likely to have included many of these ideas at some stage. It is therefore proposed that a good model of bipedal origins should actually be complemented by, and complementary to, other models and be contradicted by few of them.

D.3. Falsifiable, or at least testable

Good models of hominid bipedalism should be falsifiable or at least testable to some degree, as defined in the hypothetico-deductive scientific method.

It is well understood that actual 'proof' of any such scientific theory is unachievable, but some may be rejected on the basis that the predictions they make can be shown to be refuted.

At the very least, in this meta-analysis it is argued that models may be compared and evaluated on this basis.

Summary

These suggested characteristics of an 'ideal' hominid bipedal origins model will be used in the evaluations that follow of the specific models in the literature.

3.4. Bipedalism model evaluation

Evaluating the known bipedal origins models

This section comprises an evaluation of the proposed models of hominid bipedal origins that have been published in the literature to date, for each factor in the evaluative framework described in the previous section.

For each evaluation, the average assessment of all the models is given first of all, in order to estimate the overall strength of the published ideas this area. This is calculated using 2 for "good", 1 for "fair" and 0 for "poor". Then, a brief discussion and justification of the evaluations is given. To simplify the discussion, groups of models are often discussed en mass. Individual models are mentioned where they differ from their category. Please view the supporting documentation on-line (see www.tinyurl.com/BipedalModels) for full details.

A tentative ranking of models is then given by totalling the number of marks accrued for each criterion. At the end of the section these marks are totalled and an overall evaluation is offered.

A. "Darwinian"

A.1. Survival value

Overall rating: 1.33 (Fair + 33%)

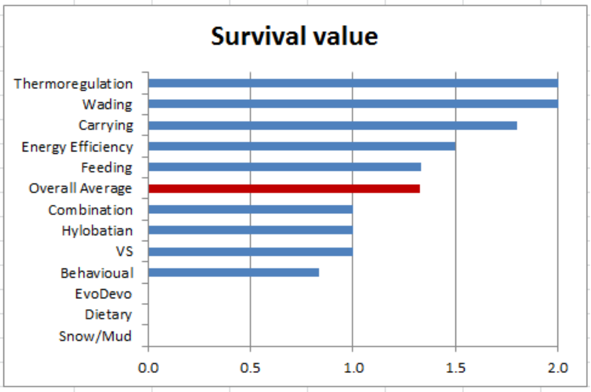

Figure 3 A1 Survival Value Summary

When evaluating survivability in the context of models of hominid bipedal origins, one is looking for clear scenarios where adopting a bipedal mode of locomotion, rather than a quadrupedal mode, would result in some distinct advantage. The more clear-cut the advantage, the better.

This criteria does not include predator avoidance which is covered specifically in criteria 5.

About 10% of reviewed models were designated as being 'poor' in this area, mostly in the behavioural category: The 'phallic display' idea, for example promoted in part by Tanner (1981); the copied gimmick idea of Dawkins (2005); the iodine deficiency idea of de la Marret (1936) and purely arboreal models such Tuttle's (1977) "upwardly mobile" hypothesis and various brachiationist models.

The first of these two models basically propose that some form of sexual selection drove bipedalism, either females being impressed by the increased visibility of the male penis, or simply by the act of moving bipedally 'catching on' as some kind of gimmick. Such specific behaviours are unlikely to be beneficial to an individual in terms of survival as they are more likely to attract predators and are likely to incur costs.

De la Marret's (1936) hypothesis is rejected as an enhancement to survival based on a lack of evidence that Iodine deficiency might act as a benefit to survival in any situation.

The arboreal models were rated poor as extant apes clearly are not hindered by their relative lack of bipedality as compared to hominins.

Almost ⅔ of the published models clearly offer a degree of survival benefit and therefore were rated 'fair'.

Just over ¼ of models were rated 'good' in this category. All the carrying models fell into this category as they all made a good case for the survival benefit of carrying various objects (Hewes 1961 p 689-701; Tanner 1981 p 30).

The energy efficiency model of Rodman & McHenry (1980) was also rated 'good' as it theoretically may provide survival benefit in terms of energy reduction (e.g. see Preuschoft 2004 p 381) as was another related model, suggesting reducing energy reduction when moving from tree to tree (Wrangham 1977).

Hunt's (1994) postural feeding model was also rated 'good' as collecting more food when in a bipedal posture clearly offers good survival benefit for its evolution.

Finally, wading models were also rated 'good' as they arguably provide the most clear cut advantage of all: In waist deep water, bipedalism raises the upper body above the surface of the water and thus prevents drowning (Morgan 1997 p 64.)

A.2. Favours sexual selection

Overall Rating: 1.19 (Fair + 19%)

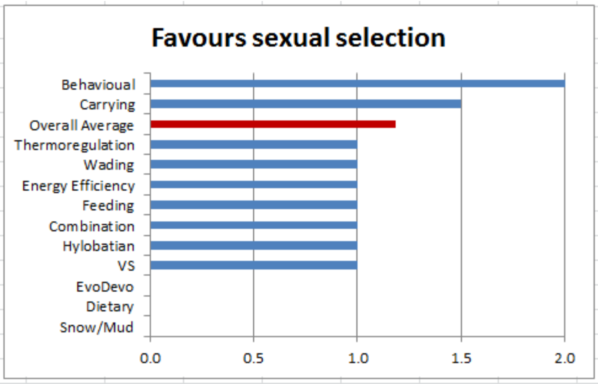

Figure 4 A2 Favours Sexual Selection Summary

This factor is included because it is a fundamental aspect of Darwinian natural selection theory and plays a major part of some models of human evolution (Parker 1987.)

When it comes to specific models of hominin bipedal origins only two were rated as being poor in this area: Köhler's (1959) idea that walking on wet substrates led to bipedalism; and de La Marret's (1936) notion that it was due to Iodine deficiency.

As most models of bipedalism promote general fitness of the individual which is likely to be recognised by the opposite sex as attractive, the majority of models reviewed were rated 'fair' in this criterion.

About ¼ of the models reviewed here were rated as offering 'good' sexual selection. These models were those that distinguish between the roles of the two genders such as the provisioning model of Lovejoy (1981), the 'nuptial gifts' idea of Parker (1987), the infant carrying models of Tanner and Zihlman (1981) and the more specific 'penile display' idea mentioned by Tanner (1981 p 165). Throwing and vigilance models were also rated 'good' as they offered potential for female selection of males based on a demonstrable behaviour that would be beneficial to survival.

Finally, Dawkins' (2005) 'behavioural meme' idea, that bipedalism arose as a kind of gimmick that was copied, was awarded a 'good' rating here.

A.3. Not teleological

Overall Rating: 0.95 (Fair – 5%)

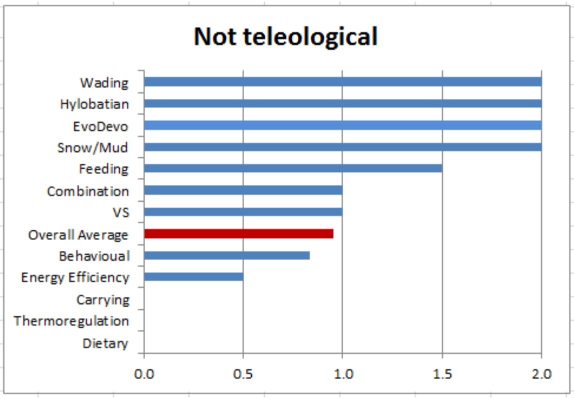

Figure 5 A3 Not Teleological Summary

This assessment evaluates whether the model is proposing causative factors that are apparent as advantages of bipedalism only in the modern human form, or whether they could also have been advantageous in a more generalised ancestral ape, and early hominins too. It therefore attempts to discriminate against models which rely on clear benefits of bipedalism, promoting consequences as causes, rather than focusing on scenarios which cause the adoption of bipedalism in the first place.

¼ of models were rated as 'poor' by this criterion. These comprised mainly the carrying and/or throwing models, including Lovejoy's (1980) provisioning model. It has been argued (e.g. Cartmill 1983, Steudel-Numbers 2006) that the ability to carry things efficiently is more likely a product of the modern human anatomy rather than a cause of it. The energy efficiency model (Rodman & McHenry 1980) and the thermoregulatory hypothesis (Wheeler 1984) have also been criticised for the same reason. Finally, Lieberman's (2007) endurance running hypothesis was rated 'poor' too for this reason.

½ the models were rated 'fair' as the cause-effect dilemma is a little more ambiguous. For example Jolly's (1970) seed eating hypothesis postulates a behaviour (crouching for seeds from tall grasses) that is not a major aspect of modern human behaviour but is nevertheless feasible in early hominins.

¼ of the models were rated 'good' in this criterion. These comprise those models which postulate that bipedalism emerged from largely arboreal apes. As this is a behaviour that is readily observed in apes, it cannot be criticised as being teleological.

Hunt's (1994) postural feeding hypothesis was also rated 'good' here as it provides strong evidence that extant apes do also adopt bipedal postures when feeding in low branches.

Finally, models suggesting habitat compulsion, such as walking on wet ground (Köhler 1959) and the various wading models are rated ‘good’ here too, as any hominid, from an early ape-human ancestor, through to modern humans or extant apes, would be predicted to move bipedally in shallow water.

‘Darwinian’ factor summary

Summary of ‘Darwinian’ Evaluations				
Code	Bipedalism Model	A.1. Survival value	A.2. Favours sexual selection	A.3. Not teleological
1.01	Carrying: Unspecified	Good	Fair	Poor
1.01.01	Carrying: Food back to gallery forest bases (Hewes 1961)	Good	Fair	Poor
1.01.02	Carrying: Scavenging (Isaac 1978)	Good	Fair	Poor
1.01.03	Carrying: Migration-carrying hypothesis (Sinclair 1986)	Good	Fair	Poor
1.01.04	Carrying: Male Provisioning (Lovejoy 1981)	Fair	Good	Poor
1.02	Carrying: Female driven infant carrying (Zihlman & Tanner 1981)	Good	Good	Poor
1.03.01	Carrying: Throwing (Fifer 1987)	Fair	Good	Poor
1.03.02	Carrying: Throwing (Dunsworth et al. 2005)	Good	Good	Poor
1.04.01	Carrying: Tool carriage (Bartholemew & Birdsell 1953)	Good	Fair	Poor
1.04.02	Carrying: Weapon wielding (Dart 1949/ Kortland 1980)	Good	Good	Poor
2.01	Behavioural: Nuptial Gifts (Parker 1987)	Fair	Good	Poor
2.02	Behavioural: Threat displays directed at other species (Kortland 1980)	Good	Good	Fair
2.03	Behavioural: Threat Display (Wescott 1967, Jablonski/Chapman 1990)	Fair	Good	Fair
2.04	Behavioural: Vigilance (Dart 1925, Ravey 1978)	Fair	Good	Fair
2.06	Behavioural: Copied Gimmick Idea (Dawkins 2005)	Poor	Good	Fair
2.07	Behavioural: Phallic Display directed at females (Tanner 1981)	Poor	Good	Fair
3.01.01	Postural Feeding: Seed-eating (Jolly 1970)	Fair	Fair	Good
3.01.02	Postural Feeding: Terrestrial squat feeding on the forest floor (Kingdon 2003)	Fair	Fair	Fair
3.02	Postural Feeding: From small bushes (Hunt 1994)	Good	Fair	Good
3.03	Postural Feeding: Arboreal predation (Eickhofft 1994)	Fair	Fair	Good
3.04.01	Postural Feeding: Stalking (Geist 1994)	Good	Fair	Fair
3.04.02	Postural Feeding: Specifically hunting (Cartmill /Carrier 1974)	Fair	Fair	Fair
4.01.01	Wading: Coastal foraging model (Hardy, 1960)	Good	Fair	Good
4.01.02	Wading: Aquarboreal model (Verhaegen 2000)	Good	Fair	Good
4.01.03	Amphibische Genalistentheorie (Niemitz 2002)	Good	Fair	Good
4.01.04	"River Apes" (Kuliukas 2013)	Good	Fair	Good
4.01.05	Wetland Foraging (Wrangham et al. 2009)	Good	Fair	Good
4.02	Walking on Snow or Mud (Köhler 1959)	Poor	Poor	Good
4.03	Habitat Variability Selection Model (Potts 1996)	Fair	Fair	Fair
4.04.01	Hylobatian Theory (Keith 1912)	Fair	Fair	Good
4.04.02	Arboreal: "Upwardly Mobile" hypothesis. (Tuttle 1977)	Fair	Fair	Good
4.04.03	Arboreal: Brachiationist Model – Gibbon-like, *Pan*-like, Bipedal (Prost 1923)	Fair	Fair	Good
5.01	Energetic Efficiency (Rodman & McHenry 1980)	Good	Fair	Poor
5.02	Biomechanical Inevitability: (Reynolds 1925)	Fair	Fair	Poor
5.03	Efficiency of moving from tree to tree	Good	Fair	Good
5.05	Running (Lieberman 2007)	Fair	Fair	Poor
6.01	Thermoregulatory hypothesis. (Wheeler, 1984)	Good	Fair	Poor
7.01	Dietary: Iodine deficiency (de la Marett 1936)	Poor	Poor	Poor
8.01	Developmental Genetic Mutation (Filler 2007)	Poor	Poor	Good
9.01	Combination: (Day 1971)	Fair	Fair	Fair
9.02	Combination: (Napier 1964)	Fair	Fair	Fair
9.03	Combination: Locomotor repertoire (Rose 1991)	Fair	Fair	Fair
9.04	Combination: Behavioural response to habitat change (Sigmon, 1971)	Fair	Fair	Fair

Table 12 Summary of ‘Darwinian’ Evaluations

According to this review of ‘Darwinian’ factors, the best models assessed here were the postural feeding and wading models, the poorest was de la Marret’s (1936) ‘Iodine deficiency’ idea, Lieberman’s (2007) ‘endurance running’ model and Wheeler’s (1984) thermoregulatory model.

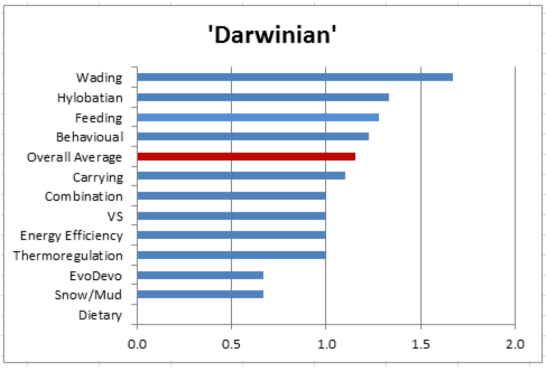

Figure 6 'Darwinian' Summary

B. Ecological

The evaluations under this heading assess each model according to how they meet various ecological considerations.

B.1. Offers improved food acquisition

Overall Rating: 1.11 (Fair + 11%)

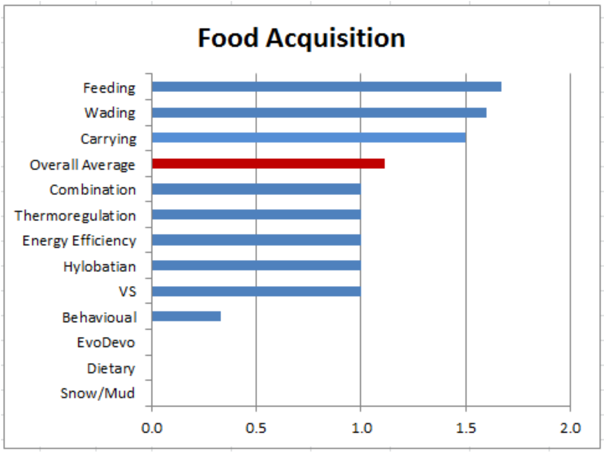

Figure 7 B1 Improved Acquisition Summary

Day (1986) suggested that improved food acquisition was probably a key ‘pressure’ for the evolution of hominin bipedalism and it is included here for that reason.

Of all the models reviewed, seven were rated as ‘poor’ by this criterion. Five of those were models which promoted weapon wielding or some other kind of aggressive posture. The other two were Filler’s (2007) genetic mutation idea and de la Marret’s (1936) Iodine deficiency model. The rest of the models fell into two groups. Half were rated ‘fair’ and half ‘good’. The ones rated fair were those models which promote some kind of scenario through which food acquisition may have been helped indirectly, or in part, as part of the model. For example Lieberman’s (2007) ‘endurance running’ model is based on the assumption that chasing antelopes to exhaustion was a factor in the lifestyle of early hominins but he would not claim that endurance running was the only means of acquiring food.

The models rated ‘good’ in this area, on the other hand, suggested scenarios where food acquisition was central to the model, including those models based on carrying food.

Bartholomew & Birdsell's (1953) 'tool carrying' model, for example, proposes that carrying tools aided food procurement in novel habitats for early hominins (Tanner 1981 p 145).

B.2. Accounts for predation vulnerability

Overall Rating: 1.02 (Fair + 2%)

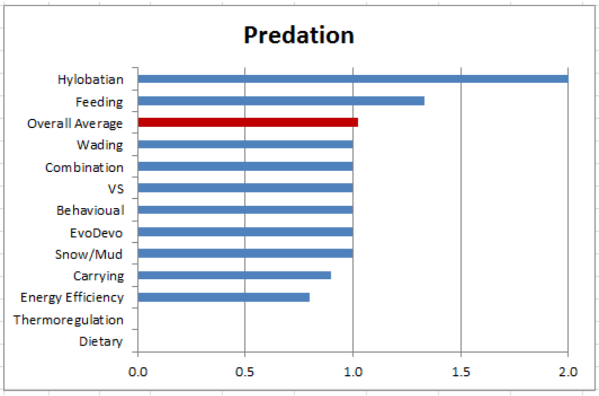

Figure 8 B2 Predation Vulnerability Summary

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 (Jolly 1970 p 9; Sigmon 1971 p 56; Isaac 1978 p 239; Geist 1978; 215; Kortland 1980; Tanner 1981; Cartmill 1983; Fifer 1987; Eickhoff 1988; Stanford 2003.) Day (1986 p 188) also treated it as a separate 'pressure' in his analysis.

In this evaluation, about ¼ of models assessed were rated 'poor' with regard to accounting for predation vulnerability. These include those models that specifically proposed carrying food and/or infants as a major factor, as such items would render the putative hominids both more attractive and also more vulnerable to predators. Models related to energy efficiency, such as Rodman & McHenry's (1980) model and Lieberman's (2007) 'endurance running model' and the thermoregulatory model of Wheeler (1984) were also rated as 'poor' because they place putative hominins in situations where long-distance, relatively slow, locomotion is given a premium without adequately explaining how they would cope with the threat of much more rapid predators.

A distinction was made about the proposed habitat in feeding models in this regard. Jolly's (1970) 'seed eating' model was rated 'poor' as it appears to place putative hominids in vulnerable open situations, whereas Hunt's (1994) 'postural feeding' and Kingdon's (2002) 'squat feeding' models were rated 'fair' because they include adequate escape routes to trees.

⅓ of models were rated 'good' by this criterion. These included those models which specifically address this issue by proposing weapon wielding or behavioural threat displays as being important factors. Models proposing a high degree of arboreality were also rated 'good' (including Niemitz's "Amphibische Generalistentheorie" as the subject was specifically addressed, especially in 2004, and 2010). It was also rated 'good' for the wading model of Hardy (1960) / Morgan (1972) because it specifically proposes a coastal niche for early hominins, allowing an escape from savannah predators.

B.3. Explains why great apes are not bipedal

Overall rating: 0.91 (Fair – 9%)

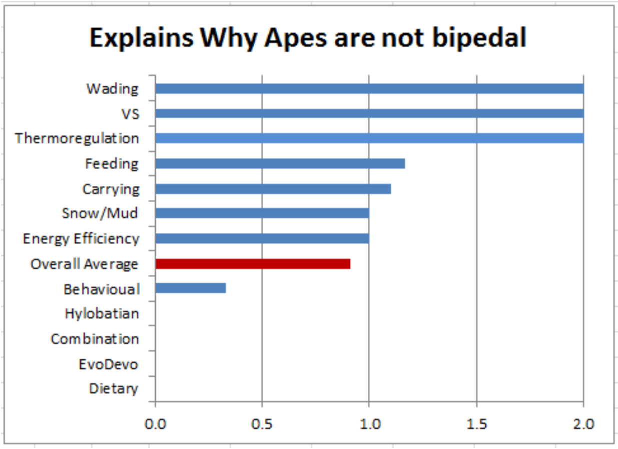

Figure 9 B3 Why Apes are Not Bipedal Summary

This criterion is similar to the third in that it assesses whether the model has an anthropocentric bias. This evaluation is a little more specific, however, in that is asks whether the model in question includes a specific 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. Although the reason supplied for this may not necessarily be an ecological one, this evaluation has been grouped under that broad heading for convenience.

This assessment was not very well met in the reviewed models with almost half being rated as 'poor'. Those models which proposed carrying items that might equally be carried by extant great apes, combinations of behaviour, specifically arboreal origins, or postural feeding models that included foods available to extant apes were considered weak in this area as they did not include any concrete reason why such an evolutionary path did not also occur to our ape cousins.

About half of the models were rated 'fair' as they did include some aspect that might explain a differentiation between the two lineages. Most of these models proposed factors that were behavioural – such as carrying some specific item unlikely to be carried by apes, throwing or running.

Six models were rated 'good' because they proposed that the key factor happened to the hominin lineage that did not to the one leading to the great apes. For example Jolly's (1970) 'seed eating' hypothesis and Wheeler's (1984) thermoregulation hypothesis propose a shift to more open savannah habitats for the early hominins that was not experienced by the ancestors of the apes. Similarly, wading models were rated as 'good' because they too suggested that it was a clear shift in habitat that was responsible. Filler's (2007) genetic mutation hypothesis was also included here because it also clearly differentiated between the two lineages.

B.4. Examples of behaviour visible in extant apes

Overall assessment: 1.05 (Fair + 5%)

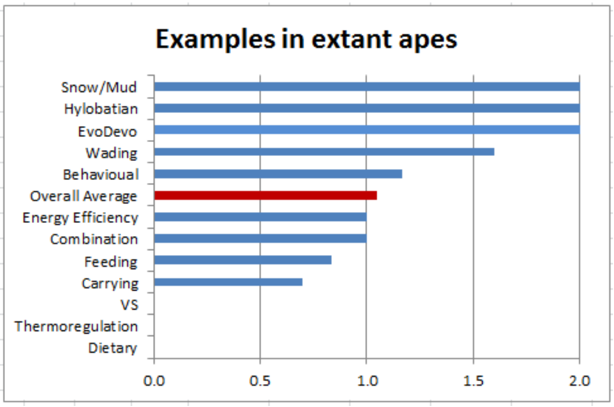

Figure 10 B4 Extant Ape Examples Summary

Hunt (1994 p 183) suggested that contexts of bipedalism in extant apes may give clues as to factors which led to the evolution of hominin bipedalism. When models of hominin bipedal origins are evaluated for this, we find that ¼ are rated ‘poor’. These comprise those models which promote behaviours which have not been observed in extant apes and is unlikely to be seen.

Half of the models were rated ‘fair’ where the model either does not promote a specific behaviour – and therefore cannot be tested in extant apes – or where the behaviour in question may be reasonably expected to be sometimes performed in extant apes, even if when such evidence is absent.

Models marked ‘good’ by this evaluation are those that promote a behaviour that has been repeatedly observed in extant apes.

B.5. Apply to both sexes

Overall assessment: 1.55 (Fair + 55%)

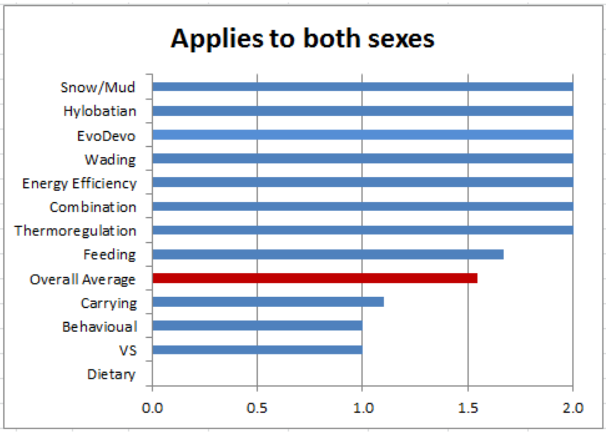

Figure 11 B5 Both Sexes Summary

Most models assessed were found to propose factors that applied equally to both sexes, however a large minority (about ¼) did not.

The models rated as ‘poor’ were those that tended to favour sexual selection or behaviours that have largely been seen as male-dominated, such as hunting or threat displays (Jablonski and

Chapman 1993). Female-dominated carrying (Tanner 1981) was also rated poorly by this evaluation.

Another quarter of the models were rated ‘fair’. These promoted scenarios that, although not exclusively practiced by one sex or another, were still unlikely to have been practiced equally by both genders. Lieberman’s (2007) ‘endurance running’ model, for example, does not preclude females but favours males as hunting was the major factor being proposed. Long distance running whilst carrying infants would also be an unlikely behaviour.

The other half of models were rated ‘good’ by this evaluation as they proposed scenarios that applied equally to both sexes.

Summary of 'Ecological' evaluations

'Ecological' Evaluation Summary						
Code	Bipedalism Model	B.1. Food	B.2. Predation	B.3. Apes not biped	B.4. Extant apes	B.5. Both sexes
1.01	Carrying: Unspecified	Fair	Fair	Fair	Fair	Fair
1.01.01	Carrying: Food back to gallery forest bases (Hewes 1961)	Good	Poor	Fair	Poor	Good
1.01.02	Carrying: Scavenging (Isaac 1978)	Good	Poor	Fair	Fair	Good
1.01.03	Carrying: Migration-carrying hypothesis (Sinclair 1986)	Good	Poor	Good	Poor	Good
1.01.04	Carrying: Male Provisioning (Lovejoy 1981)	Good	Poor	Good	Poor	Poor
1.02	Carrying: Female driven infant carrying (Zihlman & Tanner 1981)	Fair	Poor	Poor	Fair	Poor
1.03.01	Carrying: Throwing (Fifer 1987)	Fair	Good	Fair	Fair	Fair
1.03.02	Carrying: Throwing (Dunsworth et al. 2005)	Fair	Good	Fair	Fair	Fair
1.04.01	Carrying: Tool carriage (Bartholemew & Birdsell 1953)	Good	Good	Fair	Fair	Fair
1.04.02	Carrying: Weapon wielding (Dart 1949/ Kortland 1980)	Fair	Good	Fair	Fair	Fair
2.01	Behavioural: Nuptial Gifts (Parker 1987)	Good	Poor	Fair	Poor	Poor
2.02	Behavioural: Threat displays directed at other species (Kortland 1980)	Poor	Good	Poor	Fair	Fair
2.03	Behavioural: Threat Display (Wescott 1967, Jablonski/Chapman 1990)	Poor	Good	Poor	Good	Fair
2.04	Behavioural: Vigilance (Dart 1925, Ravey 1978)	Poor	Good	Fair	Fair	Good
2.07	Behavioural: Copied Gimmick Idea (Dawkins 2005)	Poor	Poor	Poor	Good	Poor
2.06	Behavioural: Phallic Display directed at females (Tanner 1981)	Poor	Poor	Poor	Fair	Good
3.01.01	Postural Feeding: Seed-eating (Jolly 1970)	Fair	Poor	Good	Fair	Good
3.01.02	Postural Feeding: Terrestrial squat feeding on the forest floor (Kingdon 2003)	Good	Fair	Fair	Fair	Good
3.02	Postural Feeding: From small bushes (Hunt 1994)	Good	Fair	Good	Good	Good
3.03	Postural Feeding: Arboreal predation (Eickhoff 1994)	Good	Good	Poor	Fair	Good
3.04.01	Postural Feeding: Stalking (Geist 1994)	Good	Good	Fair	Poor	Fair
3.04.02	Postural Feeding: Specifically hunting (Cartmill /Carrier 1974)	Fair	Good	Fair	Poor	Fair
4.01.01	Wading: Coastal foraging model (Hardy, 1960)	Good	Good	Good	Poor	Good
4.01.02	Wading: Aquarboreal model (Verhaegen 2000)	Good	Fair	Good	Good	Good
4.01.03	Amphibische Generalistentheorie (Niemitz 2002)	Good	Good	Good	Good	Good
4.01.04	"River Apes" (Kuliukas 2013)	Fair	Poor	Good	Good	Good
4.01.05	Wetland Foraging (Wrangham et al. 2009)	Good	Fair	Good	Good	Good
4.02	Walking on Snow or Mud (Köhler 1959)	Poor	Fair	Fair	Good	Good
4.03	Habitat Variability Selection Model (Potts 1996)	Fair	Fair	Good	Poor	Fair
4.04.01	Hylobatian Theory (Keith 1912)	Fair	Good	Poor	Good	Good
4.04.02	Arboreal: "Upwardly Mobile" hypothesis. (Tuttle 1977)	Fair	Good	Poor	Good	Good
4.04.03	Arboreal: Brachiationist Model – Gibbon-like, *Pan*-like, Bipedal (Prost 1923)	Fair	Good	Poor	Good	Good
5.01	Energetic Efficiency (Rodman & McHenry 1980)	Fair	Poor	Good	Fair	Good
5.02	Biomechanical Inevitability: (Reynolds 1925)	Fair	Fair	Poor	Fair	Good
5.03	Efficiency of moving from tree to tree	Fair	Good	Poor	Good	Good
5.04	Locomotor De-coupling	Fair	Fair	Fair	Fair	Good
5.05	Running (Lieberman 2007)	Fair	Poor	Good	Poor	Good
6.01	Thermoregulatory hypothesis. (Wheeler, 1984)	Fair	Poor	Good	Poor	Good
7.01	Dietary: Iodine deficiency (de la Marett 1936)	Poor	Poor	Poor	Poor	Poor
8.01	Developmental Genetic Mutation (Filler 2007)	Poor	Fair	Poor	Good	Good
9.01	Combination: (Day 1971)	Fair	Fair	Poor	Fair	Good
9.02	Combination: (Napier 1964)	Fair	Fair	Poor	Fair	Good
9.03	Combination: Locomotor repertoire (Rose 1991)	Fair	Fair	Poor	Fair	Good
9.04	Combination: Behavioural response to habitat change (Sigmon, 1971)	Fair	Fair	Poor	Fair	Good

Table 13 Summary of 'Ecological' Evaluations

In terms of these ‘ecological’ evaluations, the best models were the wading and the postural feeding models, along with those based on arboreality. The worst ranked were those promoting gender specific behaviours.

Overall ‘Ecological’ ranking

When the models are compared according to all of the ‘ecological’ factors, weighted equally, those espousing a wading factor appear strongest.

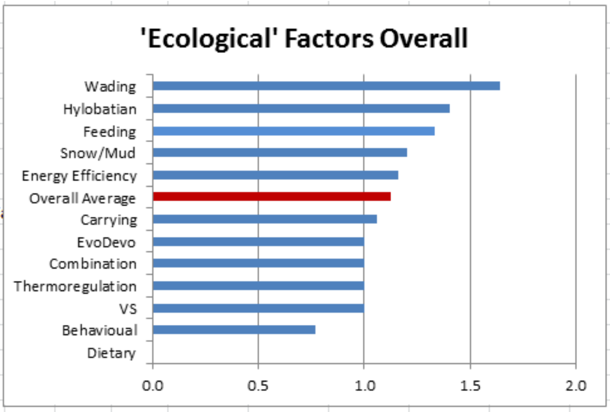

Figure 12 'Ecological' Factors Summary

C. Paleontological

The next broad heading of evaluations is labelled ‘paleontological’. These assess models of bipedalism based on how well they agree with the fossil evidence of the earliest bipeds.

C.1. Explains anatomical anomalies of early hominids

Overall assessment: 0.95 (Fair -5%)

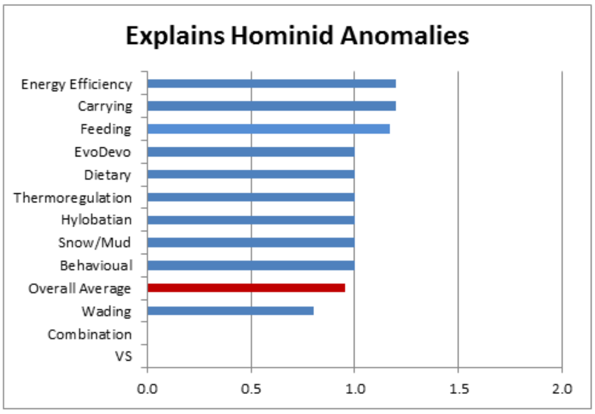

Figure 13 C1 Hominid Fossil Anomaly Summary

This review found models of bipedalism generally quite poor by this criterion. Very few authors even consider australopithecine anatomy different enough from ours to warrant an explanation and several authors do not consider australopithecines to be relevant to human evolution at all. Several models were rated ‘poor’ by this criterion largely because they promote scenarios which would probably render australopithecine locomotion less optimal than our own. Such models include the carrying models. The australopithecine post cranial anatomy, especially its platypelloid pelvis, has been described as suggesting instability when moving bipedally (e.g. Berge 1994). This instability would certainly be made worse if the individuals were carrying items at the same time and must therefore, by this criterion, make it less likely to have been a factor in its evolution.

Most models were rated ‘fair’ because they do not comment on the australopithecine post-cranial anatomy and do not promote scenarios which would render that anatomy less efficient.

Only two models were rated ‘good’ by this criterion. Kingdon’s (2003) ‘Squat feeding’ hypothesis, stands alone as an hypothesis that sets out to specifically deal with the platypelloid pelvis and its reduced anterior-posterior length. He postulates that reduced iliac wings could actually have been adaptive to squat feeding on east African gallery forest floors. The other model which is rated ‘good’ in this area is Filler’s (2007) ‘genetic mutation’ theory. This is simply because genetic mutations can cause peculiar morphologies which are not particularly adaptive.

C.2. Fits known paleoecological record.

Overall Rating: 1.11 (Fair + 11%)

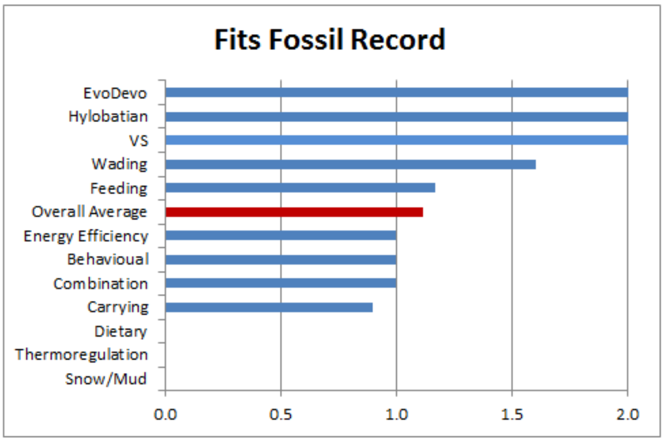

Figure 14 C2 Fits Fossil Record Summary

For this criterion, each model is evaluated according to how well it fits the currently known paleoecological record of the earliest bipedal hominids. In this regard it acts to discriminate against those models that promote a purely savannah-based paradigm. In the past twenty years, hominid finds have repeatedly urged a reassessment of that paradigm as evidence has mounted showing hominids living in relatively wet and wooded habitats. (WoldeGabriel et al. 2001, Thorpe et al. 2007).

Only five models were rated ‘poor’ according to this criterion, four of which were due to embracing the savannah paradigm. These were Rodman & McHenry’s (1980) ‘energy efficiency’ model, Wheeler’s (1984) ‘thermoregulatory’ hypothesis, Lieberman’s (2007) ‘endurance running’ model and Jolly’s (1970) ‘seed eating’ hypothesis. 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.

A fifth model, the Hardy (1960) / Morgan (1972) “aquatic ape” hypothesis which specifically promoted a coastal niche for the origin of hominid bipedalism, was also rated ‘poor’ here as there is, as yet, no good evidence associating early hominids with coastal niches.

Most of the models were rated ‘fair’ as they are either non-committal about the paleohabitat proposed or else they are ambiguous about it.

¼ of 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.

C.3. Proposed precursive locomotion overlaps human bipedalism.

Overall assessment: 1.07 (Fair + 7%)

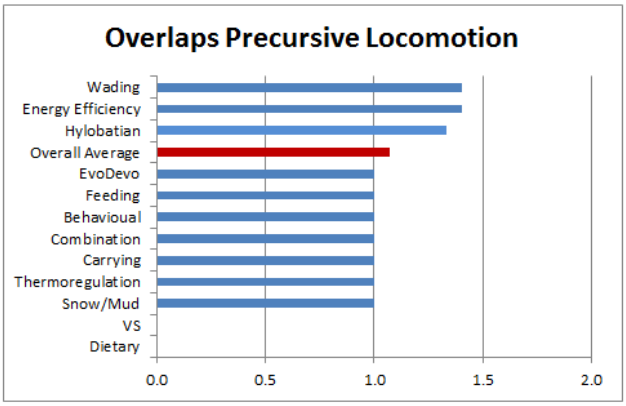

Figure 15 C3 Overlaps Precursive Mode Summary

This evaluation 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. It is therefore similar to the 'Darwinian' criterion 'not teleological' and the 'ecological' criterion 'also explains why extant apes are not bipedal' in that is assesses whether the model is also concerned with the evolution of great ape locomotion as well as human.

Unfortunately, almost all the models failed to describe what they saw as the precursive form of locomotion before hominin bipedalism and therefore 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 were rated 'poor'.

Seven models were rated 'good' because they did elaborate on the precursive form and suggested that it would be compatible with both human bipedalism and forms of extant ape locomotion. These were the arboreal models, the postural feeding ones and the 'aquarboreal' (climbing-wading) model.

'Paleontological' Evaluation Summary				
Code	Bipedalism Model	C.1. Hominid Anomalies	C.2. Fossil Record	C.3. Precursor Locomotion
1.01	Carrying: Unspecified	Fair	Fair	Fair
1.01.01	Carrying: Food back to gallery forest bases (Hewes 1961)	Fair	Fair	Fair
1.01.02	Carrying: Scavenging (Isaac 1978)	Fair	Fair	Fair
1.01.03	Carrying: Migration-carrying hypothesis (Sinclair 1986)	Fair	Poor	Fair
1.01.04	Carrying: Male Provisioning (Lovejoy 1981)	Fair	Fair	Fair
1.02	Carrying: Female driven infant carrying (Zihlman & Tanner 1981)	Fair	Fair	Fair
1.03.01	Carrying: Throwing (Fifer 1987)	Good	Fair	Fair
1.03.02	Carrying: Throwing (Dunsworth et al. 2005)	Good	Fair	Fair
1.04.01	Carrying: Tool carriage (Bartholemew & Birdsell 1953)	Fair	Fair	Fair
1.04.02	Carrying: Weapon wielding (Dart 1949/ Kortland 1980)	Fair	Fair	Fair
2.01	Behavioural: Nuptial Gifts (Parker 1987)	Fair	Fair	Fair
2.02	Behavioural: Threat displays directed at other species (Kortland 1980)	Fair	Fair	Fair
2.03	Behavioural: Threat Display (Wescott 1967, Jablonski/Chapman 1990)	Fair	Fair	Fair
2.04	Behavioural: Vigilance (Dart 1925, Ravey 1978)	Fair	Fair	Fair
2.07	Behavioural: Copied Gimmick Idea (Dawkins 2005)	Fair	Fair	Fair
2.06	Behavioural: Phallic Display directed at females (Tanner 1981)	Fair	Fair	Fair
3.01.01	Postural Feeding: Seed-eating (Jolly 1970)	Fair	Poor	Fair
3.01.02	Postural Feeding: Terrestrial squat feeding on the forest floor (Kingdon 2003)	Good	Good	Fair
3.02	Postural Feeding: From small bushes (Hunt 1994)	Fair	Fair	Fair
3.03	Postural Feeding: Arboreal predation (Eickhofft 1994)	Fair	Good	Fair
3.04.01	Postural Feeding: Stalking (Geist 1994)	Fair	Fair	Fair
3.04.02	Postural Feeding: Specifically hunting (Cartmill /Carrier 1974)	Fair	Fair	Fair
4.01.01	Wading: Coastal foraging model (Hardy, 1960)	Poor	Poor	Fair
4.01.02	Wading: Aquarboreal model (Verhaegen 2000)	Poor	Good	Good
4.01.03	Amphibische Generalistentheorie (Niemitz 2002)	Fair	Fair	Fair
4.01.04	"River Apes" (Kuliukas 2013)	Good	Good	Good
4.01.05	Wetland Foraging (Wrangham et al. 2009)	Fair	Good	Fair
4.02	Walking on Snow or Mud (Köhler 1959)	Fair	Poor	Fair
4.03	Habitat Variability Selection Model (Potts 1996)	Poor	Good	Poor
4.04.01	Hylobatian Theory (Keith 1912)	Fair	Good	Fair
4.04.02	Arboreal: "Upwardly Mobile" hypothesis. (Tuttle 1977)	Fair	Good	Fair
4.04.03	Arboreal: Brachiationist Model – Gibbon-like, *Pan*-like, Bipedal (Prost 1923)	Fair	Good	Good
5.01	Energetic Efficiency (Rodman & McHenry 1980)	Fair	Fair	Good
5.02	Biomechanical Inevitability: (Reynolds 1925)	Fair	Fair	Fair
5.03	Efficiency of moving from tree to tree	Fair	Good	Fair
5.04	Locomotor De-coupling	Fair	Fair	Fair
5.05	Running (Lieberman 2007)	Good	Poor	Good
6.01	Thermoregulatory hypothesis. (Wheeler, 1984)	Fair	Poor	Fair
7.01	Dietary: Iodine deficiency (de la Marett 1936)	Fair	Poor	Poor
8.01	Developmental Genetic Mutation (Filler 2007)	Fair	Good	Fair
9.01	Combination: (Day 1971)	Poor	Fair	Fair
9.02	Combination: (Napier 1964)	Poor	Fair	Fair
9.03	Combination: Locomotor repertoire (Rose 1991)	Poor	Fair	Fair
9.04	Combination: Behavioural response to habitat change (Sigmon, 1971)	Poor	Fair	Fair

Table 14 'Paleontological' Evaluation Summary

According to this group of evaluations, the best rated group are the Hylobatian (gibbon-like) models.

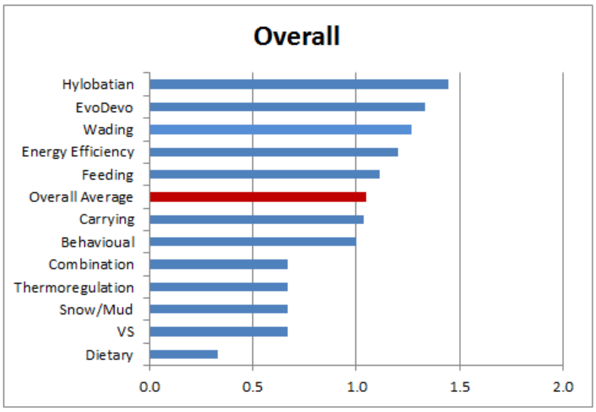

Figure 16 Paleontological Summary

D. Epistemological

The final category of evaluations assess the model in terms of its general scientific merit in the context of other models of bipedalism and human evolution generally.

D.1. Extended explanatory power.

Overall evaluation: 1.02 (Fair +2%)

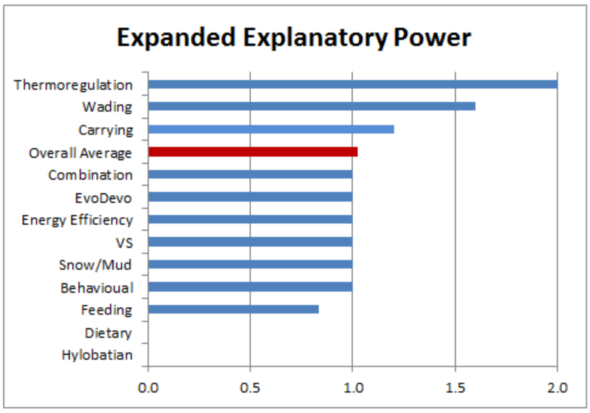

Figure 17 D1 Explanatory Power Summary

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

¼ were rated ‘poor’. Of those were mainly models suggesting arboreal origins for bipedalism, as they offer little in terms of a novel scenario that could account for other aspects of human evolution.

Most models were rated ‘fair’ by this criterion as they proposed some kind of novel scenario that may have led to other aspects of human evolution, even if the model itself did not go on to promote those aspects.

Only four models were rated ‘good’ by this criterion. These were very different in the specific idea used to promote bipedalism but all shared a willingness to explain more than this.

The female driven infant carrying idea of Tanner and Zihlman (1976), for example, also promoted increased altruism and tool use as ways of accounting for increased intelligence in ‘transitional hominids’ (Tanner 1981) Lovejoy’s (1981) ‘provisioning’ model, similarly accounts for a whole set of ape-human differences in addition to bipedalism. Wheeler’s (1984) thermoregulatory hypothesis also explains hair loss and the adoption of sweat cooling and the Hardy (1960) / Morgan (1972) ‘aquatic ape hypothesis’ accounts for this and other aspects of human evolution too.

D.2. Complementary to 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. It is this matter that this section addresses.

The models of bipedalism discussed in the previous section are considered here in terms of how they relate to each other. The methodology here is, wherever possible, to use the arguments from the authors of the models themselves to determine whether they are considered to be compatible or contradictory to each other, but to supplement this, as often authors do not comment on many alternative models, additional considerations will be made.

The results are presented in a matrix showing supportive and contradictory models.

The results of this cross-tabulation are shown in table 15.

Whilst studying the patterns of the compatibility matrix one is first struck by a very self-evident point: Models that are of a similar category tend to have a greater compatibility with each other than models from outside of those categories. These are identifiable as square-shaped blue blocks symmetrical to the diagonal.

After this, a number of more interesting generalisations appear: Carrying models, generally, are rather incompatible to arboreal ones. This is clearly a consequence of the fact that models which postulate that a key factor of early bipedalism was carrying objects with the forearms is likely to be rather incompatible with those models which suggest the forearms were used almost exclusively for climbing trees.

The combination models, *apart from being complementary to each other*, are not really complementary to many others, but neither are they contradictory to many either. The iodine-deficiency idea is almost totally contradictory to all the others. As will be elaborated upon later, most wading models are somewhat compatible with most other models but the author’s “River Apes” model (refer to section 7.4) is particularly so, as it was designed partly with this in mind.

Table 15 Model Compatibility Matrix

Code	Model	S	D	s1.1.1	s1.2.1	s1.2.2	s1.2.3	s1.2.4	s1.3.1	s1.4.1	s1.5.1	s1.5.2	s2.1.1	s2.2.1	s2.3.1	s2.4.1	s2.5.1	s2.6.1	s3.1.1	s3.1.2	s3.1.3	s3.2.1	s3.3.1	s3.4.1	s3.4.2	s3.4.3	s4.1.1	s4.1.2	s4.1.3	s4.1.4	s4.1.5	s4.2.1	s4.3.1	s4.4.1	s4.4.2	s4.4.3	s5.1.1	s5.2.1	s5.3.1	s5.4.1	s5.5.1	s6.1.1	s7.1.1	s8.1.1	s9.1.1
s1.1.1	General freeing of the hands / Forelimb pre-emption (carrying)	9	7		2	2	2	2	2	2	2	2	2	2	2	1	1	1	2	2	2	2	1	1	2	2	2	1	2	2	2	1	1	0	0	0	1	1	1	1	1	1	1	1	2
s1.2.1	Carrying food back to gallery forest bases. / Forelimb pre-emption (carrying)	5	6	2		2	2	2	2	2	2	2	2	2	2	1	1	1	2	2	2	2	1	1	2	2	0	0	2	2	2	0	2	0	0	0	2	1	2	1	1	2	0	1	2
s1.2.2	Carrying and scavenging / Forelimb pre-emption (carrying)	9	7	2	2		2	2	2	2	2	2	2	2	2	1	1	1	2	2	2	2	1	1	2	2	2	2	2	2	2	1	1	0	0	0	1	1	2	1	1	1	1	1	2
s1.2.3	Migration-carrying hypotheses / Forelimb pre-emption (carrying)	5	6	2	2	2		2	2	2	2	2	2	2	2	2	1	1	2	0	2	1	1	1	2	2	0	0	2	2	2	0	2	0	0	0	2	2	1	1	2	2	0	1	2
s1.2.4	Male Provisioning / Forelimb pre-emption (carrying)	9	7	2	2	2	2		2	2	2	2	2	2	2	1	2	2	2	1	2	2	2	2	2	2	2	1	2	2	2	1	1	0	0	0	2	2	2	1	2	1	1	1	2
s1.3.1	Female driven infant carrying / Forelimb pre-emption (carrying)	5	5	2	2	2	2	2		1	1	1	2	1	1	2	1	1	1	1	1	1	0	0	1	1	2	1	2	2	2	1	1	0	0	0	1	1	1	1	0	1	1	1	2
s1.4.1	Weapon Throwing / Forelimb pre-emption (carrying)	5	6	2	2	2	2	2	1		2	2	1	2	2	2	2	2	1	1	1	1	1	2	2	2	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	2
s1.5.1	Tool carriage / Forelimb pre-emption (carrying)	9	7	2	2	2	2	2	1	2		2	2	2	2	2	1	2	1	1	2	2	1	2	2	2	2	1	2	2	2	1	1	0	0	0	2	1	1	1	1	1	1	1	2
s1.5.2	Weapon wielding / Forelimb pre-emption (carrying)	5	6	2	2	2	2	2	1	2	2		1	2	2	2	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	0	0	0	2	1	1	1	2	2	1	1	2
s2.1.1	Nuptial Gifts / Behaviour	9	7	2	2	2	2	2	2	1	2	1		2	2	2	2	2	2	1	2	2	2	2	2	2	2	1	2	2	2	1	1	0	0	0	2	1	2	1	2	1	1	1	2
s2.2.1	Threat displays directed at other species / Behaviour	9	7	2	2	2	2	2	1	2	2	2	2		2	2	2	2	2	1	2	2	2	2	2	2	1	2	2	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2
s2.3.1	Intra-specific threat displays / Behaviour	9	7	2	2	2	2	2	1	2	2	2	2	2		2	2	2	2	1	2	2	2	2	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	1	1	2	1	1	2
s2.4.1	Sentinel behaviour / Behaviour	9	7	1	1	1	2	1	2	2	2	2	2	2	2		2	2	2	0	2	2	2	0	2	2	2	2	2	2	2	1	1	2	2	2	1	1	2	1	1	1	1	1	2
s2.5.1	Phallic Display directed at females / Behaviour	5	5	1	1	1	1	2	1	2	1	1	2	2	2	2		2	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
s2.6.1	Copied Gimmick Idea / Behaviour	5	6	1	1	1	1	2	1	2	2	1	2	2	2	2	2		2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
s3.1.1	Seed Eating / Feeding	5	5	2	2	2	2	2	1	1	1	1	2	2	2	2	1	2		0	2	2	0	1	2	1	0	0	1	0	1	0	1	0	0	0	1	1	1	1	1	2	0	1	2
s3.1.2	Terrestrial squat feeding on the forest floor / Feeding	5	5	2	2	2	0	1	1	1	1	1	1	1	1	0	0	1	0		2	2	1	2	1	1	0	1	1	2	1	0	1	2	2	2	0	1	2	1	0	0	1	1	2
s3.1.3	Other gathering / Feeding	9	7	2	2	2	2	2	1	1	2	1	2	2	2	2	1	1	2	2		2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2
s3.2.1	Postural feeding hypothesis / Feeding	9	7	2	2	2	1	2	1	1	2	1	2	2	2	2	1	1	2	2	2		1	2	2	2	1	2	2	2	2	1	1	1	1	1	1	1	2	1	1	0	1	1	2
s3.3.1	Arboreal predation / Feeding	5	6	1	1	1	1	2	0	1	1	1	2	2	2	2	1	1	0	1	2	1		2	2	2	0	2	1	2	1	0	1	2	2	2	0	1	2	1	1	0	1	1	2
s3.4.1	Stalking / Feeding	5	6	1	1	1	1	2	0	2	2	2	2	2	2	0	1	1	1	2	2	2	2		2	2	0	2	2	2	1	1	1	2	2	2	0	1	2	1	1	0	1	1	2
s3.4.2	Specific Hunting / Feeding	9	7	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2		2	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	1	1	2
s3.4.3	General scavenging/hunting / Feeding	5	6	2	2	2	2	2	1	2	2	2	2	2	2	2	1	1	1	1	2	2	2	2	2		1	1	1	2	1	1	1	0	0	0	2	1	2	1	1	1	1	1	2
s4.1.1	Coastal foraging / Habitat Compulsion	5	4	2	0	2	0	2	2	0	2	1	2	1	1	2	1	1	0	0	2	1	0	0	1	1		2	1	1	1	1	0	1	1	1	0	1	0	1	0	0	2	1	2
s4.1.2	Aquarboreal Model / Habitat Compulsion	5	5	1	0	2	0	1	1	0	1	1	1	2	1	2	1	1	0	1	2	2	2	2	1	1	2		2	2	1	1	0	2	2	2	0	1	1	1	0	0	1	2	2
s4.1.3	Amphibische Genalistheorie / Habitat Compulsion	5	6	2	2	2	2	2	2	1	2	1	2	2	1	2	1	1	1	1	2	2	1	2	1	1	1	2		2	2	1	1	1	1	1	0	1	2	1	0	1	1	1	2
s4.1.4	River Apes / Habitat Compulsion	9	7	2	2	2	2	2	2	1	2	1	2	1	2	2	1	1	0	2	2	2	2	2	1	2	1	2	2		2	2	2	2	2	2	2	1	2	1	1	0	1	2	2
s4.1.5	Wetland USO foraging / Habitat Compulsion	9	7	2	2	2	2	2	2	1	2	1	2	2	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	2		1	2	2	2	2	1	1	2	1	0	2	1	1	2
s4.2.1	Walking on Snow or mud / Habitat Compulsion	5	4	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	2	1		1	1	1	1	0	1	1	1	0	0	1	1	2
s4.3.1	Variability Selection Hypothesis / Habitat Compulsion	5	4	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	2	2	1		0	0	0	0	1	1	1	0	0	0	1	2
s4.4.1	Descent from arboreal Hylobatian locomotion / Habitat Compulsion	5	4	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1	0	2	1	1	2	2	1	0	1	2	1	2	2	1	0		2	2	0	2	2	2	0	0	1	2	2
s4.4.2	Arboreal "upwardly mobile" hypothesis / Habitat Compulsion	5	4	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1	0	2	1	1	2	2	1	0	1	2	1	2	2	1	0	2		2	0	2	2	2	0	0	1	2	2
s4.4.3	Orang-utan-like hand assisted bipedalism / Habitat Compulsion	5	4	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1	0	2	1	1	2	2	1	0	1	2	1	2	2	1	0	2	2		0	2	2	2	0	0	1	2	2
s5.1.1	Slow, long-distance walking / Locomotor efficiency	5	5	1	2	1	2	2	1	1	2	2	2	1	1	1	1	1	1	0	1	1	0	0	2	2	0	0	0	2	1	0	0	0	0	0		2	2	1	2	2	1	1	2
s5.2.1	Biomechanical inevitability / Locomotor efficiency	5	5	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2		2	1	2	1	1	1	2
s5.3.1	Efficiency of moving from tree to tree / Locomotor efficiency	9	7	1	2	2	1	2	1	1	1	1	2	2	2	2	1	1	1	2	2	2	2	2	1	2	0	1	2	2	2	1	1	2	2	2	2	2		1	2	2	1	1	2
s5.4.1	Locomotor de-coupling / Locomotor efficiency	5	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1		1	1	1	1	2
s5.5.1	Endurance Running / Locomotor efficiency	5	4	1	1	1	2	2	0	1	1	2	2	1	1	1	1	1	1	0	1	1	1	1	2	1	0	0	0	1	0	0	0	0	0	0	2	2	2	1		2	1	1	2
s6.1.1	Thermoregulatory Hypothesis / Thermoregulation	5	5	1	2	1	2	1	1	1	1	2	1	1	2	1	1	2	2	0	1	0	0	0	2	1	0	0	1	0	2	0	0	0	0	0	2	1	2	1	2		1	1	2
s7.1.1	Iodine deficiency / Dietary Factors	5	4	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1		1	2
s8.1.1	Evo Devo mutation / Random Genetic Factors	5	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	1	2	2	2	1	1	1	1	1	1	1		2
s9.1.1	Multi-factorial / Combination	9	9	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	

2 Complimentary   1 Compatibile   0 Contradictory

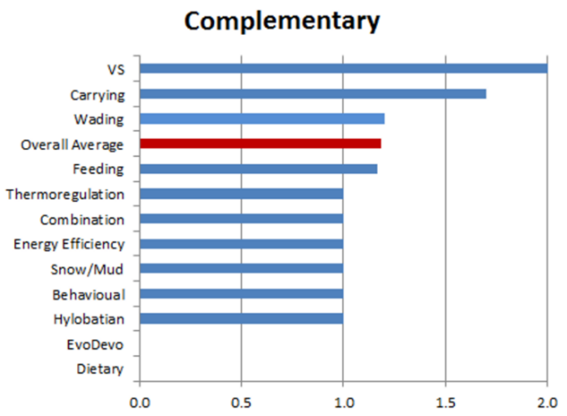

Figure 18 Complementary Summary

D.3. Falsifiable, or at least testable

Overall assessment: 0.59 (Fair – 41%)

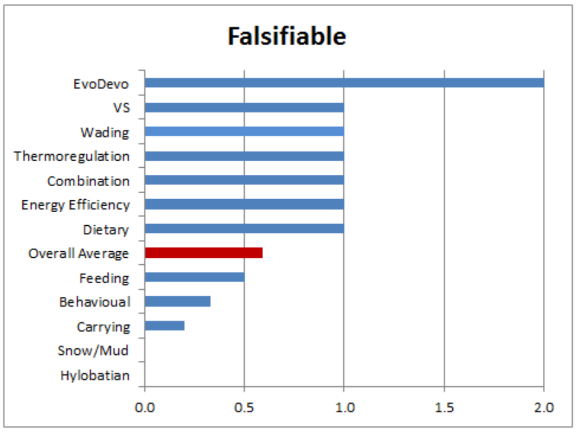

Figure 19 D3 Falsifiability Summary

This evaluation was by far the worst overall assessment of the models with almost ⅔ of models rated 'poor'. This is because most of the literature on hominin bipedal origins is largely speculative and has not been published in a scientific way. Clearly such hypotheses do not lend themselves to falsification in the Popperian sense, but as Jolly (1970) and Rose (1991) argued, 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.

Almost ⅓ of models were rated 'fair' as they did comprise elements that were testable or made some predictions. Only two models were rated 'good': Jablonski & Chapman's (2005) 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 'good' was Filler's (2007) genetic mutation hypothesis simply because it proposes a factor that may, over the course of time, prove to be invalid. His model is therefore the only one yet proposed that is falsifiable.

Again, the author's "River Apes" model scores well on this criterion because it was designed with this evaluative criteria in mind.

‘Epistemological’ summary

'Epistemological' Evaluation Summary				
Code	Bipedalism Model	D.1. Expanded Explanatory Power	D.2. Complementary	D.3. Falsifiable
1.01	Carrying: Unspecified	Fair	Fair	Fair
1.01.01	Carrying: Food back to gallery forest bases (Hewes 1961)	Fair	Good	Poor
1.01.02	Carrying: Scavenging (Isaac 1978)	Fair	Good	Poor
1.01.03	Carrying: Migration-carrying hypothesis (Sinclair 1986)	Fair	Good	Poor
1.01.04	Carrying: Male Provisioning (Lovejoy 1981)	Good	Good	Fair
1.02	Carrying: Female driven infant carrying (Zihlman & Tanner 1981)	Good	Good	Poor
1.03.01	Carrying: Throwing (Fifer 1987)	Fair	Fair	Poor
1.03.02	Carrying: Throwing (Dunsworth et al. 2005)	Fair	Fair	Poor
1.04.01	Carrying: Tool carriage (Bartholemew & Birdsell 1953)	Fair	Good	Poor
1.04.02	Carrying: Weapon wielding (Dart 1949/ Kortland 1980)	Fair	Good	Poor
2.01	Behavioural: Nuptial Gifts (Parker 1987)	Fair	Fair	Poor
2.02	Behavioural: Threat displays directed at other species (Kortland 1980)	Fair	Fair	Poor
2.03	Behavioural: Threat Display (Wescott 1967, Jablonski/Chapman 1990)	Fair	Fair	Good
2.04	Behavioural: Vigilance (Dart 1925, Ravey 1978)	Fair	Fair	Poor
2.07	Behavioural: Copied Gimmick Idea (Dawkins 2005)	Fair	Fair	Poor
2.06	Behavioural: Phallic Display directed at females (Tanner 1981)	Fair	Fair	Poor
3.01.01	Postural Feeding: Seed-eating (Jolly 1970)	Fair	Fair	Fair
3.01.02	Postural Feeding: Terrestrial squat feeding on the forest floor (Kingdon 2003)	Fair	Fair	Fair
3.02	Postural Feeding: From small bushes (Hunt 1994)	Fair	Good	Fair
3.03	Postural Feeding: Arboreal predation (Eickhofft 1994)	Poor	Fair	Poor
3.04.01	Postural Feeding: Stalking (Geist 1994)	Fair	Fair	Poor
3.04.02	Postural Feeding: Specifically hunting (Cartmill /Carrier 1974)	Fair	Fair	Poor
4.01.01	Wading: Coastal foraging model (Hardy, 1960)	Good	Poor	Poor
4.01.02	Wading: Aquarboreal model (Verhaegen 2000)	Good	Fair	Poor
4.01.03	Amphibische Generalistentheorie (Niemitz 2002)	Fair	Fair	Fair
4.01.04	"River Apes" (Kuliukas 2013)	Good	Good	Good
4.01.05	Wetland Foraging (Wrangham et al. 2009)	Fair	Good	Good
4.02	Walking on Snow or Mud (Köhler 1959)	Fair	Fair	Poor
4.03	Habitat Variability Selection Model (Potts 1996)	Fair	Good	Fair
4.04.01	Hylobatian Theory (Keith 1912)	Poor	Fair	Poor
4.04.02	Arboreal: "Upwardly Mobile" hypothesis. (Tuttle 1977)	Poor	Fair	Poor
4.04.03	Arboreal: Brachiationist Model – Gibbon-like, *Pan*-like, Bipedal (Prost 1923)	Poor	Fair	Poor
5.01	Energetic Efficiency (Rodman & McHenry 1980)	Fair	Fair	Fair
5.02	Biomechanical Inevitability: (Reynolds 1925)	Fair	Fair	Fair

5.03	Efficiency of moving from tree to tree	Fair	Fair	Fair
5.04	Locomotor De-coupling	Fair	Fair	Fair
5.05	Running (Lieberman 2007)	Fair	Fair	Fair
6.01	Thermoregulatory hypothesis. (Wheeler, 1984)	Good	Fair	Fair
7.01	Dietary: Iodine deficiency (de la Marett 1936)	Poor	Poor	Fair
8.01	Developmental Genetic Mutation (Filler 2007)	Fair	Poor	Good
9.01	Combination: (Day 1971)	Fair	Fair	Fair
9.02	Combination: (Napier 1964)	Fair	Fair	Fair
9.03	Combination: Locomotor repertoire (Rose 1991)	Fair	Fair	Fair
9.04	Combination: Behavioural response to habitat change (Sigmon, 1971)	Fair	Fair	Fair

Table 16 Epistemological Summary

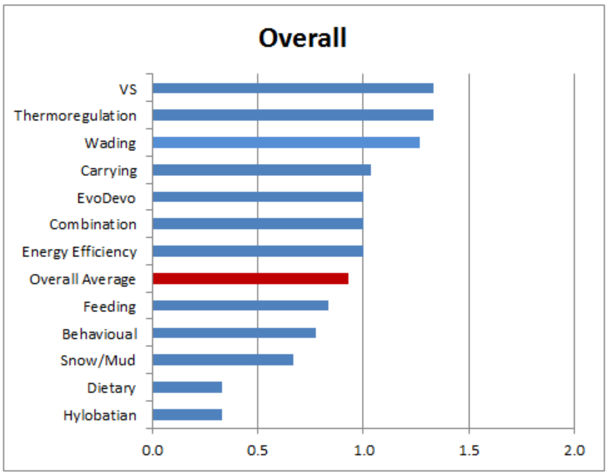

Figure 20 Epistemological Summary Chart

3.5. Summary and conclusions

Five questions will now be posed and possible answers discussed, some contributing to chapters in the rest of the thesis.

1. How can this evaluative framework itself be criticised?
2. Which model(s) is (are) rated the best?
3. Is there a discrepancy between this view and the most popular models promoted in the literature and what might account for such a discrepancy?
4. What are the weakest aspects of the best models?
5. Can these weaknesses be improved upon?

1. How can this evaluative framework be criticised?

Although this meta-analysis, like any before it, is essentially based on personal, subjective opinion, I have laid out in detail the exact criteria being used to compare and rank the various models and have offered my rankings and reasons for them for public review and scrutiny so that they too may be criticised and improved upon.

Some such criticisms and improvements are offered here.

There are a number of ways in which the evaluative framework itself might be changed. 'Predator avoidance' may, for example, be subsumed into 'survival value'. The third criteria '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 maybe even one. And, of course, there may be other criteria that might be added to bolster the overall evaluation, or some of the existing ones might be removed completely if deemed insufficiently important.

Even if the general evaluation headings were viewed as acceptable, there would still be scope for manipulating the weightings and the level of detail for each score, which would clearly affect the overall ranking. A greater range than a three-point scoring system could be devised allowing more discrimination on factors between the models to be teased out. And, some of the criteria may be weighted to reflect greater importance than others. As an example, I have provided an on-line version of the framework which includes a nine-point scale for each heading and different evaluations are weighted differently (see www.tinyurl.com/BipedalModels.)

2. Which models are the best?

Having set a cautious tone, I do feel that there are certain conclusions that can be drawn from the results of this evaluation. Most importantly, from the point of view of this thesis, is the deduction that the three wading models reviewed are highly rated and would continue to be unless very drastic changes were made to the evaluation method used here. Indeed, it might be suggested that by weighting some of the important criteria (such as criterion A.1, 'survival value') more highly this result would only be more secure.

The reader should be reminded that my own version of the wading model, labelled "River Apes… Coastal People" was specifically formulated on the basis of this evaluation in order to achieve the highest ranking possible. Although this is contrived, it at least demonstrates that the model is the result of a rigorous comparative process.

3. Is there a discrepancy between this and the most popular models promoted in the literature?

The popularity of the various types of bipedalism models may, perhaps, be best judged by the frequency that they are mentioned in university text books on human evolution. On that basis, the carrying models were clearly the most popular with approximately 86% of texts referring to them. Three others are referred to in at least half of the texts.

Wading models were ranked 7th most popular and only about 20% of texts mention them. There thus appears to be a clear discrepancy between the popularity of the wading models and their quality, as determined by this analysis. (See table 18).

Comparison of popularity of bipedalism models according to their representation in university texts and this evaluation

Rank	Model Popularity	%age popularity	%avg assessment	diff	Eval. rank	Diff
1	Carrying	86%	55%	+31%	5	+4
2	Feeding	69%	60%	+9%	2	+0
3	Energy Efficiency	58%	59%	- 1%	4	+1
4	Social Behaviour	50%	49%	+1%	8	+4
5	Thermoregulatory	47%	52%	- 5%	6	+1
6	Non-wading habitat compulsion	25%	60%	- 35%	2	-4
7	Wading habitat compulsion	22%	73%	- 51%	1	-6
8	Combination	14%	51%	- 37%	7	-1
9	Dietary	3%	18%	- 15%	9	+0

Table 17 Bipedalism Models in University Texts

The likely explanation of this discrepancy is discussed in detail in the next chapter.

4. What are the weakest aspects of the best models?

None of the models achieved evaluations that averaged closer to ‘good’ than ‘fair’ indicating that there is scope for improvement in all of them.

This is also true about the three wading models which, although generally ranked highly, all contained individual evaluations that were poor.

Verhaegen et al.’s (2002) ‘aquarboreal’ idea does not really address the postcranial differences between early hominins and the genus *Homo* (indeed Verhaegen doubts that australopithecines are ancestral to *Homo*). In addition, the Hardy/Morgan idea does not fit the known paleoecological record and is largely incompatible with most of the other models. Both of these and Niemitz’s “Amphibische Generalistentheorie” can be criticised for not providing testable predictions too.

Although the previously published wading models were rated “good’ on many criteria, all three contain several evaluations that were only ranked ‘fair’ or ‘poor’. It was to address weaknesses such as these that resulted in the development of the “River apes… Coastal People” model, which was designed to have as few weaknesses as possible. However, even this model has its own weaknesses that need to be addressed.

5. Can these weaknesses be improved upon?

It is the opinion of the author that the strength of the wading models in general outweighs their weaknesses but it is clear that even the best of them could be improved still further.

In the next chapter, the historical background to the wading hypotheses will be discussed to show how the discrepancy between the strengths of wading models and their popularity might be explained. Then, in the two following chapters, some of the weaknesses of the wading models are addressed.

CHAPTER FOUR

HISTORY OF THE WADING HYPOTHESIS

4. HISTORY OF THE WADING HYPOTHESIS

Partly reproduced from previously published papers…

Kuliukas, A.V. 2011a. A Wading Component in the Origin of Hominin Bipedalism. In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2011b. Langdon's Critique of the Aquatic Ape Hypothesis: It's Final Refutation, or Just another Misunderstanding? In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution. Bentham (Basel).

Kuliukas A. V. & Morgan E. 2011; Aquatic scenarios in the thinking on human evolution: What are they and how do they compare? In: (Verhaegen M., Kuliukas A. V., Vaneechoutte M., Eds.) Was Man More Aquatic In The Past? Fifty Years after Alister Hardy: Waterside Hypothesis of Human Evolution Basel: Bentham.

Kuliukas, A.V. 2013. Wading Hypotheses of the Origin of Human Bipedalism. Human Evolution 28 (3-4):213-236.

Abstract

The disparity between the apparent strength of wading models of human bipedal origins (as assessed here in this thesis) and their lack of coverage in university-level textbooks is discussed. The association of wading models with the so-called "aquatic ape hypothesis" is suggested as the probable cause of this disparity. The scientific literature pertaining to the wading hypothesis is reviewed, showing a remarkable paucity of serious consideration.

Weaknesses in published wading models are identified and used as research topics in chapters 5 and 6 of the thesis.

4.1. Wading and the "Aquatic Ape"

4.1.1 The rejection of the "Aquatic Ape Hypothesis" (AAH)

In the second chapter of this thesis a full literature review of all the published models of hominid bipedalism was presented. In the third, an evaluative framework was devised to compare these models and assess which ones met the criteria best. A review of the few meta analyses of bipedal models published in the literature and a survey of their portrayal in university level text books was also presented. In doing so, a discrepancy was highlighted between the strength of wading models, as rated by the evaluative framework devised here, and the level of coverage and support received in the literature.

Therefore, perhaps some justification is warranted regarding the choice of subject for this thesis. As we saw in chapter 2, almost all the literature about hominid bipedal origins has been made in the context of terrestrial or arboreal media, or a mixture of the two. Shallow water has rarely been considered. A discussion about the possible reasons for this lack of interest will therefore be presented before proceeding with the rest of the thesis.

4.1.1.1 'Aquatic ape hypothesis' (AAH) literature review

In this section, I will develop the argument that the lack of interest in, and support of, evidence pertaining to wading hypotheses has been almost entirely due to such models' historical link with the phenomenon that has been labelled the so-called 'aquatic ape hypothesis' (AAH) and the problems and controversies surrounding that hypothesis.

An example from the literature might best serve to illustrate the point.

In 2002, a series of monographs was published about the behavioural diversity of the two *Pan* species, chimpanzees and bonobos. One of the monographs, from a well-known bonobo specialist, Jo Myers Thompson, published her findings from a study of wild *Pan paniscus* at Lukuru, in the Congo. Among the many observations she reported was that her team had noticed relatively high levels of bipedal locomotion when they were observed in certain situations.

She wrote:

> *"Bonobos foraging in the pools exhibited terrestrial (aquatic) bipedal locomotion in 24.14% of encounters. Susman (1984) reported arboreal bipedal locomotion in 6% of his observations. During Susman's study, terrestrial locomotion was observed only a fraction of the time, due to the low degree of habituation. However, the propensity for bonobos to transition into bipedal locomotion during aquatic foraging as determined by this initial study, requires further examination and more extensive observation time. Also, caution must be exercised when drawing any inferences from these findings." Myers Thompson (2002 p 67)*

This might appear a rather unremarkable observation (except, perhaps for the degree of accuracy of the level of bipedality being reported!) but it provoked a quite extraordinary response in the book review of the compiled monographs (Boesch et al. 2002), published in *Folia Primatologica* by the prominent researcher into bipedal origins, Robin Crompton of Liverpool Moores University.

He wrote:

> *"It is clear also that the 'aquatic hypothesis' of Sir Alister Hardy is quite popular among chimpanzee field workers, although evidence offered in support of this 'theory' is hardly earth shattering: one paper notes that fully 24% of locomotion in water is bipedal!" Crompton (2004 p 120)*

Myers Thompson appeared to anticipate such a reaction as she urged "caution" about "drawing any inferences" from this data, but neither she, nor any of the other authors of the book chapters, made any reference to the so-called "aquatic ape hypothesis" or any of Hardy's ideas. Her monograph merely reported a significant finding which, as far as I know, is currently still (in 2015) the highest reported level of bipedality ever reported for any group of wild great apes.

This example shows how the risk of even a tentative association with the AAH could influence the general acceptance of evidence pertaining to moving through water in the context of hominin bipedal origins. These published accounts are almost certainly only the tip of the iceberg of a groundswell of opinion within the field.

This phenomenon begs a number of serious questions:

- What actually is the "aquatic ape hypothesis?"
- Why are some workers so fearful of being associated with it?
- When did this controversy arise? and
- Why should even a tentative association with it preclude wading from being considered as a plausible vehicle for the origin of hominid bipedalism?

In order to properly answer these questions it is necessary to delve into the subject in some detail.

Pro-'AAH' literature

There are at least 52 articles or books in the literature which generally promote the importance of waterside niches in human evolution. 11 of those were published together in a multi-authored publication, the proceedings of the Valkenberg symposium (Roede et al. 1991.) The earliest were from Sera (1936) and Westenhöfer (1942) but the first in the English language, and the one most often associated with the origin of the AAH, is that by Hardy (1960).

Hardy explained the gap in the fossil record between *Proconsul* and the australopithecines around the late Miocene (as it was perceived in 1960), by a shift to a coastal habitat for some apes on the human lineage. Certain ape-human differences such as improved swimming ability, reduced body hair and increased subcutaneous fat, he argued, had analogues in fully aquatic mammals and he postulated that perhaps man had gone through a "more aquatic" (Hardy 1960 p 642) phase. Sauer (1962) lent support to Hardy's idea from a geological and ecological perspective, emphasising, in particular, that coastal habitats were likely to be rich enough in food sources and safe enough from predators. However, like Hardy's, Sauer's paper was largely ignored.

The idea was briefly referenced in Desmond Morris' popular science book, "The Naked Ape", in which can be found the first references to the term "aquatic ape" (Morris 1967 p 29). Despite raising this idea as a possible explanation for the loss of body hair in humans, most of Morris' thesis promoted the view that sexual selection was a more important factor.

It was Morris' emphasis on the suggested importance for male hunting to deliver high-energy food to relatively passive and helpless females and their infants, which caught the eye of feminist playwright, Elaine Morgan and she set about trying to find an alternative model, which emphasised more the role of women and children as well as the elderly. It was Morris' reference to Hardy's idea that provided her with the idea.

Morgan attempted to publicise Hardy's thinking by using a populist writing style and by placing women and children at centre stage in her controversial book "The Descent of Woman" (Morgan 1972), provocatively published a century after Darwin's great work. Morgan wrote four more books on the subject, which succeeded in making the idea much better known to the lay public but also in giving the idea a 'fringe' reputation in academia.

The term "aquatic ape" has always been open to a wide range of personal interpretation. It is possible, for example, to take it quite literally and assume Hardy was proposing that humans evolved from some kind of mermaid or 'primate seal.' This is a view I label here a 'strong form' of the hypothesis. On the other hand, one can choose to interpret it much more modestly and recall that the question Hardy posed was relative: Was man *more* aquatic in the past? He didn't clearly spell out how *much* more other than to write…

> *My thesis is that a branch of this primitive ape-stock was forced by competition from life in the trees to feed on the sea-shores and to hunt for food, shell fish, sea-urchins etc., in the* shallow waters off the coast. I suppose that they were forced into the water just as *we have seen happen in so many other groups of terrestrial animals. I am imagining this happening in the warmer parts of the world, in the tropical seas where Man could stand being in the water for relatively long periods, that is, several hours at a stretch" Hardy (1960 p 642).*

Population genetics teaches us that even very slight selection can make profound phenotypic differences in comparatively short timescales (see e.g. Li and Graur 1991) so one may choose to interpret Hardy's idea as merely suggesting that one lineage of ape became slightly more exposed to selective pressures of moving through, and procuring food from, water than did the rest of its clade. Seen from this perspective, 'aquatic ape' is a sort of ironic term, short hand for 'the species among the ape clade (one noted for not being aquatic at all) that is merely *slightly* more aquatic than the rest.' I label this a 'weak form' of the hypothesis.

Perhaps unsurprisingly, scientists who interpreted the idea more strongly (Langdon 1997; Lowenstein & Zihlman 1980) have been most skeptical, whereas those who have interpreted it weakly, (Tobias 1998, 2001, 2002; Reynolds 1991; Sauer 1962) have been much more open to the idea.

These inconsistencies, and others, undoubtedly contributed to the skepticism that most anthropologists and anatomists have about the idea today.

Hardy and Morgan are not the only proponents of a 'more aquatic' view of human evolution. Almost 20 authors have promoted such views, many offering quite different evidence and timescales. Probably the most up-to-date scholarly summary of such views can be found in Vaneechoutte et al. (2011).

Some researchers in brain chemistry and nutrition, for example, came to the conclusion that encephalisation in the human lineage is much easier to account for if it is postulated that our evolution took place in waterside habitats.

Cunnane et al. (2007) have suggested that the essential fatty acid, docosahexanoic acid (DHA) specifically, particularly rich in oily fish, could have been a key nutrient in this process and Broadhurst et al. (1998) proposed that rift valley lakes would thus have provided an ideal habitat (although see Cordain et al. *(*2001) for an alternative account.

Ellis (1986, 1987, 1991, 1993, 1995) outlined arguments that wetland ecosystems may have provided an ideal habitat for early hominin evolution, and hence the early adoption of bipedalism. This kind of model was supported by the primatologist Bearder (2000) and, more recently in the specific context of the Okavango delta, by Wrangham (2005).

In the field of diving physiology, Schagatay (1991), Schagatay et al. (1998, 2000, 2001, 2002) and Anderson et al. (1998, 2000) suggested that humans appear to have adaptations not seen in other primates.

Evans (1992) suggested that the increased size of paranasal sinuses in humans and the presence of exostoses of the external auditory meatus of some fossil hominids may be evidence of swimming and/or diving in the human lineage. Williams (2005) suggested that the anatomy of the human kidney differs from most primates in ways which indicate either an adaptation to greater aridity or to salt water tolerance. The human capacity to sweat copious amounts of fluid is seen as evidence against the former alternative.

Verhaegen et al. (2002) promoted the view that both humans and apes evolved from “aquarboreal (climbing-wading) ancestors” and it has been argued that studies of microwear suggest that early hominins appear to have eaten a diet consisting, largely, of water-side sedges and other plant foods (Puech et al. 1986, 1992; Verhaegen and Puech 2001.)

They provided other evidence such as exostoces in the auditory meatus (Verhaegen 1993) pachyostosis (Munro & Verhaegen 2011) and coastal faunal assemblages (Verhaegen et al. 2007, Joordens et al. 2015) to suggest that *Homo erectus* appears to be coastally adapted.

More generally, some anthropologists (Tobias 2000, 2002; Cameron and Groves 2003) have simply urged for the idea to be taken more seriously than it has to date.

Finally, as reviewed in the section above, Niemitz (2002) published a detailed description of his theoretical model in support of wading through shallow water as key factor in the origin of hominid bipedalism (Niemitz 2002). Niemitz distances himself from the AAH but it cannot be denied that, like all the work above, his basic proposal is that moving through water acted as an agency of selection in human evolution.

One of the most striking characteristics of these publications is their diversity and lack of any specific common thread other than some proposal or other that moving through water, or obtaining food from it, might have been an important factor in human evolution, as can be seen in the following two tables.

Proposed ‘more aquatic’ timescale		
Period	N	Refs
Unspecified	28	Ellis (1986, 1987, 1991, 1993, 1995), Puech et al. 1986, 1992, Verhaegen and Puech 2001, Richards (1991), Fichtelius (1991), Schagatay (1991), Roede (1991), Evans (1992), Wescott (1995), Metzner (1995), Bender et al. (1997), Tobias (1998, 2000, 2002), Schagatay et al. (1998, 2000, 2001, 2002), Anderson et al. (1998, 2000), Bearder (2000), Williams (2005)
Pre-Miocene	2	Sera (1936), Westenhöfer (1942)
Late Miocene-4Ma	8	Hardy (1960, 1977), Morgan (1972, 1982, 1990, 1991a, 1991b), LaLumiere (1991), Niemitz (2000, 2002, 2004, 2006, 2007, 2010), Kuliukas (2011a, 2013)
6-4Ma	1	Morgan (1997), Niemitz (2000, 2002, 2004, 2006, 2007, 2010), Kuliukas (2011a, 2013)
Recent (genus *Homo*)	13	Sauer (1962), Cunnane (1980, 2005), Cunnane et al. (2003), Verhaegen (1985, 1988, 1991a, 1991b, 1993, 1995), Verhaegen et al. (2002), Erlandson (2001), Broadhurst et al. (1998, 2002), Niemitz (2000, 2002, 2004, 2006, 2007, 2010), Kuliukas (2011a, 2013)

Table 18 Proposed 'More Aquatic' Timescales

Main evidence used to promote waterside idea		
Evidence/Arguments used	N	Refs
Comparative anatomy of apes and humans	13	Westenhöfer (1942), Hardy (1960, 1977), Morgan (1972, 1982, 1990, 1991a, 1991b, 1994, 1997), Fichtelius (1991), Evans (1992), Wescott (1995), Kuliukas (2011a, 2013)
Comparative anatomy with aquatic and/or savannah mammals	5	Verhaegen (1985, 1991a, 1991b, 1993), Roede (1991)
Water playing some role in human evolution	3	Tobias (1998, 2000, 2002), Kuliukas (2011a, 2013)
Specific nutrition important for encephalisation from coastal habitats	5	Cunnane (1980, 2005), Broadhurst et al. (1998), Broadhurst et al. (2002), Cunnane et al. (2003),
Epistemological	4	Richards (1991) Morgan (1982, 1997), Wescott (1995), Kuliukas (2011a, 2013)
Benefits and plausibility of wetland niches	7	Ellis (1986, 1987, 1991, 1993, 1995), Metzner (1995), Bearder (2000), Verhaegen et al. (2002), Kuliukas (2011a, 2013)
Larynx and cortical control of breathing	2	Verhaegen (1985, 1995)
Anatomical differences between primates and mammals	1	Sera (1936)
Ecological/Geographical	1	Sauer (1962), Kuliukas (2011a, 2013)
Evidence of paleohabitat flooding/desiccation	1	LaLumiere (1991)
Specific diving reflex of humans compared to other mammals	7	Schagatay (1991), Schagatay et al. (1998, 2000, 2001, 2002), Anderson et al. (1998, 2000)
Human infant developmental differences with apes	1	Morgan (1994)
Bipedal wading	1	Bender et al. (1997), Niemitz (2000, 2002, 2004, 2006, 2007, 2010), Kuliukas (2011a, 2013)
Dental microwear	3	Puech et al. (1986), Puech (1992), Verhaegen and Puech 2001
Mythological references	1	Metzner (1995)
Kidney morphology	1	Williams (2005)
Archaeological	1	Erlandson (2001)

Table 19 Waterside Evidence Cited

However, few of the published "waterside" ideas specifically refer to any wading hypothesis of bipedal origins.

Treatment of wading for bipedalism		
Treatment	N	Refs
Not mentioned	33	Sera (1936), Westenhöfer (1942), Sauer (1962), Cunnane (1980, 2005), Verhaegen (1985, 1985, 1991a, 1991b, 1993, 1995), Puech et al. 1986, 1992, Verhaegen and Puech 2001, Morgan (1991a), Schagatay (1991), Roede (1991), Evans (1992), Wescott (1995), Schagatay et al. (1998, 2000, 2001, 2002), Anderson et al. (1998, 2000), Tobias (1998, 2000, 2002), Erlandson (2001), Broadhurst et al. (2002), Cunnane et al. (2003), Williams (2005)
Wading for food in coastal shallows	8	Hardy (1960, 1977), Morgan (1972, 1982, 1990, 1991b, 1994), LaLumiere (1991), Niemitz (2000, 2002, 2004, 2006, 2007, 2010) , Kuliukas (2011a, 2013)
Wading for food in wetland habitats	7	Ellis (1986, 1987, 1991, 1993, 1995), Metzner (1995), Bender et al. (1997), Bearder (2000), Verhaegen et al. 2002, Niemitz (2000, 2002, 2004, 2006, 2007, 2010) , Kuliukas (2011a, 2013)
Physiological problems of bipedalism reduced in water	2	Morgan (1990, 1997)
Suggested paleohabitat	1	LaLumiere (1991), Niemitz (2000, 2002, 2004, 2006, 2007, 2010), Kuliukas (2011a, 2013)

Table 20 Published Responses to Wading Idea

Literature critical of the AAH

Although publications in favour of the AAH are characterised by their variety and lack of any explicit suggestion as to the degree of aquatic adaptation being proposed, critiques of the AAH, which are much fewer in number, seem to be quite similar in their approach and much clearer in their assumption of what it is they are criticising.

As far as I have been able to determine, there are 22 critical papers specifically on an AAH-related subject, 11 of which are compiled in Roede et al. (1991) and the most recent being a paper by Foley and Lahr (2014). Generally speaking, they critique a "strong form" of the hypothesis rather than the "weak form" the author defined earlier, a form this thesis argues is more in line with Hardy's original question "was man *more* aquatic in the past?" (Hardy 1960 p 642.)

For example, Lowenstein and Zihlman (1980), in the first published critique, wrote:

> *"Neither present-day humans nor the earliest australopithecine fossils of three and a half million years ago show any of the skeletal adaptations to an aquatic environment that are common to all other aquatic mammals: first, reduction in the size of the limbs, especially the hind limbs, and their modification into flippers; second reduction in thickness of the pelvis, which in water is not a structural weight bearing truss as it is on land: the pelvis of whales, dolphins and manatees has nearly disappeared"(Lowenstein and Zihlman 1980 p 5).*

Pond (1987) agreed with Lowenstein and Zihlman but more important was her discussion subject of mammalian adipocity, which promoted her findings of a comparative study of the adipocity of mammals. When comparing differences in the percentage of adipose tissue of body weight and the number of adipocytes, Pond notes that humans are much fatter than is typical of most mammals, particularly primates (Pond 1987 p 64.)

Although this provided evidence supporting Hardy's original observations, Pond did not agree with his explanation for it. She critiqued Hardy's idea by showing that human adipocity is different from that of aquatic mammals and thus claimed it was maladaptive to the function of thermoregulation and streamlining.

The most substantial collection of work critical of the AAH can be found in Roede et al. (1991), eleven in all. All but two (see table below for references) reject what appears to be a 'strong' form of the hypothesis. Of these, two reject it on a paucity of evidence in the fossil record. Pickford, for example, writes "of all the pre-hominid fossils recovered in the Old World, now totalling more than 3,000 specimens from hundreds of localities ranging in age from the lower Miocene (18 Ma.) to the Holocene, only a minute proportion of specimens has, to my knowledge, been found in fully lacustrine sediments or marine (including littoral) strata." (Pickford 1991 p 130). It should be noted that this is no evidence at all against 'weak' forms of the hypothesis and may actually be strongly favourable to it as almost all of those 3,000 fossils were formed in depositional substrates.

Some papers rejected the AAH, either partly (Ghesquiere & Bunkens 1991) or wholly (Wind 1991), on the basis that humans are poor swimmers compared to what one might expect if we had been 'more aquatic' in the past. Ghesquiere & Bunkens (1991) make comparisons between humans and other terrestrial mammals and Wind's (1991) paper sets out to explain why all Hominoidea, including *Homo sapiens*, are such poor swimmers.

One paper (Leyhausen 1991) does make a good case against a 'weak' form of the AAH, namely that of predation. The threat of sharks, crocodiles, hippopotami and other aquatic threats do indeed provide a serious challenge to all strands of the AAH.

Preuschoft & Preuschoft (1991) made the case against the AAH on epistemological grounds. They took AAH proponents to task for never expressing the hypothesis in a proper scientific (i.e. falsifiable in the Popperian sense) way. They set out to test three separate 'levels' of the AAH against the known fossil evidence. As they put it, "since testable hypotheses proposed by AAT defenders are lacking, we have ourselves tried to pin down the possibilities that exist for an aquatic lifestyle" (Preuschoft & Preuschoft 1991 p 164). This leads them to specifically consider a 'weak' form (one labelled 'a marsh wader') of the hypothesis. However, the only argument the authors offer against this weak form was the claim that if human ancestors were marsh waders, then one would predict that they would have evolved long, thin stalk-like legs, like wading birds.

The chief editor, Vernon Reynolds', final assessment of the evidence presented at the symposium was straightforward enough: "Overall, it will be clear that I do not think it would be correct to designate our early hominid ancestors as 'aquatic'" (Reynolds 1991 p 340) .However it is also clear from Reynolds' justification of that conclusion, that it is a strong form of the hypothesis he is rejecting as his final comment showed a clear discrepancy between what he had just rejected and what he thought was plausible:

> *"… at the same time there does seem to be evidence that not only did they take to water from time to time but that the water (and by this I mean inland lakes and*

> *rivers) was a habitat that provided enough extra food to count as an agency for selection. As a result, we humans today have the ability to learn to swim without too much difficulty, to dive, and to enjoy occasional recourse to the water" Reynolds (1991 p 340).*

Reynold's (1991) statement illustrates a potential for confusion, with regard to the hypothesis, which is a common characteristic of most of the published discussion about it. It shows that an authority can, on the one hand, think he has rejected the AAH but, on the other, endorse the idea that the human phenotype may be the partial product of natural selection from moving through water. Apparently, Reynolds is rejecting a 'strong' form of the hypothesis, but endorsing a 'weak' one.

Colin Groves also picked up on this statement in a book review of Roede et al. whilst pondering why people had been turned away from the "AAH". Groves noted "Is this why some of the aquatic ape's more thoughtful detractors in this book, notably Vernon Reynolds, are willing to concede that (p340) "not only did they take to water from time to time but . . . The water . . . Was a habitat that provided enough extra food to count as an agency for selection"? Is this, perhaps, all that was necessary all along? Might Hardy and Morgan have seen their ideas discussed if they had taken then just this far? I suspect it might." (Groves 1993 p 1038-1040).

Since Roede et al. (1991) there have been 5 papers published specifically against the subject in the last 24 years, to my knowledge, compared to over 40 in favour of it.

The most significant of the three was Langdon's (1997) critique of the AAH, the only one to be published in a first class, anthropological journal, that this author could have read (only being conversant in the English language).

Langdon (1997), again, only evaluated a strong form of the hypothesis. His approach was to list out some 32 ape-human differences that, he suggests, AAH proponents (but especially Morgan 1991) have cited as evidence for an aquatic phase and, for each, considered if the trait might be best explained by adaptation to terrestrial or aquatic niches, as if the AAH itself posed such a dichotomy. The traits were summarised in a table and grouped according to what Langdon understood was being suggested by the AAH. For example, when considering bipedal origins, it was grouped under "traits consistent with the AAH" (along with 6 others) but dismissed it on the grounds that bipedalism is "not typical of aquatic mammals" (Langdon 1997 p 488.)

In the text, he portrayed only one of many arguments used by AAH proponents in favour of wading, namely Morgan's suggestion that modern human conditions, such as varicose veins and lower-back problems, were 'scars of evolution' from a quadrupedal past. Her point was that if our ancestors had waded in some depths of water these problems might not have been so great and therefore suggested a scenario where bipedalism may have evolved without the 'costs' that would only emerge later as we became fully terrestrial bipeds (Morgan 1990). Some might find that a reasonable point to make, but Langdon dismisses it on quite dubious grounds. Here is the full, unabridged, text of Langdon's dismissal of the wading component of the AAH:

> *"Authors who wish to recite the many disadvantages of bipedalism commonly do so by comparing humans to medium-sized terrestrial quadrupedal mammals. However, hominoid ancestry has probably never included medium-*sized terrestrial quadrupedal mammals. A comparative anatomy of living hominoids reveals a pattern of climbing and/or suspensory specializations across the taxon. *The climbing/suspensory complex both removes our ancestry from conventional*

> *terrestrial quadrupedalism and helps to bridge the gap toward human bipedalism." (Langdon 1997 p 481.)*

Langdon, however, was merely promoting a brachiationist (Hylobatian) model of hominid bipedal origins contra, especially, knuckle-walking models. As we have already seen in this review, this is only one of many, none of which are obviously better than all the others. As there is no commonly accepted candidate in the fossil record for a last common ancestor of *Homo* and *Pan* we simply do not know the size of that ancestor. Whatever size the precursor to human bipedalism was, climbing trees was probably a large part of its locomotor repertoire, a fact nobody disputes, including all AAH proponents who have commented on the matter. Equally clear however, considering that no primate other than our own species is an obligate terrestrial biped, is the probability that this climbing ancestry was not enough of a factor on its own to explain the modern human mode of locomotion.

On bipedalism, then, we see Langdon's approach was to take one of the weakest arguments in favour of the wading idea and to offer in its place another explanation, which he considered better.

Morgan's work usually stresses a handful (e.g. bipedalism, nakedness and increased adipocity) of major ape-human differences of paramount importance, giving them at least one chapter of discussion each. Minor ones are usually lumped together and treated as side issues, or in a chapter of their own such as "infrequently asked questions" (Morgan 1997 p 149-175.) However, Langdon's critique fails to weight them according to their importance at all and treats them all equally superficially. 26 such traits under examination are thus paraded, as if for ridicule.

Most of Langdon's (1997) paper, therefore, basically delivers a 'straw man' argument against the AAH. It picks out the weakest points and knocks them over with something from orthodoxy that cannot be denied. It is ironic, then, that one of his main criticisms of Morgan's work is that she invented the 'savannah theory' simply as a straw man to be knocked down. Langdon writes:

> *"The savannah hypothesis that Morgan criticizes turns out to be a straw man. Anyone who dredges up a century of hypotheses can find many to ridicule; but if the field has already rejected them, the exercise is pointless. In fact, scholars are now discarding the savannah setting for hominid divergence. Recent paleoecological work favours a woodland or mosaic habitat for early australopithecines" (Langdon 1997 p 490.)*

Recent paleoecological work certainly does tend to cite 'woodland' or 'woodland mosaic' habitats more than 'savannah' although this was not the case for most of the last century. Indeed the savannah-based paradigm of human evolution still has a great deal of support even today (Feibel 2011). To imply that the fundamental assumption that humans evolved on the savannah was merely an invention of Elaine Morgan's is an incredible one in this context. As Morgan puts it:

> *"It has been repeatedly asserted (for example on the internet) that there was never such a thing as the 'savannah theory', that it was simply a straw man constructed by Elaine Morgan for the pleasure of knocking it down again, and that no reputable scientist can be shown ever to have used the phrase 'savannah theory'. The last part of that statement is true. I would no more have expected them to use that*

> *phrase that I would expect a Creationist to refer to 'the God theory' - their faith in it was too strong for that." Morgan (1997 p 14)*

In any case, as Morgan describes below, if the current paradigm is *no longer* savannah-based, whatever it is that has replaced it cannot be all that different from the putative habitat that was ancestral to the extant apes. This only makes it more difficult to envisage how ape-human divergence could have happened.

> *"The original savannah model – though it did not stand the test of time – was argued in strong and clear terms. We are different from the apes, it stated, because they lived in the forest and our ancestors lived on the plains. The new watered-down version suggests that we are different from the apes because their ancestors, perhaps, lived in a different part of the mosaic. Say what you will, it does not have the same ring to it" (Morgan 1997 p 18-19.)*

Langdon's paper was open about the need to refute the AAH and the paucity of the response by the anthropological community to date.

He justifies writing his paper: "Thus the aquatic ape hypothesis continues to be encountered by puzzled students who wonder why mainstream paleoanthropologists overlook it. If only because of this last audience, it should not be ignored." (Langdon 1997 p 480). The early response to the hypothesis is described like this:

> *"Paleoanthropologists have been accused of being closed-minded to new ideas, sexist, and prejudiced against non-anthropologists or non-academics or Europeans. From the discipline's perspective, some anthropologists have regarded the ideas as not worth the trouble of a rebuttal. The contexts of two publications, the first a popular essay and the second a politically strident tract, diverted attention from whatever serious scientific proposal they contained." (Langdon 1997 p 480).*

Main arguments used against "waterside" hypotheses		
Evidence	N	Refs
Hominids lack features of aquatic mammals	11	Lowenstein and Zihlman (1980), Pond (1987, 1991), Preuschoft & Preuschoft (1991), Turner (1991), Leyhausen (1991), Wheeler (1991), Roede et al. (1991), Reynolds (1991), Landon (1997), Foley and Lahr (2014), Niemitz (2002, 2004, 2007, 2010).
Fossil record is lacking	2	Pickford (1991), Preuschoft & Preuschoft (1991)
Humans are poor swimmers compared to terrestrial mammals	2	Ghesquiere & Bunkens (1991), Wind (1991), Niemitz (2002, 2004, 2007, 2010).
Nasal sinus evidence contradicted	1	Rae and Koppe (2014)
Flaws in the nutritional arguments for encephalisation	1	Langdon (2006)
Aquatic predation	1	Leyhausen (1991)
Epistemological	1	Preuschoft & Preuschoft (1991)
Hominid bipeds lack features of marsh wading birds	1	Preuschoft & Preuschoft (1991)

Table 21 Arguments against Waterside Hypotheses

Arguments against wading as a factor in bipedal origins		
Evidence	N	Refs
None	8	Pond (1987, 1992), Pickford (1991), Turner (1991), Wind (1991), Roede et al. (1991), Foley and Lahr (2014), Rae and Koppe (2014)
Different models favoured	4	Leyhausen (1991), Wheeler (1991), Reynolds (1991), Langdon (1997)
Aquatic mammals are not bipedal	2	Lowenstein and Zihlman (1980), Langdon (1997)
Marsh wading predicts long thin legs, such as in wading birds	1	Preuschoft & Preuschoft (1991)
Wading is very inefficient in water "up to the armpits"	1	Ghesquiere & Bunkens (1991)

Table 22 Published Arguments against Wading Hypothesis

4.1.1.2 Niemitz's "AAH" critique

There is one author whose work must be included in both categories – both "pro" and "contra" waterside hypotheses – and accordingly given greater attention. Carsten Niemitz, as described earlier (See section 2.3 – Wading Models), is the author of the "Amphibische Generalistentheorie", a model based upon the idea that wading was a fundamental component in the origin of hominin bipedalism, a very compatible idea to the subject of this thesis. However, there is also some disagreement with Niemitz here. He also considers himself a critic of the so-called "aquatic ape hypothesis" (AAH) and strongly argues that a demarcation exists between wading and other ideas within the AAH. Niemitz certainly disagrees with the thesis, promoted here, that the AAH has been misunderstood and/or misrepresented. (Personal comment 2015). Because of Niemitz's unique position on this, his comments about the AAH will be reviewed in detail.

Amphibische Generalistentheorie (Niemitz 2002)

In his 2002 paper, as part of a review of 15 ideas on bipedal origins, Niemitz discussed the "AAH" – the concept that our ancestors passed through a transitional "more or less aquatic phase". It was a brief summary crediting the idea to Westenhöfer 1942, Hardy 1960, and especially: Morgan 1990.

No objections were raised other than the fact the idea had "caused much controversy" and was "seriously challenged" in Roede et al. (1991). Niemitz concludes that "nonetheless, this theory was elaborated further by Morgan (1997), and aspects in favour of it have recently been discussed again (Bender et al. 1997; Bearder 2000)" (Niemitz 2002 p 11).

Das Geheimnis des aufrechten Gangs ~ Unsere Evolution verlief anders (Niemitz 2004)

In his 2004 book, Niemitz wrote a chapter on this subject "Nicht aus dem Wasser" ("Not out of the water") which expanded his critique of the so-called "aquatic ape hypothesis" (AAH).

It introduces the idea with the classic "AAH" observation that human infants are relatively fat compared to other primates. "This circumstance [the high levels of subcutaneous fat in humans, especially infants] is one of the main arguments for the theory promoting aquatic apes, or The Aquatic Ape Theory as it is called in English." (Niemitz 2004 p 198).

Niemitz attributes the idea's origins to Max Westenhöfer (1942) but also gives credit to Alister Hardy and "its most prominent advocate" Elaine Morgan.

Niemitz quotes Morgan from her latest book (at that time): "The idea that bipedalism arose as a consequence of wading behaviour is a hypothesis like all the others ... None of them has been proven." (Morgan 1997 p 70.) and remarkably adds "This positions them clearly in contrast to the amphibische generalistentheorie presented here." (Niemitz 2004 p 198).

Niemitz distances himself from Morgan by claiming that she "has taken a whole series of Westenhöfer's arguments without, however, aligning them with the current state of scientific knowledge" (Niemitz 2004 p 199). This seems unfair as Morgan wrote her first book "Descent of Woman" before she was even aware of Westenhöfer's work and then, although she quoted, in full, his passage related to the idea in Roede et al. (1991), her work was always based on Hardy's (1960) published (independently conceived) ideas and substantially adds to them. It appears to have been the result of a great effort to compare them with the current paradigm.

However, having demonstrated to the reader his skepticism of Morgan's work, Niemitz then embraces one of her key arguments [infant and female adipocity] as his own: "But if we had had an ancestor who has waded much in the water longer than this, for example, species macaques are doing today, it would be of essential importance for our baby ancestors have to be well insulated against the associated heat loss." (Niemitz 2004 p 200) and "This fat distribution [in women] suggests an anatomical optimization to easily maintain the body temperature while wading in shallow water without much energy loss," (Niemitz 2004 p 201).

Niemitz's critique of Morgan's "AAH" is based on a table she prepared comparing physical attributes humans share with aquatic and savannah mammals (Morgan 1991b). He begins by questioning the fundamental nature of such comparisons: "First, the question arises whether this alternative is at all correct." (Niemitz 2004 p 201).

Niemitz's critique was based on a summary table of nine items listed by Morgan (1991b).

1) Loss of body hair
2) Habitual Bipedalism
3) Descended Larynx
4) Voluntary Breath Control
5) 180º spine/hind limb angle
6) Increased non-seasonal fat deposit
7) Ventro-ventro copulation
8) Dorsal hair sparser than ventral
9) Proliferation of sebaceous glands

Looking at this list from today's perspective, one could argue that it was not ideally conceived. For example, items 2, 5 and 7 appear to be manifestations of the same switch to bipedalism

However, there is no doubt that loss of body hair, bipedalism, descended larynx, voluntary breath control, increased adipocity and increase in sebaceous glands have always remained key arguments of Morgan's "AAH" so Niemitz's criticisms of them are of interest here.

On hairlessness, Niemitz offers no counter argument, but merely appears to sit on the fence. "The hairlessness is interesting, but plays in this context obviously no, or at least no sufficiently consistent, role." (Niemitz 2004 p 203).

Similarly, on bipedalism, the observation is merely stated that our mode of locomotion is unique among both savanna and aquatic mammals. It is perhaps peculiar that Niemitz doesn't lend

Morgan any support even here, since Niemitz's whole thesis is that wading through shallow water was the major factor in the evolution of our bipedality.

On the descended larynx, Niemitz appears to rule out any possible "aquatic explanation" on the basis that sea lions, manatees and people have "different functional requirements" (Niemitz 2004 p 204).

The voluntary breath comparison is dismissed on the basis that hippotamuses are also savannah mammals and can exhibit voluntary breath control by closing their nostrils. There is no discussion of human diving abilities which, compared to other Primates, are quite remarkable.

The other features in Morgan's list are similarly dismissed in a few sentences. Summing up, Niemitz, agrees with the concluding comments of Preuschoft & Preuschoft (1991), which argued that although the "AAH" raised a few enigmatic characters of *Homo sapiens*, it did not provide causal explanations for them.

One important aspect of human beings, not listed in Morgan's (1991b) table, but of which Hardy (1960 p 643) described as the "first and foremost", is their ability to swim – especially compared to other primates. Niemitz counters this point only by reproducing a figure from Preuschoft & Preuschoft (1991) with a caption which explains that turbulences and drag generated from various joints would make hominid swimming slow and energetically costly. Overall, Niemitz treatment of the AAH is rather superficial. Like Langdon (1997) and other critiques reviewed above, he appears to be only considering an "extreme" form of the idea and not one simply where the degree of selection from moving through water was increased – even if only slightly. This is perhaps surprising for an author of a theory which is completely based on wading in shallow water which emphasises an "amphibious" lifestyle.

The evolution of the upright posture and gait—a review and a new synthesis (Niemitz 2010)

In 2010 Niemitz added some further criticisms of the AAH, expressing doubt that it fulfilled the criteria of a hypothesis or a theory and suggested that Morgan did not intend to postulate a hypothesis of her own. Instead, Niemitz claims, Morgan merely listed analogies of features of savannah type mammals on the one hand and of aquatic mammals and man on the other, asking the scientific community for explanations other than a common aquatic ancestor of extant man.

The AAH, like many models concerning human evolution, can certainly be criticised for not being stated in a scientifically testable way, but it is clear from Morgan's books that she is considering Alister Hardy's idea of a "more aquatic" past for the ancestors of *Homo sapiens.* In particular, her chapter "The Wading Ape?" (Morgan 1997) explicitly considers the evidence for and against the idea that a component of wading was key in the evolution of bipedalism. Niemitz does not credit Morgan for this but suggests that "more recently" she "has stressed more the littoral aspects of her ideas, approaching, to some extent, Niemitz's conclusions (2000, 2004)." (Niemitz 2010 p 250).

The only argument Niemitz offers in support of a demarcation between his own wading based "Amphibische Generalistentheorie" and the "AAH" is another reference to Preuschoft and Preuschoft (1991) which, he claims, "showed that humans are far too bad swimmers ever to have been derived from a swimming ape ancestor." (Niemitz 2010 p 250.). Missing from this critique, like all the others, is any consideration of the swimming and diving abilities of humans as compared to those of chimpanzees, and the possibility that such differences might have emerged from a differential (however slight) in selection.

Niemitz does note the positive comments about "a weaker version" of the AAH made by Groves and Cameron (2004) which is, of course, the major idea behind this thesis, so it is frustrating to this author that Niemitz insists on a demarcation between wading and other modes of movement in water.

4.1.2 Literature citing the AAH in a neutral or minor way

In addition to papers specifically promoting or critiquing the AAH, there have been several papers which have given a neutral account and several that have contained very brief or marginal references to the hypothesis.

Neutral papers

There are at least four fairly neutral reviews of the AAH. Patrick (1991), evaluates putative human characteristics for swimming and concludes that, compared to aquatic and semi-aquatic mammals, they are lacking in our species. However, he suggested that 'cortical control' over normal breathing mechanisms appears to be stronger in humans which may account for some of our ability to swim and may, in fact, be a specific adaptation to do so.

Denton (1995) gave a balanced critique of the AAH but gave an alternative explanation to the observation that humans, uniquely among primates, appear to have lost their capacity for specifically detecting salt depletion through a coastal life.

Neutral accounts of "AAH"		
Paper	N	Refs
Adaptations or otherwise to swimming and diving in humans	1	Patrick (1991)
Evolution of human water-borne parasites	1	Ashford (2000)
Positive and negative aspects of Morgan's salt hunger hypothesis	1	Denton (1995)
Roede et al. Book Review, both positive and negative comments	1	Groves (1993)

Table 23 Neutral Accounts of "AAH"

Minor references

There have also been at least 13 short references to the AAH in the literature, which can be roughly equally divided between positive and negative comments.

Positive short references in the literature include those by Dawkins (2004 p 82), Calvin (2002 p 87) and Groves and Cameron (2004 p 68)

There are roughly an equal number of short negative references to the AAH including Stanford (2003 p 109), Lewin & Foley (2004), Chernova (2006 p 47), Jablonski (2006 p 41) and Dunsworth (2007 p 24).

Short references to "AAH"		
Context of mention	N	References
Positive… 7		
Positive reference to the wading hypothesis	2	Dawkins (2004), Attenborough (2002)
Generally positive to the AAH	5	Hewes (1964), Morris (1967), Dennett (1995), Cameron & Groves (2004)
Dismissive… 7		
Negative reference to the wading hypothesis	0	

Generally negative to the AAH	7	MacLarnon & Hewitt (1999), Hohman (2003), Stanford (2003), Lewin & Foley (2004), Crompton (2004), Chernova (2006), Dunsworth (2007)

Table 24 Short references to "AAH"

Conclusions from the AAH literature

Several conclusions can be made from this brief review of the so-called "aquatic ape hypothesis". Firstly, the very labelling of the idea has not been helpful, to say the least. It seems to have led to some unnecessary confusion, as it appears to be proposing a greater level of aquatic adaptation than any of its proponents have ever suggested. The term 'aquatic' is itself rather open to interpretation but most definitions would place the putative 'aquatic ape' in much deeper water than AAH proponents have usually considered. Other labels have been suggested such as the "wetland ape hypothesis" (Ellis, e.g. 1993) but it would seem that, for the foreseeable future at least, we are stuck with the presently well-known term despite all the problems it creates. Personally, I urge that people use the term "waterside hypotheses of human evolution", in the *plural*, when referring to such ideas as doing so makes it clear from the start that the degree of aquatic adaptation being proposed is not necessarily great and, perhaps more importantly, that there is not one single, narrow, idea about this but, rather a cluster of varying ones.

In addition to being misnamed, the so-called "aquatic ape hypothesis" (AAH) was never fully defined by its earliest proponents (Hardy 1960; Morgan 1972, 1980), thereby exacerbating the confusion surrounding it. Especially lacking has been any clear guide as to the level of aquatic adaptation being proposed or a consistent timescale with which to apply it. Proponents and skeptics alike have therefore been free to interpret the idea in their own personal way and make assumptions about the level of selection being proposed and the likely effects, if any, of such selection. This review has shown that the more extreme the assumptions are about the amount of aquatic adaptation being proposed, generally, the greater is the level of skepticism about it.

Despite the variety and vagueness in the pro-AAH literature, the few published critiques have all evaluated only 'strong' forms of the hypothesis. They clearly reject the idea that there could have been an 'aquatic ape' in the real sense that a seal is an aquatic mammal. The possibility that modest levels of aquatic selection may have been partly responsible for ape-human divergence has been almost totally absent from the discussions. And yet even very slight levels of natural selection have been shown to result in profound and rapid effects in the phenotype of populations (see, e.g. Haldane 1932; Li and Graur 1991), and are indeed implicit in more orthodox explanations of human evolution. This is perhaps most difficult to reconcile when one considers most orthodox models currently presume even smaller differences between the paleohabitats responsible for ape-human divergence than does the AAH.

Most relevant, in relation to this thesis, is the review showed that critics of the AAH tend to dismiss all of its arguments equally, even ones which are clearly more plausible than others. The wading hypothesis of bipedal origins appears to have fallen victim to this phenomenon more than most. If there is a general paucity of counter-arguments to the AAH overall, published criticisms against its wading component are almost non-existent.

Clearly, despite the efforts of workers to distance themselves from the AAH's poor reputation (Myers Thompson 2002 p 67; Niemitz 2002, and my own personal experience of over ten years studying this phenomenon) whilst studying aspects of bipedalism related to moving through water, there still exists a degree of skepticism against such watery ideas in anthropological circles that cannot be justified any longer.

But rather than perpetuating the controversies that have grown up surrounding this subject by continuing to avoid its mention, I take the view that the only rational approach is to get the idea out in the open and examine it carefully, as I try to do here.

The most satisfactory solution to this problem, I suggest, is to finally, unambiguously define the hypothesis. This, I have attempted to do in the final chapter, by drawing out the 'lowest common denominator' ideas that pervade all the various pro-AAH arguments published so far.

4.1.3 Weaknesses in previously published wading models

So far in this thesis, forty two different published ideas on hominin bipedal origins have been reviewed. The framework of criteria defined here to rate and compare models of hominid bipedal origins rated wading in shallow water as one of the strongest arguments. Postural feeding models were rated the next best with several other models being rated highly in various aspects. A brief summary of the reasons for this analysis now follows.

Here, the twelve evaluative criteria are reviewed once more specifically in relation to how existing wading models compare with the others and thereby clarify their relative strengths and weaknesses.

How published wading models were rated by the 14 criteria

Darwinian

A.1 Provides strong selection for bipedalism. The three published wading hypotheses were rated very highly in this area as they provide a strong immediate incentive for upright posture: To raise the upper body and head out of the water so that one can continue to breathe.

A.2 Provides strong sexual selection. The wading models generally do not make a case for improved sexual selection.

A.3 Not teleological. Extant apes, without any anatomical adaptations for bipedalism, are still able (indeed induced) to move bipedally in shallow water. Moreover shallow water, by its very nature, provides a medium with a continuum of depths from 'so deep the ape has no choice but to wade bipedally, and needs no anatomical adaptations to do so' to 'so shallow that the ape could opt for a quadrupedal mode of locomotion and indeed is likely to do so considering its lack of anatomical adaptations. For these reasons, wading models were rated highly in this area.

Ecological

B.1 Improved Food acquisition. The wading models were generally rated well on this point as they all posit that early hominins lived in food-rich areas with high biomass.

B.2 Has good answers to predator vulnerability questions. Hardy's (1960) coastal wading model does offer good answers to predation issues because these niches simultaneously provide simple escape routes from both terrestrial and aquatic predators. However, Verhaegen et al.'s (2002) wading ideas introduce new predation dangers from fresh water aquatic predators such as crocodiles.

B.3 Explains why extant *Pan/Gorilla* are not obligate bipeds. This criteria was found to favour Hardy's original wading model over the others most as it proposed simply that the human lineage found themselves by the coasts where they were more compelled to move through shallow water, whereas the lineage leading to *Pan* & *Gorilla* were not. Verhaegen et al. (2002) blur this simplicity by arguing that the last common ancestor of humans and great apes were already somewhat arboreal, but still argue that coastal living in human ancestors, but not great apes, later, made the distinction.

B.4 Is observed in extant *Pan/Gorilla* (or at least some other large primates.) Wading models are strongly supported by anecdotal evidence for wading bipedalism in extant apes and other large primates. Other models, notably for postural feeding, are also supported by similar evidence but the reported 'bipedalism' usually cited is rarely in the form of locomotion and it is generally not unsupported. However, it should be conceded that Hardy's (1960) coastal model is not supported by evidence in extant apes.

B.5 Applies to both sexes. Wading models apply equally to both sexes as do many of the other models.

Palaeontological

C.1 Explains anatomical anomalies seen in early bipeds, such as *A. afarensis*. This is an area in which published wading models were rated relatively poorly, as were most of the models. It is certainly an area that could be greatly improved upon.

C.2 Makes sense in terms of the known paleoecological record for early hominids. The earliest version of the wading hypothesis (Hardy 1960) invited strong criticism because it postulated a phase in human evolution that was not supported by any fossil evidence and has been contradicted by some fossil evidence since. The other published models have since significantly improved on this.

C.3 Proposed form of locomotion overlaps biomechanics of human bipedalism. This is a strong area for the wading hypothesis. Bipedal wading in shallow water is essentially the same kind of locomotion as bipedal walking on dry land and Verhaegen et al.'s (2002) provides an elegant precursor to both knuckle-walking and human striding bipedalism.

Epistemological

D.1 Has explanatory power beyond bipedal origins. The wading models have been historically linked to the so-called 'aquatic ape hypothesis' (AAH, see section 4.1) which has set out to explain many, if not all, physical differences between humans and the great apes. Although Niemitz (2002) goes to some lengths to distance himself from the AAH, and Verhaegen et al. (2002) have argued that bipedal origins should not be included in the AAH (pers. Comm. 2004) the idea that human bipedalism may be, at least in part, explained by wading almost certainly remains a significant part of it.

D.2 Is complementary to/complemented by other models. Niemitz's (2002) 'Amphibische Generalistentheorie' does encompass several other ideas and is argued as a complementary factor in addition to others. This is less true of the Hardy/Morgan proposal of a distinct coastal phase before *Australopithecus* which generally contradicted almost all models of bipedal origins both before and since. As Verhaegen et al. (2002) argue that australopithecines are not ancestral to humans, it is suggested that this is another area where significant improvements could be made.

D.3 Provides falsifiable, or at least testable, predictions. This was the worst criteria of all the models evaluated, overall, and the wading models were no exception. Clearly a more scientific approach would signify an improvement to the methodology behind all such models.

Main weaknesses

So, to summarise, according the evaluative framework described in this thesis, previously published wading models, although ranked among the strongest, still had some weaknesses.

Notably, for criteria C.1, D.2 and D.3 wading models can be most criticised. Namely, that the model should account for the anatomical differences between early hominin bipeds such as australopithecines and modern humans; that it should be more complementary to other models of bipedalism and, finally, that it should follow a more scientific epistemology and make testable predictions.

The wading hypothesis and the general waterside model of human evolution ("River Apes… Coastal People") proposed in the final chapter of this thesis has been formulated as a result of the strengths of the wading models, and also to meet the criticisms, described above. The author argues that it is basically an improved version of previous 'wading models', that it reduces their weaknesses and draws additional strength from some of the ideas in other models reviewed here.

4.2. Addressing criticisms

Two major perceived weaknesses of published wading models will be addressed in the next two chapters and a third will be considered in the final chapter.

One identified weakness of wading models is that they make few scientifically testable predictions. Chapter 5 attempts to address this. It makes and tests the prediction that wading should help make bipedalism less energetically costly in early hominins that must have lacked the anatomical adaptations for bipedal efficiency of modern humans. The cost differential between optimal (i.e. fully upright, extended hip, extended knee, EHEK, human-like) and non-optimal gaits (i.e. Bent Hip Bent Knee, BHBK, chimp-like), according to this test, should be reduced in water.

Another weakness of published wading models is that they offer little in the way of hard evidence from the fossil record of wading in early hominin bipeds. Chapter 6 reports a geometric morphometric study of the hominoid hip which compares the shape of the australopithecine pelvis and femur with extant great apes and humans. It tests the prediction that the shape differences between the australopithecine and human pelvis provides for biomechanical advantages for movements consistent with adaptations for more efficient wading.

In chapter 7, other anecdotal evidence pertaining to the other predictions of the wading hypothesis is discussed and a program of further study proposed to test them more thoroughly. The overall model proposed there is also much more complementary to other models than other models of bipedal origins, another perceived weakness of previously published wading models.

CHAPTER FIVE

THE COST OF ‘NON-OPTIMAL’ GAITS IN WATER

5. THE COST OF 'NON-OPTIMAL' GAITS IN WATER

Reproduced from previously published paper…

Kuliukas, A.V., Milne, N., Fournier, P. A. The relative cost of bent-hip bent-knee walking is reduced in water. *Homo* 60: 479-488, (2009).

Abstract

The debate about how early hominids walked may be characterised as two competing hypotheses: They moved with a human-like gait with extended hips and extended knees (EHEK), or with a bent-hip, bent-knee (BHBK) gait, like apes. Both have assumed that this bipedalism was almost exclusively on land, in trees or a combination of the two. Recent findings favoured the EHEK hypothesis by showing that the BHBK gait is 50–60% more energetically costly than a EHEK human gait on land. Here, these findings are confirmed, but show that in water this cost differential is reduced to about 17% in waist deep water at 0.6m/s with a 50^o *knee-flexion, and effectively eliminated in deeper water, at slower speeds, or with greater knee flexion. These data suggest that the controversy about australopithecine locomotion may be eased if it is assumed that wading was a component of their locomotor repertoire and supports the idea that shallow water might have been an environment favourable to the evolution of early forms of "non-optimal" hominid bipedalism*.

5.1. Introduction

The debate surrounding the interpretation of the postcranial anatomy of the most complete fossilised evidence for an early hominid biped, AL 288-1 ("Lucy"), can be characterised as a contest between two major competing hypotheses about their most likely bipedal gait: One is that *Australopithecus afarensis* walked in a 'fully upright human-like' or 'Extended Hip, Extended Knee' (EHEK) manner, the other that they adopted a 'bent-hip-bent-knee' (BHBK) gait. Various arguments have been put forward by proponents of one or other of the two hypotheses which are reviewed here, especially the recent evidence published against the BHBK gait model by Carey & Compton (2005).

One consideration, which has been notable by its absence in the scientific literature so far, is the question of how *A. afarensis* might have moved in shallow water. This is perhaps surprising, considering that much of the *A. afarensis* fossil record (e.g. AL 288, AL 333) is associated with the Hadar paleohabitat, which was dominated by wetland systems (Johanson & Edey 1981 p 128-129.) Yet, the vast majority of the arguments published in the literature to date have clearly been based upon an assumption that whatever bipedal gait *A. afarensis* adopted, it was being used only on land or in trees.

In this chapter, I report data comparing fully upright with bent-hip-bent-knee wading with varying degrees of knee flexion, in various shallow depths of water, at various slow speeds (Kuliukas et al. 2009).

5.2. *'Bent Hip Bent Knee'*

Bent Hip, Bent Knee versus Extended Hip, Extended Knee Gaits

Even before, but especially after, Johanson & Taieb (1976) made the remarkable discovery of the fossilised hominid popularly known as 'Lucy', (AL 288-1), there has been a debate about how putative ancestors labelled 'australopithecines' might have moved.

There is a broad consensus that they were either hominins (ancestral to *Homo*) or on another lineage separate to ours, but closer to us than to the apes, although Kleindeinst (1975 p 644-646) supported the alternative view that they may have been ancestral to apes too.

Whatever their phylogeny, there does appear to be good consensus behind the idea that generally they moved bipedally (Johanson & Edey 1981; Rak 1991), but for a contrary view see (Sarmiento 1985; 1987; 1988). There remains a clear disagreement, however, as to exactly what gait they are likely to have adopted.

There are two main schools of thought on the matter: Some workers (Lovejoy et al. 1970; Jungers 1982; Crompton et al. 1998) favour a fully upright, very human-like extended hip, extended knee (EHEK) gait whilst others (Stern & Susman 1981; Berge 1994) propose a different, more ape-like, bent-hip, bent-knee (BHBK) gait. For a full review of the arguments for and against see (Stern, 2000; Ward, 2002) but what follows here is a brief summary.

Arguments for and against the 'Bent-Hip-Bent-Knee' gait

According to Johanson and Edey (1981 p 163), the initial reaction upon seeing the first fossil proximal tibia (AL-129) from *Australopithecus afarensis* was, that this was a biped that "could walk upright". The bicondylar angle of the knee appeared to be valgus, as in the human condition, and, as a consequence, the fairest assumption seemed to be that its bipedalism included the human-like adaptation of increasing walking stability by placing the centre of mass over the stance leg (Shefelbine et al. 2002.)

However, this impression was not shared by other specialists who had studied other skeletal samples from other australopithecines. Several workers concluded that as their morphology was not very similar to our own, australopithecines were unlikely to have moved the same way we do.

For example, Zuckerman et al. (1973), in their extensive and pioneering morphometric study of the Sts 14 (*Australopithecus africanus*) pelvis, found that although it differed significantly in shape from that of the African great apes, it also differed, equally as much from *Homo*. Oxnard & Hoyles-Wilks (1994 p 19) concluded: "The deduction that stems from the investigations just described is that, because the form of the pelvis in the fossil is neither human-like nor ape-like, but uniquely different from both humans and apes, the fossil, therefore, must have had a form of locomotion uniquely different from that of both apes and humans." Their interpretation of this uniqueness was that it was due to a rare combination of existing primate locomotor activities, rather than some form of locomotion that was entirely different.

Other morphometric studies on *A. afarensis* (AL 288-1) itself (Stern and Susman, 1983; Berge, 1991, 1994) concluded, similarly, that australopithecines probably moved quite differently to *Homo*, perhaps with a swaggering side-to-side gait, probably with bent-hips and bent knees, rather like chimpanzees do on the rare occasions bipedality has been observed in them (< 3% of locomotion according to Hunt 1994). These authors have suggested that a EHEK gait is unlikely to have been stable enough on the grounds that the inter-acetabular distance is relatively large for such a small animal and as a consequence that a “waddling” or “rocking” gait with significant rotatory movements of the upper limbs is more likely to have been practiced.

More recently, however, another line of enquiry has shown that a BHBK gait is unlikely to have been adopted by any would-be biped on the grounds of energy efficiency and excessive body heat generation. Firstly, through computer modelling on simulated *australopithecine-like* figures (Crompton et al. 1998), and then through direct physical measurements of energy consumption on human subjects (Carey & Crompton 2005), it has been shown that the BHBK gait is, perhaps not surprisingly, significantly more inefficient than EHEK in humans *on land*. They found that the energy cost of locomotion almost doubled and that core body temperature was shown to rise by 0.3°C in 30 minutes by adopting this form of walking. Clearly these data indicate that BHBK walking would have been very costly for a bipedal animal living in a hot, equatorial habitat.

The outcome of this debate is important to researchers interested in the energy efficiency models of hominid bipedal origins (Taylor & Rowntree 1973). There is good evidence (Rodman & McHenry 1980) that modern, fully-upright bipedalism, as practiced by people every day, does have an efficiency edge over most forms of mammalian quadrupedalism, and particularly over the quadrupedal knuckle-walking of the genus *Pan,* during slow walking, which would offer good selective benefit for its adoption (however, for a contrary view see Halsey & White 2012). It is not difficult to extrapolate backwards from this kind of hard anatomical observation in modern humans today, to postulate that energy efficiency was an evolutionary driver for our postcranial traits. This certainly has become a majority view and most anthropologists would argue that our postcranial anatomy is the consequence of some kind of positive-feedback loop: More long distance walking provided a means for selection in ancestral populations for traits that made it more efficient, which allowed those individuals with such traits to do more long distance walking than their competitors which improved their fitness. Whether it be in the ecological context of savannahs, woodlands or littoral zones, scavenging or foraging for food provide compelling reason for such selection for greater locomotor efficiency to have taken place.

Assuming the majority view is right and human bipedalism does have some energetic advantage over quadrupedalism, it has still not been demonstrated how the very traits that allow this efficiency could have evolved in the first place. Indeed if it were so beneficial, it begs the question: Why did chimpanzees and gorillas not adopt it too? Clearly, if the earliest proto-hominin bipedal apes did move in an inefficient BHBK gait, this would argue against the energy efficiency argument, as it would provide a significant energetic ‘rubicon’ that somehow had to be crossed. Unless there was some other factor involved in the early adoption of bipedalism, which dampened down the effect of this rubicon, it would appear that the argument for an early BHBK gait was contradictory to the argument which favours energy efficiency as a major driver of the evolution of human bipedalism.

The common assumption from both sides of this debate has been that whichever way the australopithecines moved, they did so either on land, or in trees, or both. As Richmond put it: “The focus has shifted instead [from a gibbon-like brachiating model] to whether bipedalism was preceded by exclusively or nearly exclusively climbing and suspensory behaviours, including vertical climbing, in a large-bodied ape, or whether the ancestral condition included a significant terrestrial, possibly knuckle-walking component (Richmond et al. 2001 p 73)

The possibility that they may have moved bipedally in water seems to have been discounted, although it is not clear from the literature as to when, how, or why this idea was ever rejected.

This is particularly surprising because many of the fossil sites associated with *A. afarensis* were close to, or dominated by, significant wetland systems (Johanson & Edey 1981 p 128-129).

The biomechanics and kinesiology of human walking in water has, in recent years, begun to be studied (Barela et al. 2006,) especially in the context of rehabilitation therapy in the sick or elderly (see, for example, Shono et al. 2000, 2001; Fujishama et al. 2003; Wadell et al. 2003; Masumoto et al. 2004) but the phenomenon is most noteworthy by its absence in the literature on human evolution and bipedal origins.

If it was assumed that australopithecines practiced at least some of their bipedalism whilst moving through shallow water, in accord with Rose's (1991 p 39) premise that the proto-hominids probably practiced a repertoire of locomotor behaviours, and not just one or two, it is possible that several key counter-arguments from both schools of thought could be removed and the energy efficiency model would therefore be enhanced significantly:

The energy efficiency disadvantage of the BHBK gait, as compared to EHEK, might not be so marked in water, where moving is likely to be more expensive in any case.

If moving through shallow water acted as a 'level playing field' for early bipeds, neutralising them from the inefficiencies of one gait over another, it might have provided a reduction in whatever energetic rubicon might have been present to inhibit the early adoption of bipedalism, and therefore facilitate the onset of a positive feedback loop of anatomical adaptations leading to ever greater efficiencies.

The problem of overheating by adopting a BHBK gait is likely to be nullified whilst moving through natural shallow water.

The stability of an EHEK gait, even with an anatomy that appears not to be adapted for it, could be greater in waist deep water than on dry land.

Previous studies done on the energetics of human gait in water

A number of studies have looked into the biomechanics of walking in shallow water from the point of view of exercise physiology (for a review see Rebutini et al. 2012). These studies have largely been motivated to provide more data pertaining to recuperation therapies for people recovering from various operations or in athletes recovering from injuries of other trauma.

Only two studies, to the knowledge of the author, have looked at the energetics of wading in water from the perspective of the evolution of bipedality.

The first study, by Ghesquiere & Bunkens (1991) compared the energetics of wading up to the arm pits in water with walking on dry land and found that the costs were 4x higher in water. On that basis they dismissed the wading hypothesis. Shallower depths were not considered. The study did not vary knee or hip flexion, other gait parameters or speed.

The second was a short pilot study in a variable depths pool by this author for his master's thesis. (Kuliukas 2001). The study found that in water shallower than around waist depth, most people could wade through water faster than they could swim. The study showed that a sideways or side-to-side gait was faster than a standard "face on" fully-frontal gait. Only speed, and not energetic cost, was measured.

A more comprehensive study of the energetics of wading (Kuliukas et al. 2009) is reported here.

5.3. Testing BHBK in water

This section describes a set of experiments that were conducted to test the effect of wading in shallow water on the relative cost of bipedal locomotion using bent-hip bent knee and fully upright, extended hip and knee, gaits. It specifically tests one of the predictions made by the wading hypothesis – that shallow water should provide a scenario and environment which supports the early adoption of bipedal locomotion.

5.4. Materials and methods

Experimental protocol

Thirty fit and healthy volunteers (14 males, 16 females, means and standard deviations, respectively, for age=39.13 and 15.36 years, weight=76.54 and 15.25 kg, height=1.72 and 0.10 m, BMI=29.51 and 3.70 kg/m2) were involved in a series of wading experiments with approval granted by the University of Western Australia Ethics Committee.

The experiments were designed to calculate the energy consumption of various walking trials administered to each individual following a counterbalanced design. Each set of trials was performed on the same day and examined the effects of speed, depth of water and degree of knee flexion on the cost of locomotion. Typically the volunteer either walked along one end of a pool or waded from side to side at a given depth, speed and knee flexion, for about three minutes in order for their oxygen consumption to reach a steady state. The speed was maintained by synchronising the volunteer's location against a series of markers along the pool. Knee flexion was measured as the angle the tibia makes away from the continuation line from the femur. The degree of knee flexion was maintained by suspending a cord across the pool at a height corresponding to the eye-level of the volunteer whilst standing with bent knees. Once steady state was reached, expiratory gases were collected via a Douglas bag for about 1 min and subsequently analysed to calculate the rate of O2 consumption and CO2 production. Heart rate was recorded before and after each trial and used to ensure the volunteer was rested before the next trial in the set.

A (not exhaustive) selection of permutations of speed, knee / hip flexion and water depth were tested:

Variables being tested	Details	Permutations
Speed of wading (m/s)	0, 0.1, 0.2, 0.3, 0.4, 0.5; 0.6, 0.7; 0.8; max	10
Depth of water (cm)	0, 96, 120, 144	4
Flexion of knee during BHBK or EHEK gait	0 (EHEK), 30, 50, 70	4

Table 25 Permutations of speed, depth and knee flexion measured

Although this would potentially lead to at least 160 data points per individual, due to time constraints, not all permutations were tested. As a compromise, a reduced protocol was followed. For example only postures (i.e. speed 0 m/s) were studied at all the different depths, and speed itself was only thoroughly investigated at one depth (0.96m). Overall, 275 individual trials were undertaken on 25 separate days, to cover 45 of the 160 permutations.

The 'standard' experimental protocol was as follows:

Volunteers first performed a set of four trials testing two gaits, human-like, fully upright extended hip, extended knee (EHEK) and ape-like, bent-hip, bent-knee (BHBK) on land and in water.

They were asked to walk, at 0.6 m/s, up and down one end of a swimming pool. This speed was maintained by synchronising the volunteers' location against a series of cones and the two sides of the pool using software written specifically to generate such timely audible signals. 0.6m/s was selected as a suitable speed because although not optimally efficient for walking or wading at the depths chosen for this study, it nevertheless represented a comparable speed which was towards the 'more efficient' end of the range for both and therefore appeared to be a good compromise. (See efficiency results for more discussion about this.)

During each trial, a number of widths were walked to reach "steady state" before the expiratory gases were captured using a Douglas bag, carried alongside the volunteer by the author. The period of time used to reach steady state was around 3 minutes, and was always consistent for all the trails in a given set.

Respiratory gases were then recorded for a fixed amount of time, or a fixed number of widths of the pool, for each set of trials, usually for about 60 seconds.

The exact order of the four trails was randomised, but during the colder months volunteers performed the two trials on the side of the pool before getting into the water to minimise discomfort. For trials done in the summer months this was totally randomised.

An estimate of the number of strides taken by the volunteer was also recorded.

For the BHBK gait, the volunteer was asked to assume a posture with a knee flexion of 50º and an estimated hip flexion of 30º (from now on, be referred to as BHBK50.) This was measured with a rotating protractor. Whilst standing in that posture, the height at eye-level was recorded. A length of light string was suspended across the width of the pool at this height as a guide to help the volunteer maintain the BHBK50 posture as they walked. For the wading part of the trial set, the string was lowered to the same eye level whilst in the water (at 0.96m depth.)

Heart rate was measured during the recording phase of trial.

Volunteers were asked to rest for five to ten minutes between trials, usually until their heart rate had returned to close to their resting rate. Air and pool temperatures were noted, as was the start time and duration of the exercise. A few randomly selected volunteers were also asked to give a small sample of blood before and after some of the trials to measure blood lactate. Resting VO2 was also recorded for volunteers when their time allowed it. A DEXA scan was taken for a sample of volunteers. Douglas Bag gas fractional concentrations were accurately estimated using a gas analyser, which was calibrated at the beginning and the end of the trial set against cylinders of known Oxygen and Carbon Dioxide gas volumes. The volume of the respiratory gases was measured by pumping the air into a calibrated cylinder. Oxygen consumption was thus calculated and expressed in terms of standard temperature and pressure, and recalculated in terms of the body mass of the volunteer (VO2/kg/min.)

After a twenty minute rest period, the volunteer was asked to perform a second set of trials from one of the supplementary experimental sets described below, to obtain data for one of three more specific experimental trail sets:

- To find the most cost-efficient speed whilst wading in either EHEK or BHBK50 gait.
- To find the effect of increasing knee flexion on the efficiency of wading and walking.
- To find the cost of standing posture in different depths and using different knee flexions.

Volunteers, where possible, were allocated to one of the three trials randomly. However, if they were unable to perform the knee flexion study, they were allocated to an alternative. Towards the end of the study some of the volunteers were asked to do two of the supplementary tests instead of the standard test and one supplementary one.

Paired student's t-tests were used to compare the differences in oxygen consumption (VUO2) for BHBK and EHEK on land and in water, and two-way unbalanced ANOVA followed by Fisher LSD a posteriori tests, using Genstat for Windows software, were adopted where depth and knee flexion variables were compared. Statistical significance was accepted at the po0.05 level.

Some additional notes on the experimental protocols are now given for each of the supplemental trial sets:

Supplemental trial set 1: To find the most efficient wading speed

Two sets of four trials were done on the same day, to measure the efficiency of BHBK50 and EHEK gaits at various speeds. The first trial in each set was to find their maximum speed using this gait. The volunteer was asked to wade up and down as fast as they could, ensuring that one foot was always in contact with the bottom of the pool. Once the max speed was known (usually around 1m/s in a 0.96m depth pool) then three other speeds were selected from a pre-planned list to provide a good range of speeds in addition to the 0.6 m/s already conducted in the first set of trials. The order of the remaining three trials was randomised. After a rest period the volunteer would repeat the trial set but using the alternative gait.

Supplemental trial set 2: To find the effect of knee flexion of wading and walking efficiency

A further set of four trials was conducted; two more on land, two more in water. Only volunteers that had no recent knee complaints were able to do this quite difficult exercise. Two further knee flexion angles were used, one easier (40º) and one more difficult (70º), and the eye height was measured for each. The same technique as before was used to collect data. The data from these gaits will be labelled BHBK40 and BHBK70 from this point onwards.

Supplemental trial set 3: To the effect of depth and knee flexion on the cost of standing posture

Six more trials were conducted in this trial set: Four in water, at two different depths (out of 0.96m, 1.2m and 1.4m, depending on the height of the volunteer) and two on land. Each pair was done using a different posture: one EHEK and one with a bent-hip, bent-knee gait, either BHBK50 or BHBK70.

5.5. Results

Comparison of BHBK and EHEK gaits at medium speeds in shallow water

Reduced differential in efficiency between BHBK50 and EHEK at speeds between 0.5 and 0.6 m/s in 0.96 m depth, as compared to moving on land

In agreement with Carey and Crompton (2005), it was found that the cost of a BHBK gait (Fig. 20a) with 501 knee flexion (BK50) at 0.3 m/s was approximately 57% higher (student's t-test, po0.05) than an EHEK gait on land. 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 EHEK and BHBK gaits, (p=0.631, Fig. 20a).

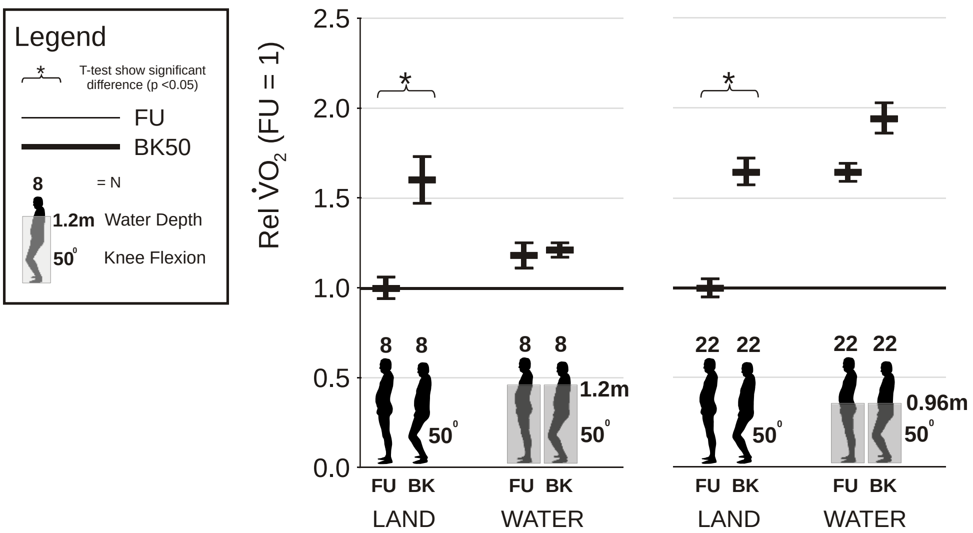
a (0.3 m/s)
b (0.6 m/s)

Figure 21 Relative cost of walking with EHEK and BHBK gaits.

(Fig compares on land versus (a) chest-deep water at 0.3 m/s or (b) waist-deep water at 0.5 - 0.6 m/s. All results for each panel are expressed as means ± S.E. relative to the cost of the EHEK gait on land. * indicates statistically significant difference at $p < 0.05$.)

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. 20b). As knee flexion increased, there was a greater difference between the cost of EHEK and BHBK walking on land, but this effect was diminished in water (two-way, unbalanced ANOVA, substrate: F=33.40, $p > 0.001$, flexion: F=14.27, po0.001; Fig. 21).

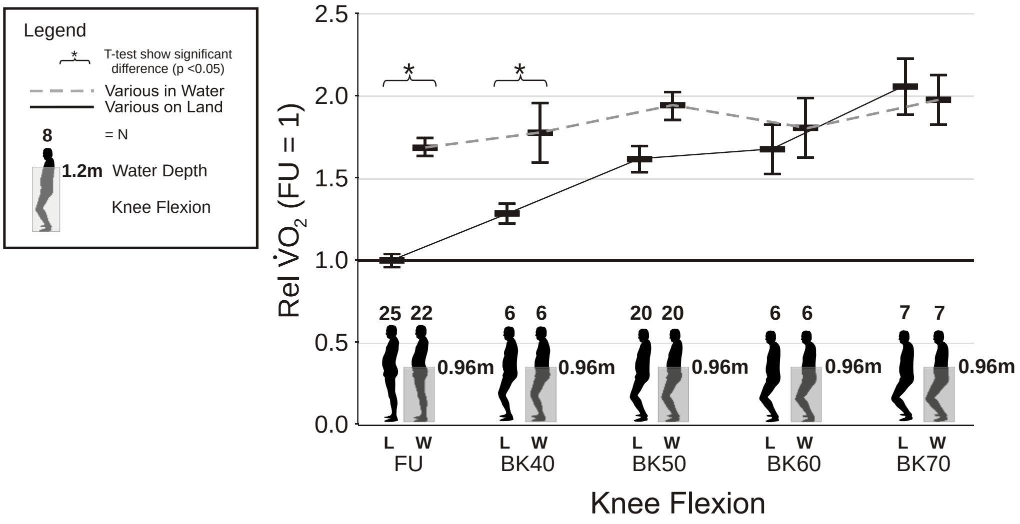

Figure 22 Relative cost of walking with EHEK and BHBK gaits

(Fig shows on land versus waist-deep water at 0.6 m/s with varying knee flexion. All results are expressed as means ± S.E.M. relative to the cost of the EHEK gait on land. *, indicates statistically significant difference at p < 0.05.)

It was also found that it was about 73% more costly to move with an EHEK gait in water than on land, but that this ratio gradually diminished as knee flexion increased. Walking with a knee flexion of 601 or more was actually found to be just as costly (no significant difference) in water as on land. The effect of increased knee flexion on the cost of standing still was also found to be 50–70% more than a EHEK posture on land, with the cost falling away as water depth increased up to 1.4 m, where there was no significant difference between postures (two-way, unbalanced ANOVA, flexion: F=19.86, po0.001, depth: F=6.20, p=0.004; Fig. 22).

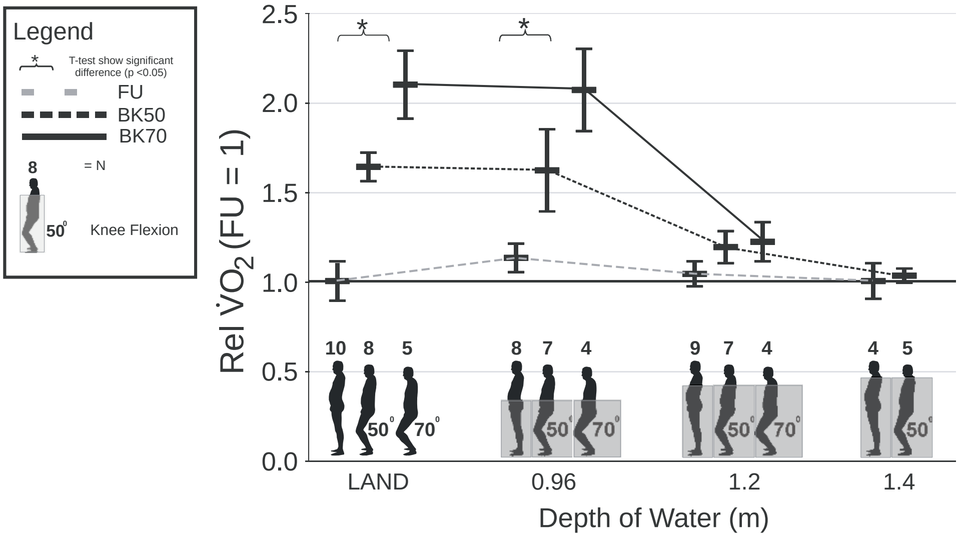

Figure 23 Relative cost of standing still in varying depths and knee flexions.

(All results are expressed as means ± S.E.M. relative to the cost of standing still EHEK on land. *, indicates statistically significant difference at p < 0.05.)

Finally, as with walking on land, it was found that the cost of locomotion per metre travelled was highest at very low speeds (o0.2 m/s), reached lowest levels in the mid-range (between 0.3 and

0.7 m/s at this depth) and then rose again as maximal speeds were reached, with the EHEK gait being 20–25% less costly over the 0.3–0.7 m/s range (Fig. 23).

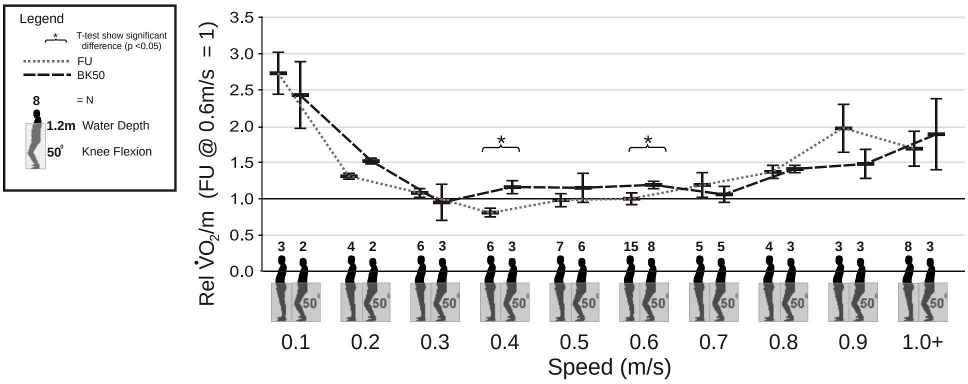

Figure 24 Relative cost of wading with EHEK and BHBK (50°).

Fig shows at varying speeds in 0.96 m water. All results are expressed as means ± S.E.M. relative to the cost of wading with EHEK gait at 0.6m/s. *, indicates statistically significant difference at $p < 0.05$.

5.6. Discussion

The results of this study show that the cost differential of BHBK compared to EHEK gait is less in water than on land. This 'gait-cost equalising effect' varies with the angle of knee flexion, depth of water, body height and speed of movement. The greater the knee flexion, the deeper the water and the slower the speed, the less is the differential between the cost of movement of a BHBK gait compared to the cost of a EHEK gait. Under some conditions (knee flexion greater than 60º at speeds less than 0.3 m/s in depths of water about the xiphisternum level) the cost of moving in water is not significantly different from that on land.

These findings may have a bearing on some important issues in the debate about the evolution of hominid bipedalism, generally, and about the possible mode of locomotion of early hominid bipeds such as *A. afarensis* in particular: Assuming that the results of this study would be as valid in the typical muddy substrata found in flooded forest habitats as in our ideal swimming pool experiments, they suggest that for early hominids not yet anatomically specialised for human-like bipedalism, the cost of moving through shallow water bipedally may have been less affected by gait in water than on land.

Although there is good evidence, for example from Laetoli, that australopithecines walked on land habitually (Leakey & Hay 1979) and moving through water would have entailed significant predation risks from crocodiles and territorially defensive hippopotami, there is good reason to suppose that early *Homo* retained a significant ecological relationship with waterside habitats, along with their australopithecine-like forebears.

Firstly, it is likely that early *Homo* needed to maintain an adequate water budget for thermoregulation, in the context of mobility and stealth activity in semi-arid tropical mosaics (Wheeler 1991, 1992) and would therefore have been unlikely to have wandered too far from drinking water. Such locations, including gallery forests adjacent to rivers, swamps and lakes would also have attracted game ungulates for similar reasons, and contained usable lithic materials with the potential for tool-making.

Secondly, as tropical rainforest made way for savannah in the Plio-Pleistocene, woodland would not have shrunk in a random manner but systematically, closer to permanent water courses in the form of gallery forests. Our early hominin ancestors, like most forest adapted species, are likely to have clung to these forest refugia (Hughes 1988;Meave et al. 1991) placing them closer to water courses, clung paradoxically, the more arid the climate became. Riparian forests are prone to seasonal flooding, a phenomenon likely to have exposed these hominins (Reed 1997 p 309) to the need for occasional movement through water and it has been suggested that habitats such as the Okavango inland delta, may have acted as relatively food-rich refugia for taxa, including early hominids, adapted to forests (Wrangham 2005).

Thirdly, some *A. afarensis* paleohabitats indicate a close association with water including Taharin (KHN-TH 13510), whose faunal assemblage was described as "including lacustrine animals and those that would be found along a lake margin and in the catchment area" Hill (1985 p 222), Hadar (AL 288-1) dominated by local wetlands (Johanson et al. 1982 p 391), Denen Dora (AL-333) associated with distinct water channels and the Dikika area (DIK-1) described as a "river-dominated delta system" (Wynn et al. 2006 p 332). The association with water-side niches is even stronger in some earlier hominids (e.g. *Sahelanthropus tchadensis,* Vignaud et al. 2002) which, according to some recent studies, have "apparent adaptations for bipedality, close to or even antedating accepted dates for hominin/panin divergence" (Thorpe et al. 2007 p 1330). The anticipated objection of taphonomic bias in this evidence can be countered, most importantly, by simply understanding that although death close to water courses doesn't have to indicate a more aquatic life style, it certainly doesn't provide evidence against it. The matter at hand is simply the question as to whether such habitats may have provided sufficient pressure of selection to favour increased levels of bipedality. Indeed, considering those current models of ape-human divergence that place the phenomenon in the context of wooded-savannah mosaics, it is difficult to see how such scenarios differ from the habitats of extant chimpanzees. If such a slight (or even non-existent) shift in habitat is perceived to have been sufficient to drive early hominin evolution it can only be suggested that waterside habitats could be more powerful in doing so.

Figure 25 Chimpanzee (*Pan troglodytes)* female, with infant, wading bipedally.

Fig shows chimpanzee in approximately 75cm deep water at the Conkouati reserve, Congo. Photo: Philippe Vallas/HELP International.

It is worth considering which habitat settings might provide the most feasible setting for bipedal wading. Extant great apes have been observed moving quadrupedally in very shallow water.

Fruth reported quadrupedal wading in bonobos in the context of foraging for invertebrates in shallow forest streams (interviewed in De Waal & Lanting (1997 p 79-82). Chimpanzees have been reported moving quadrupedally in shallow water too (Kortlandt 1999 p 27-31) and Gorillas have been observed moving quadrupedally in shallow swampy 'beis' in the Congo in the context of gathering roots and shoots of aquatic sedges (Parnell & Buchanan-Smith 2001).

However, in deeper water there is good evidence, including photographic and film, that chimpanzees (Karlovski 1996; Tutin et al. 2001; BBC / Discovery Channel 2002), bonobos (Myers-Thompson 2002 p 24; Kuliukas 2002), gorillas (Doran & McNeilage 1998 p 124; Parnell & Buchanan-Smith 2001; Breuer et al. 2006) and orang-utans (Ellis 1991 p 56; Sommer & Amman 1998; Galdikas & Erickson-Briggs 1999 p 72-80) tend to switch to bipedal locomotion (Fig 24), often in the context of foraging for food. As I have not been able to find reports of other mammalian taxa that share this locomotor behaviour, other than brief instances of postural bipedalism seen in film footage of the grizzly bear (*Ursus arctos*), bipedal wading would seem to be an almost unique characteristic of Hominoidea amongst mammals.

One of the two species most closely related to humans, the bonobo (*Pan paniscus*), perhaps the extant species most closely associated with the general body shape of *A. afarensis* (Zihlman & Cramer 1978), has been shown to habitually move both bipedally and quadrupedally with a knee flexion typically much greater (40˚ – 130˚) than that in humans (0˚ - 75˚) (D'Aout et al. 2002). Such general body shapes, therefore, may be seen as ideal candidates to benefit from moving through water bipedally, as shown in this study.

It is proposed that the results of this study should be considered in the light of the fossil evidence, provided earlier, linking the paleohabitats of early hominins to waterside habitats, and in the context of a climatically variable time period in human evolutionary history (Potts 1998). It is suggested, in that context, that this study indicates that intermittent wading in seasonally flooded habitats, either for food or as a necessity to cross flooded open patches of woodland, could have been a significant factor in leading some apes on an evolutionary trajectory towards obligate bipedalism. Furthermore, our findings might help to satisfy the apparently contradictory concerns of paleoanthropologists about the putative gait of the australopithecines: The suggested instability of the EHEK posture in australopithecines (Berge 1994; Stern 2000) would certainly not be as great, and concerns that a BHBK gait would have been too energetically costly and likely to have resulted in overheating (Crompton et al. 1998; Carey & Crompton 2005) may be eased, if it is assumed that at least some of their bipedal locomotion was performed in water.

I believe this study should stimulate further research in a number of areas. It would be useful to repeat this experimental protocol in various natural habitats to determine how the results might be affected by real world under-foot substrates. It should also be possible to conduct research into the shape of the australopithecine hip and, specifically, how it differs biomechanically from the human form. A 3D morphometric geometric study of the pelvis and femur should be able to yield enough data to determine the kinds of hip movements this hominid could perform with a biomechanical advantage better than the human form. Then, further similar studies to this one, varying gait by including components of lateral motion (e.g. twisting and sideways), could be done to test the hypothesis that the hip movements, found to be most effective in the australopithecine hip, might be explained as some adaptation to efficient wading.

CHAPTER SIX

A 3 DIMENSIONAL GEOMETRIC MORPHOMETRIC STUDY OF THE HOMINOID HIP

(OR “WHY WERE LUCY’S HIPS SO DIFFERENT?)

6. 3D GEOMETRIC MORPHOMETRIC STUDY OF THE HOMINOID HIP

OR "WHY WERE LUCY'S HIPS SO DIFFERENT?"

Original work, not previously published.

Abstract

In this chapter, a 3D Geometric Morphometric (GM) analysis of the shape of the pelvis and femur of various extinct hominids and extant humans and apes is described. Observed differences in shape of the pelvis and femur, between early hominids and the genus Homo, are then discussed in the context of the wading hypothesis.

A historical summary of previous morphometric studies of the australopithecine hip is provided to place this study into context with what has been done before and to highlight relatively new methodologies using various computer software techniques, some written by the author.

The general shape of the pelvis of Australopithecus afarensis *is shown to be fundamentally different from both* Homo *and extant great apes, and not intermediate between them. Although it includes many human-like traits indicating a strong propensity to bipedalism, there are also sufficient differences to indicate a very different mode of locomotion to the relatively efficient striding gait associated with modern humans. Basically, the australopithecine pelvis is remarkably platypelloid, even compared to humans, which is itself more platypelloid than those of extant apes.*

An analysis of putative muscle lever arm ratios is described. Triangular sets of landmarks including hip muscle origin, the centre of rotation of the acetabulum, and a generated (fixed point) landmark modelling an insertion point on the femur, were used to calculate the lever arm of the major muscle blocks involved with hip movement. For each specimen, each lever arm was expressed as a ratio of all the others, yielding over 135,000 ratios in all. This data was then explored using a business analysis data summarising tool, the Pivot Table feature of Microsoft Excel. This allows the rapid production of succinct species summaries of broad lever arm groups, such as those pertaining to abduction compared to those pertaining to extension, or for rotation, compared to flexion. The pivot table feature is designed so that these broad summary data can be "drilled down" to get at ever increasing detail, ultimately to the individual level arm ratio pairs.

The results indicate that the australopithecine hip was more adapted, than modern humans or extant great apes, to adduction, abduction and rotation of the thigh during locomotion. This is more logically consistent with a greater component of wading than other ideas published about a putative locomotor repertoire for early hominid bipeds.

6.1. ***Introduction***

The anatomy of the australopithecine pelvis is now reasonably well known thanks largely to two major fossil finds (STS14, AL 288-1) which have been extensively studied (Le Gros Clark, 1955; Lovejoy and Heiple,1970; Zuckerman et al., 1973; McHenry and Corruccini, 1975; Oxnard, 1975; Ashton et al., 1981; Stern Jnr and Susman, 1983; Berge, 1984; Berge and Kazmierczak, 1986; Häusler, 1992; Berge, 1994; Abitbol, 1995; Häusler and Berger, 2001.) Despite this work, anatomists have been unable to agree on what the shape of the australopithecine pelvis tells us about the way they moved.

Although there is a broad consensus that australopithecines were generally bipedal in their locomotion, there remains a large disagreement about whether their form of bipedalism was human-like.

Some, e.g. Lovejoy (1979), have suggested that the anatomy is consistent with human-like fully-upright bipedalism, whilst others (Stern Jnr and Susman, 1983) have disagreed, suggesting that it is more indicative of an ape-like bent hip, bent knee gait, others that it might have been something rather unique.

When Oxnard summarised over two decades of study into the shape of the australopithecine pelvis, he wrote:

“The deduction that stems from the investigations just described is that, because the form of the pelvis in the fossil is neither human-like nor ape-like but uniquely different from both humans and apes, the fossil, therefore, must have had a form of locomotion uniquely different from that of both apes and humans” (Oxnard and Hoyland-Wilkes 1994 p 19.)

When I read that, it occurred to me that perhaps all that was missing in Oxnard’s analysis was to propose a mode of bipedal locomotion that was plausible in ape-like ancestors, but that was sufficiently different from human walking to have selected for a different anatomical shape. Wading through shallow water seemed to me to be the ideal candidate.

This chapter considers this possibility in the light of previous studies into the shape of the hominid pelvis and femur. It then describes the methods of a 3D GM study designed to compare the overall shape of the australopithecine hip to humans and extant apes and then to attempt to draw out evidence pertaining to the possibility of wading in the australopithecine locomotor repertoire by analysing Lever Arm ratios of putative hip muscle formations.

6.2. Literature review

The purpose of this section is to review the extensive literature describing studies of the shape of the australopithecine hip.

By 2006, the most studied postcranial fossils of early hominid bipeds were the australopithecines: *Australopithecus africanus* (Sts 14) and *Australopithecus afarensis* (AL 288-1) and there is a considerable volume of literature speculating about their functional anatomy (see, for example, McHenry & Temerin 1979; Stern & Susman, 1983; Stern 2000; Richmond et al. 2001; Ward 2002 for comprehensive reviews.)

The findings, and resulting conclusions about how australopithecines might have moved, from 16 such studies are reviewed here briefly (See tables 6.1 and 6.2 for summaries.)

More recent finds, such as *Ardipithecus ramidus* (Lovejoy et al. 2009), have not been included in this study because the fossil remains are not complete enough to make significant comparisons using the methods described here.

Studies of the shape of the australopithecine pelvis

Robinson 1972: Early hominid posture and locomotion.

(Sts 14 – *Australopithecus africanus*)

The first serious study of note about the morphology of australopithecines (Sts 14, *Australopithecus africanus*) was that published by John Robinson in 1972. His approach was to record a series of carefully defined inter-landmark distances on the hip bone and sacrum of Sts14 and to calculate from them a set of ratios highlighting various aspects of the shape of the pelvis (see fig 25 below). He repeated these measurements on 136 pelvic samples from 6 different species of primates, including *Homo sapiens* and performed univariate analyses on the resulting data.

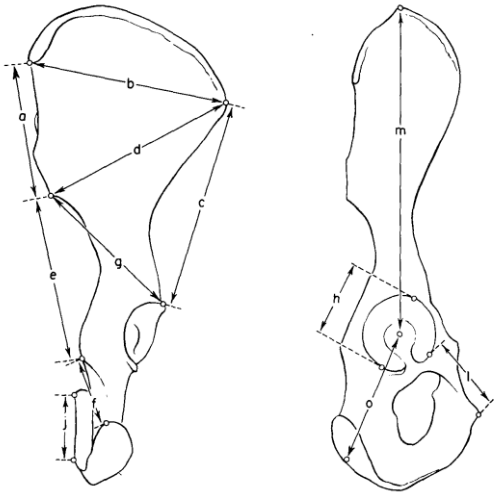

Figure 26 Inter-landmark measurements of the hip used by Robinson (1972 p 354.)

The results, presented in ratio diagrams and histograms, generally showed that, in each individual ratio measured, *Australopithecus africanus* tended to fall within the range for *Homo*, or at least or closer to it than to that of the great apes.

This conclusion drew Robinson into calling for *Australopithecus africanus* to be reassigned to the genus *Homo* and consequently he referred to it as *H. africanus* throughout his book (Robinson 1972 p 6.)

Zuckerman et al. 1973: Some locomotor features of the pelvic girdle in primates; & Ashton et al. 1981: Further quantitative studies of form and function in the primate pelvis with special reference to *Australopithecus*

(Sts 14 – *Australopithecus africanus*)

Solly Zuckerman and collaborators Oxnard, Ashton, Spence and Flynn, studied the shape of the Sts14 hip bone extensively in two separate studies. They examined the evidence promoted by Robinson and others to see if it supported the view, growing at the time, that the australopithecines were ancestors of *Homo.*

Zuckerman et al. 1973 pioneered the use of computers[1] to perform multivariate analyses on data from 11 landmarks and 9 measures of the hip bones of 44 extant species in addition to *A. africanus*. Later, Ashton et al. 1981 extended these data from 20 landmarks and 25 measures. Their results showed that although Sts14 did appear to cluster closely with *Homo* in aspects concerned with weight bearing, it did not appear to do so in those concerned with muscle attachments.

Their evidence suggested that australopithecines were not only different from both *Homo* and the African great apes, they were not even intermediate between them. In fact their data indicated a triangular relationship, where the distance between *A. africanus* and *Homo sapiens* was as great as the distance of either of them from the African great apes. They concluded that the australopithecines exhibited a form of bipedalism, but one that was unlike our own.

McHenry & Corruccini 1975: Multivariate analysis of early hominid pelvic bones

(Sts 14 – *Australopithecus africanus* & SK 3155 *Paranthropus robustus*)

Using what was, at the time, the novel technique of recording distinct 3D co-ordinates for pelvic landmarks, McHenry & Corruccini (1975) examined the pelvis of Sts 14 and SK 3155 and compared them to five extant species of primate, including humans. These 3D co-ordinates were used to generate inter-landmark-distances (ILDs) which were then analysed using multivariate analysis.

They showed, firstly, that SK 3155 (*Paranthropus*) was more similar to Sts14 (*Australopithecus*) than either fossil is to any extant hominoid species; secondly, that of the living hominoids, all of the fossils were closer to modern *Homo sapiens* than to the apes; and thirdly that the robust and gracile forms of southern African australopithecines were somewhat different from one another, the gracile form falling nearer to *Homo sapiens*, but neither form demonstrably closer to the pongids.

Steudel 1978: A multivariate analysis of the pelvis of early hominids

(Sts 14 – *Australopithecus africanus*, SK 3155 *Paranthropus robustus* and OH 28 *Homo erectus*)

The most comprehensive study of the hominoid pelvis, in terms of the number of samples measured, was published by Karen Steudel in 1978. Her canonical analysis examined three fossil samples, OH 28, SK 3155 and STS 14, and compared them with 568 pelves from 26 extant species.

Eight inter-landmark distances were chosen which could be measured on all three fossils. As a consequence, none of these landmarks were on the ischium or pubis, the parts of the bone which were in the prior studies of Zuckerman et al. (1972) and Ashton et al. (1981). This might explain why her results revealed a similarity between these three fossil hominids and modern man in pelvic structure. The differences she did find between the pelves of fossil and modern hominids were discussed, and she concluded that these would not have reduced the capacity for fossil forms to engage in bipedal striding.

However some peculiarities in the results cast some doubt on her claims. Firstly, the species which lay closest to *Homo sapiens* in her results was, in fact, the squirrel monkey, *Saimiri*

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[1] The KDF9 used had 32K of RAM, a ‘clock speed’ of 1KHz and took two weeks to perform a multivariates analysis of the 11 landmarks. (Oxnard pers. Comm. 2005)

sciureus. Steudel (1978 p 589) suggests that this was an anomaly from allometric scaling, as squirrel monkeys were amongst the smallest in the study. Secondly *Homo erectus* appeared more distant from *Homo sapiens* than either form of australopithecine, a result that no other study has repeated to my knowledge.

Stern & Susman 1983: The locomotor anatomy of *Australopithecus afarensis*

This study covered all post-cranial elements, including the pelvis and femur.

Following the methodology of Robinson, they made several measurements of the pelvis and compared various ratios of these measurements to those from humans. Unlike Robinson, their study was based on *Australopithecus afarensis.* They found several ratios (e.g. the hamstring moment arm to iliac breadth ratio) which placed the AL 288-1 fossil well outside the normal human range and others (e.g. the “acetabular arc ratio”, the ratio of the acetabular diameter with the maximum perpendicular distance between the acetabular rim and a line connecting the tips of the acetabular horns) which showed that *A. afarensis* showed characteristics seen in African apes.

Another aspect of the australopithecine pelvis they reviewed was the orientation of the iliac blade. Here, they found that the pelvis of AL 288-1 was more sagittally aligned than in humans and closer to *Pan troglodytes*.

Please refer to the section below for details about their study of the australopithecine femur.

Berge 1984: Multivariate analysis of the pelvis for hominids and other extant primates: Implications for the locomotion and systematics of different species of australopithecines

(AL 288-1 & Sts 14)

In support of the findings of Zuckerman et al. (1973) and contrary to Steudel (1978), Christine Berge (1984) reported the findings of another comprehensive multivariate study on the australopithecine pelvis. She analyzed the shape of AL 288, MLD 7 (*A. afarensis*); OH 28 (*H. erectus*); SK 50, SK 3155 (*P. robustus*) and Sts14 (*A. africanus*), comparing them with 19 species of extant primates, including *H. sapiens.*

The data were presented using a technique called correspondence analysis (Benzecri et al. 1973) which plots the dispersion of individual specimens against each other rather as in a canonical variates analysis.

Her results indicated, firstly, that the australopithecine pattern differed from that of Homo (*H. erectus, H. sapiens*) and thus seemed to correspond to another type of bipedal adaptation; Secondly, that the gracile species (*A. africanus, A. afarensis*), which appeared to be less “advanced” in the australopithecine specialisation than the robust one (*P. robustus*), clustered quite closely to the human lineage; Thirdly, regarding pelvic morphology, the results indicated that species *A. africanus* and *A. afarensis* belonged to the same morphological pattern, the differences between them being merely allometric.

Abitbol 1991: Ontogeny and evolution of pelvic diameters in anthropoid primates and in *Australopithecus afarensis* (AL 288-1)

Obstetric pelvimetry, (both anterior-posterior, AP, and transverse, TR, diameters, for example) was investigated by Abitbol (1991). The ratios of diameters (AP/TR) in three pelvic planes (inlet, mid-pelvis and outlet) were calculated. Also, the length of the iliac, pubic and ischial axes and the angles between these axes were determined.

The study showed that the AP/TR ratio in AL 288-1 was significantly smaller than in humans or apes and not intermediate between them (0.58 in *A. afarensis*, 0.87 ± 0.08 in *H. sapiens* and 1.53 ± 0.17 in apes.) The other pelvic measurements studied showed a similar pattern, again with *A. afarensis* not intermediate to apes and humans. Abitbol explained this as the "result of early adaptation to erect posture" (p135), suggesting that as early bipedal hominids began to support their body weight on the sacrum it widened in order to fulfil the support function better. The later reversal of the trend, to increase the AP/TR ratio, is attributed to contrary obstetric pressure due to increased encephalisation in later human evolution.

Oxnard & Hoyland-Wilkes 1994: Hominid bipedalism or bipedalisms? The pelvic evidence.

Stress bearing is one of the most important functions of bone. Therefore both the gross anatomy of fossilised bones, as well as the micro anatomy of the orientation of the trabeculae in spongy bony, can potentially offer a great deal of evidence as to how early hominids bore stresses.

This kind of evidence has been often studied in the femur (see below) but less so in the pelvis. Oxnard & Hoyland-Wilkes (1994) is one of the few papers to do so. Using a very simplified model of a the weight bearing region of the pelvis (from the ischium, through the acetabulum to the vertebral body of the sacrum) they found that although australopithecines appeared to have had pelves that were human-like and upright in their orientation and weight-bearing, they appeared to be quite different from the human condition.

This paper extended the earlier studies by Oxnard and co-workers on the australopithecine pelvis. It confirmed their general findings that although the australopithecine pelvis did indicate some kind of bipedality, it appears to be a quite different one to our own.

Kepple et al. 1998: A three-dimensional musculoskeletal database for the lower extremities

Although their study did not include any hominids or apes, Kepple et al.'s (1998) extensive study did provide a comprehensive framework of landmarks against which other investigations, including this one, of the functional anatomy of the lower limb might be compared.

The locations of idealized muscle attachments on the pelvis, both femurs, both tibias and fibulas, and both feet were accurately digitized for 52 dried skeletal specimens. The study derived a database from 54 anatomical landmarks of the pelvis and 41 for the femur. Although neither the database itself nor the detail of the landmarks were published, they were communicated by the author (Kepple pers. comm. 2005.)

Marchal 2000: A new morphometric analysis of the hominid pelvic bone

A different approach to the analysis of hominid pelvic shape was used by François Marchal in 2000. The technique provided seven size, and five shape-derived variables, from two-dimensional images of seven selected areas of the pelvis.

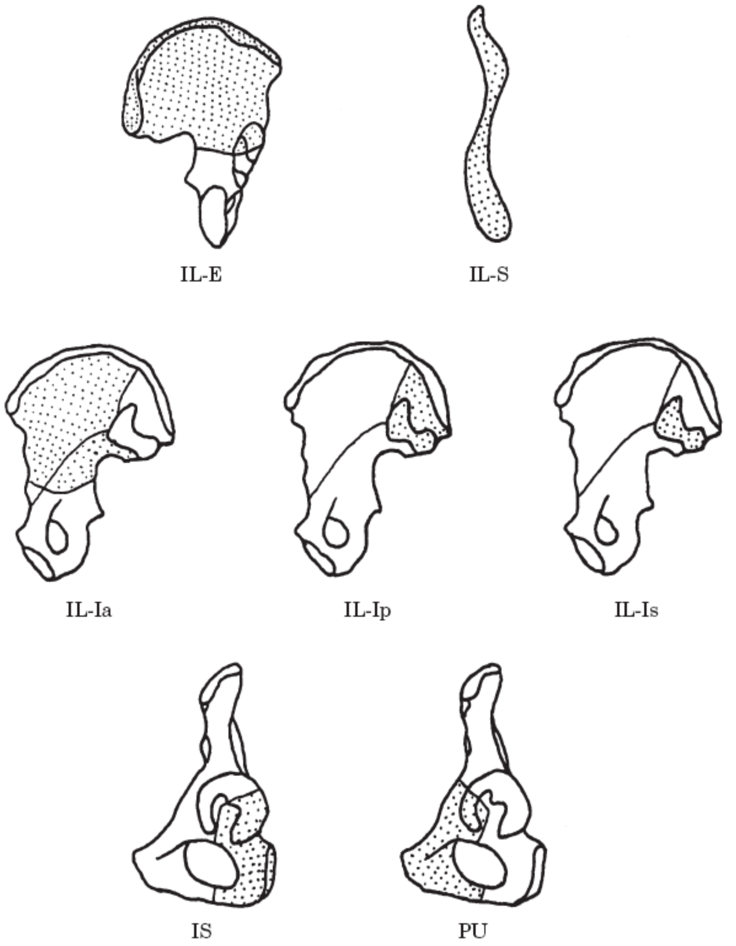


Figure 27 Areas of the pelvis analysed by Marchal's (2000) study.

These were repeated over 200 pelvic bones of various hominoid species both extant and extinct. Ratio diagrams were used to show comparative data of the shape variables across the species. The study found the ilium to be the most different of the three parts of the pelvic bone and that there were two levels of differences therein: The first separated *Australopithecus* from *Homo*, and could be seen as reflecting locomotor differences between both genera; The second splits both *Homo erectus* and Neanderthals from modern human pelvic bones.

Marchal speculated that two periods of stasis existed separated by a period of very rapid evolution corresponding to the emergence of the genus *Homo* and that the same could be true for the split between African ape and hominid lineages at the end of the Miocene.

Weaver 2003: Morphometric study of the neanderthal pelvis, sacrum, coccyx and femur

The most recent, comparable, study on the hominid pelvis was published by Timothy D. Weaver in 2003. It looked primarily at the question of how and why Neanderthal femora are distinct from contemporaneous near-modern human femora, testing the hypothesis that their characteristically robust shape was climate induced. He concluded that when placed in the context of variation within modern human populations, living in climatically varying locations, the differences between *Homo sapiens* and *Homo sapiens neanderthalensis* were relatively insignificant.

Weaver's study mirrors the present study in a number of techniques, including the collection of a significant number of 3D landmarks on the pelvis and femur, and in the generation of whole pelvic morphs from hemi-pelvic samples. These studies on the pelvis are summarized in the table below:

Id	Year & Author(s)	Description	Species (in. fossils)	Sample size	Data Collected
1	1972 Robinson	Comparison of univariate analyses of Sts14 and other hip bones	6 (Sts14)	136	Hip bone: 13 inter-landmark distances ILDs) and 12 ratios using 14 different landmarks. Sacrum: 4 ILDs and 1 ratio using 5 different landmarks.
2	1973 Zuckerman et al.	Multivariate analysis of Sts 14 in comparison with hip bones of several extant primates	45 (Sts14)	431	9 ILDs or angles using 11 different landmarks.
3	1975 McHenry & Corruccini	Multivariate analysis of hominid hip bone	7 (Sts14, SK3155)	10	16 landmarks
4	1978 Steudel	Multivariate analysis of early hominids and extant primates	26 (OH 28, SK 3155 and STS 14)	568	8 ILDs using 14 different landmarks.
5	1981 Ashton et al.	Further multivariates analysis of Sts14	44 (Sts14)	424	25 ILDs using 20 different landmarks.
6	1984 Berge et al.	Multivariates analysis of Australopithecine pelvis	19 (Sts14, AL 288-1)	367	11 ILDs
7	1991 Abitbol	Investigation of pelvic diameters in *A afarensis* AL 288-1	15 (AL 288-1)	217	3 ILDs using 4 different landmarks.
8	1994 Oxnard and Hoyland-Wilkes	Further analysis of Sts 14 hip bone shape and stress-bearing features.	4 (Sts 14)		
9	1998 Kepple *et al*	3D musculoskeletal database of hip bone	1	52	N landmarks
10	2000 Marchal	Morphometric analysis of hip bone shape using 2D image analysis of various shape variables.	7 (Sts 14, MLD 7, MLD 8, MLD 25, KNM-ER 3228, Neanderthal, Kebara, Skhul 4, AL 288-1-ao, OH 28, La Chapelle-aux-Saints	200	14 shape variables
11	2004 Weaver	Morphometric study of the Neanderthal pelvis, sacrum, coccyx and femur	1 Neanderthal	100	39 landmarks

Table 26 Summary of Pelvic Morphology Studies

In addition to these studies, specifically on the pelvis, listed below are a number of studies have been conducted into the morphology of the femur of the earliest bipeds.

Studies of the australopithecine femur

Napier 1964: The evolution of bipedal walking in hominids

One of the first papers to specifically investigate the anatomical differences between the femur of humans and australopithecines in the context of their possible gait, was that of Napier.

The study found "striking differences" in morphology between *Paranthropus* and *Australopithecus* but otherwise found many similarities between australopithecines and humans.

Heiple & Lovejoy 1971: Distal femoral anatomy of *Australopithecus*

Following on from a previous paper, the year before, which attempted a reconstruction of a whole australopithecine femur from several proximal and distal fragments, Heiple & Lovejoy reviewed the anatomy of some distal femoral fragments attributed to *Australopithecus africanus* with respect to its putative locomotor pattern and compared it with other hominids and a number of quadrupedal primates. The most significant aspects of the femur they considered were the obliquity and robustness of the shaft, the anterior intercondylar groove, the intercondylar notch, and the contrast between the medial and lateral articular surfaces, which have been associated as traits indicative of human-like bipedalism. They concluded that no feature was found which was inconsistent with completely bipedal locomotion but they also suggested that there was a need for a reanalysis of possible gait patterns in these early Pleistocene hominids.

Walker 1973: New *Australopithecus* femora from East Rudolf, Kenya

Australopithecine fossils of femora discovered the previous year by teams led by Richard Leakey in East Rudolf, Kenya, formed the basis for a three-dimensional reconstruction of a complete femur. The fossils described, KNM.ER.738, KNM.ER.815, KNM.ER.736 and KNM.ER.993, have since been tentatively assigned to *Paranthropus boseii*. The reconstruction was compared with the femora of *Homo sapiens* and several other known fossils: SK 82; SK 92; OH 20; Sts 34; TM 1513 and MLD 17, assigned to *Australopithecus africanus* or *Paranthropus boseii*.

Walker's findings were that many of the features of the fossil bones fell within the overall ranges for modern humans, but he detected, nevertheless, "a distinctive total pattern in the femoral anatomy of *Australopithecus*".

He found 9 major differences between the australopithecine femora when compared to those of *Homo sapiens*:

- They were more robust.
- They had relatively small femoral heads.
- They had femoral necks which were relatively long, well outside the human range.
- Their neck-shaft angles were smaller (i.e. more nearly at right angles to the shaft.)
- The femoral neck was more antereoposteriorly compressed.
- The greater trochanter did not flare out from the lateral profile of the shaft as it does in *H. sapiens.*
- The bicondylar angle was greater (i.e. more *valgus*) than in *H. sapiens.*

Although having a greater range the australopithecine femora were, generally, smaller than those of *Homo sapiens.* [It should be remembered here, that Walker's study comprised of samples which were probably from at least two distinct species.]

These differences appear to indicate a distinctive australopithecine pattern.

McHenry & Corruccini 1976: Fossil hominid femora and the evolution of walking

This short paper analysed the shape of the proximal femur of australopithecines and from the genus *Homo* and compared them to 215 femora from extant humans and apes. They used ten measurements: vertical head diameter, vertical neck diameter, anterior-posterior neck diameter, anterior-posterior neck diameter, transverse shaft diameter, anterior-posterior shaft diameter, the projected distance from the centre of the head to the lateral surface of the greater trochanter measured perpendicular to the shaft axis, neck length, two measurements from the inferior border of the lesser trochanter: one to the superior surface of the neck and one to the centre of the head, and the projection of the greater trochanter above the neck. The data were analysed using canonical variates analysis, having been first adjusted for possible allometric effects.

Their findings support the idea that there were two distinct forms of hominids, one more closely related to humans than the other, and that the early forms had a distinctively long femoral neck which appears to have provided an ability for a strong abductor lever arm. The authors suggest that this would provide favourable lateral support system in the hip as required during human-like walking.

Stern & Susman 1983: The locomotor anatomy of *Australopithecus afarensis*

This very comprehensive review of the locomotor anatomy of *Australopithecus afarensis* covered the whole post-cranial skeleton and not just the femur (see the section above for their treatment of the pelvis). The paper aimed to determine (1) the extent to which this ancient hominid practiced forms of locomotion other than terrestrial bipedality, and (2) whether or not the terrestrial bipedalism of *A. afarensis* was notably different from that of modern humans.

Their main finding was that *A. afarensis* possessed anatomical characteristics that indicate a significant adaptation for movement in trees and that their mode of locomotion appeared to involve less extension of the hip and knee than occurs in modern humans. They suggested that in their opinion "*A. afarensis* from Hadar is very close to what can be called a 'missing link'" and predict that "earlier representatives of the *A afarensis* lineage will present not a combination of arboreal and bipedal traits, but rather the anatomy of a generalised ape."

Aspects of the proximal femur studied included the shape of the articular surface of the femoral head the angle, and biomechanical length, of the femoral neck, and the presence or otherwise of a groove for the obturator externus tendon on the posterior surface of the femoral neck.

Here, their overall conclusion was that the proximal femur of one australopithecine fossil, AL 333-3, was much more similar to humans than another, AL 288-1. The edge of the articular surface was extended in the anterior-medial direction in AL 333-3, presumably reflecting greater weight bearing whilst being upright. They found the proximal femur of AL 288-1 to be very ape-like.

Aspects of the distal femur studied mainly surrounded the shape of the articular surface with the tibia. Firstly, they found that the bicondylar angle was very high at between 9º and 15º consistent with previous studies. Secondly, they calculated various measures of the distal surface of the femur to assess the shape of the patellar groove and the condyles. Overall, again, their conclusions varied according to the fossil being sampled. They found the smaller Hadar hominid knees were rather ape-like and, other than its characteristic valgus angle, had no significant trait suggestive of a large degree of terrestrial bipedalism. The larger specimens they found "enigmatic" (Stern & Susman 1983 p 299,) being more similar to the modern human form than the smaller samples but still quite distinct. They suggested that "for the present we are unable to interpret this other than to suggest that stresses and movement at the knee during locomotion were unlikely to have been the same as in modern humans (Stern & Susman 1983 p 299.)

Lovejoy et al. 2002: The Maka femur and its bearing on the antiquity of human walking: Applying contemporary concepts of morphogenesis to the human fossil record

In 2002 a new fossil femur found at Maka, in the Middle Awash, Ethiopia, was reported. Dated at around 3.4 Ma and attributed to *Australopithecus afarensis*, it represented some of the oldest skeletal evidence of locomotion in early hominins. This very comprehensive study analyzed the femur from a morphogenetic perspective. They obtained X-ray, CT, and metric data are compared them to humans and extant apes.

Among the bony features studied were:

- The platymeric index (anterior-posterior shaft diameter as a percentage of the lateral diameter).
- The depth of the obturator externus groove.
- The length of the femoral neck.
- The diameter of the femoral head.
- The height of the greater trochanter.

Their findings indicated that the hip joint of *A. afarensis* was like that of modern humans, and that the dramatic muscle allocation shifts which distinguish living humans and African apes were already present in a highly derived form in this species. According the authors, its anatomy provided no indication of any form of locomotion save habitual terrestrial bipedality, which very probably differed only trivially from that of modern humans.

These studies on the femur are summarized in the table below:

Id	Year & Author(s)	Description	Species (in. fossils)	Sample size	Data Collected
1	1964 Napier	Femoral Neck	SK 97, SK 82		
2	1971 Heiple & Lovejoy	Study of bicondylar angle in hominid fossils	8 (Sts14, TM 1513)	11	12*
3	1973 Walker	Study of bicondylar angle in hominid fossils	Sts 14, KNM-ER-815, KNM-ER-738, SK 82’ SK 97, OH 20, KNM-ER-993, KNM-ER-736	7	6 measures, 2 dimensions
4	1976 McHenry & Corruccini	Canonical variates analysis of proximal femur shape	KNM-ER 1503, KNM-ER 1472, KNM ER 1481c, Sk 82, Sk 97	220	10
5	1983 Stern and Susman	Comprehensive study of locomotor anatomy of *A afarensis.* (inc. pelvis and femur)	AL 333-4, AL-129		
6	Lovejoy et al. 2002	Detailed study of new (Maka) Femur	MAK VP-1/1		

Table 27 Summary of Femoral Morphology Papers

A New 3D Geometric-Morphometric method

Before going on to further summarise these studies and to outline the aims of the study described here, one more item from the literature will be reviewed, namely a relatively new method of investigating shape.

The studies of the pelvis listed above used a variety of techniques in order to acquire data. Largely, this involved the traditional approach of obtaining inter-landmark distances (ILDs) between two easily-identifiable points and then presenting ratios of ILDs.

One technique notable by its absence, however, was the use of 3D geometric-morphometrics and related software.

In this technique, a series of 3D co-ordinates, operating within the shape’s space, are collected for each sample and then analysed, using specific processing software, to investigate patterns of shape variation in the sample.

The two processing phases are, first, a procrustes analysis followed by, second, a principal components analysis.

In the procrustes analysis phase, the average position of landmarks is calculated for each morph, giving the centroid. This centroid is then subtracted from each landmark, transforming the morph so that it is centred about the origin. Each morph is also scaled so that they are all approximately the same size. This is done by calculating the centroid size, the square root of the sum of squared Euclidean distances from each landmark to the origin, and then dividing the distance from the origin for each landmark by that value.

Finally, each morph is rotated so as to minimise the sum of squared distances between the set of equivalent landmarks on each morph.

Effectively, at this stage, all the morphs are superimposed upon one another, scaled to the same overall size and rotated so that they are orientated in the same direction. This is also known as Kendall’s shape space (Kendall, 1984) and prepares the morph data so that it may be analysed in terms of differences in shape: correlations in shape difference can then be drawn out against other variables, such as age, sex, size, phylogeny etc.

The second phase, to carry out a principal components analysis, looks at the variation within the population of shapes and derives a list of principal components (PCs) which provide the greatest variation in shape. PC1 has the greatest variation, PC2 the next greatest and so on.

What do these studies of hominid pelvis and femur indicate?

The overall conclusion from the studies listed above appears to be the same, largely dichotomous, one that has characterised the debate about how australopithecines might have moved: On the one hand, there appears to be a great deal of evidence from studies of the shape of the pelvis and femur (Heiple & Lovejoy 1971; Steudel 1978; Lovejoy et al. 2002) which suggest that these early hominid bipeds actually moved rather like we do. On the other hand, there appears to be an equally strong body of evidence (Walker 1973; Zuckerman et al. *1973;* Stern & Susman 1983) which suggest that they moved in a manner that was quite *dissimilar* to the way we do.

These contradictory positions are softened only slightly by a few studies (McHenry & Corruccini 1976), whose findings were a little ambivalent in suggesting that perhaps the australopithecine fossil sample itself might include some variation within it, perhaps satisfying both positions at the same time. However, considering that most of the studies reviewed here still arrived at opposing views even when examining exactly the same fossil, we have to discount that as the main cause of the dilemma.

It seems appropriate to consider how these seemingly contradictory findings might possibly be resolved into a model that supports both views. The literature review begs the question: How could a form of bipedalism appear to be human-like when certain traits are studied but dissimilar when others are taken into account?

Oxnard & Hoyland-Wilkes (1994 p 22) suggested that the resolution might lie in australopithecines performing a unique combination of activities in their typical locomotor repertoire: A combination, presumably, made up of components of locomotion rather typical in the primates today and classified by Oxnard (1973 p 105) as, for example, acrobatic, brachiation, branch running, burrowing, climbing, cursorial, grasping, hanging by upper/lower limbs, leaping, quadramanous quadrupedalism, slow climbing, and habitual (part-time) terrestrial bipedalism. As there appears to be good evidence (Stern & Susman 1983) that australopithecines were, at least in part, arboreal, this would seem to be a reasonable hypothesis even if it is contradicted by some (Lovejoy et al. 2002) proponents of the human-like gait.

However there is another possible solution to this dilemma. Perhaps the australopithecines regularly moved in a way which is simply not seen much in any extant species today. Oxnard (1994 p 22), tongue-in-cheek, discounted “a totally unique form of locomotion (such as jumping up and down on its thumbs)” but there is a type of movement that would indeed represent a rather unique form of locomotion and yet still very much qualify as a form of bipedalism if it existed today which has not been seriously considered to date. Perhaps the australopithecines merely included some regular bipedal wading in their locomotor repertoire.

The evidence presented by Zuckerman et al. (1973) and Ashton et al. (1981) suggested that they practiced bipedal locomotion, but not *our kind* of bipedal locomotion. Bipedal wading, it is suggested here, is a candidate for such a form of locomotion. It is certainly worthy of scientific consideration, although there is clearly a difficulty in devising a way of testing it. Perhaps the answer may be resolved by using a more powerful technique, such as 3D geometric morphometrics, than earlier studies.

Study objectives and hypotheses to be tested

Based upon the earlier work done in this area, it was decided to perform a 3D geometric morphometric study of the shape of the ape pelvis.

The broad objectives of the study were:

- To apply the relatively new technique of 3D geometric morphometrics (using the Morphologika package (O'Higgins & Jones 2006) to the long-held question of the functional anatomy of the australopithecine pelvis and its relation to forms in extant cousins.
- To better visualise and describe the pelvic shape differences between modern human, other *Homo* and australopithecines.
- To analyse the lever arm ratios of all the major muscle groups involved in the movement of the hip across extant and extinct Hominoidea to determine if the anatomical differences might infer mechanical advantage to some hip movements.
- To attempt to arrive at adaptive scenarios which might account for such anatomical differences.

The null hypotheses tested by this study are as follows:

- The general shape of the australopithecine pelvis is not significantly different from the modern human form.
- Any differences in shape are unlikely to have conferred any biomechanical advantage to postcranial movement in the australopithecines, as compared to modern humans.
- Any biomechanical advantage inferred by the anatomy of the australopithecine pelvis would not have given them any advantage whilst wading in waist deep water.

If all three hypotheses can be falsified, it is proposed that this study will support the wading hypothesis.

6.3. General 3D GM study

6.3.1 Methods

Introduction

This study was originally designed to be as inclusive as possible of all previous studies in terms of their methods used and their measurements taken. This was so that it would be possible to verify the findings of this study against previous work, and also to complement them. Several studies, for example, had some omissions which this study aimed to complete: Robinson (1971), Zuckerman et al. (1973), McHenry & Corruccini (1975), Steudel (1981), Ashton et al. (1981) did not study AL 288-1, but only Sts14. Abitbol (1991) studied AL288-1 but not Sts14. It remains a possibility for future studies to perform this extra work.

Following on from McHenry & Corruccini (1975) but using modern 3D geometric-morphometric techniques, a thorough analysis of the shape of the pelvis was conducted in apes.

All of the previous studies contained specific landmark sets which, although overlapping to some extent, were different from each other. Therefore this study was built on a superset of all of the key landmarks used in order to potentially consolidate and enhance the existing studies.

Landmarks types

A comprehensive series of landmarks was determined for the pelvis and femur for several species of Hominoidea (extant or extinct.)

Three broad categories of landmarks types were obtained, the first based on the taxonomy of landmarks as defined by Bookstein 1991 and Marcus et al. 1996.

1) Easily-recognisable ‘point’ landmarks. These are the types that have been traditionally used in morphometric studies of the skeleton in the past both classically, where direct, instrumentally derived, measurements have been taken between two points, and more recently in studies such as this, where individual 3D co-ordinates have been captured, from which the traditional measures can still be derived.

As O’Higgins (1999 p 106) described them, they comprise...

Type 1 landmarks are those “whose homology from case to case is supported by the strongest (local) evidence (meeting of structures or tissues; local unusual histology etc.)”

Type 2 landmarks are those “whose claimed homology from case to case is supported by geometric (tooth tip etc.), not local or histological evidence. Type 2 landmarks include landmarks which are not homologous in a developmental or evolutionary sense but which are equivalent functionally such as wing tips.”

Type 3 landmarks “have at least one deficient coordinate (which means that they can be reliably located to an outline or surface but not at a specific location, e.g. tip of a rounded bump).”

2) Semi-landmarks. Several series of semi-landmarks have been included to provide a means of analysing linear shapes e.g. the linea aspera, of the femur and the iliac crest, the brim inlet and outlet of the pelvis.

Pelvic landmark schema

The landmark schema devised for this study included landmarks which were sufficiently similar to the landmarks used in all the previous studies listed above so as to be able to repeat them using this data. Software was written by the author to manipulate the 3D co-ordinate points so that any of the measures used in any of the previous studies could be converted and compared to any other (See the section on MorphDb below.)

‘Point’ Landmarks used on the Hip Bone

LM	Type	Code	Description	Also used in studies
Left Side Hip bone Landmarks (right side has 46 corresponding symmetrical ones with ‘R’ suffix)				
1	1	AcCentL	Deepest & most central point in the acetabulum and point of fusion of ischium, ilium and pubis.	1, 5, 6, 7, 10
2	3	AcRimIschL	Rim of the acetabulum at the intersection of the axis of the ischium - as defined by the linear buttress emanating from it in the direction of the Ischial tuberosity generally.	1, 3, 5
3	3	AcRimILL	Rim of the acetabulum at the intersection of the cranio-lateral border of the iliac blade.	3, 4.
4	3	AcRimPubL	Point on the rim of the acetabulum intersected by the axis of the pubic bone.	1, 3
5	3	AcRimPubOpL	Point on the opposite rim of the acetabulum intersected by the axis of the pubic bone.	
6	3	AcNchVntL	Ventral margin of acetabular notch (on rim.)	
7	3	AcNchDrsL	Dorsal margin of acetabular notch (on rim.)	
8	3	AcArtSL	Most central limit of the inner acetabular articular surface on the line perpendicular to [AcNchDrsL] and [AcNchVntL].	
9	1	oRecFemRHL	Origin of the rectus femoris reflected head on groove just above acetabulum.	
10	1	AIISL	Anterior inferior iliac spine, most caudal (i.e. furthest along the ilium from the sacrum) point.	1, 3.
11	1	ASISL	The most caudal point on the anterior superior iliac spine which, when observed perpendicularly to the iliac plane, has the greatest curvature.	1, 2, 3, 4, 5, 9
12	3	oTFLL	Mid point of IL-TUB-GL and ASIS (origin of Tensor Fascia Latae.)	9
13	1	IlTubExL	Iliac Tubercle, external. The point on the gluteal margin of thickest width of iliac crest cranial to ASIS.	9
14	1	IlTubInL	Iliac Tubercle, internal. The point on the interior surface on the crest of thickest width of iliac crest cranial to ASIS.	
15	3	CranIlL	Furthest (most cranial) point on the Iliac crest from AcCentL.	1
16	1	CrstSacIntL	Intersection of the iliac crest (interior margin) with the buttress leading to the sacrum	2, 5
17	1	CrstSacExtL	Intersection of the iliac crest (exterior margin) with the buttress leading to the sacrum	
18	3	DorsILL	The most dorsal point on the iliac crest. (This lies close to the posterior superior iliac spine)	2, 5
19	1	PSISL	Posterior superior iliac spine.	1, 3, 4, 9
20	1	oES-LatL	Most lateral point on the erector-spinae origin surface at the midpoint of PSIS and oPirif-GScNL. Indicates strength of erector spinae.	
21	1	oES-MedL	Most medial point on the erector-spinae origin surface at the midpoint of PSIS and oPirif-GScNL. Indicates strength of erector spinae.	
22	1	oPirif-GScNL	Medial end of the greater sciatic notch, where smooth curvature ends. (also in humans acts a partial origin to piriformis)	
23	1	SIJ-CranL	Junction of cranial limit of sacro-iliac joint and iliac crest.	2, 3, 5
24	1	SIJ-BrimL	Junction of the auricular surface with the pelvic brim.	
25	1	SIJ-CaudL	Caudal limit of auricular surface close to Posterior inferior iliac spine PIIS.	2, 3, 5
26	4	LatInletL	Most lateral point on the iliopectineal line on hip bone (forms transverse diameter with opposite) On fully articulated only. May calculate from disarticulated by taking a trace of points on the inlet.	6
27	4	MidInletL	Mid point of PUBSA to SIJ-PI on the pelvic	
28	1	IPEL	ILIO-pectineal eminence	

29	4	OBLIQUEL	Oblique diameter with opposite SIJ-PI) on the margin of the brim alongside IPE (from: Midwifery-based True pelvis dimensions)	
30	4	oPectL	Half way point between IPEL and PubTubL (origin of Pectineus)	
31	1	PubTubL	Most ventral corner of caudal surface of the pubic tubercle (origin of Adductor Longus)	
32	1	PubCranL	Most cranial point, at maximum height, of the pubic symphysis.	1
33	1	PubCaudL	Most caudal point on pubic symphysis.	2, 3, 5, 6, 9
34	1	PubDorsL	Closest point on the pubis to the sacral promontory indicating maximum D-V extension of pelvic inlet.	
35	3	SciNotL	That point situated on the margin of the greater sciatic notch which is most distant from the PSISL-IschSpL axis.	3
36	1	IschSpL	Point of greatest curvature on the ischial spine.	1
37	3	oObtIntL	The rim of the lesser sciatic notch (origin of Obturator internus and Gemelli)	9
38	1	IT-CranL	Most cranial limit of ischial tuberosity	1, 9
39	1	IT-CaudL	Most caudal point on the ischial tuberosity.	9
40	1	IT-ExtL	Most lateral (external) point of ischial tuberosity.	1, 9
41	1	IT-IntL	Most medial (internal) point of ischial tuberosity.	9
42	4	IT-CentL	Central point of the ischial tuberosity (intersection of IT-ExtL + IT-IntL, and IT-CranL + IT-CaudL).	
43	3	OFI-AcL	Closest point on the interior rim of the obturator foramen to the mid-point of [AcNchVntL] and [AcNchDrsL]	
44	3	OFI-PubL	The point on the obturator foramen border closest to the cranial margin of pubic symphysis.	
45	3	OFI-IschL	The point on the obturator foramen border closest to [IT-CentL].	
46	3	OFI-RamL	the mid-point between OFI-PubL and OFI-IschL on the most caudal interior margin of obturator foramen	

Table 28 Pelvic Landmark Schema (Hip bone)

These landmarks are illustrated graphically in the figures below:

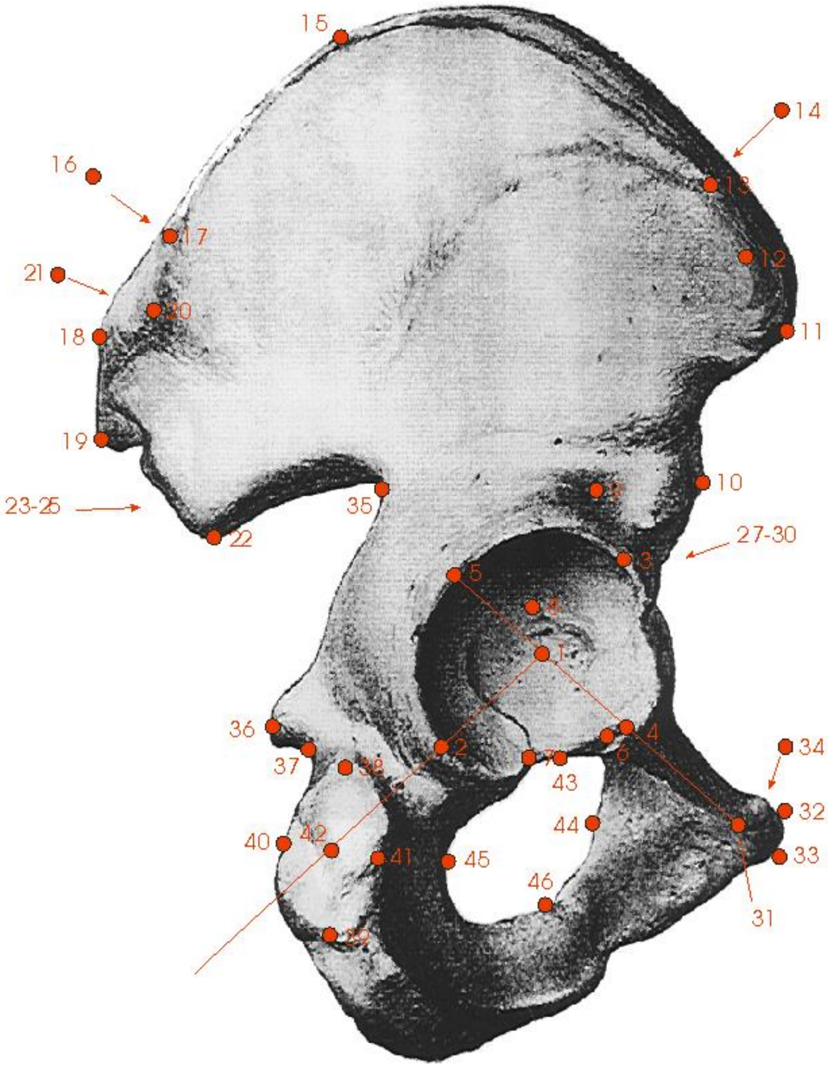


Figure 28 Landmarks of the Hip bone (lateral view)

Landmarks on the Sacrum				
93	1	sSIJ-CranL	Junction of cranial limit of sacro-iliac joint and iliac crest.	
94	1	sSIJ-BrimL	Junction of the auricular surface and the pelvic brim, left side.	
95	1	sSIJ-CaudL	Caudal limit of auricular surface.	
96	1	sSIJ-CranR	Opposite Junction of cranial limit of sacro-iliac joint and iliac crest.	
97	1	sSIJ-BrimR	Junction of the auricular surface and the pelvic brim, right side	
98	1	sSIJ-CaudR	Opposite caudal limit of auricular surface.	
99	1	sVertProm	Sacral promontory in the plane of the pelvic inlet. Most cranio-ventral point on the sacral body.	
100	1	sVertDors	Most dorsal point on the sacral body	
101	1	sVertLatR	Most lateral point on sacral vertebral joint right.	
102	1	sVertLatL	Most lateral point on sacral vertebral joint left	
103	1	sSacTip	Most caudo-ventral tip of the sacrum.	
104	1	sCoxTip	Most caudal tip of the coccyx.	
105	3	oPirif-SACR	Ventral surface of the right side sacrum between second and third foramen midway between midline of foramen and lateral border.	10

106	1	oGluMaxInfR	Right infero-lateral angle, marking corner of sacrum (origin of coccygeus) where medial border of sacrum begins to taper towards the coccyx. (origin of Gluteus Maximus inferior fibers.)	10
107	1	oGluMaxInfL	Left infero-lateral angle, marking corner of sacrum (origin of coccygeus) where medial border of sacrum begins to taper towards the coccyx. (origin of Gluteus Maximus inferior fibers).	10
108	3	oPirif-SACL	Ventral surface of the left side sacrum between second and third foramen midway between midline of foramen and lateral border (first sacral foramen is most cranial) (origin of Piriformis).	10

Table 29 Pelvic Landmark Schema (Sacrum)

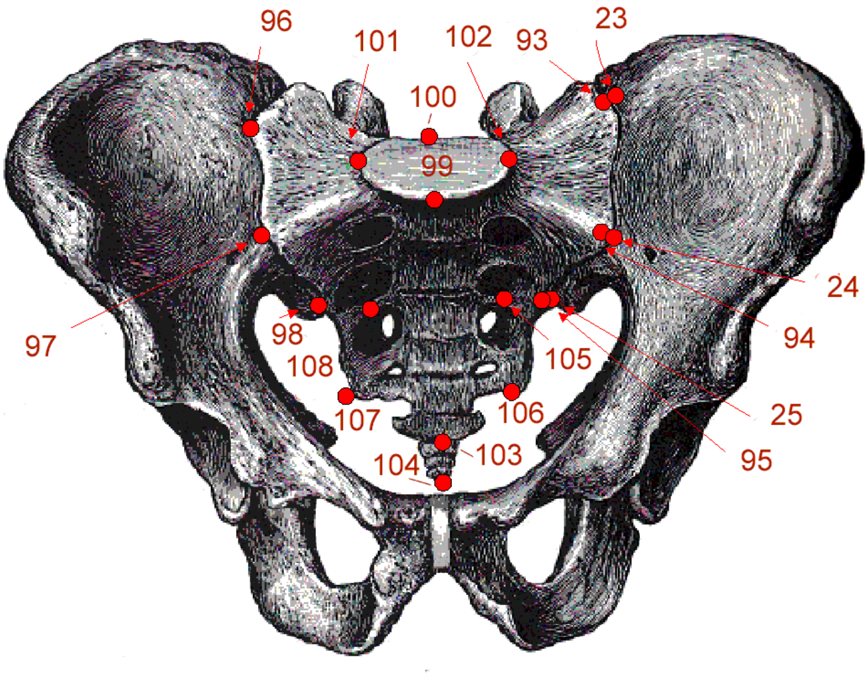


Figure 29 Landmarks of the Hip bone and Sacrum (Frontal View)

'Point' Landmarks of the Femur			
Lnk No	LM Type	Landmark Name	Description
1	2	FemHeadCtr	The centre of the femoral head in line with the axis of the femoral neck
2	1	GtTrochPost	Most ant.-posterior point on the greater trochanter
3	2	GtTrochAnt	Most anterior-superior point of greater trochanter (corresponds with insertion of Gluteus minimus
4	1	GtTrochAnt	Most superior point on the greater trochanter
5	1	TrochFossa	Deepest point in the trochanteric fossa
6	1	LesTrochSup	Most superior point on the lesser trochanter
7	1	LesTrochInf	Most inferior point on the lesser trochanter
8	2	FemHeadRimSup	Most superior point on the rim of the femoral head
9	2	FemHeadRimPost	Most posterior point on the rim of the femoral head
10	2	FemHeadRimInf	Most inferior point on the rim of the femoral head
11	2	FemHeadRimAnt	Most anterior point on the rim of the femoral head
12	2	FemHeadMaxSup	Most superior point on the head at maximum distance from the femoral head axis
13	2	FemHeadMaxPost	Most posterior point on the head at maximum distance from the femoral head axis
14	2	FemHeadMaxInf	Most inferior point on the head at maximum distance from the femoral head axis

15	2	FemHeadMaxAnt	Most ant. point on the head at maximum distance from the femoral head axis
16	2	FemNeckSup	Most sup. point on the mid-point of the femoral neck
17	2	FemNeckPost	Most post. point on the mid-point of the femoral neck
18	2	FemNeckInf	Most inf. point on the mid-point of the femoral neck
19	2	FemNeckAnt	Most anterior point on the mid-point of the femoral neck — point of attachment of ilio-femoral ligament
20	2	FemAxis	Estimated point on the lateral extremity of the axis of the femoral neck
21	2	TrochLat	Most lateral point on the greater trochanter
22	2	QuadTub	Quadrate tubercle — most medial point
23	2	AntIntTrochLine	Most anterior point on the inter-trochanteric line, borders the femoral neck
24	2	ThrdTroch	3rd Trochanter or most sp. point on gluteal ridge
25	2	Shaft1Med	Medial-most point quarter of the way down the shaft
26	2	Shaft1Lat	Lateral-most point quarter of the way down the shaft
27	2	Shaft1Ant	Anterior-most point ¼ way down the shaft
28	2	LinAsp1Med	Medial-most point on the linea aspera, quarter of the way down the shaft
29	2	LinAsp1Lat	Lateral-most (if any) point on the linea aspera, quarter of the way down the shaft
30	2	Shaft2Med	medial-most point quarter of the way down the shaft
31	2	Shaft2Lat	Lateral-most point quarter of the way down the shaft
32	2	Shaft2Ant	anterior-most point 1/4 of the way down the shaft
33	2	LinAsp2Med	Medial pt on the linea aspera on mid pt of the shaft
34	2	LinAsp2Lat	Lateral-most point on the linea aspera, on mid point of the shaft
35	2	Shaft3Med	medial-most point on the shaft ¾ of the way down[1]
36	2	Shaft3Lat	lateral—most point on the shaft ¾ of the way down[1]
37	2	Shaft3Ant	anterior-most point on the shaft ¾ of the way down
38	2	LinAsp3Med	Point three quarters of the way down the shaft on the medial side on the medial supracondylar line
39	2	LinAsp3Lat	Point three quarters of the way down the shaft on the lateral side on the lateral supracondylar line
40	2	LatCondyle	Most lateral inferior point on the popleatal surface (opposite adductor tubercle)
41	2	MedAddTub	Adductor tubercle
42	2	LatLatCond	Most superior-lateral point on the lateral condyle
43	2	LatMedCond	Most superior-medial point on the lateral condyle
44	2	MedLatCond	Most superior-medial point on the lateral condyle
45	2	MedMedCond	Most superior-medial point on the medial condyle
46	2	MedPostCond	Most posterior point on the medial condyle
47	2	LatPostCond	Most posterior point on the lateral condyle
48	2	MedEpiCond	Medial epicondyle
49	2	LatEpiCond	Lateral epicondyle
50	2	IntCondNotSup	Intercondylar notch superior point
51	2	IntCondNotInf	Intercondylar notch inferior point
52	2	AntMedCondyle	Most anterior-medial point on articular surface of the patella surface
53	2	AntLatCondyle	Most anterior-lateral point on articular surface of the lateral condyle
54	2	DistMedCondyle	Most distal point on the medial condyle[1]
55	2	DistLatCondyle	Most distal point on the lateral condyle[1]
56	2	Fovea	The centre of the fovea capitis

Table 30 Femoral Landmark Schema

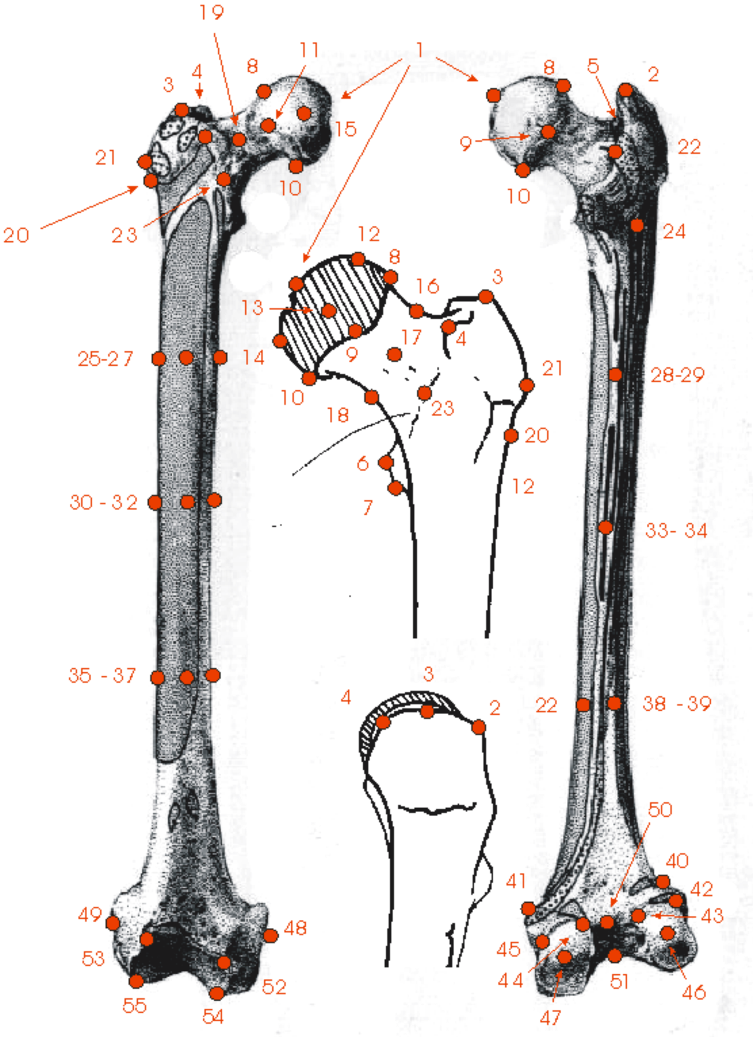


Figure 30 Landmarks of the Femur

Species studied

Species list

This study does not cover the full range of primates covered by some of the previous studies, neither are the sample sizes used as great as in most of them, but it does cover all the major fossil hominids found before the discovery of *Ardipithecus ramidus* (Lovejoy et al. 2009). Due to the relatively incomplete nature of that fossil specimen it was decided to omit it from this study.

	Species Studied		
Phylogenetic Grouping	Latin Name	Code	N
1	*Lemur catta*	LEC	1
2	*Ateles geoffroyi*	ATG	1
3.01.1.1	*Cercopithecus aethiops*	CEA	2
3.01.2	*Mandrillus sphinx*	MSL	1
3.01.3	*Theropithecus gelada*	TGL	1
3.01.4	*Nasalis larvatus*	NSL	2
3.02.1	*Hylobates syndactylus*	HYL	4
3.02.2	*Hylobates agilis*	HYL	2
3.02.3	*Hylobates lar*	HYL	1
3.02.4	*Hylobates moloch*	HYL	5
3.02.5	*Hylobates muelleri*	HYL	3
3.03.1	*Pongo abelii*	PPA	5
3.03.2	*Pongo pygmaeus*	PPY	11
3.04.1	*Gorilla gorilla gorilla*	GGO	17
3.04.2	*Gorilla gorilla graueri*	GGB	10
3.05	*Pan paniscus*	PNP	19
3.06	*Pan troglodytes*	PNT	16
3.07X	*Australopithecus afarensis (AL 288-1)*	AFA	1
3.08X	*Australopithecus africanus (STS 14)*	AFR	1
3.09X	*Homo erectus (WT 15000)*	HER	1
3.10	*Homo sapiens sapiens*	HSS	32

Table 31 Species Studied

Data capture

The 3D landmarks were captured and written directly to Microsoft Excel data files using a Microscribe Digitiser (Immersion Corporation, San Jose, CA), and associated software. As shown in Figure 30. The sample and the digitiser remained fixed during the recording of a set of landmarks. Where, occasionally, the sample or digitiser needed to be moved (perhaps to get access to landmarks that were hidden from the first orientation), the two sets of 3D points were re-aligned digitally through software using four reference landmarks common to both sets.

The digitiser has a heavy base and the samples were fixed to the work surface either with a clamp or adhesive material.

Figure 31 Digitising a Model Pelvis

Pre-processing techniques

A number of generated landmarks and landmark processing methods were used in this study through software written by the author (programmable database called MorphDb – see section later.)

Generated landmarks on the hip

In order to analyse muscle Lever Arms, two generated landmarks were derived from the landmark schemas described above. One estimates the centre of rotation of the acetabulum and one estimates a hypothetical insertion point on the femur (at the greater trochanter). The following describes the method used to derive these landmarks.

Generated landmarks

A number of generated landmarks were derived from those listed above.

Generated Landmarks	
Landmark Name	Description & Method of Calculation
CntRotAcetab	Estimated centre of rotation of the femoral head. Calculated as the mean point of the two pairs of opposite landmarks on the rim of the acetabulum (landmark nos 2 & 3, and 4 & 5)
FemNeckExtended	Estimated position of the greater trochanter, assuming a continuation line from the centre of the acetabulum (landmark 1) through the calculated centre of rotation of the femoral head to a point at a distance equal to the length of the femoral neck of the associated femur for the individual.

Table 32 Generated Landmarks

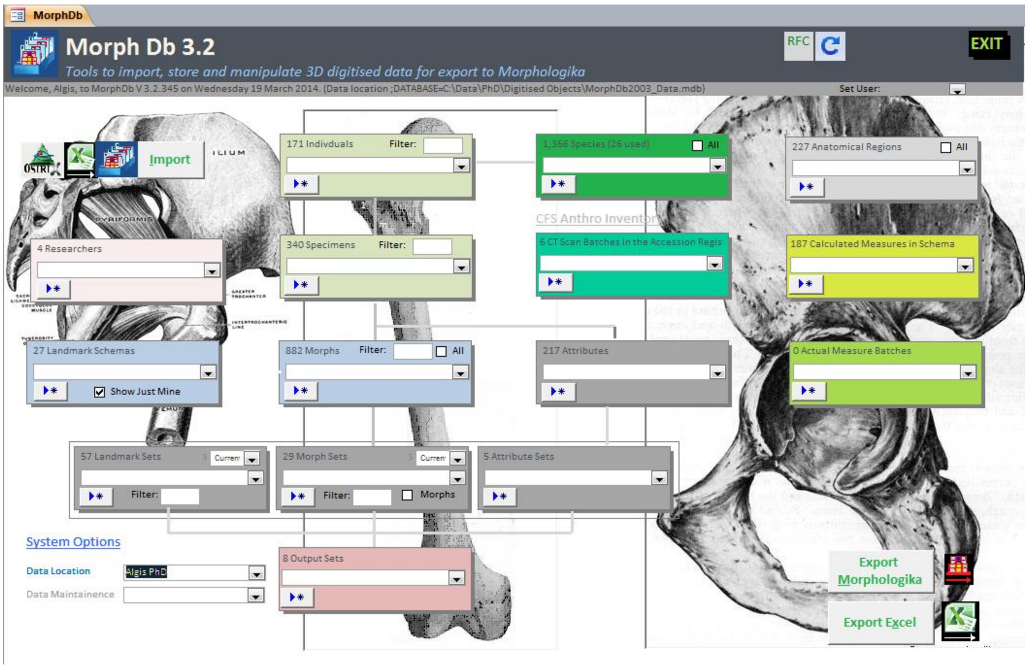
MorphDB relational database

Introduction

Throughout the study, hundreds of specimen of skeletal samples were digitised in multiple ways, generating over a million 3D co-ordinates. When collecting large quantities of digitised data, one soon accumulates many data files which require careful storage and organisation. Therefore it was decided that such a vast amount of data should be stored in a fully functional, programmable database.

As the database was almost exclusively for personal use, Microsoft Access was chosen, rather than a “higher end” solution, such as Oracle, SQL Server or MySQL. Microsoft Access is a popular (SQL-based) relational database with sophisticated development features such as a rich windows forms event model and uses a relatively simple programming language, Visual Basic for Applications (VBA), but is simpler and more accessible to others than developing in Java or the Microsoft .Net framework.

Figure 31 shows the front screen of the database which gives an indication of the structure of the database entities, each of which can be searched individually.



Morph Db 3.2

Tools to import, store and manipulate 3D digitised data for export to Morphologika

Welcome, Algis, to MorphDb V 3.2.345 on Wednesday 19 March 2014. (Data location ;DATABASE=C:\Data\PhD\Digitised Objects\MorphDb2003_Data.mdb)

Data Location: Algis PhD

Figure 32 MorphDb - Home Page

The study required inter-landmark distances (ILDs), angles and other calculations to be performed on the captured data. Equally, when using shape analysis software, such as Morphologika, it is necessary to carefully prepare complex data files in order to analyse pre-defined sets of morphs, landmarks and attributes.

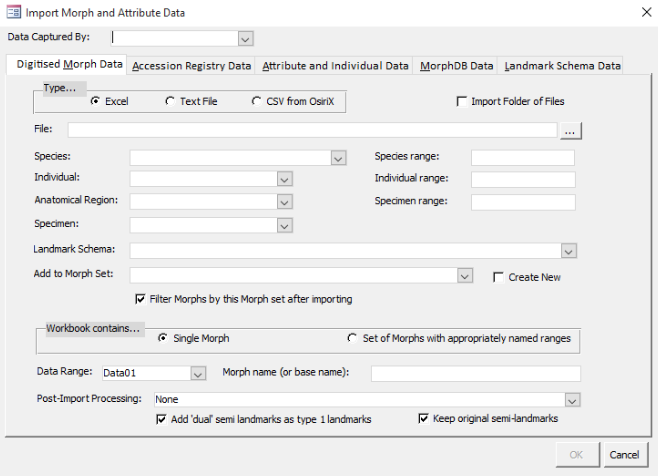
General function

The database was designed to import 3D landmark data captured in the study from Comma separated variable (CSV), Excel and other file formats, store it in an easy-to-query relational database where the data can be manipulated and calculations performed before export data to other GM related software. An almost infinite number of sets of morphs, landmarks and attributes can be created and combined with each other before being analysed in Morphologika. Any combination of 3D landmarks can be used to calculate inter-landmark distances (ILDs), angle, and other metrics. This section briefly describes the database, which was designed by the author of his thesis.

Functional specification

Importing

MorphDb can import digitised data captured either by a 3D digitiser (saved into Microsoft Excel format) or via Osirix DICOM reader (saved as Excel readable comma separated variable, CSV, files). Fig 32 shows the import dialog box and its various option.



Import Morph and Attribute Data

Data Captured By:

Type...
● Excel ○ Text File ○ CSV from OsiriX
☐ Import Folder of Files

File:

Species:
Individual:
Anatomical Region:
Specimen:
Species range:
Individual range:
Specimen range:
Landmark Schema:
Add to Morph Set:
☐ Create New
☑ Filter Morphs by this Morph set after importing

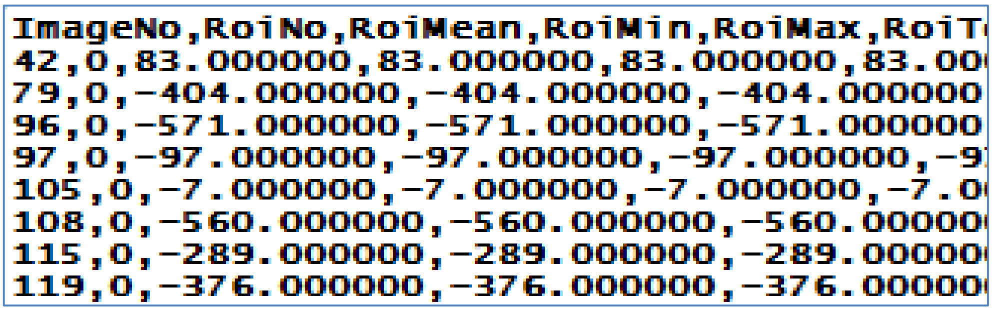
Workbook contains...
● Single Morph ○ Set of Morphs with appropriately named ranges

Data Range: Data01
Morph name (or base name):
Post-Import Processing: None
☑ Add 'dual' semi landmarks as type 1 landmarks
☑ Keep original semi-landmarks

Figure 33 Import Dialog Box

As the data is imported into the database it is assigned to an existing species, individual, specimen, anatomical region, or such other entities as are necessarily created if they do not already exist.

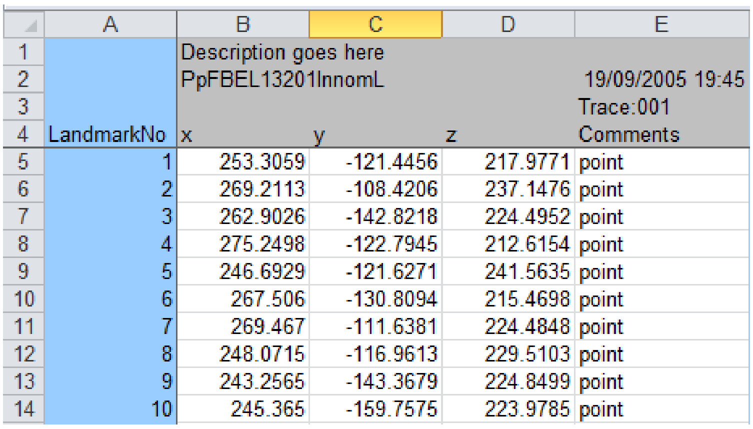
MorphDb can import data in several pre-defined formats. For example, “region of interest” (ROI) files capture 3D landmarks from within the DICOM file rendering program, OsiriX. (See example from such a file in Fig. 33.) Various processing steps are performed whilst importing some kinds of morph data, for example semi-landmarks can be generated from pre-defined sets of points.



```
ImageNo,RoiNo,RoiMean,RoiMin,RoiMax,RoiT
42,0,83.000000,83.000000,83.000000,83.00
79,0,-404.000000,-404.000000,-404.000000
96,0,-571.000000,-571.000000,-571.000000
97,0,-97.000000,-97.000000,-97.000000,-9
105,0,-7.000000,-7.000000,-7.000000,-7.0
108,0,-560.000000,-560.000000,-560.00000
115,0,-289.000000,-289.000000,-289.00000
119,0,-376.000000,-376.000000,-376.00000
```

Figure 34 Sample data from an OsiriX ROI file to be imported

Figure 34 shows an example of an Excel file generated by the 3D scanner…



	A	B	C	D	E
1		Description goes here			
2		PpFBEL13201InnomL			19/09/2005 19:45
3					Trace:001
4	LandmarkNo	x	y	z	Comments
5	1	253.3059	-121.4456	217.9771	point
6	2	269.2113	-108.4206	237.1476	point
7	3	262.9026	-142.8218	224.4952	point
8	4	275.2498	-122.7945	212.6154	point
9	5	246.6929	-121.6271	241.5635	point
10	6	267.506	-130.8094	215.4698	point
11	7	269.467	-111.6381	224.4848	point
12	8	248.0715	-116.9613	229.5103	point
13	9	243.2565	-143.3679	224.8499	point
14	10	245.365	-159.7575	223.9785	point

Figure 35 Sample data from Microscribe Digitiser file to be imported

Multiple files in a particular folder can be imported in one go to speed up the process.

Other file types (such as attribute files, landmark schemas and data from other MorphDb files) can also be imported.

Storage

MorphDb was designed to store morphs in a normalised database structure, allowing them to be grouped and queried in very flexible ways. Millions of morphs can be stored, each containing potentially thousands of landmarks, and associated with hundreds of attributes.

Put simply, the database is organised hierarchically. Although defaulting to human anatomical data, any number of species can be imported for analysis. Individuals are stored along with any number of attributes, including sex and age. Each individual may have one or more associated specimens for a specific anatomical region (e.g. the pelvis or femur) of them. Each specimen can have associated one or more morphs. Each morph is linked to a landmark schema, which defines the landmarks to be captured, and a researcher. The database is multi-user and can contain and manipulate data from any number of researchers.

Each landmark schema may include any number of measures which define formulae to calculate inter-landmark distances, angles and other calculations from the landmarks. Once data has been imported into a morph, MorphDb will calculate all these defined measures automatically. Wireframe and polygon maps can also be stored in MorphDb for export to Morphologika.

The database is made of approximately 70 permanent tables in all, some of which are displayed in Figure 35.

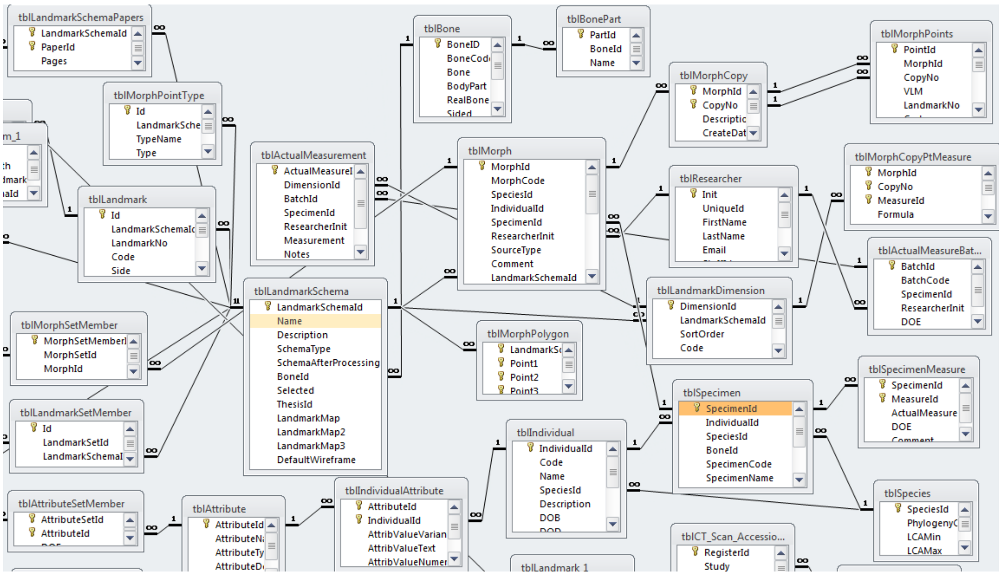
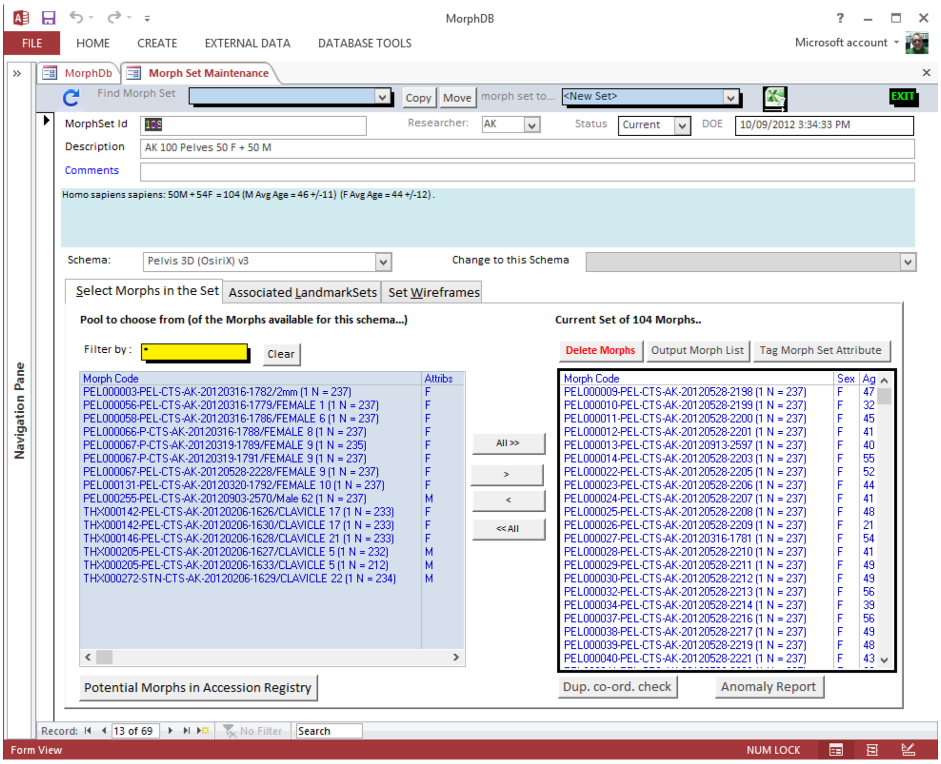


Figure 36 A Section of the Entity Relationship Diagram (ERD) of MorphDb

Manipulation

Set manipulation

Morphs, landmarks and attributes can be grouped into many thousands of easily customisable sets (Figure 36 shows how individual landmarks are collected into an example set) which can be combined into almost infinite permutations. Any number of wireframes and polygons can be associated with each landmark schema and selected for output.



MorphSet Id	108
Researcher:	AK
Status	Current
DOE	10/09/2012 3:34:33 PM
Description	AK 100 Pelves 50 F + 50 M
Comments	
morph set to...	<New Set>

Homo sapiens sapiens: 50M + 54F = 104 (M Avg Age = 46 +/-11) (F Avg Age = 44 +/-12) .

Schema: Pelvis 3D (OsiriX) v3

Change to this Schema

Pool to choose from (of the Morphs available for this schema...)

Filter by : *

Morph Code	Attribs
PEL000003-PEL-CTS-AK-20120316-1782/2mm (1 N = 237)	F
PEL000056-PEL-CTS-AK-20120316-1779/FEMALE 1 (1 N = 237)	F
PEL000058-PEL-CTS-AK-20120316-1786/FEMALE 6 (1 N = 237)	F
PEL000066-P-CTS-AK-20120316-1788/FEMALE 8 (1 N = 237)	F
PEL000067-P-CTS-AK-20120319-1789/FEMALE 9 (1 N = 235)	F
PEL000067-P-CTS-AK-20120319-1791/FEMALE 9 (1 N = 237)	F
PEL000067-PEL-CTS-AK-20120528-2228/FEMALE 9 (1 N = 237)	F
PEL000131-PEL-CTS-AK-20120320-1792/FEMALE 10 (1 N = 237)	F
PEL000255-PEL-CTS-AK-20120903-2570/Male 62 (1 N = 237)	M
THX000142-PEL-CTS-AK-20120206-1626/CLAVICLE 17 (1 N = 233)	F
THX000142-PEL-CTS-AK-20120206-1630/CLAVICLE 17 (1 N = 233)	F
THX000146-PEL-CTS-AK-20120206-1628/CLAVICLE 21 (1 N = 233)	F
THX000205-PEL-CTS-AK-20120206-1627/CLAVICLE 5 (1 N = 232)	M
THX000205-PEL-CTS-AK-20120206-1633/CLAVICLE 5 (1 N = 212)	M
THX000272-STN-CTS-AK-20120206-1629/CLAVICLE 22 (1 N = 234)	M

Current Set of 104 Morphs..

Morph Code	Sex	Ag
PEL000009-PEL-CTS-AK-20120528-2198 (1 N = 237)	F	47
PEL000010-PEL-CTS-AK-20120528-2199 (1 N = 237)	F	32
PEL000011-PEL-CTS-AK-20120528-2200 (1 N = 237)	F	45
PEL000012-PEL-CTS-AK-20120528-2201 (1 N = 237)	F	41
PEL000013-PEL-CTS-AK-20120913-2597 (1 N = 237)	F	40
PEL000014-PEL-CTS-AK-20120528-2203 (1 N = 237)	F	55
PEL000022-PEL-CTS-AK-20120528-2205 (1 N = 237)	F	52
PEL000023-PEL-CTS-AK-20120528-2206 (1 N = 237)	F	44
PEL000024-PEL-CTS-AK-20120528-2207 (1 N = 237)	F	41
PEL000025-PEL-CTS-AK-20120528-2208 (1 N = 237)	F	48
PEL000026-PEL-CTS-AK-20120528-2209 (1 N = 237)	F	21
PEL000027-PEL-CTS-AK-20120316-1781 (1 N = 237)	F	54
PEL000028-PEL-CTS-AK-20120528-2210 (1 N = 237)	F	41
PEL000029-PEL-CTS-AK-20120528-2211 (1 N = 237)	F	49
PEL000030-PEL-CTS-AK-20120528-2212 (1 N = 237)	F	49
PEL000032-PEL-CTS-AK-20120528-2213 (1 N = 237)	F	56
PEL000034-PEL-CTS-AK-20120528-2214 (1 N = 237)	F	39
PEL000037-PEL-CTS-AK-20120528-2216 (1 N = 237)	F	56
PEL000038-PEL-CTS-AK-20120528-2217 (1 N = 237)	F	49
PEL000039-PEL-CTS-AK-20120528-2219 (1 N = 237)	F	48
PEL000040-PEL-CTS-AK-20120528-2221 (1 N = 237)	F	43

Record: 13 of 69

Figure 37 Morph Set Maintenance Screen

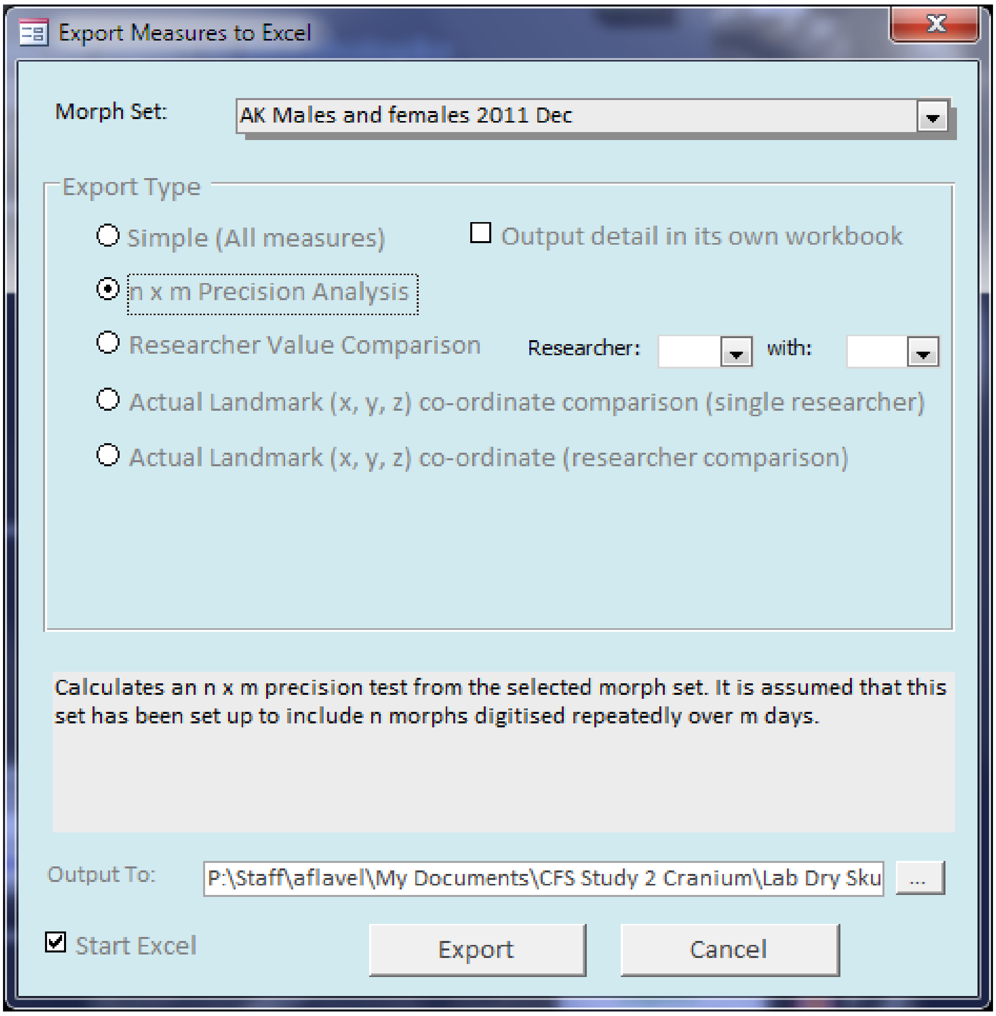
ILD and other calculations

MorphDb can store any number of pre-defined formulae in each landmark schema which are then automatically calculated when data is imported and stored in a morph. Formulae may be simple inter-landmark distances, angles between three landmarks, subtenses – or calculated distances between a landmark and a segment between two other landmarks, and many other types of calculation.

MorphDb therefore acts both as a pre-processor for complex 3D morphological analytical software, such as Morphologika, as well as a tool to calculate more traditional 'linear' measures. These traditional measures can be validated and analysed for accuracy.

For example…

- An n x m precision analysis, where the researcher captures the same n specimen on m separate days. Here, standard estimates of accuracy are included, such as TEM, rTEM and coefficient of variability.
- A inter-researcher comparison, where the same specimen have been captured by two different researchers.


Export Measures to Excel

Morph Set: AK Males and females 2011 Dec

Export Type

○ Simple (All measures) ☐ Output detail in its own workbook

● n x m Precision Analysis

○ Researcher Value Comparison Researcher: with:

○ Actual Landmark (x, y, z) co-ordinate comparison (single researcher)

○ Actual Landmark (x, y, z) co-ordinate (researcher comparison)

Calculates an n x m precision test from the selected morph set. It is assumed that this set has been set up to include n morphs digitised repeatedly over m days.

Output To: P:\Staff\aflavel\My Documents\CFS Study 2 Cranium\Lab Dry Sku

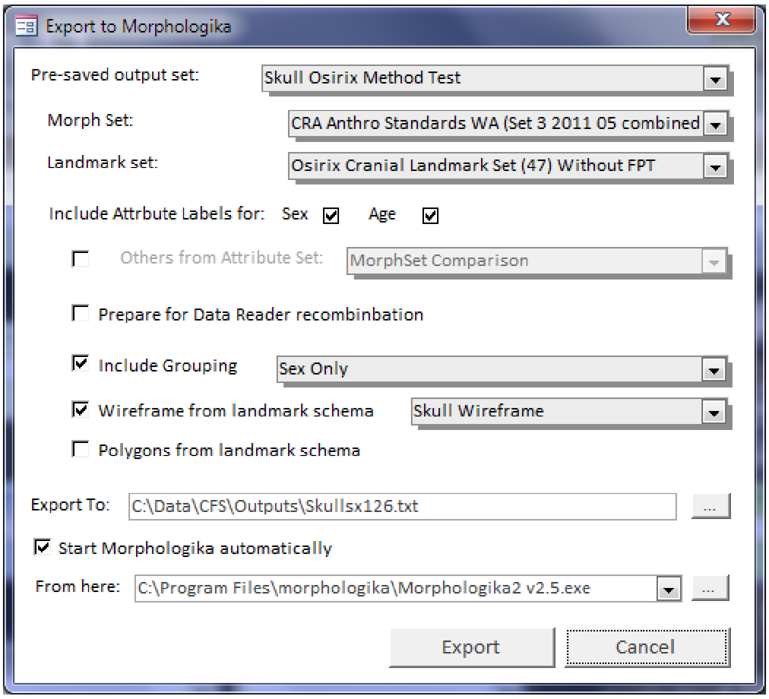
☑ Start Excel

Figure 38 Some MorphDb export options

Export to morphologika

Along with calculating 'traditional' linear measures, the major function of MorphDb is to output data to the 3D geometric morphometric analysis program Morphologika. Morphologika inputs a text file in a very specific format and MorphDb prepares these file in flexible ways.

Basically, MorphDb combines sets of morphs, landmarks and attributes into a single Morphologika file. It also will generate a wireframe and/or 3D polygons to render the shapes in 3D.



Pre-saved output set: Skull Osirix Method Test

Morph Set: CRA Anthro Standards WA (Set 3 2011 05 combined

Landmark set: Osirix Cranial Landmark Set (47) Without FPT

Include Attrbute Labels for: Sex ☑ Age ☑

☐ Others from Attribute Set: MorphSet Comparison

☐ Prepare for Data Reader recombinbation

☑ Include Grouping Sex Only

☑ Wireframe from landmark schema Skull Wireframe

☐ Polygons from landmark schema

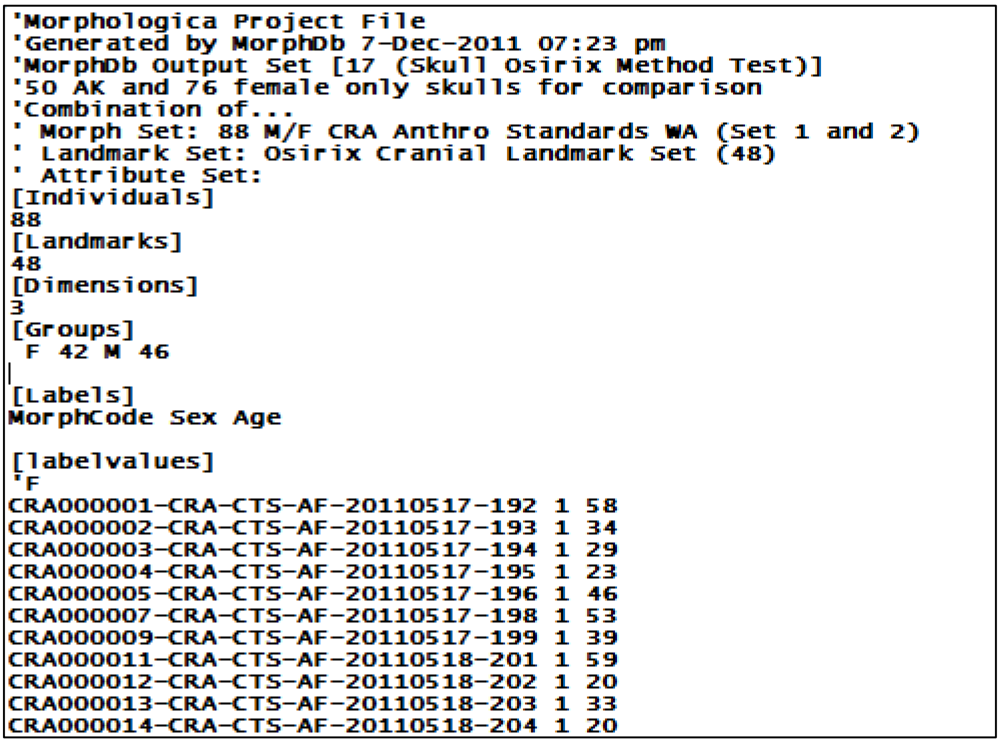
Export To: C:\Data\CFS\Outputs\Skullsx126.txt

☑ Start Morphologika automatically

From here: C:\Program Files\morphologika\Morphologika2 v2.5.exe

Figure 39 Exporting data to Morphologika

An example target Morphologika file is shown in Figure 39.



```
'Morphologica Project File
'Generated by MorphDb 7-Dec-2011 07:23 pm
'MorphDb Output Set [17 (Skull Osirix Method Test)]
'50 AK and 76 female only skulls for comparison
'Combination of...
' Morph Set: 88 M/F CRA Anthro Standards WA (Set 1 and 2)
' Landmark Set: Osirix Cranial Landmark Set (48)
' Attribute Set:
[Individuals]
88
[Landmarks]
48
[Dimensions]
3
[Groups]
 F 42 M 46

[Labels]
MorphCode Sex Age

[labelvalues]
'F
CRA000001-CRA-CTS-AF-20110517-192 1 58
CRA000002-CRA-CTS-AF-20110517-193 1 34
CRA000003-CRA-CTS-AF-20110517-194 1 29
CRA000004-CRA-CTS-AF-20110517-195 1 23
CRA000005-CRA-CTS-AF-20110517-196 1 46
CRA000007-CRA-CTS-AF-20110517-198 1 53
CRA000009-CRA-CTS-AF-20110517-199 1 39
CRA000011-CRA-CTS-AF-20110518-201 1 59
CRA000012-CRA-CTS-AF-20110518-202 1 20
CRA000013-CRA-CTS-AF-20110518-203 1 33
CRA000014-CRA-CTS-AF-20110518-204 1 20
```

Figure 40 Example of a Morphologika File

Filtering and grouping by taxa

Before the data were exported into Morphologika, they were filtered, allowing any combination of landmarks to be analysed, and sorted and grouped according to taxa (usually by sex/species permutations). By filtering on selected landmarks which formed the sets from previous studies, a direct comparison of this studies' data with previous studies' could be made.

Wire-frame construction

Before exporting the processed data to a Morphologika file a wire-frame is constructed according to the landmarks selected. This enables a simple 3D frame structure to be visualised and manipulated in 3D for each skeletal sample as shown in Figure 40.

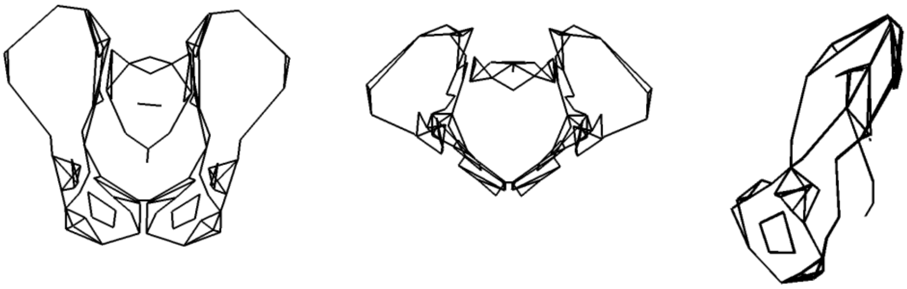


Figure 41 Example wireframes of fully the articulated pelvis.
Fig shows Os Coxa wireframe from dorsal, cranial and lateral, respectively, perspectives. These show the procrustes mean of 7 species used in this study with 108 point landmarks.

Processing in morphologika

Once in the Morphologika software the data was processed in the following two steps:
Procrustes Analysis (with reflections enabled) was performed. This process involves a number of steps:

- The centroid (average *x,y,z* co-ordinate for each morph) is calculated.
- The root mean square (RMS) is calculated for each landmark, giving its distance from the centroid. An average value for the whole morph is calculated.
- The centroid is subtracted from each landmark, translating all morphs to the same centroid around the origin.
- All landmark-centroid distances were divided by the average of the all distances, scaling all morphs to be the same size.
- Finally, each morph is rotated so as to minimise the RMS of the distances of all the landmarks.

Principal Components Analysis. Next a principal components analysis was performed. This process effectively analyses all the 3D data point combinations and selects the ones which provide the greatest variation. These are then labelled principal component 1 … 32. (PC1… PC32.) At the end of the process the morphs are plotted on a chart showing the two largest PCs (1 and 2). Ideally the morphs from the same taxa/sex should cluster together indicating that they have similar shape. Differences between clusters on the different PCs can then be analysed to see what might be inferred about them.

6.3.3 Results

General 3D morphological study

A morph set comprising 125 hip bones from 23 species was chosen for the study of the pelvis. A slightly smaller set of 102 Specimen contributed to the study of the sacrum. 71 femora specimen were used.

	Species Studied			
Phylogenetic Grouping	Latin Name	Code	N	Symbol
1	*Lemur catta*	LEC	1	🔷
2	*Ateles geoffroyi*	ATG	1	◆
3.01.1.1	*Cercopithecus aethiops*	CEA	2	◆
3.01.2	*Mandrillus sphinx*	MSL	1	♦
3.01.3	*Theropithecus gelada*	TGL	1	◆
3.01.4	*Nasalis larvatus*	NSL	2	🔶
3.02.1	*Hylobates syndactylus*	HYL	4	△
3.02.2	*Hylobates agilis*	HYL	2	△
3.02.3	*Hylobates lar*	HYL	1	△
3.02.4	*Hylobates moloch*	HYL	5	△
3.02.5	*Hylobates muelleri*	HYL	3	△
3.03.1	*Pongo abelii*	PPA	5	🟠
3.03.2	*Pongo pygmaeus*	PPY	11	🟠
3.04.1	*Gorilla gorilla gorilla*	GGO	17	▫
3.04.2	*Gorilla gorilla graueri*	GGB	10	■
3.05	*Pan paniscus*	PNP	19	⬛
3.06	*Pan troglodytes*	PNT	16	🟦
3.07X	*Australopithecus afarensis (AL 288-1)*	AFA	1	✳
3.09X	*Homo erectus (WT 15000)*	HER	1	✕
3.10	*Homo sapiens sapiens*	HSS	32	🟩

Table 33 Species of Pelves Analysed

For those species with ten or more samples collected, females are represented with a smaller rectangle or circle.

In the Principal Component Figures (41 - 44) that follow the wire diagrams represent the shape of the morph at the position of the cloud indicated.

<u>Pelvis</u>

The shape analysis of 125 morphs of 19 species using 45 Hip bone landmarks is shown in figure 41.

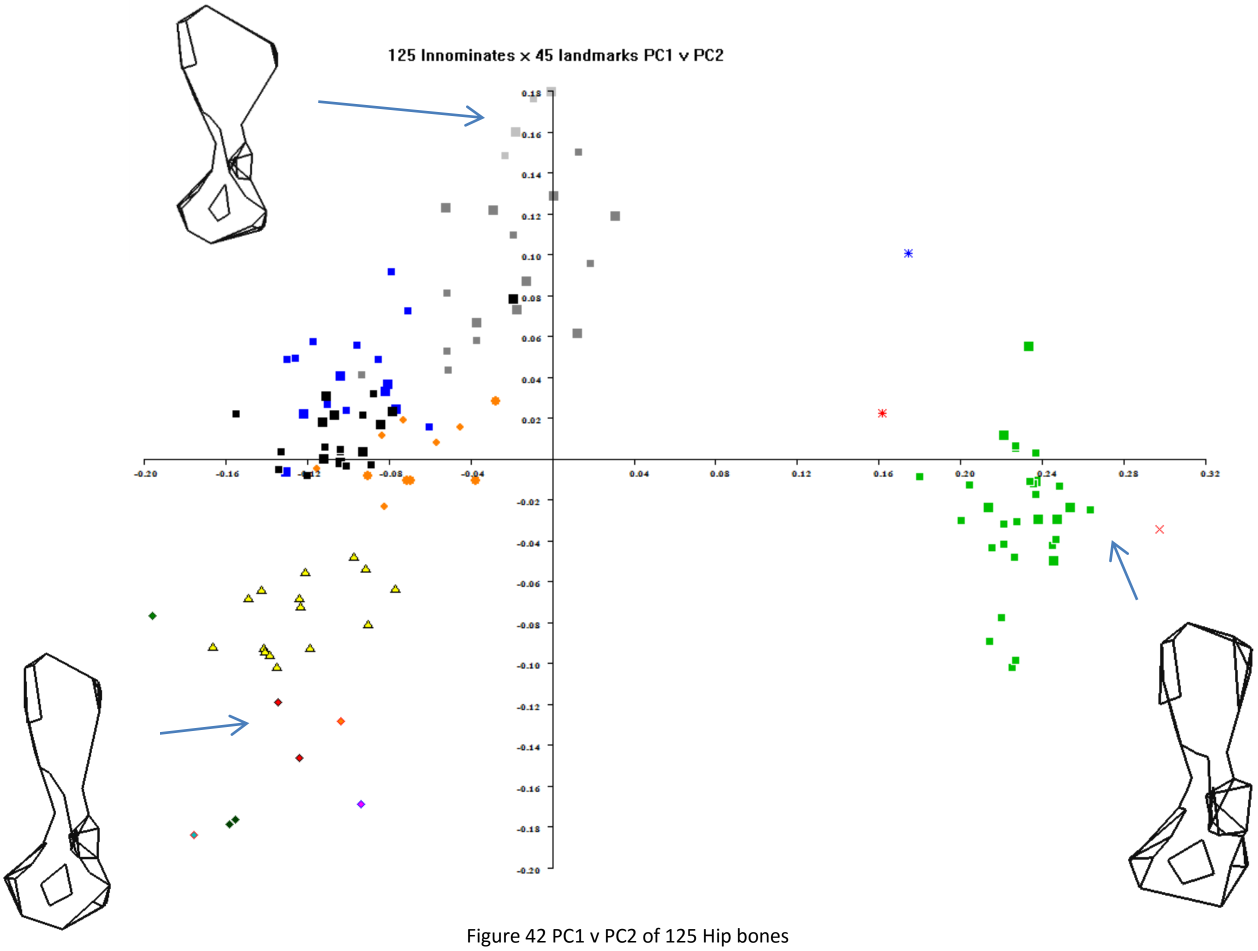


Figure 42 PC1 v PC2 of 125 Hip bones

The percentage eigenvalues of the 4 most significant principal components were:

PC	Variation	Cumulative
PC 1	51.3%	51.3%
PC 2	12.7%	64%
PC 3	4.3%	68.3%
PC4	3.08%	71.4%

Over 71% of the variation were represented by these 4 PCs, the majority of which was represented by PC1.

PC1 represents a distortion of the overall shape, generally, of the hip bone from one elongated in the Superior-Inferior (S-I) axis and narrowed laterally, to the opposite, shortened in the S-I axis and widened laterally. This PC appears to correlate more specifically with widening/shortening of the ischium rather than ilium.

PC 2 represents a specific widening/shortening of the width of the ilium. For example, at one extreme one finds mostly Gorilla with relatively broad ilia, at the other old world monkeys, with relatively narrow ones.

The key finding of note here is that the shape of the australopithecine hip bone, although lying closer to *Homo* than to the great apes, is still significantly different from it, especially in *A. africanus*. This implies that although the australopithecines were very likely to have been bipedal, it is unlikely that their mode of locomotion was exactly the same as ours.

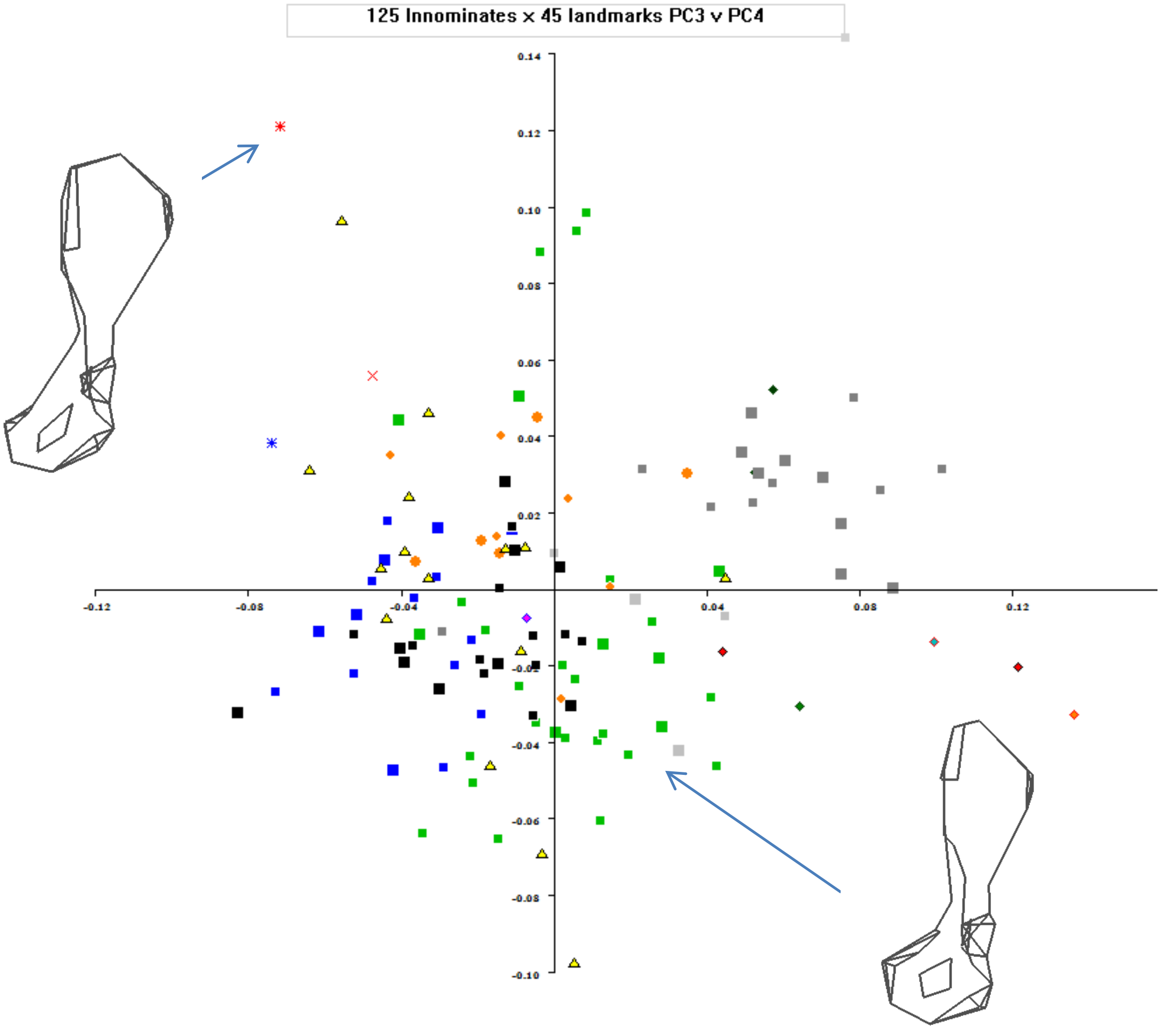


Figure 43 PC3 v PC4

PC3 and PC 4

Principal Components 3 and 4 together make up only 7% of the variation (compared to over 51% for PC1) but it is interesting to note that *Australopithecus afarensis* appears an outlier on the two combined. This seems to represent a lateral twisting of the iliac blade with respect to the rest of the hip bone and an inferior shearing of the pubic region including the pubic tubercle. Again this implies that australopithecines probably adopted a different gait to our own.

Sacrum

Not all the specimens measured included sacra, notably the paleospecies *Australopithecus africanus*.

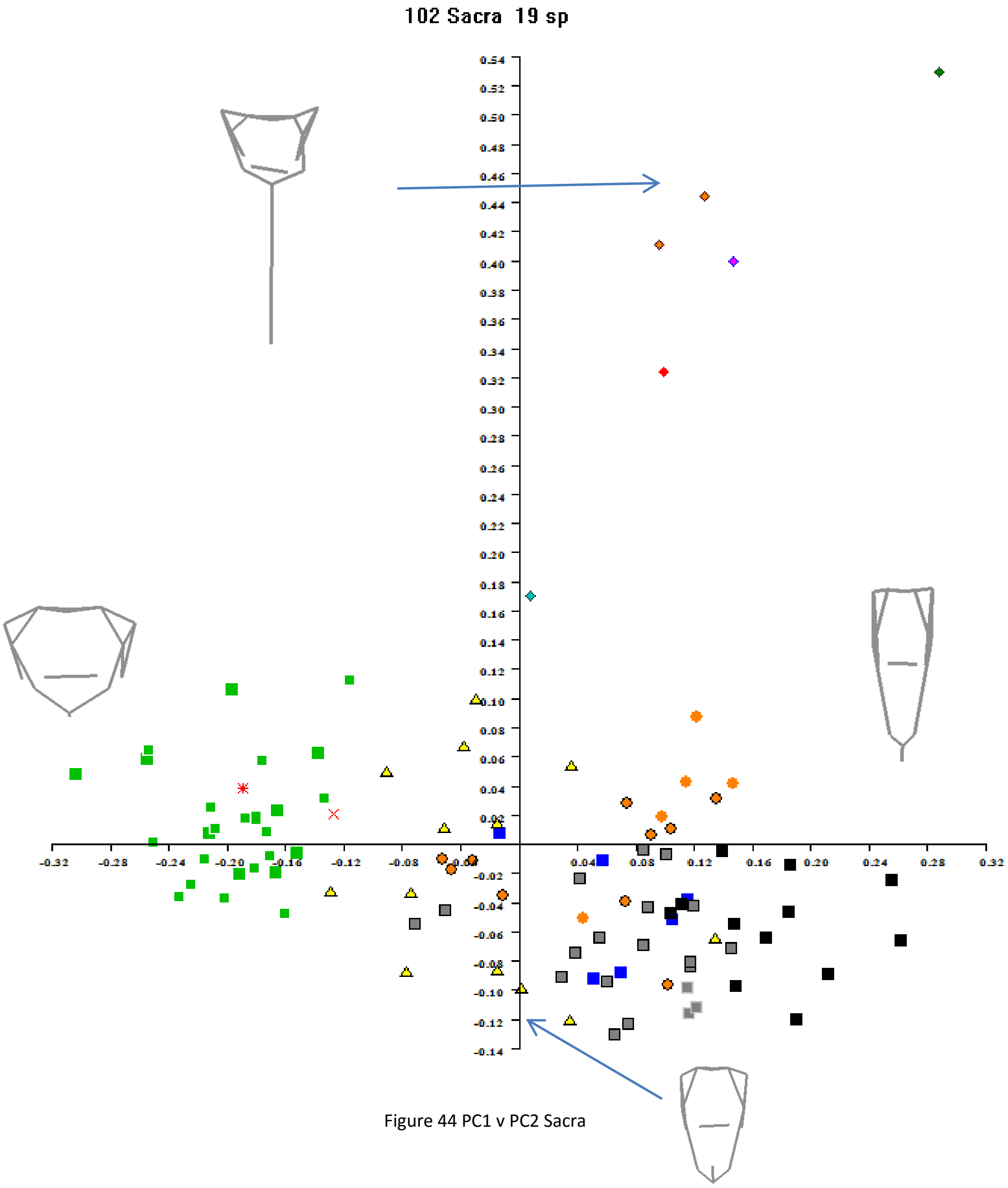


Figure 44 PC1 v PC2 Sacra

Percentage	Variation	(Cumulative)
PC 1	34.2%	34.2%
PC 2	21.8%	56.0%
PC 3	11.4%	67.4%
PC 4	6.3%	73.7%

Australopithecus afarensis clustered well within the range of *Homo sapiens* on the main principal components indicating a similar shape and weight bearing function.

Proximal femur

As the key paleo species in this study *Australopithecus afarensis* only contains a sample of its proximal femur, only the landmarks representing that part of the bone are analysed here.

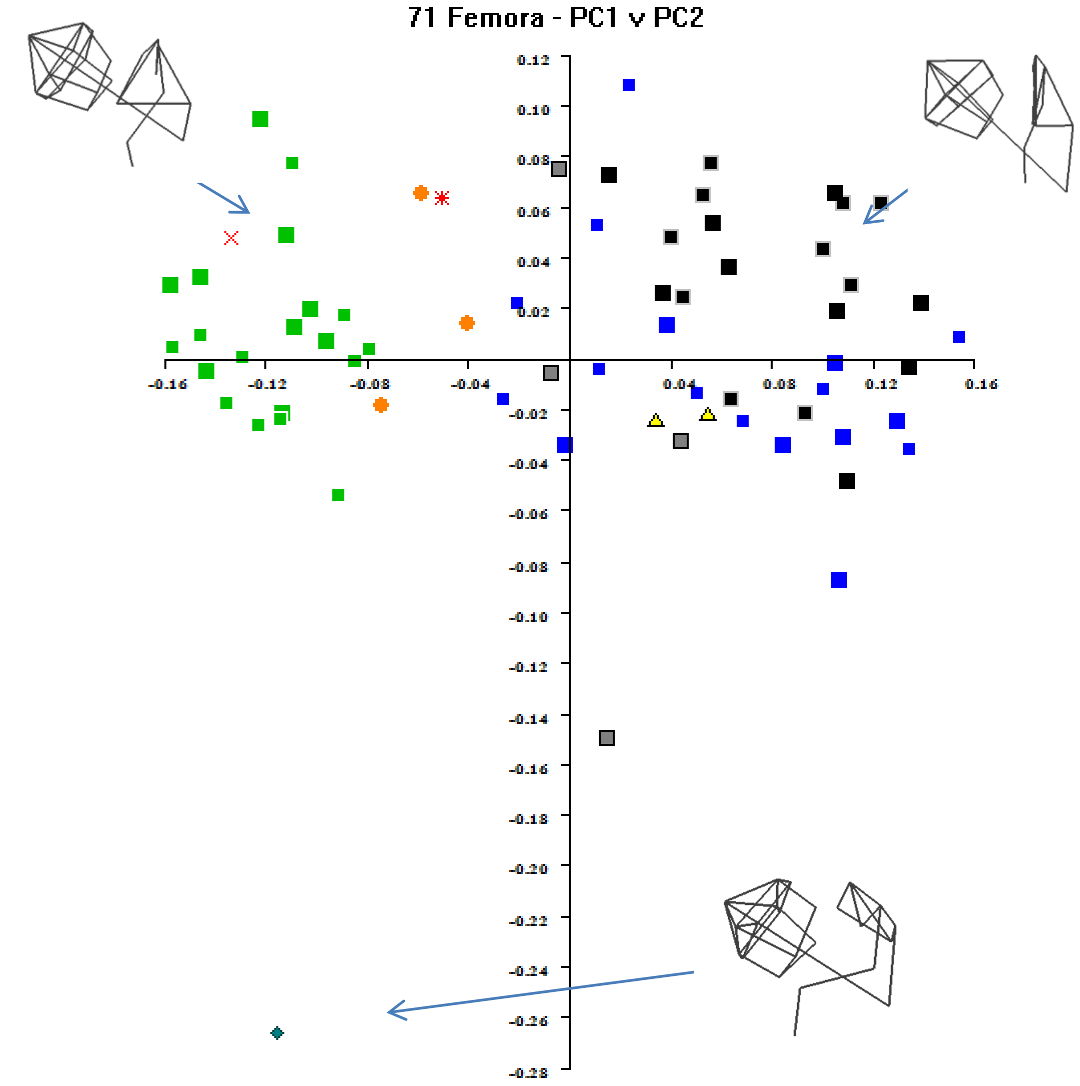


Figure 45 PC1 v PC2 Proximal Femur

Percentage	Variation	(Cumulative)
PC1	24.4%	24.4%
PC2	11.0%	35.4%
PC3	8.9%	44.3%
PC4	8.1%	52.4%

52.4% of the variation was found in the first 4 principal components.
The shape of the proximal femur of *Australopithecus afarensis* clustered close to that of *Homo sapiens* in the two major principal components this analysis, along with the genus *Pongo.*

Summary

The shape analysis of sacrum and proximal femur generally clustered australopithecines close to, if not within, the normal range for *Homo sapiens* for those traits characteristic of bipedalism pertaining to weight bearing.

They differed somewhat in the shape analysis of the hip bone. The significant twisting of the ilium, with respect to the ischium, is quite different in australopithecines compared to other apes and their remarkable platypelloid shape is very different from *Homo.* These characteristics suggest that australopithecines has differences pertaining to muscle action and therefore perhaps are indicative of locomotor differences as first shown by the findings of Zuckerman et al. (1973) and Ashton et al. (1981).

This is not a remarkable observation, as it is pretty obvious from even a cursory glance at the australopithecine, *Pan* and *Homo* pelves. In terms of the ratio between the lateral diameter and the A-P diameter, australopthecines and *Pan* are at the extremes, with *Homo* intermediate.

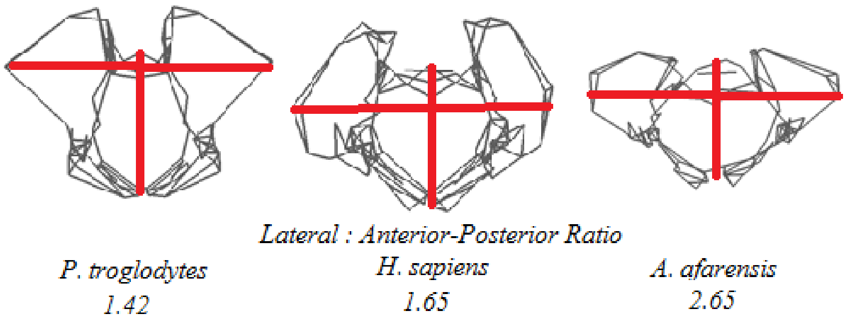


Figure 46 Lateral: Anterior-Posterior Diameter Ratios (figures from MorphDb data set)

This part of the 3D GM study of the shape of the australopithecine hip bone concludes that the australopithecine pelvis differed so markedly from that of *Pan* and *Homo* that it likely adopted a mode of bipedal locomotion that was very differed from ours.

The next part of the study, then, sets out to investigate the muscle lever arms involved at the hip to try to identify those muscle blocks which were likely to have been favoured most by the australopithecine skeletal anatomy. In this way, it might be possible to discern the kind of gait that australopithecines may have adopted, and why.

6.4. Relative muscle lever arm study

Of the three bones analysed for shape, only the hip bone showed major deviation in the australopithecine form from that of the genus *Homo*. The femur and sacrum did not show such marked deviation. As discussed in the previous section, the next logical step in this study, therefore, was to analyse the shape differences of the hip bone between the australopithecines and the genus *Homo* from the perspective of muscle action.

The objective here is to analyse **all** the muscle lever arms involved in the movement of the hip, and to compare them against each other in order to try to identify those muscle blocks which were likely to have been favoured most by the australopithecine skeletal anatomy and therefore the nature of the gait they adopted. Put simply, it will test the assumption, arriving from even a cursory glance at the remarkably platypelloid shape of the australopithecines pelvis, that their postcranial skeletal anatomy would appear better adapted to adduction/abduction of the thigh, relative to humans and chimpanzees.

The following section describes the method used for all the muscle origins and insertion points.

6.4.1 Method

Triangular sets of three points were derived for each hip bone landmark associated with a muscle origin for each skeletal sample, including two generated landmarks. The following method was the basis for the calculation of lever arms. It should be noted that it describes a simplified, unspecified muscle. Known caveats and difficulties with the method are described afterwards.

1. A pseudo landmark (landmark 0 – AcCenterGen) was generated to represent the centre of rotation of the acetabulum on each hip bone. As shown in figure 46, it was calculated as the midpoint of four landmarks (2, 3, 4 and 5) on the rim of the acetabulum.

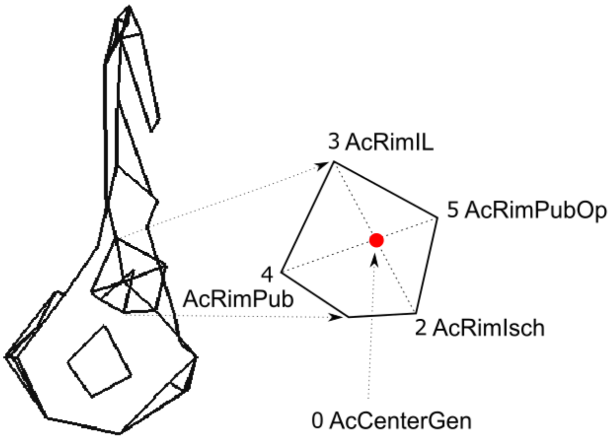


Figure 47 – Calculation of pseudo-landmark for centre of rotation of the acetabulum

2. Another pseudo landmark was generated to represent a standard position of the greater trochanter of the femur relative to each hip bone. It was calculated, as shown in figure 47, using a vector from the landmark at the centre of the acetabulum (landmark 1 - AcCent) through the calculated landmark just described (landmark 0 AcCenterGen

– fig. 47 A), the centre of rotation of the acetabulum, through to a point away from the hip. The distance was calculated by using the actual length of the femoral head from the same individual (fig. 47 B). In this way, a landmark on the hip bone was generated to represent a generalised muscle insertion point (fig. 47 C).

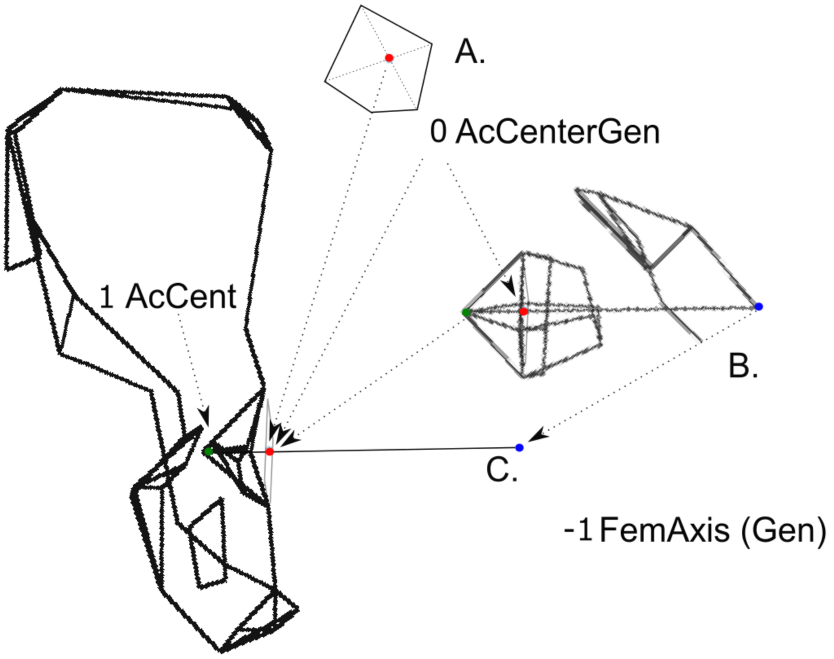


Figure 48 Method of calculation for pseudo landmark (FemAxis)

3. On each hip bone, for each landmark representing a muscle origin, the lever arm was calculated using the following procedure:
    a) A triangle of 3 3D co-ordinates was processed:

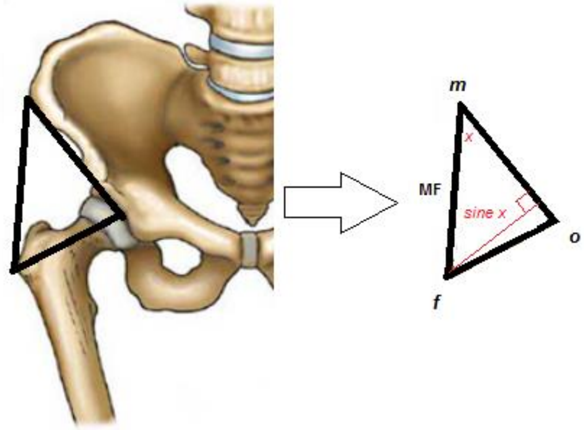


Figure 49 Lever Arm Calculation

o = the centre of rotation about the centre of the femoral head

f = the generated landmark representing the end of the femoral neck

m = the landmark representing the muscle origin.

b) the angle (x) is calculated for <omf>
c) the distance MF is calculated
d) MF is multiplied by sine(x) to get the lever arm

Caveats

A number of significant limitations of this study should be noted here before describing the results.

A single static hip position was assumed

There are thousands of possible permutations of the hip. Obviously, as femur moves relative to the hip bone, any specific muscle lever arm will change greatly. For example, the lever arm of *Gluteus medius* is very different when the hip is extended from when it is flexed. To analyse hip muscle lever arms in full then, one would need not only to consider every muscle lever arm, but to do so in every possible position the hip could be orientated. In order to greatly simplify the study, only one fixed position was assumed. Although this greatly reduces the scope of the study and what might be interpreted from them, it is argued that even this one position will allow the lever arm ratios to be calculated and compared across species, thus elucidating the likely effects on muscle action on the shape of the australopithecine pelvis.

All insertion points on the femur were identical

For similar reasons all muscle insertion points on the femur were estimated to be at the same point – approximating to the most lateral point on the greater trochanter on the femoral axis. As each muscle lever arm greatly depends on the position of the insertion point of the femur relative to the hip, and as the orientation of the femur can vary greatly, it vastly reduces the number of permutations to consider if it is assumed that the femur is in a static position and that all muscles insert at the same point.

Although this is obviously an unrealistic model of the true overall biomechanics of the hip, it will consistently show the shape differences of the hip bone in terms of muscle lever arms against a fixed point in space, one that is the true insertion point for some of the muscles. The generated landmark is calculated using the actual femoral length of the individual in question.

A future study is proposed (see final chapter) to greatly enhance the data set produced to overcome this weakness.

Soft tissue and muscle wrapping ignored

Many muscles, particularly those in the pelvis region, are known to wrap around bone and soft tissue, including other muscle layers. Again for reasons of simplicity these problems were largely ignored in this study. Where muscles are known to wrap around the hip bone significantly (e.g. the superior and inferior gemelli) an estimated muscle origin was estimated to be near the point of wrapping.

Again, it is suggested that despite this limitation the results can still infer the most significant effects of hip bone shape on the locomotion of the hip.

Large muscle origins and muscle blocks were grossly simplified

Some hip muscles, such as the gluteal block, originate on relatively large surface areas of the hip bone and can perform more than one muscle action, for example both extension and abduction. For this reason, landmarks were clustered according to likely muscle action, rather than specifically for which muscle origin they were likely to correspond to in the technical sense. Many areas of the hip bone, where large muscles such as these originate, had no corresponding landmark.

Paleospecies muscle function is speculation

Although the muscle action of extant species is now well known, the actions of the muscles in the paleospecies used in this study were, of course, based on speculation and the principle of homology.

Morphs used

For this study, 70 hip bones were selected for those specimens with corresponding femora from 12 species, including 2 paleospecies: *A afarensis and H erectus*. (for example *A. africanus* could not be included here because there is no corresponding femoral neck specimen)

Processing

The following procedure was used to derive and analyse the lever arm data:

1) A subset of 44 landmarks of the hip bone were used, from which the lever arm from the centre of the acetabulum to the generated landmark representing the greater trochanter was calculated for muscles of the hip as described above.
2) Each of these calculated lever arms were expressed as a ratio of all the other calculated lever arms for each specimen.
3) The average of each permutation was calculated for each species.

Thus a data set of 1,936 (44^2) lever arm permutations was derived for each specimen, showing the ratio of each lever arm against each other.

One example will be followed through here to demonstrate this process.

Abduction versus extension muscle block example.

One key muscle involved in abduction of the thigh is the *tensor fasciae lata*. The origin of this muscle is identified on the hip bone schema here as landmark 12.

In humans the gluteal muscles also perform this function to a degree. The origin of these muscles is a very large area, however, so to contrast the biomechanical Lever Arm of extension, a landmark was selected that was more central: landmark 16.

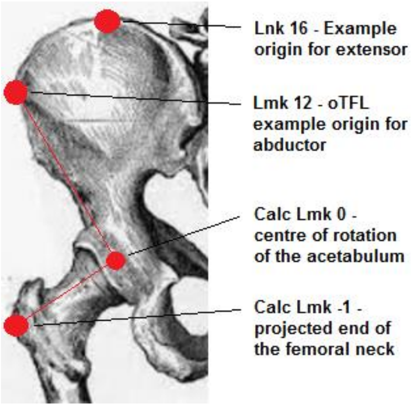


Figure 50 Sample landmarks to compare Abduction v Extension of the Hip

3D co-ordinates of these landmarks

Here are a set of sample 3D co-ordinates for two paleo-species and two randomly selected human specimen (one male, one female)

AFA002881-HIP-DIG-AK-20050620-461 - *Australopithecus afarensis*

Lmk	x	Y	Z	Lever Arm	Ratio 16/12
-1	330.51	-41.3	198.41		
0	316.32	-66.2	178.36		
12	284.67	-0.8	145.17	33.87	0.49
16	262.53	-77.21	101.97	16.67	

HER005000-HIP-DIG-AK-20050627-465 - *Homo erectus*

-1	-273.94	-146.68	209.06		
0	-283.91	-86.79	189.72		
12	-198.13	-95.15	153.76	55.24	0.78
16	-246.96	-56.83	76.69	42.71	

HSSM00029-HIP-DIG-AK-20080520-913 - *Homo sapiens sapiens* (Male)

-1	179.08	-295.38	287.73		
0	115.83	-321.81	280.12		
12	110.74	-278.48	354.05	59.51	0.67
16	39.22	-334.65	365.76	39.78	

HSSF00054-HIP-DIG-AK-20080813-977 - *Homo sapiens sapiens* (Female)

-1	250.45	1.45	421.01		
0	277.41	6.30	360.13		
12	254.10	-67.89	331.31	48.34	0.67
16	318.29	-69.71	283.31	32.49	

Once the load arm ratios have been calculated, they are then averaged in extant species. Here, for just two specimen considered, *Homo sapiens* would end up with an average ratio of 0.67. Finally, all the ratios for all the species are expressed as a ratio of that for *Homo sapiens.*

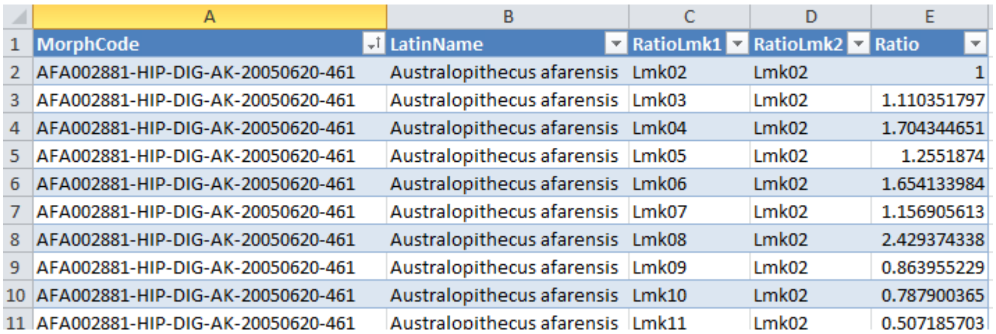
So, for this small example…

Homo erectus	1.16
Homo sapiens	1.00
Australopithecus afarensis	0.74

This indicates that australopithecines have a smaller lever arm ratio for extension as a percentage of that for abduction of the thigh than the other two species.

Pivot table analysis

As the data set is relatively large (> 135,000 rows) and a degree of flexibility was required in order to perform relevant queries pertaining to the muscle actions of the hip muscles, the data was inserted into a single, large “fact table” which lends itself to the modern business practice of performing a “pivot table” summary analysis on it.

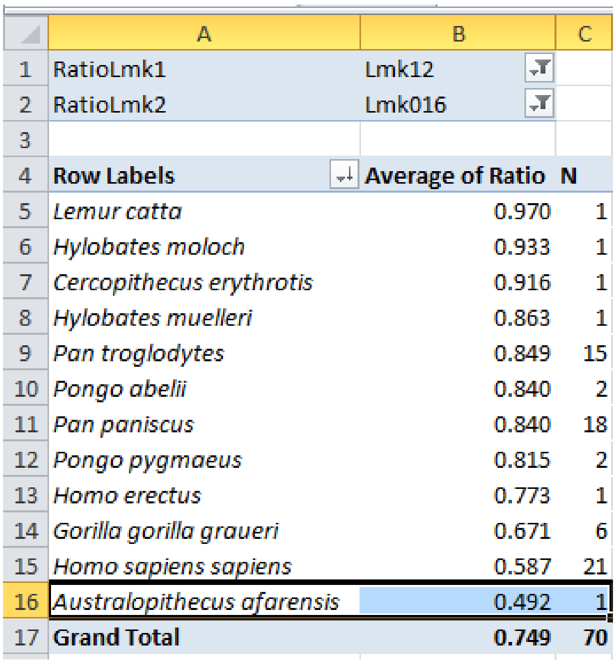


	A	B	C	D	E
1	MorphCode	LatinName	RatioLmk1	RatioLmk2	Ratio
2	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk02	Lmk02	1
3	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk03	Lmk02	1.110351797
4	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk04	Lmk02	1.704344651
5	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk05	Lmk02	1.2551874
6	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk06	Lmk02	1.654133984
7	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk07	Lmk02	1.156905613
8	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk08	Lmk02	2.429374338
9	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk09	Lmk02	0.863955229
10	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk10	Lmk02	0.787900365
11	AFA002881-HIP-DIG-AK-20050620-461	Australopithecus afarensis	Lmk11	Lmk02	0.507185703

Figure 51 Sample of Fact Table Data.

Figure shows one row for each specimen load arm permutation

Many users of Microsoft Excel will be familiar with this technique and the Excel Workbook containing the Pivot Table is available in the supplementary materials for personal use, if required.



	A	B	C
1	RatioLmk1	Lmk12	
2	RatioLmk2	Lmk016	
3			
4	**Row Labels**	**Average of Ratio**	**N**
5	*Lemur catta*	0.970	1
6	*Hylobates moloch*	0.933	1
7	*Cercopithecus erythrotis*	0.916	1
8	*Hylobates muelleri*	0.863	1
9	*Pan troglodytes*	0.849	15
10	*Pongo abelii*	0.840	2
11	*Pan paniscus*	0.840	18
12	*Pongo pygmaeus*	0.815	2
13	*Homo erectus*	0.773	1
14	*Gorilla gorilla graueri*	0.671	6
15	*Homo sapiens sapiens*	0.587	21
16	*Australopithecus afarensis*	0.492	1
17	**Grand Total**	**0.749**	**70**

Figure 52 Example Pivot Table

The figure shows the same sample comparison as above, but for the whole set of hip bones

Using this method it was possible to group sets of multiple landmarks to represent more widely distributed origins for various muscle blocks and thus generate summary ratio data for all the permutations of the major locomotor groups pertaining to the hip.

Muscle action groupings

As some muscles are known to perform multiple actions (e.g. Gluteus maximus can act as an extensor, an abductor and a medial rotator) it was decided to simplify the analysis by pooling antagonistic or opposing muscle actions and grouping them into three major categories.

- Flexion / Extension
- Abduction / Adduction
- Lateral / Medial Rotation

The task was then to compare the results from these three major muscle action groups against each other in order to determine the major differences among the species being studied.

In order to tease out the differences between these muscle action groups, in terms of this hip bone shape analysis of lever arm ratios, any landmarks that were common to different paired groups were eliminated.

Hip muscles analysed

The following table lists the major muscles of the hip concerned with locomotion, their origin and the landmarks used from the schema here to calculate their lever arms.

Where significant muscle wrapping is known, a local "proxy" on the hip bone was used as the landmark from which to calculate the lever arm.

Muscle	Origin as used on Hip bone (or proxy)	Landmarks
Flexors		
Iliacus	Illiac fossa (Proxy used on pelvic brim)	28, 29
Psoas	lumbar vertebrae (Proxy used on pelvic brim)	28, 29
Pectineus	Pectineal line on superior ramus of pubis	30
Adductus longus	Pubic Tubercle	31
Rectus femoris	Anterior Superior Iliac Spine (ASIS)	9, 11
Sartorius	ASIS	11
Extensors		
Semitendinosus	Ischial Tuberocity	40, 42
Biceps femoris	Ischial Tuberocity	40, 42
Semimembranosus	Ischial Tuberocity	38, 41
Gluteus maximus	Medial edge of ilium	17, 18, 19, 20
Gluteus medius	Gluteal surface of ilium	15, 22, 14
Gluteus minimus	Gluteal surface of ilium	14, 12, 22
Medial Rotators		
Pectineus	Pectineal line on superior ramus of pubis	30
Adductus longus	Pubic Tubercle	31
Adductus Magnus	Inferior ramus of pubis & Inferior ramus of ischium	39, 33
Obturator internus	Inner surface of Obturator foramen (sciatic notch)	37
Lateral Rotators		
Gemelllus superior	Ischial spine	37
Gemelllus inferior	Above Ischial tuberocity	37
obturator externus	Medial margin of obturator foramen	45
Piriformis	Closest point on sciatic notch to the sacrum	22
Quadradus Femoris	Exterior border of the ischial tuberocity	38, 40
Biceps femoris	Ischial tuberocity	40, 42
gluteus maximus	Gluteal surface of ilium	17, 18, 19, 20
Abductors		
TFL	ASIS	12
Gluteus medius	Gluteal surface of ilium	15, 22, 14
Gluteus maximus	Gluteal surface of ilium	17, 18, 19, 20
Adductors		
Adductor longus	Pubic Tubercle	31
adductor brevis	Pubic Tubercle and inferior towards ramus	31, 32
Adductor magnus	Along inferior ramus of ischium and pubis	39, 33
Gracilis	Lower pubic symphysis to upper half of public arch	33
Pectineus	Pectineal line on superior ramus	30

Table 34 Landmarks used in Muscle Load Arm Calculations

From this, groups of landmarks were derived to represent the three major categories of muscle action: flexion/extension; medial/lateral rotation and abduction/adduction.

Landmarks for Muscle Action Group

Flexion/Extension	9, 11, 14 ,15, 17, 18, 19, 20, 22, 28, 29, 30, 31, 38, 40, 41, 42
Rotation	17, 18, 19, 20, 22, 30, 31, 33, 37, 38, 39, 40, 42, 45
Abduction/Adduction	12, 14, 15, 17, 18, 19, 20, 22, 30, 31, 32, 33, 39

Finally, each of these three groups of landmarks were permuted against each other and common landmarks to each pair were removed.

Extension/Flexion (ER) v Rotation	ER: 9, 11, 14, 15, 28, 29, 41	R: 33, 37, 39, 45
Extension/Flexion v Abduction / Adduction	ER: 9, 11, 28, 29, 38, 40, 41, 42	A: 12, 32, 33, 39
Rotation v Abduction /Adduction	R: 37, 38, 40, 42, 45	A: 12, 14, 15, 32

These sets of landmarks were then used as filters in the pivot table analysis to generate average lever arm ratios for all the permutations of landmark pairs.

6.4.2 Results

The "data mining" technique, commonly used in the world of business and commerce by using tools like Pivot Tables, allows a vast amount of data to be summarised in a few lines of data. From these summaries, interesting data can be "drilled through" to get to the detail of what is going on behind the big picture.

This will be the approach used here to analyse the large data set produced by this study – more than 135,000 lever arm ratios.

Top level summary

The overall averages of the permutations of lever arms grouped by muscle action for australopithecines as compared with *Homo sapiens* are summarised in the table below – in the cells above and to the right of the diagonal. Below and to the left are the relative rank order of *Pan troglodytes* relative to *Australopithecus afarensis* and *Homo sapiens*, among the 12 species analysed.

Australopithecus v *Homo sapiens* Ratio

	Flexion / Flexion	Rotation	Abduction / Adduction
Flexion / Extension		0.730	0.754
Rotation	12, 11, 1		0.997
Abduction / Adduction	12, 5, 1	5, 2, 4	

Australopithecine, *Pan troglodytes* , *Homo sapiens* ranking out of 12 species

So, for example, the ratio of the mean lever arm values for muscles associated with Flexion / Extension for australopithecines is approximately 75% of that for *Homo* shown in the red cell at the top right.

When compared to the 12 species analysed, australopithecines ranked lowest for this ratio, *Homo* highest and *Pan troglodytes* ranked 5th – shown in the yellow cell in the bottom right.

The key finding is that the lever arms of muscles involved in flexion and extension, compared to those involved in rotation or abduction and adduction, are most different between *Homo sapiens* and australopithecines. The *Australopithecus* specimen AL 288-1 had an average lever arms ratio figure that was approximately 75% of that for *Homo sapiens*. It was ranked lowest of the twelve species studied, whilst *Homo sapiens* was ranked 1st.

When lever arms for muscles pertaining to adduction and abduction are contrasted with those involved with rotation, there is relatively little difference between *Homo sapiens* and australopithecines, both ranked in the middle of the list of species.

2nd tier summary

Drilling down on those two data points, one can see the figures in context of the full set of species and more statistical information about them.

Extension/flexion against rotation

The figure 0.73 above is itself a ratio of two ratios for AL 288-1 and *Homo sapiens*: 0.908 / 1.243. These figures each represent the average ratio of all permutations of lever arms of landmarks representing muscle origins involved with extension and flexion that are distinct from landmarks involved with rotation compared to those involved with rotation.

Rank	Row Labels	Min.	Avg,	Std. Dev.	Max.	N
1	*Homo sapiens sapiens*	0.432	1.243	0.553	3.747	588
2	*Homo erectus*	0.567	1.156	0.605	3.012	28
3	*Gorilla gorilla graueri*	0.477	1.112	0.493	3.167	168
4	*Pongo pygmaeus*	0.495	1.106	0.506	2.474	56
5	*Lemur catta*	0.429	1.106	0.548	2.327	28
6	*Pongo abelii*	0.560	1.098	0.495	2.635	56
7	*Hylobates moloch*	0.509	1.078	0.594	2.505	28
8	*Pan paniscus*	0.285	1.066	0.484	2.712	504
9	*Cercopithecus erythrotis*	0.594	1.037	0.447	2.073	28
10	*Hylobates muelleri*	0.550	0.995	0.334	1.607	28
11	*Pan troglodytes*	0.431	0.993	0.454	2.335	420
12	*Australopithecus afarensis*	0.586	0.908	0.231	1.315	28

Table 35 Extension/Flexion v Rotation

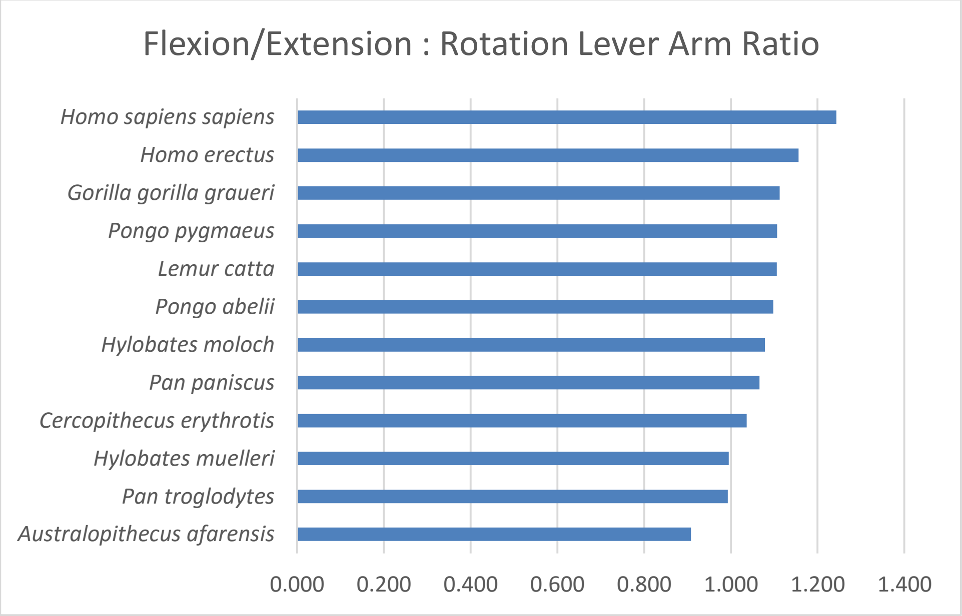


Figure 53 Extension/Flexion v Rotation Summary

The most striking point of note here is that *Homo sapiens* and AL 288-1 are at opposite ends of the ranked list of species.

The relatively high standard deviations inherent in these figures (e.g. *Homo sapiens* Mean = 1.243; Standard Deviation = 0.553) are due to the large variation of the landmark permutations used to make the extension/flexion and rotation muscle groups as the Pivot table generates an average for every landmark pair permutation.

Extension/flexion against abduction/adduction

Similarly, the headline figure of 0.754 for extension/flexion compared to abduction/adduction in the summary table earlier can be 'drilled through' in the same way.

Rank	Row Labels	Min.	Avg.	Std. Dev.	Max.	N
1	*Homo sapiens sapiens*	0.626	1.408	0.567	4.242	672
2	*Homo erectus*	0.625	1.399	0.640	3.488	32
3	*Pongo pygmaeus*	0.449	1.246	0.582	3.178	64
4	*Gorilla gorilla graueri*	0.516	1.239	0.577	4.298	192
5	*Pan paniscus*	0.330	1.212	0.591	4.356	576
6	*Pongo abelii*	0.518	1.212	0.563	3.483	64
7	*Lemur catta*	0.620	1.198	0.550	2.528	32
8	*Pan troglodytes*	0.394	1.155	0.594	3.392	480
9	*Hylobates moloch*	0.324	1.108	0.731	3.640	32
10	*Cercopithecus erythrotis*	0.479	1.103	0.551	2.717	32
11	*Hylobates muelleri*	0.521	1.093	0.423	2.077	32
12	*Australopithecus afarensis*	0.659	1.061	0.296	1.871	32

Table 36 Extension/Flexion versus Adduction/Abduction

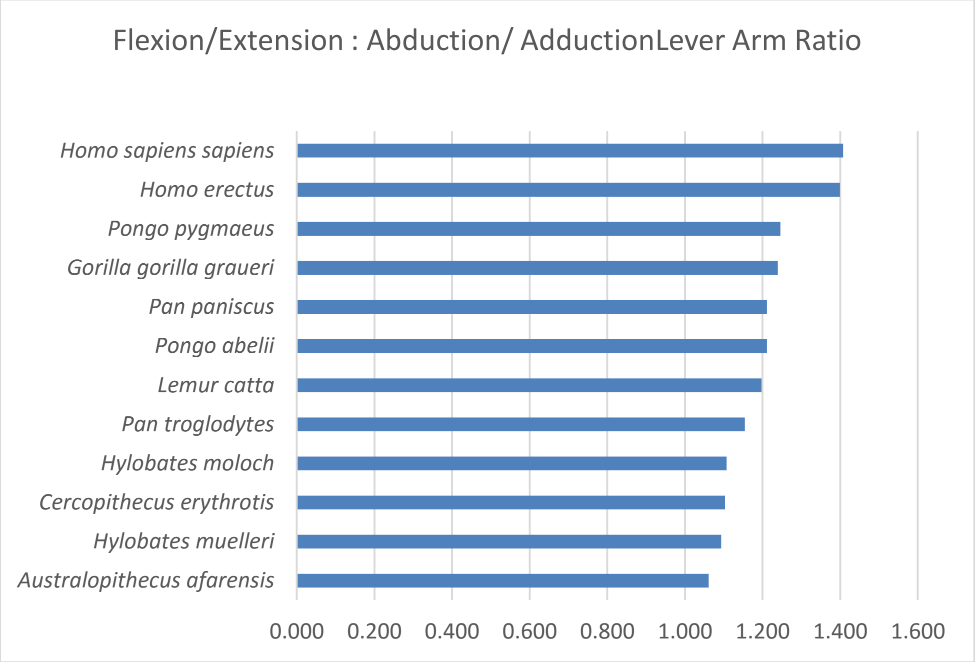


Figure 54 Extension/Flexion versus Abduction/Adduction Summary

Again, the distance between *Homo sapiens* and AL 288-1 is remarkable, considering both species are considered to be bipedal. The implication from these data is that the shape of the australopithecine pelvis must have been adapted to a different locomotor repertoire than the modern human form.

3rd tier summary

Drilling down further, one might next tease out more specific muscle groupings, some which give even clearer results, and others which give more ambiguous findings. For example flexion and extension can be split apart and compared with either lateral or medial rotation, or with adduction and abduction, individually.

Taking one example, if one compares lever arm ratios for muscles exclusively involved with flexion with those exclusively involved in medial rotation, one finds an even greater difference between *Homo sapiens* and AL 288-1.
Here the ratio is 0.648 (1.082/1.669).

Rank	Row Labels	Min.	Avg.	Std. Dev.	Max.	N
1	*Homo sapiens sapiens*	0.635	1.669	0.641	3.747	168
2	*Lemur catta*	0.753	1.589	0.531	2.327	8
3	*Homo erectus*	0.664	1.581	0.769	3.012	8
4	*Pongo pygmaeus*	0.535	1.481	0.587	2.474	16
5	*Gorilla gorilla graueri*	0.685	1.480	0.541	3.167	48
6	*Pongo abelii*	0.666	1.449	0.577	2.635	16
7	*Pan paniscus*	0.413	1.427	0.509	2.712	144
8	*Hylobates moloch*	0.608	1.411	0.680	2.482	8
9	*Cercopithecus erythrotis*	0.604	1.349	0.487	2.073	8

10	*Pan troglodytes*	0.498	1.312	0.468	2.335	120
11	*Hylobates muelleri*	0.679	1.279	0.357	1.607	8
12	*Australopithecus afarensis*	0.702	1.082	0.246	1.315	8

Table 37 Flexion versus Medial Rotation

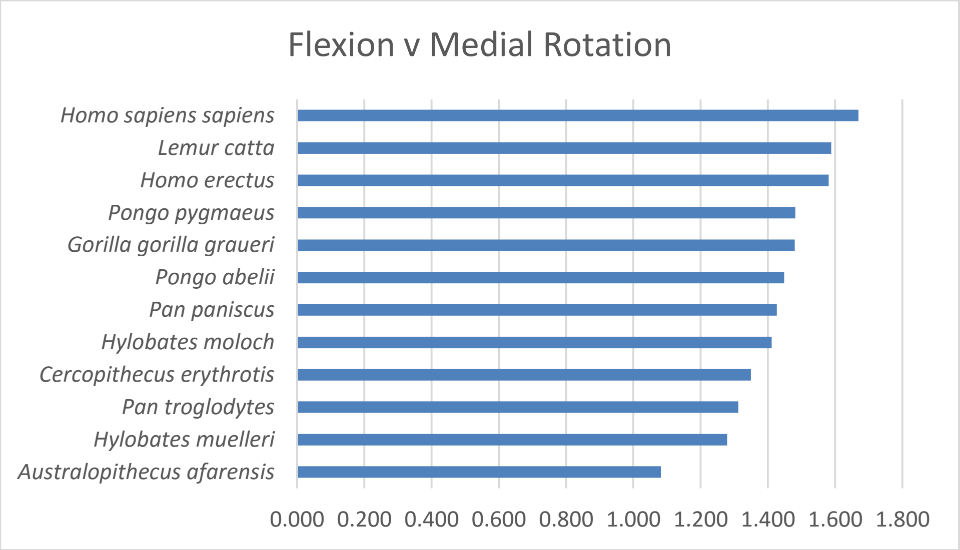


Figure 55 Flexion versus Medial Rotation Summary

By contrast, if one compares the lever arms for extension with those for adduction, one finds very little difference between *Homo sapiens* and AL 288-1 (Ratio 0.951).

Rank	Row Labels	Min.	Avg.	Std. Dev.	Max.	N
1	*Homo sapiens sapiens*	0.512	1.264	0.461	3.617	1155
2	*Australopithecus afarensis*	0.687	1.202	0.442	2.146	55
3	*Homo erectus*	0.513	0.940	0.226	1.632	55
4	*Gorilla gorilla graueri*	0.483	0.903	0.259	1.871	330
5	*Pongo abelii*	0.487	0.877	0.235	1.656	110
6	*Pongo pygmaeus*	0.462	0.867	0.268	1.916	110
7	*Hylobates muelleri*	0.530	0.760	0.175	1.279	55
8	*Pan paniscus*	0.330	0.759	0.213	2.176	990
9	*Lemur catta*	0.510	0.720	0.150	1.141	55
10	*Pan troglodytes*	0.392	0.681	0.162	1.520	825
11	*Cercopithecus erythrotis*	0.473	0.628	0.134	1.021	55
12	*Hylobates moloch*	0.327	0.530	0.188	0.915	55

Table 38 Extension versus Adduction

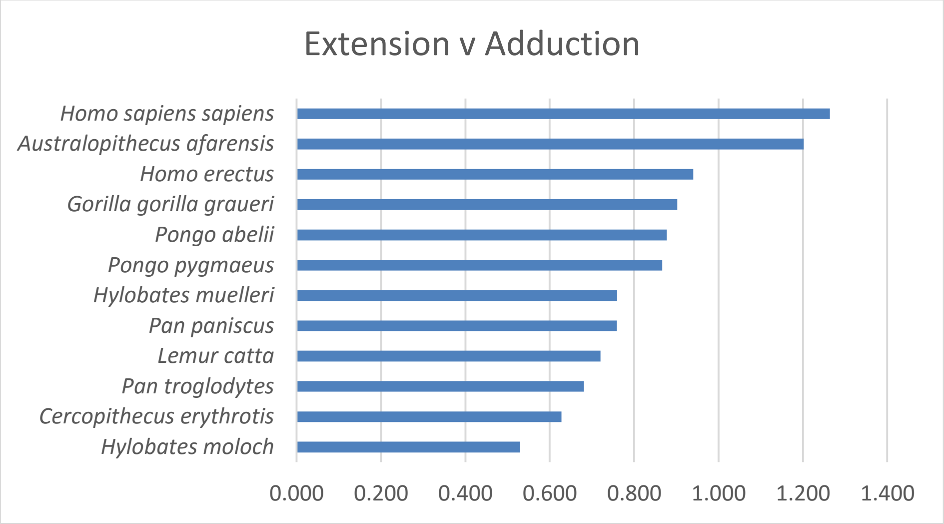


Figure 56 Extension versus Adduction Summary

As one can see, there is a vast number of permutations of pairs of landmarks and landmark groups that could be used to perform analysis with this data. But considering the significant caveats about the data outlined earlier, perhaps it would be better to end at this point, to step back from the detail a little and to discuss what the results may or may not indicate. In the next chapter, a potential program of further research will be outlined which might be useful to tease out more specific implications from this analysis.

6.5. Discussion

This chapter has built upon a significant foundation of decades of morphological studies of the hip. After a broad review of techniques used in the past, methods using 3D Geometric Morphometric (GM) analysis were chosen and were described here using a custom built database and software.

Australopithecines had different shaped pelves to humans

A 3D GM analysis of the shape of the hip bone, sacrum and femur confirmed earlier studies (Zuckerman et al. 1973) that indicated that australopithecines were similar to humans in many aspects pertaining to bipedalism, and support the long held conviction that they were almost certainly obligate bipeds, like us. The shape of the australopithecine proximal femur and sacrum, in particular, clustered particularly well within that of *Homo sapiens*. However, sufficient differences in the shape of the hip bone between the AL 288-1 specimen and *Homo sapiens* were identified to indicate that australopithecines might have used a bipedal gait that was quite unlike the striding, “inverted-pendulum” gait of modern humans.

Lever arm analysis indicates a greater utility for adduction/abduction in australopithecines

A more detailed investigation of load arms of potential muscle origins, grouped by major muscle action, was consistent with this and identified differences in lever arms in muscles pertaining to flexion in particular, as compared to rotation and abduction/adduction of the hip, as being largest between humans and australopithecines in the species studied.

Clearly, many individual muscle lever arm ratios could be analysed to increase the depth of this study and to derive quantitative data but even this limited study shows approximately a 25% difference in the lever arm ratio between muscles involved with flexion/extension compared to those involved with abduction/adduction and rotation.

Putative side-to-side wading gait

It is interesting to speculate about what form of locomotion might best account for such a radically different hip bone shape and to consider which types of muscle action would best be biomechanically favoured by the australopithecine hip as compared to the human form.

If the australopithecine pelvis indicates bipedality, but not our kind of bipedality, what other kinds might there be? As the morphology of the australopithecine hip is most certainly unlike most of the (largely arboreal) more primitive forms analysed here, it seems unlikely that such a departure from the Primate ‘norm’ could be explained by a peculiar combination of exclusively terrestrial and arboreal locomotion as suggested by Oxnard and Hoyland-Wilkes (1994 p 22.)

It is argued here that the simplest and most satisfactory potential explanation for their pelvic shape anomalies is a significant wading component in their locomotor. A twisting, side-to-side gait (one perhaps likely in waist deep water) would be easier to perform with a hip which gave biomechanical advantage to rotation, abduction and adduction of the hip. The remarkably platypelloid shape of the australopithecine pelvis (Tague and Lovejoy 1986) might similarly be explained as a streamlining adaptation to moving though water using such a twisting, side-to-side gait as illustrated in figure 56.

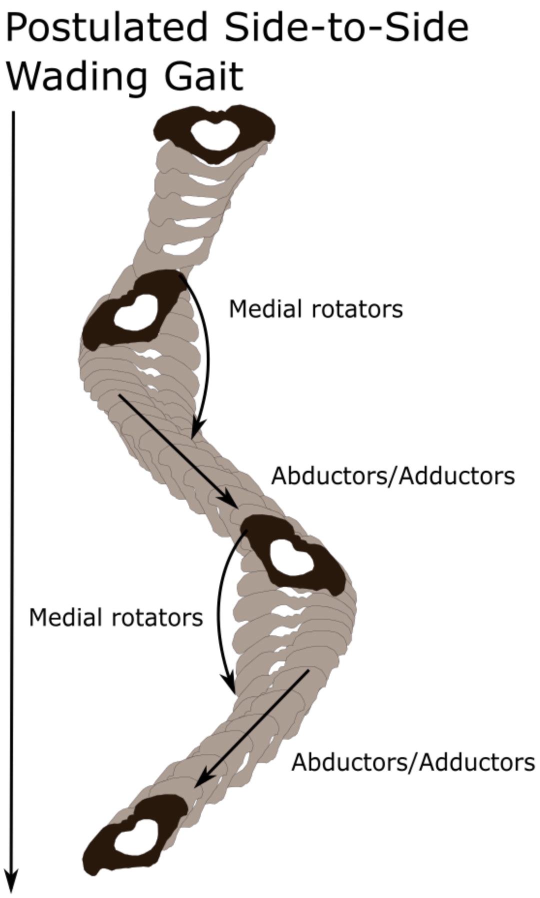


Figure 57 - Postulated side-to-side "wading" gait

Drag reduction speculation "explains" platypelloidy

Motion in water incurs far greater drag forces than in air and so it is logical that any hominid adapted to significant amounts of wading would be expected to have evolved traits to reduce that drag. The area of the lateral profile of the australopithecine at the hip must have been significantly less than one would expect if they had a pelvis shaped like most apes or large primates. As drag is calculated to be proportional to the area of the shape, it can be inferred that having a lateral profile that has half the area of, say, a chimpanzee could be expected to reduce drag by a significant amount (Kuliukas 2001).

Side-to-side gait speculation "explains" lever arm differences

The side-to-side gait postulated would also predict a greater biomechanical premium on those muscles involved in rotation and adduction/abduction of the thigh. It is argued here that no other explanation of the peculiarly platypelloid shape of the australopithecine pelvis has been so succinctly argued.

Of course, such speculation could be criticised as being fanciful and/or circular: One layer of speculation placed on top of another. However, the fact remains that the australopithecine pelvis does indicate a form of bipedalism that is not quite like ours and it as form that is remarkably different from the 'prototype' Primate form, one clearly strongly associated with arboreality.

Extant ape wading behaviour support

If one ties this in with anecdotal evidence of observations of extant great apes moving in shallow water (see e.g. Bruer 2000; Tutin et al. 2000;Myers-Thompson 2002;Kuliukas 2002), the idea is greatly supported. There is no other scenario in the natural world where otherwise committed quadrupedal great apes will so predictably switch to moving (not just posing momentarily) bipedally – and remain doing so as long as the conditions prevail – than in waist deep water.

Evaluating predictions of the wading hypothesis

Earlier in this chapter three falsifiable hypotheses were proposed to test the wading hypothesis of hominin bipedal origins.

- The general shape of the australopithecine pelvis is not significantly different from the modern human form.
- Any differences in shape are unlikely to have conferred any biomechanical advantage to postcranial movement in the australopithecines, as compared to modern humans.
- Any biomechanical advantage inferred by the anatomy of the australopithecine pelvis would not have given them any advantage whilst wading in waist deep water.

It is argued that the first two hypotheses have been falsified here and that the findings described here, although not falsifying the third, are consistent with what one would predict if it were false.

To conclude, it is argued, that the wading hypothesis works just as well whether the ancestors of all the great apes were already somewhat bipedal, or not.
If the genus *Homo* uniquely gained bipedalism, or the genera *Pan* and *Gorilla* both lost it, wading in shallow water must surely take its place as a plausible, evidence based, model to help explain the origins of hominin bipedalism and/or why some hominins stopped using that form of locomotion.

CHAPTER SEVEN

WATERSIDE SPECULATIONS, HYPOTHESES AND POTENTIAL RESEARCH

7. WATERSIDE SPECULATIONS, HYPOTHESES AND POTENTIAL RESEARCH

Partly reproduced from previously published papers…

Kuliukas, A.V. 2011a. A Wading Component in the Origin of Hominin Bipedalism. In: Vaneechoutte, M., Verhaegen, M., Kuliukas, A.V. Eds. Was Man More Aquatic In The Past? Fifty Years After Alister Hardy: Waterside Hypothesis Of Human Evolution. Bentham (Basel).

Kuliukas, A.V. 2013. Wading Hypotheses of the Origin of Human Bipedalism. Human Evolution 28 (3-4):213-236.

Abstract

This chapter confronts and aims to help resolve the controversy surrounding wading hypotheses of hominin bipedal origins and the so-called "aquatic ape hypothesis" (AAH) to which they are commonly associated. It does this by re-defining the AAH as a series of "waterside hypotheses of human evolution" which simply propose that many human phenotypic traits may be the result of a slightly increased differential in selection from moving through water and procuring food from aquatic habitats, as compared to our great ape relatives.

An improved wading hypothesis of hominin bipedal origins, the "River Apes… Coastal" Model, is developed and offered for criticism. Counter arguments to the model are anticipated and discussed. The "River Apes… Coastal People" Model is compared and contrasted with other wading models and other waterside hypothesis of human evolution, using the evaluative framework introduced in chapter 3.

Testable predictions of the model are made, and the progress that have been made in testing them is reviewed. Although some of that work has been done here there is still a great deal more to be done and the thesis concludes by proposing the initial outline of a research program to do further tests as required.

7.1. Introduction

Many ideas about human origins have been published over the years, showing "a theatre for intellectual daring" (Kingdon 2003 p 16) to the extent that some of them have been criticised as "just-so" story-telling in the way that Rudyard Kipling made famous. Proponents of the so-called "aquatic ape hypothesis" have notoriously been associated with this kind of thing. After all, wondering "how humans lost their pellet?" is a similar question to "how the tiger got its stripes?" That's where the similarity starts to end, however. Hardy's speculation, and Morgan's promotion of it, have always been carefully phrased in Darwinist terms. Kipling's, by contrast, are, quite literally, pure fantasy.

As reported in Chapter 4, a literature search of the critical science pertaining to "more aquatic" models of human evolution in general, and wading-related ideas about human bipedal origins in particular, yields a paltry return. The review of the literature showed that most of it critiqued stronger versions of an "aquatic ape", ones that can be more easily knocked down.

Long overdue, is a dispassionate, scientific assessment of exactly what these ideas are (and are not) proposing. This thesis has been written to do just that with one such idea. It has focused on the argument given most coverage, in the most recent books, on the subject by its most well-known proponent, Elaine Morgan: that wading in shallow water could have been a major factor in the evolution of our bipedality. This chapter concludes this work on the wading hypothesis by defining it as clearly as possible, setting out its testable predictions, reviewing the relevant anecdotal evidence and previously published scientific research, as well as that added here, and by proposing possible future research which might help to further test those predictions.

In addition to the wading hypothesis, however, there are at least five or six other key arguments in Morgan's books that this thesis could have used as its main focus and so this chapter also turns its attention to other "more aquatic" ideas of human evolution in general and places the wading hypothesis in that context.

The so-called "aquatic ape hypothesis" has been much criticised, but even its harshest critics usually fail to spell out exactly what they think it is. The fault is not all theirs. Certainly, the early proponents of these kind of ideas could be accused of being rather vague and rarely attempted to define exactly what they are proposing, with a clear timescale, geography and mode of selection.

It is time to finally bring some clarity to this debate and *re-define* the so-called "aquatic ape hypothesis." What follows is a proposal to define *them* (in the plural, for there is more than one idea) as "waterside hypotheses of human evolution". They vary a great deal in terms of timescale, degree and mode of selection being proposed and geographical location, but what they all have in common is the proposal that the human condition, to a greater or lesser extent, differs from that of our great ape cousins as a result of a differential in selection pressure from moving through water and procuring food from aquatic habitats.

The author offers his own "River Apes… Coastal People" version which, it is argued, is the strongest and most evidence-based current waterside model of human evolution.

It is often forgotten that Hardy's original article on the idea in 1960 was very modestly written and ended with an appeal for more science to be done: "My thesis is, of course, only a speculation - an hypothesis to be discussed and tested against further lines of evidence. Such ideas are useful only if they stimulate fresh inquiries which may bring us nearer the truth." Hardy (1960 p 642-645.) In accordance with that spirit, this thesis ends by listing some testable predictions of the River Apes… Coastal People Model along with a brief outline of a scientific research program which should be done to test them.

7.2. Waterside Hypotheses of Human Evolution

The wading hypothesis of hominin bipedal origins is only one of several water-related ideas about human evolution. As described earlier (chapter 4) it is probably the association of the wading hypothesis with the so-called "aquatic ape hypothesis" that has helped make it so unpopular and put off many would-be researchers from investigating it scientifically.

It has been the intention of this thesis to rationally and scientifically look at the wading hypothesis in isolation of other "more aquatic" ideas of human evolution. The goal has been to show that if one applies an objective rigour to the different bipedal origin models, then the wading model can only be seen as one of the more credible and evidence-based ideas published on the subject. This, however, does not really grasp the full nature of the problem. It is time to re-define the so-called “aquatic ape hypothesis” itself and place the wading hypothesis in the proper context of that redefined framework.

7.2.1 Redefining the “AAH”: Waterside Hypotheses of Human Evolution

As described earlier, the so-called “aquatic ape hypothesis” has received a very poor reception in mainstream anthropology. It is my considered opinion that this poor reception has largely been due to a misconception about what is being proposed. Some of the blame for this misunderstanding certainly lies with the proponents themselves. Labelling it the “aquatic ape hypothesis” may have been a way of grabbing people’s attention and causing a bit of stir, but unless one understands the use of the term “aquatic” in a somewhat ironic sense (“of the apes, which are generally not aquatic in any way at all, we are the *most* aquatic”), it is easy to see how one could arrive at an understandably bad first impression. Elaine Morgan’s first book on the subject “The Descent of Woman” was designed to tease the authorities of anthropology for what she perceived (albeit through popular accounts by Morris 1967 and Ardrey 1961) a largely male-orientated view of human evolution. This almost guaranteed that sympathetic ears (in palaeoanthropology) to her ideas would be rare.

However, any lack of sympathy for Morgan should be placed in the context of Hardy’s (1960) original request for comments. He was very much part of the scientific establishment, a Fellow of the Royal Society, no less. Unlike Morgan’s books, his article was written in a very unassuming and non-challenging way, and yet it too was still largely ignored for 12 years, long before Morgan got involved.

Morgan’s later books were certainly written to be less controversial and more scholarly than her first, but it seems that the damage to her reputation was already done as far as most anthropologists were concerned. One cannot blame specialists, who have spent decades scientifically investigating their chosen fields, for resenting being told that they had got it all wrong by a non-specialist popular playwright. But it is surely time to put the “blame game” behind us, move on and try to look at the ideas behind this so-called “aquatic ape theory” scientifically and objectively, as the late Phillip Tobias, urged: “… I believe that scientists have a duty to re-examine these claims, much as Langdon (1997) has done.” (Tobias 2002 p 15).

In 2011 some of the proponents of related ideas wrote the latest multi-authored, scholarly book on the subject (Vaneechoutte et al. 2011). It was the first such volume since Roede et al. (1991). The majority of the authors are either professional scientists or people aspiring to be, this author included. Although its pages contain a real diversity of views related to the idea that moving through water may have played a role in human evolution, all the authors are united in their disappointment about the continuing skepticism to the idea prevalent in mainstream anthropology and all of them are keen that more science be done to test these ideas. The book’s title (and subtitle), I think, was very apt: Was Man More Aquatic in The Past? 50 Years after Alister Hardy: Waterside Hypotheses of Human Evolution. See Langdon (2012) for a critique of the book and Vaneechoutte et al. (2012) for a reply.

The ‘Aquatic Ape’ misnomer

Most skeptics of the so-called “aquatic ape hypothesis” (AAH) continue to critique what I think can best be described as an exaggerated, singular, ‘strong’ version of the idea. Foley and Lahr

(2014), for example, recently attempted to discriminate between what they considered legitimate enquiries about human evolution pertaining to water and those ideas they were keen to demarcate as part of the AAH. In doing so they made several statements indicating a confusion about the idea they were critiquing. For example, they latched onto arguments from quite different ideas and reported them as if they were contradictions of the same single model, characterising the “aquatic ape” with “enormous adaptability”, that it “has been able to move chronologically from the Miocene to the Middle Pleistocene, as well as from the ocean to the beach” (Foley and Lahr 2014 p 59). The paper did cite Vaneechoutte et al. (2011), but made no reference to the diversity of related ideas it contained, outlining different timescales, geographical and ecological scenarios (Kuliukas 2014).

It should, in fairness, be pointed out that not all “aquaskeptics”, fail to see this point. Interestingly, by contrast, a sister paper in the very same journal (Rae & Koppe 2014) made it clear they recognised that most proponents had moved on from the original Hardy/Morgan “U-turn” concept.

So what are these ideas? What divides them, and what unites them?

One of the chapters in Vaneechoutte et al. (2011) was specifically written to fill the gap in the literature and provide a concise description of the various scenarios proposing that human evolution was affected, to some extent, by selection from wading, swimming and diving through water (Kuliukas & Morgan 2011).

It is not surprising that most of the critical literature about the AAH tends to focus on just one scenario, the one that was first proposed by Hardy and promoted by Morgan. This suggested that a more aquatic interlude was contemporaneous with, and probably caused, the split between *Pan* and *Homo*, and was followed by a U-turn back to a fully terrestrial life, as may have been the case with several other species, such as echidnas, moles, hyraxes and elephants (Mirceta et al. 2013). Kuliukas and Morgan (2011) describe various “more aquatic” models in detail, including ones that preceded Hardy, such as those from Max Westenhöfer (1942) and Guiseppe L Sera (1938). Of particular note is the model proposed by Verhaegen et al. (2002) which differs quite markedly in timescale, the proposed degree and mode of aquatic selection, and in terms of the evidence used in support of it.

More than ten such scenarios are reported and the differences between them clarified (summarised in Table 41).

Proponents	Timescale of "More Aquatic" Phase	Geographical location	Ecological scenario
Hardy	Between *Proconsul* and *Australopithecus*, ~15-10 Ma.	African and Indian Ocean coast, followed by a "U turn" to a more terrestrial lifestyle.	Coastal niche provided food.
Morgan	Around the time of the *Pan*/*Homo* split, ~6 Ma.	Unspecified waterside habitats (sea coasts, lakes, rivers) followed by a "U turn".	Food procurement after ecological inundation.
Verhaegen et al.	Pleistocene *Homo* < 2.5 Ma, especially during Glacials? But also with early (> 6Ma) wading-climbing phase for the last common ancestor of all great apes.	African and Indian Ocean coastal shallows including continental shelves now submerged.	Littoral diving and beach-combing for shell fish and other sea food.
Crawford, Cunnane, Broadhurst et al	Unspecified.	Indian ocean coasts.	Nutrients in the marine food chain key in encephalisation.
Ellis	~5 Ma.	Red Sea and East-African coasts.	Various coastal wetlands provide reliable food supply with low predation risk.
Williams	10-2.6 Ma.	Mediterranean islands, then Danakil and Afar triangle.	Coastal food procurement.
Kuliukas	River Apes: 5-2.6 Ma, Coastal people: 2.6-0.2 Ma.	Seasonally flooded riparian habitats east of the Rift, then Indian Ocean coasts.	Seasonally flooded gallery forests, then coastal shallows.

Table 39 Waterside Hypotheses

Two other ideas about human evolution were also reported that can also be linked to waterside habitats. Although they somewhat overlap with some of the ideas listed above, their authors have made varying efforts to distance themselves from the so-called "aquatic ape" so were respectfully not included in the main analysis. The "Amphibische Generalistentheorie" of Carsten Niemitz (2000, 2002, 2004, 2006, 2007, 2010), described in section 2.3.10, is basically a wading hypothesis of early hominin bipedalism but the author insists a demarcation exists between his ideas and other ideas of the so-called "aquatic ape" hypothesis (see section 4.1.1.2). Philip Tobias, as described above, has urged that anthropologists take a greater interest in these ideas and has promoted his "Water and Human Evolution" ideas Tobias (1998, 2001, 2002), but it would be wrong to characterise him as an "AAH" proponent.

By pointing out the diversity of models that have all broadly been described as the "aquatic ape hypothesis", Kuliukas and Morgan (2011) show that a single, and rather ironic (or extreme, depending on one's point of view) label is no longer appropriate for these ideas.

They conclude by offering a broad umbrella term for all such ideas, as well as a working definition which acts as a kind of "lowest common denominator" for them. This, and the reasoning behind it is described later.

The recent "Waterside Hypotheses" London symposium

Since the publication of Vaneechoutte et al. (2011), a symposium was held in London, organised by Peter Rhys Evans, an Ear Nose and Throat specialist at the Royal Marsden Hospital and presented by Sir David Attenborough. The participants included "aquaskeptics" such as John Langdon, Stephen Oppenheimer and Donald Johansen as well as proponents of various waterside hypotheses. The presentations were video recorded and the proceedings were published in the journal "Human Evolution" (see, e.g. Kuliukas 2013).

Once again, the most striking impression one gets from this work is the diversity of the ideas pertaining to human evolution that are linked to moving through, or procuring food from, water. One can only conclude that there is no singular "aquatic ape hypothesis."

7.2.2 Definition of a 'weak' form of the AAH: 'Waterside Hypotheses'

As the review of the "AAH" literature in chapter 4 has indicated, the AAH has never been adequately defined by its proponents and the only forms of it that have ever been critiqued in the literature are ones which have assumed it to have been 'strong', that is proposing a level of aquatic adaptation that is similar to those which must have acted upon aquatic and semi-aquatic mammals such as dolphins and seals. What has very rarely been considered is any 'weak' form of the hypothesis.

A number of criticisms of the label "aquatic ape hypothesis" need to be addressed in order to avoid misunderstanding.

- The degree of 'aquatic' selection (from wading, swimming and diving and from collecting foods from aquatic habitats) need not be as extreme as is implied by using the term 'aquatic'. Even if procuring food from, and moving through, water may have only comprised a relatively small proportion of the locomotor repertoire, it may still have provided a significant difference in selection pressure in the lineage leading to *Homo* as opposed to that leading to *Pan/Gorilla*. The term 'waterside' is therefore preferred to express this sentiment.
- Although the original idea from Hardy (1960) promoted by Morgan (1972, 1980, 1998) certainly proposed an early (pre-*Homo*) "more aquatic" ape phase, this is not necessarily the end of the story. It is equally possible that any (even slightly) "more aquatic" pressure occurred later, since the split with *Pan*. Therefore the term 'ape' is dropped from the label and a more general indication pertaining to human evolution generally is sought.
- There is not one single "waterside" model. Like any area of speculation about historical science, such as human language origins, there are several competing ideas in this area, each with different proponents arguing for different timescales, modes of selection and citing different types of evidence. Although such proponents may broadly agree on some aspects of the role of adaptation to waterside habitats in human evolution, it would be unfair to expect them to agree on everything or to use contradictions between them in arguments to discredit the broad idea in general. Therefore a term indicating plurality has been chosen.

Rather than "aquatic ape hypothesis" (implying a single, rather strongly 'aquatic' phase, that is *pre-Homo*) the term "waterside hypotheses of human evolution" (plural, more modest and also alluding to time since the split with *Pan/Gorilla*) is offered.

Finally, to avoid the kind of ambiguity and misunderstanding that has been seen surrounding "the aquatic ape hypothesis", they are clearly defined:

> **Waterside hypotheses of human evolution** assert that selection from wading, swimming, diving and procurement of food from aquatic habitats, have significantly affected the evolution of the lineage leading to *Homo sapiens* as distinct from that leading to *Pan.*
>
> (Kuliukas & Morgan 2011)

It should be noted that other proponents of "more aquatic" ideas of human evolution may prefer other labels and definitions. Marc Verhaegen, for example, has recently promoted the terms "Littoral Hypothesis" and "Coastal Dispersal of Pleistocene archaic *Homo*". However, I believe the term "waterside" is simpler and quite sufficient.

Underneath the broad, "lowest common denominator," definition of waterside hypotheses that attempt to explain overall ape-human differences, I think there is room both for a number of distinct, scientifically testable, sub-hypotheses formed to explain specific human traits, as well as overall models of human evolution, such as those published by Verhaegen et al. (2007).

The specific waterside hypothesis of human evolution of this author will now be presented. It is called the "River Apes… Coastal People" model, which includes a wading hypothesis of hominin bipedal origins at its core.

7.3. The "River Apes … Coastal People" model

What follows is a presentation of a model of human evolution that aims to combine the best mainstream ideas from orthodox science about human evolution with strands from waterside hypotheses of human evolution backed up with most evidence. The model has a number of unique features which distinguish it from, and answer criticisms of, other ideas on human evolution.

7.3.1 The force of slight selection

One unique aspect of the model outlined here is that it stresses the importance of slight selection. More precisely, it is fully cognisant of a basic principle of population genetics that for selection to overcome drift, it need only be greater than the reciprocal of twice the effective population size (Li and Graur 1991.)

$$s > 1 / 2Ne$$

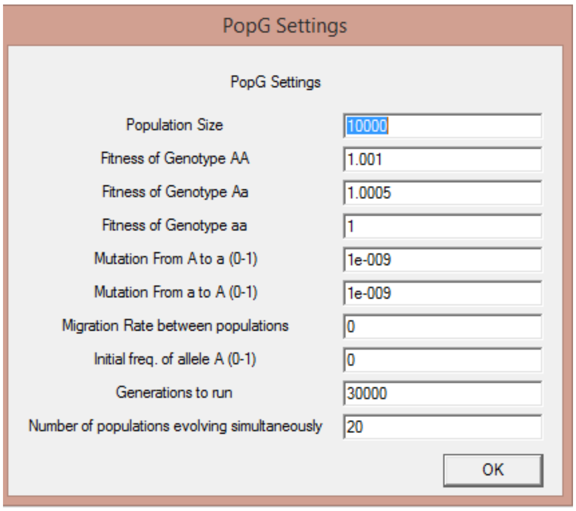
(s = selection, Ne = Effective population size)

One can easily demonstrate this point for oneself by running any basic population genetics simulator, for example popG.exe, available from the University of Washington (http://evolution.gs.washington.edu/popgen/popg.html)

In the simulation below, the following parameters were chosen based on a number of assumptions:

- 20 simultaneous populations were run so that a significant set of results could be compared.
- The mutation rate of a single nucleotide is approximately 2.5×10^{-8} (Nachman & Crowell 2000), setting a lower bound for a typical gene. In this simulation it was set lower still (at 1×10^{-9}) so as not to unrealistically diminish the effect of drift.
- A population size of 10,000 was chosen – a typical consensus number for estimates of hominin populations (see Chen 2001).
- A fairly slight (+0.1%) positive effect on selection was assumed for a given allele in the homozygous form and half of that in the heterozygous form.

- It is assumed that the allele did not exist at all to start with.

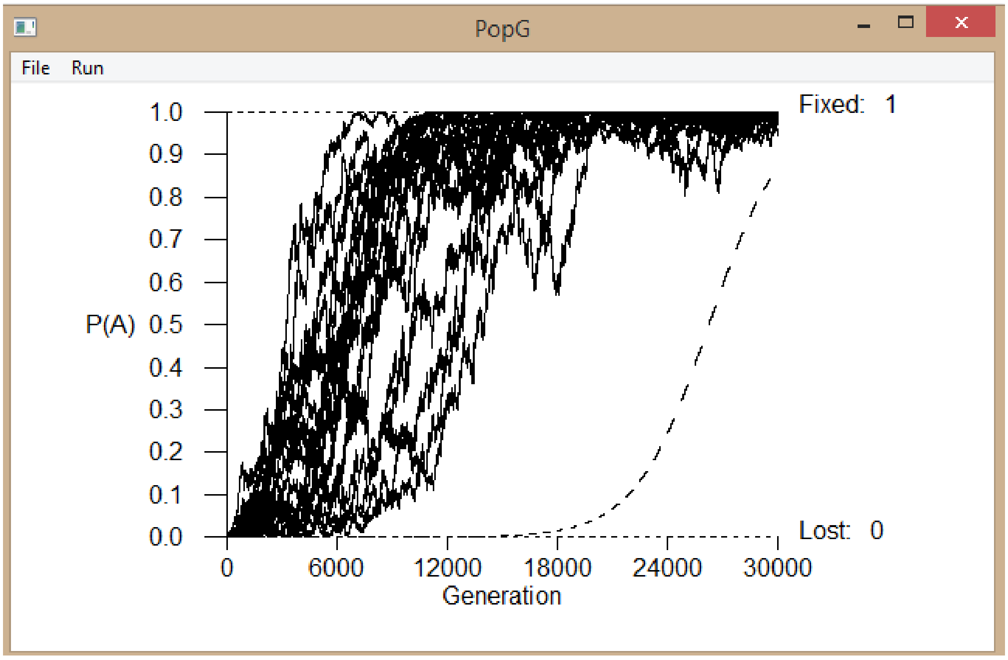


PopG Settings

Population Size	10000
Fitness of Genotype AA	1.001
Fitness of Genotype Aa	1.0005
Fitness of Genotype aa	1
Mutation From A to a (0-1)	1e-009
Mutation From a to A (0-1)	1e-009
Migration Rate between populations	0
Initial freq. of allele A (0-1)	0
Generations to run	30000
Number of populations evolving simultaneously	20

Figure 58 PopG.exe Run Settings

In this run, the allele became close to fixation in most of the 20 populations by the end of 12,000 generations.



Fixed: 1

Lost: 0

Figure 59 PopG.exe Run

Obviously, reducing the degree of selection or the population size still further would make the case for slight selection less clear cut, but there is no doubt that, generally, when this sort of simulation is left to run, it invariably results in the frequency of the given allele increasing steadily over time. Of course, through random drift, some populations will lose the allele, but even with such modest estimates of slight selection and low mutation rates in fairly small populations, the force of slight selection generally will overcome that of drift and most populations will reach something close to fixation of the allele in remarkably rapid timescales.

Of course, this kind of simulation is open to many criticisms, but it establishes a fundamental point – that selection need not be great to have a dramatic effect on a population's phenotype in relatively short evolutionary timescales. Hence for a phenotype to radically change, it requires very much less selection than one might intuitively think, and less than most models of human evolution appear to assume.

This is especially relevant in the context of the so-called "aquatic ape hypothesis" where the degree of "aquatic" exposure one imagines is being proposed is often directly proportional to the degree of skepticism one might have about the idea. Put it this way: If one imagined that for a trait to have evolved as a result of selection for diving, it required mermaid-like human ancestors converging with dugongs, it would be perfectly understandable that one might find the idea grotesque. If, on the other hand, it turned out that relatively infrequent and modest levels of diving activity, in otherwise almost totally terrestrial human ancestors, could still be expected to cause significant phenotypic change, over relatively short evolutionary timescales, then it is hard to see what the fuss is all about.

In a nutshell, Alister Hardy asked "Was man more aquatic in the past?" but few seem to have wondered "… and if so, how ***much*** more aquatic might that have been?"

Many proponents and skeptics, alike, agree in thinking that for any "aquatic ape" idea to work at all, then a radically different (and much more 'aquatic') lifestyle must be imagined. This thesis disagrees. It is argued here that even relatively infrequent and short exposures to wading, swimming and diving, for a species that was almost 100% terrestrial, would still be sufficient to allow these ideas to work.

Critics of this thinking have suggested that this is no longer any kind of "aquatic ape" model at all and that it is just "shifting the goalposts" to make it work, but this is not the case. The model about to be described still insists that the primary, new, selective force, that worked to make humans so phenotypically different from our great ape cousins, came from an increase in the amount of wading, swimming and diving in the locomotor repertoire of our ancestors compared to that of the ancestors of chimpanzees. That is still very much the same argument used by Elaine Morgan for 45 years and Hardy before her. The key differences between this model and theirs are simply ones of timescale and degree.

As outlined below, the model assumes wading was a component of the ancestor of all the great apes, Hardy & Morgan did not. It assumes a coastal lifestyle for human ancestors being important up until, and including, the "Out of Africa II" diaspora, whereas they argued for a 'U' turn back to a more terrestrial lifestyle after a 'more aquatic' interlude, millions of years ago. Compared to Hardy & Morgan the degree of selection for a 'more aquatic' lifestyle being proposed here is probably nowhere near as high.

It seems to this author that even an infrequent exposure to the risk of drowning for relatively short periods of time would still be expected to add a significant component to the regime of selection in populations that lived by the water's edge compared to populations that, generally, did not. After all, it only takes a few moments to drown. If a population of hominids migrated to a shoreline habitat and occasionally had the need to wade, swim and/or dive for food, it is only common sense to assume that some of them might drown. If a sister population stayed away from such habitats, it would surely create a different regime of selection that would inevitably cause rapid phenotypic divergence between the two.

It is difficult to know exactly how much selection from moving through water Hardy was imagining, but a couple of quotes on the matter provides a hint.

He wrote "My thesis is that a branch of this primitive ape-stock was forced by competition from life in the trees to feed on the sea-shores and to hunt for food, shell fish, sea-urchins etc., in the shallow waters off the coast. I suppose that they were forced into the water just as we have seen happen in so many other groups of terrestrial animals. I am imagining this happening in the warmer parts of the world, in the tropical seas where Man could stand being in the water for relatively long periods, that is, several hours at a stretch" (Hardy 1960 p 642-645).

And…

"It may be objected that children have to be taught to swim; but the same is true of young otters, and I should regard them as more aquatic than Man has been." (Hardy 1960 p 642-645)

Arguing for 'several hours at a stretch' and for only just less aquatic exposure than otters might still seem an overly high degree of aquatic pressure to some but I would argue that this is really just setting an upper bound. It is certainly not arguing for any mermaid-like convergence with manatees. Of course, what Hardy doesn't say, but is clearly true, is that the degree of selection could undoubtedly have been far less than that, and some phenotypic effects would still be predicted to happen. Hardy obviously could not have taken advantage of the sort of computer based evolution simulators referred to earlier that we can now take for granted today.

It seems to me that this rather simple point has been overlooked by both sides in this controversy, and that taking it on board offers an elegant way of satisfying both sides' skepticism of each other's position.

The following model, then, assumes that even very slight levels of selection would still result in significant phenotypic change, relatively quickly. It is argued that if human ancestors went into water, even only slightly more regularly than chimpanzee ancestors, this alone would be enough to induce a wide range of phenotypic differences over a 5Ma period.

7.3.2 "River Apes… Coastal People" model

What follows is an evidence-based, triphasic model of human evolution, based on the strongest points made by proponents of so-called "aquatic ape" models, including Hardy, Morgan, and Verhaegen et al. but modified to meet the exceptions of their harshest critics. Similarly, it draws upon the most compelling, evidence-based, parts of mainstream models such as that characterised as "the savannah theory" but at the same time is cognisant of the criticisms made of those models by Morgan and others. It also draws upon some models of human evolution that use varying dependence on waterside niches, such as Tobias, Niemitz and Wrangham.

The model has been designed with the evaluative framework, described in chapter 3 of this thesis, in mind. As a result, it scores most highly on that framework.

Phase 1 – Wading-climbing great ape LCA (Miocene 15Ma – 5.2Ma)

Along with the growing modern consensus (e.g. Lovejoy & McCollum, 2011), this model assumes that the Last Common Ancestor (LCA) of *Gorilla/Pan/Homo* (GPH-LCA) was already somewhat bipedal, but does not assume that they were already the efficient, obligate, *terrestrial* bipeds that *Homo sapiens* are. The increasing fossil evidence of early hominids with anatomical traits consistent with upright posture but different from our own, at the very least, backs this assumption and is therefore rated highly in criterion C.2 ("Fits the palaeoecological record"). This phase is very similar to the "aquarboreal ancestors" idea postulated by Verhaegen et al. (2000), Verhaegen et al (2011), but differs from Niemitz (2002, 2010) in that it very much assumes our ancestors were arboreal and came down from the trees, and from Hardy (1960) and Morgan (1998) in that it assumes the ancestors of both *Homo* and *Pan/Gorilla* were already regularly moved through water. Like Verhaegen, but contra other wading models, it assumes that GPH-

LCA was already somewhat bipedal and that whereas *Homo* went on to consolidate and optimise that bipedalism, *Pan* and *Gorilla* effectively lost it.

It should be noted here that despite some authors' (e.g. Lovejoy & McCollum, 2011) confidence about how the GPH-LCA moved, there is still actually no generally agreed consensus fossil candidate for that palaeospecies, and therefore no good evidential basis for any proposed locomotor repertoire they might have used. Contrary to most authorities, but in agreement with some (Harrison, 1991), it is suggested that *Oreopithecus bambolii* is as good a candidate in the currently known fossil record as any other. There is contradictory evidence about this palaeospecies, some indicating that *Oreopithecus bambolii* was somewhat bipedal (Harrison, 1991; Rook et al., 1999; Kohler et al., 2003) whilst others take an opposing view (Susman, 2005; Lovejoy & McCullom, 2011).

It is suggested that positing a locomotor repertoire comprising significant amounts of wading and climbing may well solve this paradox. The palaeological evidence suggests that *Oreopithecus bambolii* lived in a swampy island niche (Harrison 1989) consistent with a locomotor repertoire comprising significant wading and climbing. It is these two substrates together that, it is suggested, provide an ideal scenario for early hominid upright posture and the earliest forms of bipedalism.

Bipedalism in waist deep water, rather uniquely among the various models, offers the strongest possible and most acute survival value (evaluative framework criteria A.1, as described in chapter 4), as the alternative, quadrupedalism, would result in the face being immersed in water. Evidence from extant apes would seem to indicate that shallow water compels bipedal locomotion (not just posture) like no other substrate. This is another strength of this model and it scored maximum marks by criteria A.3 ("Not teleological") and B.4 ("Extant analogues") of the evaluative framework. Many models, such as those invoking carrying, rely on an assumption that as modern humans benefit from a feature of bipedalism, it is likely to have driven its evolution. Not so here. And few other models can be demonstrated so easily using Hunt's (1994 p 183) premise that contexts of bipedalism in extant apes may give clues as to factors which led to the evolution of hominin bipedalism. No other model of bipedal origins can, as confidently, predict that placing a group of extant apes in a given scenario would result in their continued, unsupported bipedal locomotion as placing them in waist deep water.

Whereas in dry land habitats, extant vertical climbing apes tend to switch to quadrupedal locomotion once they have climbed down from trees, in swampy habitats they stay upright in the shallows. This indicates that vertical climbing alone is an insufficient precondition for early bipedalism. The terrestrial "bipedalism" of *Hylobates* or *Ateles* can be seen as a highly derived condition from very specialised brachiation.

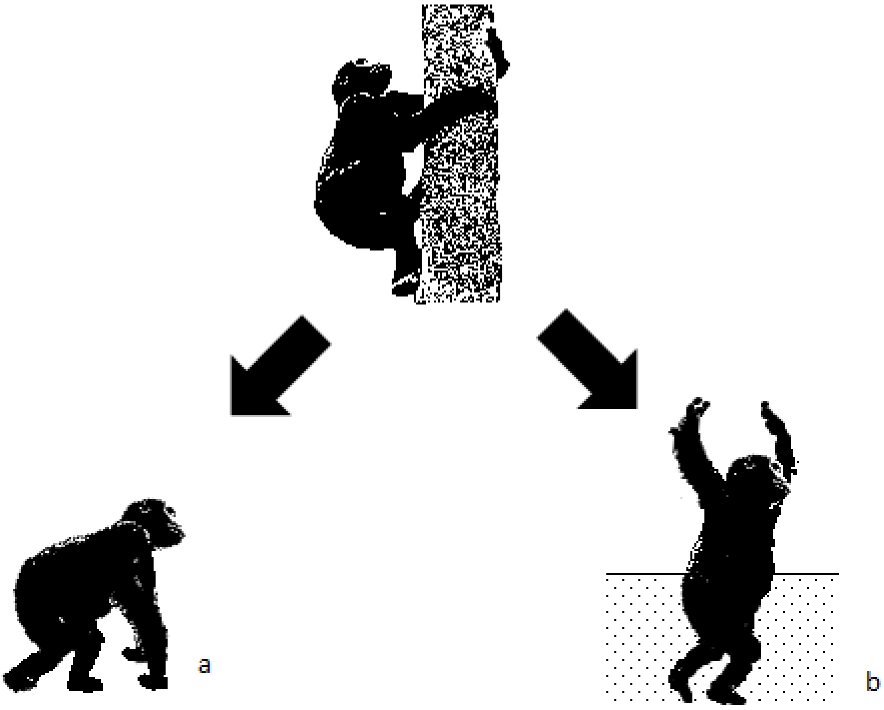


Figure 60 Wading-Climbing Early Bipedalism.

Vertically climbing extant apes switch to quadrupedal knuckle-walking on dry ground (a), but continue to move in an upright posture when in shallow water (b).

This phase helps explain both the early origin of some kind of bipedalism, seemingly increasingly likely to precede the split between *Pan/Gorilla* and *Homo*, and the idea that one lineage moved from that early (climbing-wading) form to a more-or-less terrestrial only, efficient type, whilst the other 'reverted' to a peculiar form of quadrupedalism with echoes of some kind of bipedal precursor – knuckle-walking. A wading-climbing ancestor, it is argued, is an ideal theoretical precursor to both knuckle-walking and terrestrial bipedal descendants. As such, it is argued that this model also meets criterion C.3 ("Precursor to strider and knuckle-walker") in the evaluative framework better than any other model.

The phase also helps to explain the geographical distribution of the great apes, in particular the fact that *Pongo* migrated to south east Asia, whilst the others, moved south into Africa (as per criterion C.2 in the framework). Coastal habitats along the Tethys sea could well have contained habitats where these Miocene great apes lived and the closing of the Tethys Sea channel could have been a key event in the isolation of *Pongo* from the other great apes.

As well as *Oreopithecus*, discussed above, another early candidate for the hominid lineage is *Sahelanthropus tchadensis*, also consistent with this phase of the model. The hominid, dated at around 7 Ma, was found in the middle of what was the huge, paleo Lake Chad, in a layer of rock labelled the anthracotheriid unit due to the prevalence of those amphibious creatures found there (Vignaud et al 2002).

Phase 1 can therefore be seen as a wading hypothesis for very early hominid bipedal origins.

Some testable predictions can be made of this phase of the model (as per criterion D.3):

1. The earliest fossil evidence for hominid bipedalism, still to be discovered perhaps between 10 Ma and 5Ma, should be associated with swampy/ wooded habitats.

2. Earlier candidates for the LCA of *Pongo* and African great apes should be found in Mediterranean/Tethys coastal habitats, again indicative of swampy habitats.
3. The LCA of African great apes and *Homo* should be found migrating south from the Mediterranean/Tethys, perhaps closely associated with *Sahelanthropus* and its Lake Chad habitat.

Phase 2 – Terrestrial bipedalism evolving in seasonally flooded gallery forest refugia in australopithecine-grade hominins, knuckle-walking in other African pes (Pliocene, 5.2 Ma – 2.6 Ma)

Consistent with the "savannah-based paradigm" held by most anthropologists for most of the last hundred years, and specifically Coppens' (1994) "East-Side Story", the second phase proposes that rifting in East Africa was the major factor in the *Pan-Gorilla* / *Homo* split. Of the previously published wading models, this phase overlaps considerably with Niemitz' (2002, 2004, 2010) "Amphibische Generalistentheorie" and Ellis' (1991) "Wetland Ape" ideas in habitat and timescale and somewhat with Verhaegen et al.'s (2000) "Aquarboreal Ancestors" idea. It differs from Hardy's (1960) and Morgan's (1998) wading ideas in terms of habitat. It therefore scores well by criterion C.2 ("Fits the palaeoecological record".)

The model suggests that west of the rift valley, ancestors of chimpanzees and gorillas became adapted to tropical rainforest habitats resulting in more climbing and less wading. Moving through dense, forested, vegetation in uneven substrates favoured a reversion to more quadrupedal locomotion and knuckle-walking specifically, as a formerly somewhat-bipedal ape increasingly looked to move on all fours and support its weight with extended forelimbs.

This is another strength of this model, as judged by criteria B.3 in the evaluative framework, as it accounts not only for why the human lineage became bipedal, but why the great apes did not.

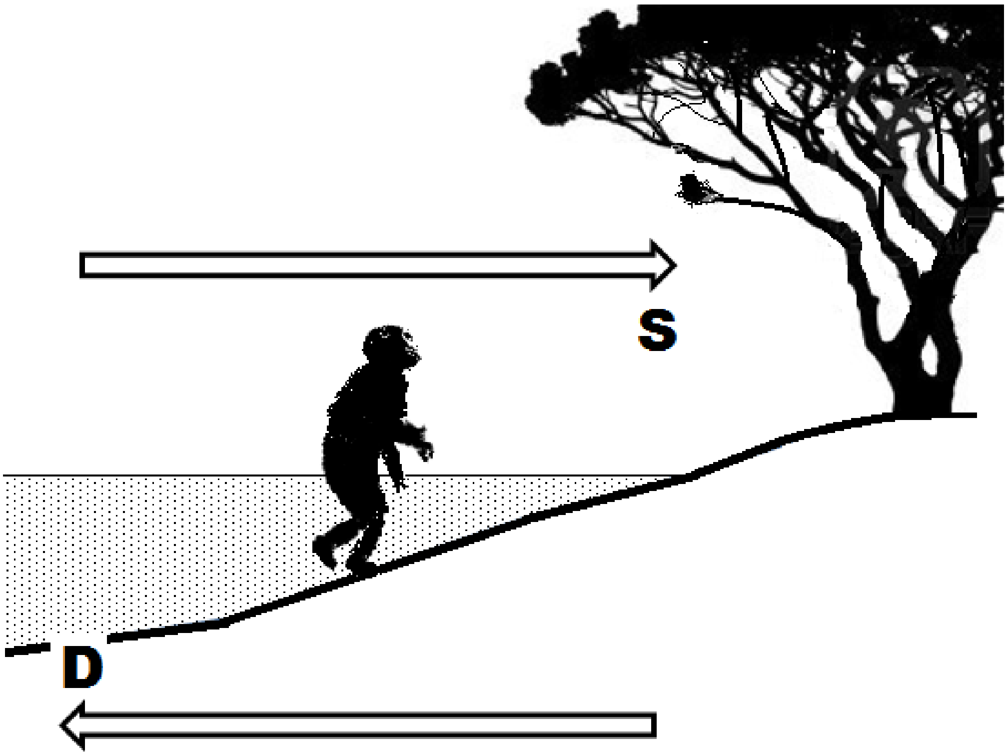


Figure 61 Rivers provides a continuum of depths .

East of the rift, it is suggested (again consistent with the orthodox 'savannah theory') that the lineage represented by australopithecine grade hominins were exposed to a shift to a much more arid environment. Savannahs, however, are still characterised by seasonal rainfall and although, generally speaking, forests were replaced by open plains, tree density would not have been reduced evenly. Gallery forests would have provided suitable refugia for hominins that had evolved in wet and wooded habitats for millions of years (compare, for example, with Wrangham et al. 2009). Seasonally flooded for several weeks, perhaps twice a year, such habitats provide an ideal scenario to simultaneously (in evolutionary timescales) guarantee more bipedalism (in waist deep water, hominins have little choice) and also encourage greater efficiency for ***terrestrial*** bipedalism.

As shown in Fig 60, in shallow water (S), there is less hydrostatic support for upright posture, less compulsion to move bipedally but, it is proposed, greater selection for anatomical traits to make terrestrial bipedalism more efficient. In deep water (D), there is more hydrostatic support and more compulsion to move bipedally, but less selection for traits to make bipedalism efficient. See the following "key points and criticisms section" 7.4, for more arguments in support of this.

Even though the two scenarios (flooded rivers compelling bipedal locomotion in even the least anatomically adapted hominid on the one hand, and flat, dry river beds and banks, allowing a modern human-like extended limb, inverted pendulum gait to evolve, on the other) are almost polar opposites of each other, they would coexist alongside each other, alternating in short temporal cycles. In a single year, a hominid inhabiting such a habitat might be exposed to two or three periods when they are exposed to each scenario. Over a lifetime, they would need to be adapted to both. The "river apes" phase of this model thus proposes that australopithecine-grade hominids were adapted to seasonally flooded gallery forest habitats. Selection for wading in shallow water during wet phases, and for walking bipedally short distances on parched river beds and banks during dry ones, as well as for some tree climbing, it is argued, explains the postcranial anatomy of australopithecines better than any alternative scenario.

Many traits would favour both forms of bipedalism, such as having longer legs and more laterally orientated pelvic ilia. Longer legs in water would provide more stability and greater safety from the risk of drowning. On land, they would help to make the striding gait more efficient. Having more laterally orientated ilia would favour strong abduction of the thigh, ideal for propelling the body bipedally through waist deep water efficiently, perhaps with some lateral motion, whilst on dry land they would help stabilise the body during the stance phase.

As many models of bipedal origins (and certainly the most popular ones, currently) argue that locomotor efficiency on dry land alone was sufficient to drive this process, it can only add strength to such models to add a wading component. It is complementary, not contradictory.

One of the key debates in hominin bipedal origins has been whether our ancestors needed to cross some "rubicon" of energy efficiency. See section 7.4.4 for detailed discussion of that but suffice it say here that this phase of the "River Apes… Coastal People" model supports the notion that a threshold had to be crossed. (Ironically the term "rubicon", which means a "point of no return", arose historically from Julius Caesar's army crossing the river Rubicon in 49 BC.)

Once the locomotor repertoire included more terrestrial bipedalism than shallow water wading or climbing, this phase of the model proposes that the selection for yet more efficient bipedalism would accelerate and become somewhat optimised.

The Pliocene was characterised not only by a shift towards greater aridity, but also to greater shifts in seasonality both in phase frequency and amplitude (See Fig 61, after Potts, 1998), perhaps synchronised with variations in solar orbits such as Malinkovitch cycles (Wynn 2004). Many hominin fossils have been associated with riparian habitats both generally (Wynn et al., 2006) and specifically for *Ardipithecus ramidus* (Gani and Gani 2011). Lakes are also associated with *Australopithecus anamensis.* ‘Anam’ means ‘lake’ in the Turkana language (Ward et al. 1999). Even the famous Hadar fossil site, where *Australopithecus afarensis* (or ‘Lucy’) was discovered, appears to have been a wetland for over a million years (Johanson and Edey 1981 p 129).

Kingdon’s (2003) evidence-based thesis for bipedal origins is wholly based on gallery forest habitats flowing east into the Indian Ocean. The key difference here is that, following Niemitz (2002, 2010), it is proposed here that wading through the riverine borders on the inside of such habitats was the major driver for greater bipedalism, rather than the dry forest-floors on the outside borders where, Kingdon argues, ground-dwelling hominins’ haunching would give them anatomical exaptations for bipedalism.

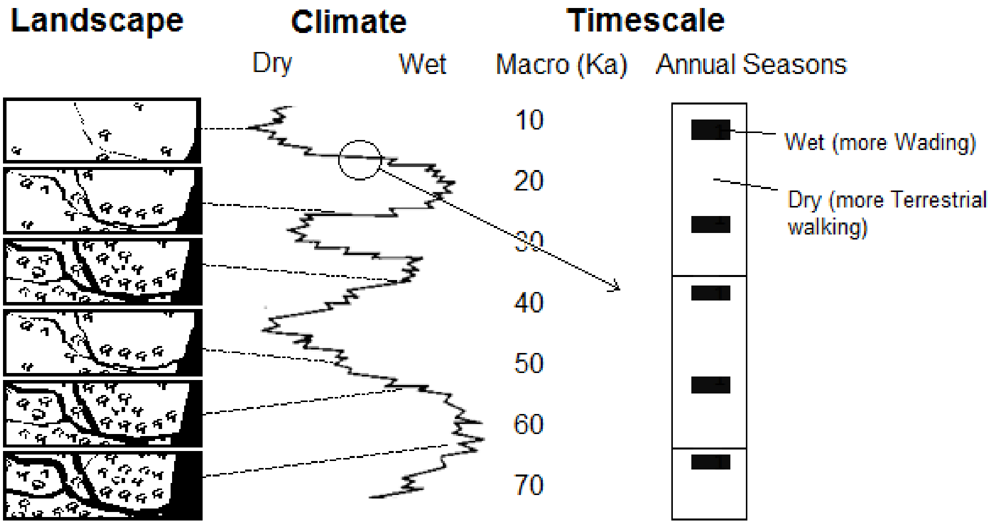


Figure 62 Short and Long Term Climate Variation

Seasonally flooded gallery forests favour both wading and Terrestrial Bipedalism (Adapted from Potts 1998)

As climate varies on a macro scale (over thousands of years), tree cover recedes closer to permanent water courses during periods of aridity, or spreads out generally during wet periods. These broad macro-changes are superimposed upon regular annual seasons with one or two wet seasons per year, where local gallery forest habitats would become flooded or have exposed, dried out river beds.

Another strength of this model, as compared to others based on a general savannah macro habitat, is that it applies equally to both sexes (criterion B.5). Unlike many hunting, scavenging or provisioning models, it does not propose that just one sex drove the evolution of a novel form of locomotion. Better still, is that it rather elegantly supports both savannah-based ideas of human evolution and more aquatic ones, simultaneously (criterion D.2).

A potential weakness here is predator vulnerability (criterion B.2) as relying on seasonally-flooded gallery habitats would clearly increase the risk of predation from crocodilians. However, it is assumed that australopithecine-grade hominins were still adept climbers and would have been smart enough to learn strategies to minimise this risk. Certainly, the risk of predation would seem greater if they were to wander away from the trees into open savannah grasslands.

It is suggested that this model's phase, rather uniquely, may help explain the peculiar traits of early bipedal hominins, such as *Australopithecus*. As shown in chapter 6, the shape of the pelvis appears to provide biomechanical advantage to abduction/adduction and rotation of the thigh. This is consistent with a putative wading gait and completely different from the classic Primate form, which is almost certainly adapted to arboreal modes of locomotion. The very platypelloid shape is also possibly adapted to improved streamlining when moving laterally, or using a side-to-side gait in water. Although this is largely speculation, there is clearly a great deal more science that could be done to test this idea. The early evidence seems to support criterion C.1 of the evaluative framework better than most models.

Phase 2 is therefore promoted as a very strong wading hypothesis for transitioning early, facultative, wading-climbing, bipedalism, common to all ancestors of the great apes, into a more obligate form, that is more optimised for walking on dry land.

This phase predicts (as required in criterion D.4) that:

1. Anatomical differences (such as the shape of the australopithecine pelvis, relatively large feet etc.) between Pliocene hominins and modern humans may be explicable as adaptations for more wading.
2. Gallery forest and other wetland habitats will continue to be associated with australopithecine-grade hominins.

Phase 2, also predicts phase 3. Simply by postulating seasonally flooded gallery forest habitats as an ecologically stable niche for bipedal hominids, it suggests that sooner or later, some of this population would find themselves in coastal habitats with more stable, less seasonally sensitive food supplies.

The first two phases of the "River Apes… Coastal" model are pretty exclusively concerned with hominin bipedal origins so, at this point the chapter will digress from the narrative of the model in general and summarise and focus on the wading hypothesis component of it. Phase 3 will be covered shortly.

The 'River Apes' wading hypothesis

The wading hypothesis of hominid bipedal origins is defined as a sub-hypothesis of an overarching group of broadly related ideas, labelled in this thesis "waterside hypotheses of human evolution" as described earlier.

Definition:

> ***The 'wading hypothesis' of hominid bipedal origins*** *proposes that bipedal wading through shallow water was a significantly greater component in the locomotor repertoire in the lineage leading to the genus Homo than in the lineage leading to the African great apes and that this differential was the key factor that led to our lineage alone ultimately becoming obligate bipeds.*

Assumptions:

It makes the following assumptions:

- That at some point in the past, the ancestral stock of all apes were predominantly quadrupedal when moving on dry land as are (but not in the manner of) the Old World Monkeys.
- That a major part of the lives of early bipeds was spent in trees and that a significant component of their locomotor repertoire was vertical climbing, degrees of arm suspension and/or brachiation.
- That, additionally, the earliest hominin bipeds also regularly waded through water, reinforcing the propensity to upright posture, which is probably provided by their large size and arboreality (as per Tuttle, 1981; Crompton et al. 2008.)
- That since the split with *Pan/Gorilla*, human ancestors became less arboreal but continued to regularly wade through shallow water until they crossed a rubicon after which they became obligate bipeds on dry land too, whereas *Pan*/*Gorilla* continued their arboreality but moved through water less, and thus reverted to quadrupedalism.

<u>Assumption 1: Quadrupedal ancestry</u>

As all apes are descended from the *Catarrhini* (The Old World Monkeys) and practically all species of that clade are quadrupedal when moving on land, this suggests that the ancestors of all apes were quadrupedal at some point in time. The only question really is: When? Until recently it has been largely assumed that even the Last Common Ancestor of *Homo, Pan* and *Gorilla* (*G*PH-LCA) was largely quadrupedal but recent publications (Brunet et al. 2002; Filler 2007; Filler 2007; Sayers et al. 2012) have called that view into question, largely because the emerging fossil evidence now places the earliest hominin bipeds in a timescale which is close to, if not before, the consensus estimate for *Pan* / *Homo* divergence.

It is argued here that the wading hypothesis helps explain the current disparity between humans and their great ape cousins, irrespective of whether the last common ancestor of their ancestors was largely quadrupedal or already somewhat bipedal, although the author now favours the later view due to the emerging fossil evidence just described..

If GPH-LCA was largely quadrupedal, then the wading hypothesis would help explain why humans uniquely became bipedal as it would argue that our ancestors did more wading than those of *Pan* or *Gorilla*. If GPH-LCA was already somewhat bipedal, then the wading hypothesis argues that this bipedality was, in part, explained by a significant amount of wading and that *Pan* and *Gorilla* lost this bipedality as the habitats of their ancestors (rainforest west of the rift valley) became less conducive to wading as compared to those of the ancestors of *Homo* (seasonally flooded gallery forests, east of the rift.)

<u>Assumption 2: Vertical climbing component</u>

The wading hypothesis does not argue that wading behaviour alone would be sufficient to drive the evolution of hominid bipedalism. Many mammalian species regularly wade, but are not bipedal. It assumes that an arboreal component is equally important in its origin. Throughout the Primates, those species noted for (albeit rare) observations of bipedality tend to be the largest in their respective clades: The Sifakas among the Lemurs and *Ateles geoffroyi* (spider monkey) among the *Platyrrhini* (New World Monkeys) are classic examples. The exception appears to be *Hylobates* among the apes, but these are themselves large compared to the Old World Monkeys from which they are derived.

The point here is that being relatively large makes it difficult, if not impossible, to traverse the smallest branches of a tree on all fours. A large arboreal Primate will therefore tend to stick to thicker branches and either exhibit thick vertical branch climbing or below branch brachiation where they are more horizontally orientated.

Consequently, as apes are generally large relative to most Primates, our ancestors would have exhibited a tendency to orthograde (upright) posture simply from vertical climbing and/or brachiation.

Assumption 3: Wading component

The wading hypothesis differs from most ideas on bipedal origins, however, in that it argues that a locomotor component of vertical climbing and/or brachiation is insufficient alone to lead to hominid bipedalism. *Hylobates, Ateles* and sifakas adopt bipedalism when (rarely) on land quite predictably, but they exhibit forms of bipedalism quite unlike ours.

Critically, those Primates closest to humans, the great apes *Pongo, Gorilla* and *Pan*, which are all predictably quadrupedal on dry ground, all switch to bipedalism in water that is around waist deep. Such incidents are, admittedly, rare, indicating that for most great apes today there is usually very little need or compulsion to enter shallow water. However, if one posits a scenario where similar apes inhabited forested swamps, it is not difficult to conceive very plausible motivations for much a more regular wading and significant wading component. Wading for sedges near the banks, selecting fruit off low branches overhanging the water are just two obvious examples. There may be other motivations too: The need to cross stretches of water to get to new patches of woodland, to gain access to mates or simply to cool down.

Assumption 4: *Pan/Gorilla Homo* divergence

As stated above, due to recent fossil evidence placing the earliest bipeds close to and perhaps beyond the estimated dates for *Pan / Homo* divergence, this author assumes that the GPH-LCA was already somewhat bipedal, due to a significant wading component of their locomotor repertoire. The question then remains: Why did *Pan* and *Gorilla* lose that bipedality and why did *Homo* become a specialised terrestrial biped?

Just as this model assumes it was environmental change that drove the early adoption of bipedal locomotion in great apes in the first place, it assumes that a change in environment later caused the divergence between *Homo* and the other great apes.

The African Miocene inhabited by the "wading-climbing" GPH-LCA was a much wetter place than in the Pliocene (Potts 1998). It is assumed that this population of great apes inhabited swampy habitats similar to mega lake Chad, the site where *Sahelanthropus tchadensis* was found (Brunet 2002). In the Pliocene, African climate changed, especially east of the rift valley. It was this climate change that the wading model assumes drove *Pan-Gorilla/Homo* divergence. West of the rift, equatorial rainforest persisted albeit with reduced rainfall and less swamp habitat, east of the rift, rainforest gradually made way for more open habitats criss-crossed with permanent water courses enveloped in gallery forest refugia where hominid ancestors would have persisted. The locomotor repertoire of apes that inhabited seasonally flooded gallery forests would have required regular wading, where bipedalism was practically unavoidable. In addition they provide scenarios where walking on relatively flat, firm vegetation-free substrates would have favoured traits to make the inverted pendulum gait more efficient. This is logical as lifting the lower limb, even slightly, during the swing phase, will incur greater energy cost than if it can swing though more fully extended.

Finally, as rivers flow into lakes and oceans, it is suggested that some of these gallery forest dwelling "river apes" would have eventually found themselves in coastal habitats with fewer trees to climb and more flat, firm, vegetation-free substrates on which to forage for food. In this way, it is proposed that *Pan-Gorilla/Homo* divergence may be accounted for.

It is at this third (coastal) phase of the model that we will now resume the presentation of the "River Apes … Coastal People" Model.

Phase 3 – Efficient coastal foraging in *Homo* (2.6 Ma – 150 Ka)

The final phase of the model attempts to explain the undoubted anatomical adaptations for efficient terrestrial bipedalism, as well as a whole host of other peculiar human physical features, that distinguish modern humans from our great ape cousins, in a waterside context. As rivers lead to the sea, it is proposed that it would only be a matter of time before populations of hominins inhabiting local wetland microhabitats (seasonally flooded gallery forest refugia), in a broad savannah macrohabitat context, would find themselves by the large rift valley lakes or by the Indian ocean coast, where the effects of aridity and seasonality on food supplies would be less severe.

The shores of the Indian ocean, envisaged for colonisation by early *Homo*, are known to include a significant amount of high coasts where, even in times of aridity, significant amounts of ground water would seep out providing ample fresh water (Sauer 1962.) The littoral zone, between high and low tides, would provide a very energy rich and relatively reliable and easy to procure food, source largely in the form of shellfish. The marine food chain is soft and particularly rich in terms of brain nutrients, such as Iodine, Iron, Copper and Selenium and essential fatty acids, such a DHA or docosahexaenoic acid (Cunnane 2005) and thus is compatible with the well-known simultaneous trends in later human evolution for masticatory and dental reduction and encephalisation. This food procurement could be easily supplemented by relatively easy wading at low tides, or swimming, to off shore rocks and islands and diving into the coastal shallows.

Consistent with many purely terrestrial models, (so scoring well on criterion D.2 "Complementary to other models") this phase assumes that these provided a selective advantage to early humans for slow, long distance locomotion. However, it notes that this efficiency is optimal on the kind of specific substrates that modern humans have designed for themselves – those that are perfectly flat, firm and vegetation-free. This is because walking over even the smallest of obstacles requires greater knee and hip flexion in the swing phase than would be required on perfectly flat substrates, adding to the energy consumption of such locomotion. It proposes that for human anatomy to have evolved optimally for such habitats, it is logical that they moved through substrates analogous to them for much of the time. In the natural world, substrates that are ideal for walking (i.e., flat, firm and vegetation-free, analogous to the man-made carpets and pavements which came along much later) include waterside habitats. Dried out river beds, coastal flats and beaches, right by the water's edge are, almost uniquely in the natural world, flat and firm enough to allow the kind of fully extended striding gait that allows for our bipedal efficiency. Following behind massive herds of savannah ungulates might also qualify, perhaps, but it is argued that even savannah grasslands often have significant vegetation which would hinder efficient bipedalism and, of course, there is the matter of the risk of predation.

The topology of coastal habitats, such as river deltas coastal lagoons and spits by their very nature, are likely to be convoluted and oddly shaped, requiring longer distances to be covered, per km^2, than in-land niches. Furthermore the ecology of coastal habitats makes them less vulnerable to predation (criterion B.2), compared to open savannah and other in-land habitats where the absence of herds of grass-grazing ungulates precludes the biomass necessary to support significant number of predators. The littoral zone provides a relatively reliable, non-seasonal, food supply (criterion B.1) making slow, efficient, locomotion a more plausible adaptive benefit. In a nutshell, it proposes that the earliest members of the genus *Homo*, and later, *Homo sapiens*, were costal foragers.

This is supported by at least two lines of evidence. Firstly, the earliest evidence of *Homo erectus* as well as anatomically modern humans, with recognisably human cultural artefacts, are both coastal.

The oldest artefacts of art yet found, attributable to the genus *Homo* and dated at around 500 Ka, were recently found at Trinil on the island of Java. Joordens et al. (2015) describe various use of freshwater shells, for food, tools as well as art which they attributed to *Homo erectus*. Marean et al. (2007) reported strong evidence for fully modern humans inhabiting a coastal site in South Africa, called Pinnacle Point. The remains are dated at 164 Ka, close to the estimates for the origin of *Homo sapiens.* The site also includes strong evidence for the procurement and use of shellfish.

Secondly, several "Out of Africa" Hypotheses (e.g. Stringer 2003) include an assumption of coastal migration routes as *Homo* (both *erectus, sensu lato*, and *sapiens*) left Africa to populate other regions of the world. As argued earlier, even modest selection from a few thousand years of exposure to a coastal life could have made a significant phenotypic difference to human populations migrating out (and back) to/from Africa.

Thus phase 3 provides a rather optimal scenario for the evolution of modern, energy-efficiency human bipedalism too.

Figure 63 The ideal naturally occurring substrate to walk?

High coasts guarantee that seeping ground water be easily accessible to people walking along the coasts providing reliable sources of fresh water. The littoral zone is rich in high energy (and brain nutrient-rich) foods.

Selection from swimming and diving?

Perhaps most controversially, this phase also proposes that members of the genus *Homo* regularly procured food from coastal shallows through swimming and diving.

Like Verhaegen et al.'s "Littoral *Homo*" ideas, this model disagrees with the Hardy/Morgan "U-Turn" hypothesis, in that it does not assume that the "more aquatic" phase *preceded* the evolution of *Homo sapiens* and caused the split with the other great apes, but instead that selection from swimming and diving continued with the evolution of *Homo*. Unlike Verhaegen et al. however, the "River Apes… Coastal People" model assumes relatively little swimming and, especially, diving behaviour was practiced by early *Homo* and proposes that the (quite low) peak of 'more aquatic' adaptation happened later, around the time of the origin of *Homo sapiens* itself, around 250Ka. It suggests that a population of coastal foraging people would regularly swim and dive for food, but perhaps rarely even for the "few hours at a stretch" Hardy (1960 p 642) proposed. Remembering the earlier point about the force of slight selection, it argues that even if this was as little as half an hour per week, it would still provide a sufficiently greater risk of drowning, as compared to chimp ancestors that were not coastal foragers, to cause a wide variety of phenotypic changes.

The key phenotypic changes being considered here are the main unique human features Hardy, Morgan and others noted (the state of the evidence for these features and specific detailed testable sub-hypotheses are described later in section 7.6.2):

Reduced body hair

A remarkable change in the general pattern of body hair, leading to the majority of the body being largely denuded or even glabrous. What little body hair remaining is explained as protecting from the sun's rays whilst swimming (i.e. the scalp), deflecting water from the eyes (eyebrows and lashes) or specific manifestations of sexual signalling (pubes, axilla hair.) Drag reduction in water is the major factor being proposed for most of these changes.

Increased adipocity

An increase in female and (in particular) infant adiposity, as a buoyancy aid to improve the chances of parental rescue in near drowning situations.

Respiratory tract changes

Respiratory tract changes including the evolution of a 'hooded nose' with inferiorly orientated nostrils and the descended larynx. The relatively large paranasal sinuses in humans might also be included here. These again are suggested as mildly adaptive of swimming and diving.

Voluntary breath control

The evolution of highly tuned voluntary breath control as an adaptation to swimming and diving, but acting as the perfect exaptation for the evolution of speech.

Encephalisation, masticatory reduction and early stone tool use

The remarkable increase in the (highly energetically costly) human brain size at the same time as masticatory power reduction, is consistent with a dramatic change in diet which appears to have begun around the time of early *Homo* (ca 2.6Ma). Although the use of fire in food preparation was surely a key factor in this dietary switch later, it is also possible that an earlier switch to the marine food chain was also a key component. Several nutritionists (e.g. Crawford, Broadhurst, Cunnane) have long argued that essential micronutrients (such as Iodine) and essential fatty acids, best found in the marine food chain, are key in the process of encephalisation. A point to note here is the elegant way this idea dovetails another remarkable aspect of human evolution – the use of stone tools. The point can be made that a three-year old can be taught to smash open a shellfish with a pebble.

By extending the explanatory power (criterion D.1) of the model in this way, it argued that it only adds to its strength without over-extending itself or contradicting the known fossil record.

Again, the key point to stress here is that the degree of aquatic locomotion being proposed is not very high. If one considers, merely that human ancestors did a little more swimming and diving than the ancestors of the chimpanzee – sufficient to change the regime of selection slightly – then isn’t a seemingly random list of peculiar phenotypic changes, such as this, exactly what one would expect?

The common “aquaskeptic” response to these suggestions is that most aquatic mammals have far superior and highly evolved traits for such things, and they discount the idea on that basis. But if one imagines humans as remaining almost 100% terrestrial, but merely adding a small extra component of swimming and diving to their locomotor repertoire, then such objections can be rebutted.

At the end of the day, these traits certainly did evolve for some reason or another. Why should adding a small, entirely plausible and evidence-based, swimming and diving component to the scenario be seen as being in any way unhelpful? Whatever orthodox (entirely earthbound) explanation there might be for such traits, they cannot be hindered, only helped, by adding a more aquatic component.

This phase makes several predictions (criterion D.3):

1. Evidence of the very earliest modern humans should be found in or near coastal habitats (see, e.g., Marean et al., 2007, for some evidence of this.)
2. The most optimal naturally occurring substrates to walk efficiently are waterside habitats such as dried out river beds and flat, wet sandy beaches.
3. The earliest *Homo erectus/ergaster* grade hominins should also be found in coastal habitats (see Joordens et al., 2015 for evidence of this.)

Some words on hybridisation

One, perhaps odd, aspect of the River Apes… Coastal People model that should be noted here is its relationship with hybridisation-based models of speciation. It basically proposes that the karyotypic difference in human chromosome number compared to other great apes is due to a natural hybridisation event of two closely related species of hominin. This is not an essential part of the model but it is mutually supportive of it and, it is argued, supported by it.

One of the most remarkable (but phenotypically invisible) differences between *Homo sapiens* and *Pan*/*Gorilla* is to be found in the number of chromosomes found in their cells. The large human chromosome (no 2) appears to have resulted from a telomeric fusion of two ancestral chromosomes of our great ape ancestors, a feature they do not share (Ijido et al. 1991). Various evolutionary models explain this kind of phenomenon (see, e.g. White 1978) but few are as satisfying as models of introgression (hybridisation.)

The problem with most models of karyotype change is that they rely on a very unlikely event – a chromosomal fusion in this case – happening at least twice in the same generation in a given population and producing not only viable, but mutually fertile offspring. Furthermore, such models require that these odd F1 individuals with the new karyotype are born sufficiently frequently, without any deleterious effects, as to allow them to grow into a new population of interbreeding individuals that is genetically isolated from parental populations.

Postulating a hybrid zone helps in every regard here.

Let's take two extremes: On the one hand, if two populations become separated for a sufficiently long period of time they eventually become absolutely genetically isolated from each other, and speciation could be said to have occurred. On the other hand, if they did not become isolated at all, no such speciation would occur at all and a continually breeding population would be maintained.

The hybrid model of speciation through karyotype change postulates something in between: There must be a period of time, intermediate between these two extremes, when populations that have been separated, come back together again, at a time when the mechanics of syngamy would still be successful enough produce a viable embryo, albeit with problems in chromosome alignment. It is in exactly this situation that karyotype change (such as telomeric fusion) is most likely to occur and, elegantly, it is in such scenarios where there would be a constant source of interbreeding parents generating exactly the same new F1 generation individuals with the new karyotype. Sufficient individuals, in fact, for them to be able to form their own subpopulation which could then interbreed themselves, effectively forming a new species with a new karyotype that is effectively genetically isolated from both parental groups at the same time.

How is all this related to waterside hypotheses? Well, over evolutionary timescales, sea levels rise and fall, and land masses come closer together and/or further apart again. If two populations of waterside hominins found themselves geographically isolated from each other because of a rise in sea level, they could just as easily be thrust back together again later, when sea levels fell.

If one assumes, as this model does, that human ancestors were never very aquatic, but just swam and dived a little more than chimpanzee ancestors, then such rises in sea levels could easily cause sufficient genetic separation for long enough periods of time for this sort of speciation through hybridisation to occur. The idea is that either *Homo erectus* or *Homo sapiens* was the result of such an interbreeding of two closely related, coastally dwelling, species.

It is well known that hybridisation events cause extra variability in the phenotypes of the F1 generation, from which very rapid evolution can act to produce novel forms very quickly (See, e. g. Arnold 1997). This is exactly the sort of situation that could lead to what would appear salutatory leaps in evolution.

If one population of hominins were more adept at swimming and diving than the other, perhaps by being more coastal dwelling, and as a consequence had better breathing control, whilst another, more terrestrial, group had the rudiments of group communication, perhaps as a result of some early hunting strategies, then a hybrid of two such populations might be more likely to inherit fortunate combinations of traits resulting in a predisposition to syntactical speech.

Such a saltatory leap towards the ability to use language may have been critical in human evolution.

Such speculations are, of course, rather fanciful and need more thought to start to flesh out testable hypotheses let alone a potential research program, but it was decided to report them here because they show how pursuing the concept of waterside hypotheses of human evolution has the potential to generate a whole cluster of novel and useful approaches to solving problems about human evolution.

Compatibility with other Models

One of the main design goals of this model was to make it as compatible with other models as possible. This was not motivated by the desire for a "political fudge" but simply a recognition that a great deal of intelligent thought and effort has gone into solving this question by many experts in many different fields and any new idea is unlikely to prove them all absolutely wrong.

Some of the best advances in science have been the result of a synthesis of two or more previously published ideas and it is anticipated that whatever model of hominin bipedal origins becomes accepted by the consensus, it is likely to be characterised by synergy not exclusivity.

Here, the compatibilities of this wading hypothesis with other models are listed.

Carrying

A variety of objects have been proposed as the thing being carried in models of forelimb pre-emption but relatively little attention has been given as to where the carrying took place. Although carrying models are clearly rather contradictory to climbing models, there is no such contradiction with wading models. Indeed one could argue that for some objects, for example infants, moving through water provides a far more compelling argument for the adaptive benefit of bipedal carrying than on dry land.

Behavioural

Some of the evidence for behavioural models of bipedalism, such as threat displays by gorillas, are compatible with wading models. Splash displays were reported by Parnell & Buchanan-Smith (2001) and tool-use in gorillas, reported by (Breuer et al. 2005) was essentially a depth gauge used before wading in Congo swamps.

Feeding

As waterside habitats are among the richest in terms of biomass, it is reasonable to expect wading models to be compatible with those espousing postural feeding. Many food items, such as sedges and low-lying branches in flooded forests, would only be accessible from shallow water. Wrangham et al. (2009) makes the case that procuring fall-back foods from wetland refugia could have been a key survival strategy for early hominins.

Arboreality

As this model, like Verhaegen et al.'s (2002) "aquarboreal" idea, assumes a climbing-wading last common ancestor, it is very compatible with those models citing an arboreal past, such as Keith's (1923) Hylobatian model.

Thermoregulation

Even Wheeler's (1994) thermoregulatory model of bipedal origins overlaps with the "river apes… coastal people" model to some extent. One could argue that the best possible way of cooling down for an overheating hominin is simply to go for a dip. Furthermore, the problem provided by Wheeler's notion of sweat-cooling assisted model of bipedalism - the need to replenish the water lost – is more easily resolved if one assumes that hominins lived in waterside habitats.

Energy Efficiency

Even energy efficiency models of bipedal origins, such as those by Rodman & McHenry, need not be contradicted by wading models if one assumes that wading helped ease the energy-inefficiencies of the gaits of the earliest bipeds, and if one accepts that, once a rubicon was crossed, humans did indeed become well adapted to efficient terrestrial bipedalism. The river apes… coastal people model does assume this and, in addition, proposes that the most ideal habitats for the efficient, striding human gait are those characterised by flat, firm and vegetation-free substrates – most commonly found by the water's edge on sandy flats at low tide or dried out river beds.

7.4. ***Answers to potential criticisms***

Several counter-arguments and criticisms have been raised against various wading hypotheses over the years. In anticipation of such objections, this section has been prepared to answer some of the more common ones.

7.4.1 Many animals wade in, water but they are not bipedal

Perhaps the strongest argument of the wading hypothesis is that, uniquely among models of hominin bipedal origins, it provides a simple scenario in which otherwise quadrupedal apes and other large primates will predictably switch to bipedalism. In waist deep water all extant species of great apes and some of the Old World monkeys have been observed to move bipedally (Kuliukas 2001, 2002; Myers-Thompson 2002; Parnell 2001).

Unlike other models based on ape behaviour, wading compels a form of bipedalism that is actually a form of locomotion and not merely postural, as is Hunt's (1994) "Postural Feeding Hypothesis". As long as apes remain in the context of waist deep water they are likely to continue to move bipedally. This is in contrast to much more transitory forms of behaviour used as the basis of some other models such as the threat display hypothesis (see, e.g. Jablonski & Chaplin 1993).

As discussed in section 1.3.2, various examples of bipedalism have been observed in mammals, but few of them are in water. Crucially to this argument, only large primates in general and great apes in particular, having a predisposition to upright posture which has probably evolved through vertical climbing, exhibit the peculiar phenomenon of switching their preferred form of locomotion from quadrupedalism on land to bipedalism in shallow water. There are examples in Ursidae, where normally quadrupedal bears have been observed switching to bipedalism in shallow streams whilst looking for fish, but even here they switch back to quadrupedalism again, or swim, when they begin to move.

Thus, wading bipedalism in Hominoidae has the appearance of a phylogenetic constraint, a key argument when discussing hominin bipedal origins.

As the best evidential basis of the model is great ape behaviour, it cannot be criticised for being anthropocentric, as can many of the other models (e.g. forelimb prehension, energy efficiency, male provisioning and thermoregulation.).

Another possible criticism is that extant apes rarely move bipedally. This is countered by the observation that Africa in the Miocene was a much wetter place than it is today (Potts 1998) and that early hominid fossil sites are usually associated with permanent water courses (Brunet et al. 2002; Vignaud et al. 2002).

Another counter-argument is to question why apes would want to spend much time in water and their motivation for doing so. This objection is addressed next.

7.4.2 Why would these apes go into the water?

There are many habitat scenarios where an ape population would have no choice but to move through water. Even in swampy woodland with an extensive canopy, apes living there would be compelled to occasionally come down from some trees and move across to others by wading through water. Gallery forests are known to become seasonally flooded, sometimes twice a year (e.g. Potts 1998). At such times there may be no dry land for several kilometres.

There are also other, less obligatory, reasons why hominin ancestors may have chosen to move into the water.

1) Food procurement. There are several potential sources of that would only be accessible by physically entering the water. Reeds and sedges have been observed being procured in shallow beis in modem western lowland gorillas (Doran and McNielage 1998). Fruit and leaves in low-hanging branches of the water’s edge would also provide a motivation. This is consistent with many models of bipedal origins based on food procurement.

2) To move to other territories for finding mates. Whatever the mate selection method was of the earliest hominids, males or females would occasionally need to migrate to other groups to find mates. In swampy or seasonally flooded habitats this is likely to require some wading.

3) Keeping cool. One of the most commonly cited models of bipedal origins is Peter Wheeler’s Thermoregulatory hypothesis (Wheeler 1991, 1992). This argues that early humans may have begun to walk upright on the open savannah as a means of keeping cooler where the upper body would be exposed to convective cooling. It hardly need be said that entering water is a far more efficient way of cooling down.

4) Unlimited availability of fresh water. Clearly, as Africa became more arid, access to permanent water courses would have gained greatly in importance.

The bottom line in this argument is that the evidence suggests that when extant apes find themselves in shallow water they have an overwhelming propensity to switch from quadrupedalism to bipedalism. It follows that if human ancestors were exposed to wetter habitats than either humans or extant apes experience today, this would provide a rather simple and plausible scenario for them, to regularly adopt bipedal locomotion long before any anatomical adaptations had evolved to make this bipedalism more efficient. It is the very nature of this efficiency that is addressed next.

7.4.3 Is modern human bipedalism really more efficient?

Some might criticise the later phases of the model for its assumption that the modern human postcranial anatomy, and its characteristic inverted pendulum gait, evolved to optimise the energy efficiency of walking. It therefore might be necessary to expand on this aspect of the thesis explicitly here.

Clearly, many animals have adopted forms of bipedal locomotion that are unlike humans and many of them may be superior to ours in terms of speed or even energy efficiency. Emus, ostriches and kangaroos, for example, are faster and more efficient than ours (Rubenson et al. 2007). Such examples, however, do not detract from the argument that the evolution of modern human postcranial traits was due to adaptations to make walking more energetically efficient (see chapter 5). Just as specific anatomical traits that help kangaroos to leap further would not be expected to be found in emus, the lack of human-like traits in other bipedal animals is not evidence that energy efficiency optimisation did not help to drive human evolution.

It is not argued here that human bipedalism is the optimum form of bipedalism in the animal world, but that the evidence suggests that human walking, a peculiar mode of animal bipedalism, is relatively energetically efficient (perhaps as much as 75% more) compared to great apes (Sockol et al. 2007) and that this is, at least in part, due to several anatomical traits. It follows, that the explanation of human bipedalism must include a component that addresses this issue.

So, in phase two of the model, a plausible ecological scenario is proposed where otherwise quadrupedal extant great apes are very predictably compelled to switch to bipedalism, and, in phase three, a body of evidence which suggests that the modern human form of bipedalism is energetically efficient compared to the bipedal gait of extant apes, which depends on a series of anatomical traits that appear to have evolved for that purpose.

The challenge is to connect these two elements into a co-ordinated, evidence-based model. One obstacle to overcome is to explain how a behaviour that relies on traits to make it efficient could have begun in the first place, before such traits had started to evolve.

7.4.4 How did overcoming an "energetic rubicon" lead to a positive feedback loop?

There appears little doubt among most experts that human postcranial anatomy "speaks of" improved bipedal efficiency, even if the degree of improvement over quadrupedal species is not great. "The unity of form and function" is a phrase often used to describe anatomy. It seems particularly apt in the way that the parts of the human body concerned with locomotion are so closely tied to their function.

Almost all authors of models of hominin bipedal origins agree on this and attempt to weave it into their story. Working backwards from anatomically modern *Homo sapiens*, this provides few difficulties. All that is needed is to conceive of some evidence-based scenario where efficient, long-distance walking might be adaptive and to postulate a feedback loop whereby this resulted in increased fitness for individuals with those traits. Most models are based on some specific variant of this.

One problem with such feedback models, as Jolly (1970) elucidated, is in explaining how they began in the first place. Some solutions assume something else "kick started" the bipedal behaviour, whilst others propose that the behaviour that drove the bipedalism was self-generated, perhaps simply through random forces.

The former idea proposes that some "rubicon" was crossed after which the feedback loop kicked in. According to this idea, some other factor was at play encouraging bipedalism before the point where energy efficiency became a factor.

The second approach argues against the need for any "rubicon" to be crossed, at least for reasons of greater parsimony. As long as there was variation in the population of those early hominids that adopted facultative bipedalism, so the argument goes, then this would be sufficient to cause the feedback loop to begin on its own.

A recent study (Sockol et al. 2007) provided evidence in support of the "no rubicon needed" argument. They found that variation in limb sizes of five chimpanzees studied correlated with variation in their recorded energy consumption whilst moving bipedally, although less efficient than humans.

However, evolution shows countless examples of traits evolving, only to be *exapted* for something completely different, later. And even if variation in population might have been sufficient for a trait to evolve on its own, it does not preclude the possibility that an earlier use of that trait could, nevertheless, have acted as a precursor to later forms and therefore helped it to evolve.

The review of models here showed that few of them offer plausible arguments for the “crossing the rubicon” kind of idea. This may indeed have been the reason for the increased popularity of models which assume that energy efficiency was a major driving force from the beginning, *and throughout,* the evolution of human bipedalism.

It is argued here, however, that wading models elegantly provide a plausible scenario for a kind of facultative bipedalism that would precede the modern human obligate (and energy efficient) form, and hence act as a means for such a “rubicon” to be crossed.

Furthermore, as will be argued next, they also provide a scenario that neatly dovetails into the energy efficiency model itself.

7.4.5 How or why did the transition from BHBK to EHEK happen?

Assuming the principle that, in evolution, many traits or behaviours are *exapted* or “co-opted” for a different use from which natural selection had originally favoured them, and assuming that bipedal wading could have acted as the former - *an ape-like, bent-hip, bent-knee (BHBK) gait,* and efficient terrestrial walking actually became the later - *a modern human, extended-hip, extended-knee (EHEK) gait,* the question arises: How could the former transition into the later? It is a question that is crucial to this particular wading hypothesis, so one that requires an answer. Let’s recapitulate on what needs to be explained here.

The model is based on the notion that, in shallow water, early human ancestors spent sufficient time wading in shallow water to move bipedally even though they had no anatomical adaptations to help them to do so efficiently.

Later, the model assumes that our more recent ancestors spent sufficient time moving on dry land on relatively flat, firm, largely vegetation-free substrates for anatomical adaptations to evolve that made such locomotion more efficient, as less knee and hip flexion is required on the swing phase, requiring less energy.

A key argument of the wading hypothesis that these two are connected through a rather elegant dovetailing of the two scenarios. Namely, it reminds that rivers provide a continuum of depths where the compulsion to move bipedally and the masking of anatomical inefficiencies gradually morph into terrestrial walking (See Fig 60) as one moves from deeper to more shallow water. It proposes this merging of scenarios, both through the continuum of depths at any given specific contemporary waterside habitat, and also temporally over evolutionary time. Perhaps this argument needs spelling out in a little more detail.

Water depth variation at a point in time

Let’s consider an hypothetical waterside habitat at a given point in time and a range of depths of water in which a putative human ancestor might have occasionally needed or desired to move through.

Let’s start with water that is quite deep and then progressively reduce that depth. In waist-chest deep water, extant species of great ape appear to be compelled to switch from quadrupedalism to bipedalism. At such depths they could theoretically choose to swim, but the evidence seems to indicate that unless the water is too deep to do so, they prefer to stand up and wade. This may be due to some inherent inability for apes to swim (Wind 1991) or simply that they judge it safer to wade. Opting for quadrupedal locomotion is not possible in such depths as the face would be submerged in water.

This tendency to bipedal wading is likely to have been true of all the ancestors of the great apes and their common ancestors with us. Apes, and therefore our earliest hominid ancestors, need no anatomical adaptations to do this other than a predisposition to upright posture which they probably inherited simply from being relatively large and arboreal. It is sufficient a predisposition that its absence precludes all other mammalian species from making this locomotor switch. Bears, for example, may adopt postural bipedalism in shallow water, momentarily, perhaps whilst looking for salmon to hunt, but when the want to move they do quadrupedally, or else they swim.

The point is that here we have a scenario, perhaps a unique one, where ape-like human ancestors would be compelled to move bipedally even though they may have almost no anatomical traits to help them to do so. This is largely because the water is deep enough to provide sufficient hydrostatic bodily support so that the hominid would be able to maintain an upright posture whilst moving with little need for any specialism for balance, such as traits that help keep the centre of mass above the midline.

Now let’s consider a shallower depth. Knee deep water is very likely to be too shallow to be able to swim but extant great apes would still have a theoretical choice of mode of locomotion in such scenarios: They could wade bipedally, or quadrupedally. However, the evidence seems to suggest (e.g. Van Lawick-Goodall 1968; Myers Thompson 2002) that even at these depths extant great apes still tend to switch to bipedalism whilst entering knee deep water, or else remain moving bipedally if moving into shallower water from deeper areas. Again, the possible reasons for this phenomenon are speculative, but it intuitively feels safer to keep the face further away from the water, particularly if the water is murky and the nature of the substrate on the bottom unknown.

Compared to waist deep water, ankle depths provide significantly less hydrostatic support, and therefore would require early hominids to exert greater effort and skill in order to balance and move bipedally. Intermediate depths between waist deep and knee deep would provide a gradient of such hydrostatic support. The deeper the water, the easier it would be to stay upright, the shallower, the more difficult.

As the depths of water becomes shallower than the knee, what little hydrostatic support there was, gradually disappears. So, in terms of substrate, moving through ankle deep water is practically the same as walking on certain non-ideal substrates on dry land. There is anecdotal evidence (Van Lawick-Goodall 1968) that even on wet ground chimpanzees are more likely to move bipedally than normal, so even here there is a greater tendency, according to this model, for bipedalism to be selected.

The argument, then, is that any hominid inhabiting a wetland habitat could, in the course of any day, be likely to need to move through a range of depths from those where the water would provide sufficient hydrostatic support as to require no effort to balance the body, to those which would practically the same as walking on dry land, but at all those depths there would be a greater likelihood for bipedalism to be adopted.

Variation in depth across time

In addition to variation in depth of water, in a given habitat, at a given point in time, the model also argues that such habitats varied in depths across time too. The evidence appears to show

(Potts 1998) that East Africa did not become drier from the Miocene to the Pleistocene in a simple, linear, way, but that its aridity repeatedly oscillated back and forth between wet and dry. In increasing tone and phase as the Pliocene progressed, albeit with a general underlying trend toward greater aridity. These cycles lasted hundreds and even thousands of years, proving enough time for whole ecosystems to change from wet rain forests, through gallery forest refugia, to relatively arid local savannah microhabitats, and then back again, repeatedly (Potts 1998). Superimposed on these broad cycles, were also seasonal climate patterns. Even today, where some East African savannah habitats are close to their driest, seasonal rainfall still occurs and often cause whole river basins to flood for months at a time (e.g. Hughes 1988).

The net result of all this wetland variability would act upon any hominids fortuitous enough to inhabit such regions. It would subject them to selection for a range of habitats from wet to dry and everything in between. Specifically, for this wading model, it would subject them to a regime of selection that encouraged more bipedalism and therefore more efficient than would otherwise be the case.

7.4.6 What changes are expected in wading hominids?

It might be worth spelling out exactly the kind of effects such selection for wading might have on such a putative group of hominids. Generally, as shown in figure 63, a hominid that regularly waded and moved through different depths of water would be subject to varying selection from different aspects of the environment. A key argument here is that many of the traits one would expect to evolve in response to such selection would considerably overlap with traits one would expect to evolve for an early hominid that began to walk on land, even if they did not include wading in their locomotor repertoire at all.

Elongation of lower limbs

Assuming a population of hominids lived in a habitat in which they regularly in waist-chest deep water, one likely adaptation would be for the lower limbs to increase in length. This is a trait seen, for example, in wading birds.

Improved weight bearing in lower back and hips

Assuming the population also regularly waded bipedally in shallower depths one would also expect traits consistent with upright posture to evolve. Specifically, the kind of weight bearing traits in the lower back and hips one would expect to find as evidence of bipedalism, generally, would also be expected to be found in hominids that regularly waded in shallow water.

Wading traits overlap walking traits

The wading model argues that populations of hominids regularly waded in a full range of depths over long periods of evolutionary time and so predicts that traits for both deeper and shallower wading would be found.

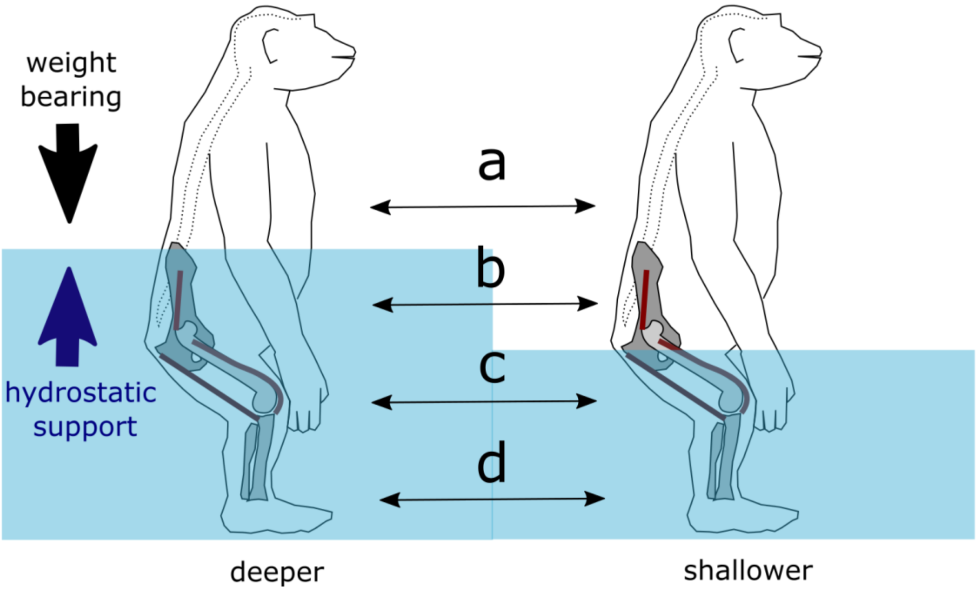


Figure 64 Weight Bearing in a Wading Environment

The key point here is that such traits would also make it more likely that such hominids would also be more likely to move bipedally on dry ground too. Having longer legs would make moving quadrupedally more difficult and having better support for upright posture in the lower back and hips would make walking on dry land easier.

In this way, the wading hypothesis proposes that increased wading in the locomotor repertoire helps nudge populations of hominids ever closer towards, and then beyond, a “rubicon” where they would not only be likely to opt for bipedal locomotion in water, but on land too. Regular wading, in a full range of depths of water, therefore, eventually would push the anatomy of hominids past a point of no return where they would be most likely to move bipedally whenever they moved on dry land.

7.4.7 What is the explanatory value of gallery forest habitats?

The “river apes” phase of the “river apes… coastal people” model, described in earlier, is a wading hypothesis of hominid bipedal origins that specifically proposes seasonally-flooded gallery forest habitats as being the key habitat involved in ‘driving’ the evolution of our bipedality. It is argued that these riparian habitats are both theoretically ideal for the purpose and are evidentially heavily implicated as being part of the paleohabitat of many putative human ancestors via the fossil record.

As explained above, habitats that vary in terms of water depth, both geographically and temporally, may be ideally suited to select for a range of traits that encourage greater bipedality in hominids that already possess a predisposition to upright posture. If that is true, it would be difficult to imagine a better habitat on the planet than seasonally flooded gallery forests as they typically pose a range of depths in close proximity to each other and are subject to great change over time, from extensively inundated flood plains to parched landscapes with little or no running water. It should be noted that even at the driest of times, the kind of seasonally flooded gallery forest habitats being envisaged for this model are ones where water is never far away, either geographically or temporally.

As described later, many of the palaeohabitats of early fossil hominids have been associated with such habitats and it is well understood that climate variability increased during the Pliocene. Undoubted traits indicative of climbing ability in these hominins is also explained by positing a gallery forest habitat.

7.4.8 How optimal for walking are dry river beds and coasts flats?

It may be contended that the inverted pendulum gait (phase three) need not have evolved in the sort of the relatively flat, firm, vegetation-free substrates proposed by this model.

However, logic and some empirical evidence appear to contradict this commonly held view.

The efficiency of the modern human inverted pendulum gait relies on the locomotion being largely due to forward momentum (the body is effectively gently falling forwards) and for the swing phase limb to be placed above the center of mass of the body for the next step with very little muscular activity. This, in turn depends on the substrate being close to ideal. It is logical that having to lift the foot above vegetation or obstacles on the ground during the swing phase, no matter how slightly, will require more muscular action than if no such obstacles existed. This inevitably would cause walking to be less energetically costly on flat, firm, vegetation-free than it would be elsewhere.

A number of studies have shown that the efficiency of walking rapidly diminishes if these conditions are not met. My own (very limited and unpublished) pilot studies showed that walking in long grass at 1 m/s was about twice as energetically costly than on a treadmill.

A major factor of the 3rd phase of the “river apes … coastal people” model is specifically that waterside habitats, such as seasonally flooded gallery forests, at times of relative aridity, and many coastal habitats are rather ideal for this purpose. They are perfectly flat – as they literally are traced by the water’s edge and continually shaped to be flat by wave action. They usually are relatively firm – as they are largely composed of wet compacted, eroded material such as sand and silt. And many are relatively vegetation free as in times of aridity the water levels will drop and at coasts few plants can survive the effect of salt water and waves.

Of course, it may be objected that many riverside habitats are dense with vegetation and many coastal habitats are rocky – neither being suitable for walking. However, it is argued that in a broad savannah-based context, such permanently vegetated riverside margins are rarely found during times of aridity and that even at rocky coasts there often exists, at low tides, narrow pathways at the water’s edge along which people can walk.

It should also be remembered that the “river apes … coastal people” model is postulating seasonally flooded gallery forest habitats as being the main driver for bipedal origins, up and until a rubicon was crossed after which time human-like bipedalism was preferred on dry land too. It is only after this point has been reached that the model proposes that coastal flats primarily drove the anatomical adaptations we see in modern humans for the efficient inverted pendulum gait. It also should be remembered that no extremes are being postulated here. It is not being suggested that early hominid waded exclusively and later hominids only ever walked by the water’s edge on beaches or dried out river beds, just that there was a shift in the degrees of these behaviours in the locomotor repertoire over time, and that a sufficient large shift in the regime of selection resulted to cause a phenotypic affect.

7.4.9 Slight selection is subject to noise, not just drift

Another potential criticism that needs to be addressed is the one relating to slight selection. One could argue that the insistence that only minimal amounts of selective pressure are needed to drive evolutionary change is speculative, not backed by good data, and fundamentally flawed in that it assumes that the only obstacle to evolutionary change is the process of evolutionary drift. It has been argued by some that it ignores “noise”, the inputs of many other, tiny effects of drift and selection.

It is argued here that slight selection should not be discounted, *a priori*, particularly when it comes to consideration of movement through water being a factor of selection. This is simply because it only takes a few moments to drown. Therefore, it should not be assumed that a great deal of time spent wading (or swimming or diving for that matter) would be needed to invoke a change in the regime of natural selection.

The evidence is not speculative, but theoretical. Anyone can demonstrate this for themselves using simple population genetics simulators. Very slight levels of selection overcome drift in even relatively small population sizes.

The idea certainly does not assume that the only obstacle to evolutionary change is drift, but is simply cognisant of the fact that, all things being equal, even very slight selection will overcome drift.

The material point here is that human bipedality *did* evolve for some selective pressure or another. Whether the regime of selection for it were strong or weak, they were no doubt sufficient to overcome drift as well as any of the well-known negative factors or “costs” associated with it. The point in emphasising slight selection is simply to remind the reader that sometimes evolution need not be driven by blatantly obvious factors. In the context of seasonally-flooded gallery forests, this model suggests a whole range of subtle advantages for regular but occasional bipedal wading in certain scenarios would be sufficient to select for traits that made a disposition to bipedalism, even on dry land, increasingly more likely.

It seems obvious to this author that whatever drove the evolution of human bipedalism, adding a component into the scenario in which our ancestors would have been compelled to move bipedally and made it easier to do so, cannot hinder the process. Adding a wading component can only help any model of hominid bipedal origins.

7.4.10 What about crocodiles?

One of the biggest criticisms of the “river apes… coastal people” model is surely on Criterion B.2, “accounts for the risk of predation.” It was rated it only 4 out of 10 in this regard the mortal danger provided by crocodiles and hippopotami are probably the greatest concern for a proponent of the wading hypothesis.

The counter-argument is predictable, however. Early hominids were still adept climbers and lived in gallery forests so it may be suggested that the “river apes” model is no worse than savannah-based ideas on this criteria. Whereas many savannah-based predators are able to climb some trees to go after their prey, the same is less likely for crocodiles and hippopotami.

Just as the adoption of smart group strategies and weapons has often been coined as an argument against savannah predators (e.g. Kortland 1980) and even as a factor in the evolution of human characteristics such as language, combative strategies could have been adopted by smart “river apes” who spent their lives in close proximity to populations of potentially dangerous crocodiles. It is interesting to speculate how long it might have taken such ancestors to learn how to steal the eggs and young of these predators and hence unwittingly reduce their danger from them in the long term.

7.5. Evaluating the River Apes… Coastal People Model

Evaluative Framework Revisited

The evaluative framework described in chapter 3 was devised in order to compare all the published models of hominin bipedal origins and begin to answer the question “which ones are the best, and why?”

Simultaneously, the “River Apes… Coastal People” was devised in order to provide a model of hominin bipedal origins specifically, and human evolution generally, which was at least as good, if not better than those previously published.

It should be no surprise, therefore, that this was achieved. In the opinion of the author, this is the not only the best waterside hypothesis of human evolution, but the strongest, most evidence-based hypothesis of hominin bipedal origins.

As described in section 3.5, even previously published wading models were already assessed as amongst the best. Weaknesses were nevertheless identified, which this thesis attempted to address with an improved Wading Hypothesis.

Criticisms of the evaluative framework, my assessments and the “River Apes … Coastal” model are, of course, encouraged and welcomed. The on-line Bipedal Model Evaluator tool (www.tinyurl.com/BipedalModels) was designed in order than anyone can read my assessments in detail and try their own.

Here, the “River Apes… Coastal People” model is compared and contrasted with previously published wading models using the evaluative framework so that the reader can more clearly assess its strengths and weaknesses.

Hardy/Morgan’s “Coastal Foraging” Model

The first discussion in the literature of the idea that wading bipedally in shallow water may have contributed to the origin of hominin bipedality is probably attributable to Alister Hardy (1960) although some may argued that distinction be attributed to Westenhöfer (1942).

The original idea, followed up and promoted by Morgan (1972, 1982, 1993) largely suggests a coastal environment for the earliest bipeds and this is where, it is argued, it is at its weakest as there is very little evidence for coastal habitation of early hominin bipeds. Conversely, since Hardy article was published, a growing body of evidence has accumulated placing the earliest hominin bipeds in land, albeit in wetland, lakeside and riverine habitats.

Morgan, more recently, (e.g. 1997) increasingly considered inland wetland habitats too and must be given full credit for taking Hardy’s original idea and shaping it into a significant wading hypothesis of bipedal origins. Where Morgan can be criticised is in her reluctance to consider the growing evidence that hominin bipedalism came very early, perhaps even pre-dating the *Pan*/*Homo* split. She was determined, to the end, to argue that bipedalism was a key component in causing the divergence between humans and the other apes.

Verhaegen et al.'s (2002) "Aquarboreal" Model

Marc Verhaegen, in contrast, has always been remarkably cognisant of the possibility that hominin bipedalism may have preceded the split of *Pan* and *Homo* and has argued that the earliest forms of bipedalism may have been wading-climbing or "aquarboreal" in form (Verhaegen et al 2002).

The model described here therefore, follows Verhaegen et al., not Morgan, on this early origin aspect as, since the discovery of *Sahelanthropus* (Brunet et al. 2002), it appears to fit the fossil evidence better.

Where the "aquarboreal" model appears weakest to this author, however, is how it explains this early wading-climbing form of bipedalism evolved into the modern human form. Verhaegen et al. deny the evidence that anatomically modern humans are adapted to efficient bipedal locomotion. Verhaegen (personal correspondence 2012) has stated that *Homo erectus* "was almost certainly not adapted to bipedalism." Instead, the argument is put forward that "linear build" as an adaptation to simming and (largely) diving was the essential precursor needed for human bipedalism.

It frankly seems grotesque to this author that horizontal motion in an effectively weightless medium could be invoked as a possible explanation for modern human bipedalism when so much unequivocal evidence for upright weight-bearing exists not only in modern humans but in the fossil record of hominins.

This bizarre lack of compatibility with orthodox thinking on human evolution surely severely weakens the "aquarboreal" model.

Ellis' (1990) "Wetland foraging" Model

Ellis' ideas on human evolution are among the most sensible ideas in the literature, in the opinion of this author. Ellis applied the ideas of Hardy and Morgan and applied them to a plausible wetland habitat in a paleohabitat scenario set in the early Miocene in the context of early Red Sea rifting.

Much of the first two phases of the "River Apes… Coastal People" model are based on Eliis' ideas but, obviously, in the course of developing the model, various improvements have been made, and the results of scientific investigations applied. It is therefore argued that this model supercedes Ellis'.

Niemitz's (2002) "Amphibische Generalistentheorie"

Niemitz's (2002, 2007, 2010) "Amphibische Generalistentheorie" is another strong wading hypothesis of hominin bipedal origins which shares a great deal in common with the "River Apes… Coastal People" model.

The major difference between Niemitz's ideas and the ones presented here appear to be mainly concerning the relationship of wading to the so-called "aquatic ape hypothesis". Niemitz does not credit the wading hypothesis to Morgan and insists on a clear demarcation between wading ideas of hominin bipedal origins and other "more aquatic" ideas espoused by her.

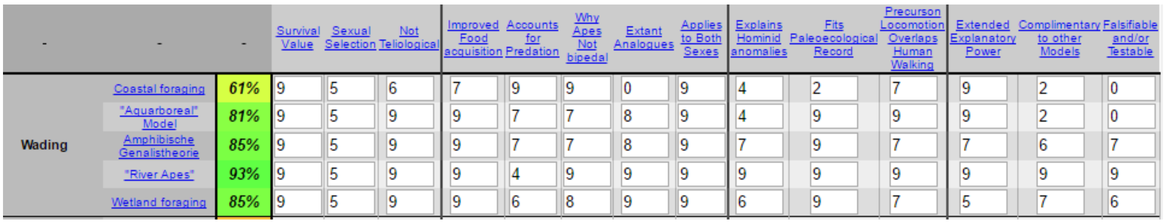
To this author, it is illogical to argue that perhaps the most significant feature of the human condition (our bipedality) evolved as a response to wading through water whilst at the same time denying that our ancestors ever swam and dived to any significant extent. Niemitz offers little to justify this demarcation (see section 4.1.1.2) and seems to hold an exaggerated view of waterside hypotheses of human evolution.

Summary of Wading Models

The subjectivity of this kind of assessment is obvious but it is argued that critically assessing written work by teasing out individual components that can be evaluated in this way has been the currency of academic progress for centuries and so it cannot be argued that the concept of applying a "marking rubric" to assess a set of complex ideas is radically new.

My assessments, summarised below, were actually done in a very self-critical way, especially in criterion B.2 "predator avoidance".

I feel confident, therefore, in offering the "river apes… coastal people" model as the best current model of hominin bipedal origins as well as the most evidence-based waterside model of human evolution.



-	-	-	Survival Value	Sexual Selection	Not Teliological	Improved Food acquisition	Accounts for Predation	Why Apes Not bipedal	Extant Analogues	Applies to Both Sexes	Explains Hominid anomalies	Fits Paleoecological Record	Precurson Locomotion Overlaps Human Walking	Extended Explanatory Power	Complimentary to other Models	Falsifiable and/or Testable
Wading	Coastal foraging	*61%*	9	5	6	7	9	9	0	9	4	2	7	9	2	0
	"Aquarboreal" Model	*81%*	9	5	9	9	7	7	8	9	4	9	9	9	2	0
	Amphibische Genalistheorie	*85%*	9	5	9	9	7	7	8	9	7	9	7	7	6	7
	"River Apes"	*93%*	9	5	9	9	4	9	9	9	9	9	9	9	9	9
	Wetland foraging	*85%*	9	5	9	9	6	8	9	9	6	9	7	5	7	6

Figure 65 Wading Model Evaluation

Screen shot from www.tinyurl.com/BipedalModels shows "River Apes... Coastal People" and Ellis' "Wetland Apes" models ranked highest.

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7.6. Future Potential Research

It is the honest, considered opinion of this author that wading hypotheses of hominin bipedal origins are among the strongest yet published. 66 years after Alister Hardy first published his "More Aquatic" ideas, I think it can be fairly stated that this wading hypothesis is now more than "only a speculation." But as Hardy concluded his New Scientist article in 1960, this is an hypothesis that remains "to be discussed and tested against further lines of evidence." Hardy (1960 p 645.) Such ideas really are only useful if they stimulate fresh inquiries which may bring us nearer the truth.

There is clearly a huge amount of science that remains to be done to test this hypothesis properly. In this section some of the falsifiable tests that could be done are outlined, firstly, pertaining to the wading hypothesis itself, and then other waterside hypotheses of human evolution.

7.6.1 Research Pertaining to the Wading Hypothesis

Falsifiable Tests

Although no theory of evolution is fully testable in the Popperian sense, some scientific rigour may be applied to any tests or prediction that they may make.

The wading hypothesis of hominin bipedal origins makes several such predictions which are directly testable. They are briefly outlined here, after which the current existing evidence for each is outlined and further research proposed to improve our understanding.

Extant ape bipedalism in waist deep water

Throughout this thesis, it has been regularly claimed that, in waist deep water, extant apes will switch from quadrupedalism to bipedalism. There, they will move, not just pose, bipedally, without the support of their upper limbs and continue to do so as long as the conditions prevail. There is excellent good anecdotal evidence for this and the few, and limited, studies that have been done unquestionably support it, but it must be conceded that more science needs to be done in this area to support the claim.

Anecdotal evidence

Great apes have long been considered so fearful of water that moats are often used to contain them in captivity (Kortlandt 1975 p 648) but of course, these are moats with high walls. More recently, evidence (mainly film or photographic) has accumulated showing that there are scenarios where all members of the Hominoidea are prepared to enter shallow water and move through it. This section briefly reviews the anecdotal evidence for how they do on these occasions.

Orang-utan (*Pongo*)

A growing amount of photographic and other evidence suggests that orang-utans wade bipedally when they find themselves in shallow water. Galdikas (1980 p 835) wrote that “Orang-utans have surprisingly little fear of water.” The article was accompanied by a photograph of an infant-carrying female wading bipedally in a swamp. Ellis (1990 p 56) provides photographic evidence of an orang-utan wading bipedally in a moat at Singapore zoo. Sommer & Amman (1998) use a photograph of a bipedally wading orang-utan on the front cover of their book. Ammann (personal comment) reported the photo was taken “at Tanjung Puting crossing the river and using the stick to gauge depth or give him a better hold should it get too deep. That was my assessment.” Galdikas (1999 p 72-80) also includes a sequence of photographs of an orang-utan wading through a swamp.

Gorilla (*Gorilla*)

Doran & McNeilage (1998 p 121) review the ecology and behaviour of sub-species of gorilla, including the least studied until then, the lowland gorillas. They report “it was long thought that gorillas avoided water” but “recent work has demonstrated that western lowland gorillas routinely wade into swamps in forest clearings to feed on aquatic herbs.” Studies at Mbeli Bai, at the Nouable-Ndoki National Park of “spectacular splash displays” (Parnell 2001 p 294) in male silver backs have been particularly interesting. Parnell was working as a scientific consultant for a film crew making documentaries about western lowland gorillas (*Gorilla gorilla gorilla*). Parnell 2001 (personal communication) noted thirteen incidents of bipedal wading in several weeks of observation. He noted that “when crossing any expanse of open water too wide to bridge by reaching and clinging to swamp vegetation and dragging oneself cross, in water over about 2 feet deep, most adult gorillas waded bipedally. Water up to approximately 100-150cm deep has been crossed in this way.”

Chimpanzee (*Pan troglodytes*)

In addition to early anecdotal evidence of chimpanzee bipedalism on wet and muddy ground (Nishida 1980 p 201; Van Lawick-Goodall, 1968) there has recently emerged some significant photographic footage of chimpanzees wading bipedally in fairly deep (chest high) water. Research at a chimpanzee sanctuary in the Conkouati reserve lagoon (See Tutin et al. 2001) revealed more anecdotal evidence. Chimpanzees there are placed on three islands in a lagoon where they live semi-natural lives. Because there is not enough vegetation on the islands to sustain them, every day fresh food supplies are brought to them by boat. Karlovski (1996), describes what happens when the boat comes in "The biggest group of chimpanzees lives on Grand Ile which is almost 1 km long… Generally the whole group runs into the water, when the boat carrying the caretakers and the food arrives on the island - holding their arms high to keep as dry as possible. Chimpanzees usually go into water only in emergencies, but the food is so tempting that they lose their fear of water."

Perhaps the most dramatic and graphical anecdotal evidence for chimpanzees bipedalism whilst wading in shallow water was shown in the BBC Documentary "Life of Mammals" in the episode about Primates called "Food for Thought". David Attenborough, wading up to his hips in galoshes, spoke as members of the group of Conkouati chimpanzees described above waded behind him in the water.

"Suddenly an image from our remote past comes vividly to life, the time when our distant ancestors, in order to keep up with the changing environment, had to wade and keep their heads above water in order to find food; that crucial moment when our far distant ancestors took a step away from being apes and a step towards humanity."

Bonobos (*Pan paniscus*)

Bonobos have generally been studied less than the other great apes. However there does seem to be evidence that they are less fearful of water and show a greater tendency to wade than their chimpanzee cousins. A study of bonobos in the Congo (Uehara 1976) reported them to feed on aquatic plants for at least two consecutive months. In doing so, they immersed themselves in water up to the shoulders. De Waal (1996 p 185) reports various anecdotal accounts that bonobos had entered streams wading bipedally and that "…two female bonobos [had been seen] walking upstream, in the water. They snatched handfuls of floating dead leaves, picking out things to eat." Later he added that it was observed that numerous tracks along streambeds lack knuckle prints indicating that bonobos had avoided getting their hands wet by assuming bipedal postures when crossing streams.

Myers Thompson (2002 p 67) reported possibly the highest levels of bipedal locomotion observed in the wild. "Bonobos foraging in the pools exhibited terrestrial (aquatic) bipedal locomotion in 24.14% of encounters." Apparently aware of how controversial some anthropologists might find reporting such findings, she argued "that the propensity for bonobos to transition into bipedal locomotion during aquatic foraging as determined by this initial study, requires further examination and more extensive observation time" and also that "caution must be exercised when drawing any inferences from these findings."

Studies Done

Very little research effort has been made in this area to date. The only known study which has attempted to gather new empirical data specifically pertaining to extant apes wading locomotion in the context of hominin bipedal origins is the pilot study done by this author (Kuliukas 2002.)

The 2002 study was very limited in its scope as it was only a small part of a master's thesis 3rd term project. It basically involved observations of captive bonobos over three days in April 2001, at Planckendael zoo, in Belgium. The study sought to record how bonobos moved when they were in water. A focal study of bonobos found only 38 seconds of their time was spent in water, confirming that wading in shallow water was very rare in these captive bonobos. These rare incidents usually consisted of occasional forages into the moat that surrounds their enclosure in order to reclaim food items thrown to them (against all the instructions of the zoo keepers!)

Despite the rarity of these incidents, the study set out to video record these incidents for frame by frame analysis later. It was found that when in water their bipedality was remarkably high. About 90% of their time in fully water was spent in a bipedal posture, compared to approximately 2% on dry land. An interview with a field researcher who had been working there for two months suggested that these observations were quite usual.

There are several weaknesses in this study which should be addressed in any future research program:

The length of this pilot study was far too short. Kevin Hunt collected over 700 hours of chimpanzee behaviour for his landmark paper (Hunt 1994). A greatly extended observation time would give the results much more significance.

The bonobos were studied in captivity. There is always the possibility, particularly with intelligent animals such as our nearest relatives, that some of their bipedal behaviour is due to "aping" human visitors. Also the enclosure and its surrounding moat are not particularly representative of the natural world and having to go into shallow water to collect food being thrown at them is certainly an unusual phenomenon.

Only bonobos were studied. For this prediction of the wading hypothesis to be tested properly, all four great ape species should be studied.

Proposed research

In order to properly test this prediction of the wading hypothesis, ideally, extended field studies should be carried out on all four species of great ape in their natural habitat.

Locations

The chimpanzees of Conkouati, although not in a totally natural environment, would at least provide ample opportunities to observe movement in the water. Chimps have rarely been seen moving in the water elsewhere. The field site of Lomako in the Congo, where Myers Thompson studied bonobos, would also appear to be an ideal location, where wild bonobos have been reported to occasionally move through water. The Mbeli Bei location, where Parnell et al. studied western lowland gorillas, would appear to be an ideal spot to gather wading data on gorillas. And Tanjung Puting national park in Borneo appears to be a good candidate for conducting a similar study of *Pongo pygmaeus*.

Study methods and objectives

The pilot study outlined earlier would form the basis of the data collection. The study objective would be to video record as much locomotion as possible that occurred in water to determine how much of it was bipedal, how much was supported with forelimbs and to determine the main reason for such locomotion. This would be contrasted with similar observations on land and in trees to test the hypothesis that wading induces bipedalism in great apes like no other substrate.

For each incidence of movement through water, the depth of the water would also be determined and expressed as a ratio of hind limb and/or forelimb length so that any relation between the chosen mode of locomotion and the depth might be determined.

Shallow water and energy efficiency

Similarly, the experiments conducted on the energy efficiency of wading, reported here in chapter 5, could also be improved upon and augmented.

Proposed research

There were several weaknesses of the Kuliukas et al. (2009) paper (and hence chapter 5) that could be addressed:

The study could be extended to include more natural habitats. The floor of a swimming pool is very unnatural and it would be interesting to repeat this study in lakes, rivers and in shallow coastal areas.

No attempt was made to change the gait being used to wade other by varying the degree of knee and hip extension. It would be interesting to repeat the experiments using different types of wading gait, for example a twisting side-to-side gait and a sideways gait.

EMG recordings could be taken to find out exactly which muscles are involved in such locomotion, compared to the standard forward-only mode used in the study. Natural variation of hip shape (e.g. A-P versus lateral diameter) in volunteers doing the wading could be recorded to see if there was any correlation between hip shape and the relative efficiency of the type of gait.

The natural variation in volunteers' hip shape (especially the ratio of A-P to lateral diameters) could be measured to see if there was any correlation between the energetics of wading particular gaits. The hypothesis would predict that people with a more platypelloid shaped pelvis should be better suited to lateral movements in water. Perhaps natural differences between the sexes could be observed here. This effect might even be artificially exaggerated to represent a more australopithecine-like (platypelloid) profile in such a study.

Australopithecine anatomy consistent with wading

The studies done into the morphology of the australopithecine, reported in chapter 7 could, similarly, be improved upon.

Proposed research

In order to better test whether the australopithecine (and/or other early hominins) post cranial anatomy had adaptations to wading, the following research program is proposed.

The study reported here should be followed up and greatly enhanced. Logical morphs of fully articulated pelves could be derived from the data reported here, as well as significant parts of the postcranial anatomy, including lower vertebrae, femora, tibiae and bones of the foot. These could be used to construct realistic biomechanical models in various established modelling software programs (e.g. SIMM). By taking EMG readings of humans wading in water with different gaits, the muscle profiles used in various gaits could be reconstructed in australopithecine models to test whether the shape of their hip gave any biomechanical advantage to wading in various gaits. Using fluid mechanics modelling software (e.g. FLUENT) 3D models of australopithecines could be tested for drag coefficients to see if their platypelloid pelves may be indicative of some adaptation for drag reduction in water whilst wading with certain gaits.

The anatomy of the hominid knee and foot, completely ignored here, could also be investigated in the context of wading generally, and a side-to-side, twisting gait in particular.

Some research questions might be…

Is the australopithecine foot likely to be adaptive to wading? Is its relatively large size (Foot: Stature ratio of 0.162 according to Jungers 2005 p 230) potentially helpful for stability and to grip on muddy substrata? Are there any differences in the orientation of the tarsals and metatarsals which indicate some adaptation to lateral, or twisting, torque?

Does the australopithecine knee joint have any features which indicate an improved robustness or biomechanical advantage for abductive movement, twisting and rotation?

Paleohabitats conducive to regular wading

Clearly, if the wading hypothesis of hominin bipedal origins was valid, one would predict that the paleohabitats associated with the earliest fossil evidence for bipedality in hominins would be conducive to regular wading.

If a major part of their locomotor repertoire was both climbing and wading, swampy forested habitats should be strongly associated with them.

Anecdotal evidence

A well understood fact of palaeontology is that the most common mode of fossilisation is in depositional substrates. These are often formed by the effect of silting in waterside habitats, such as margins between rivers and lakes. Rapid silting can bury dead animals and thus protect them from scavengers and erosion and allow fossilisation to take place. Other modes of fossilisation are possible, of course, that have nothing to do with water, such as burial in volcanic ash.

The fact that most fossils are found in waterside, depositional substrates is known as “taphonomic bias” and clearly a difficulty arises to us here: Just because a large number of fossils are found by the water’s edge, it does not mean that it is where they lived. Equally, however, it cannot be used as an argument to suggest that they did not live there.

This must be borne in mind as the following review of the palaeohabitats of early hominin bipeds is presented.

Review of the palaeohabitats of early hominins

Review of the palaeohabitats of early bipedal hominins. (See Kuliukas 2001) for more discussion.

Species	Site	Notes	Age (Ma.)
Sahelanthropus tchadensis	Toros-Menalla, Chad	"The diversity of aquatic and amphibious forms clearly demonstrates the presence of aquatic environments. … Moreover, there is a great abundance of taxa related to amphibious and bank habitats, particularly the well-preserved anthracotheriids and hippopotamids (including some complete skeletons), otters, trionychid turtles and the snake Python cf. P. sebae. The liana-like character of the papilionoid plants from TM 266 is compatible with a gallery forest bordering a lake." Vignaud et al (2003 p 155.)	7.0 Ma
Orrorin tugenensis	Tugen Hills (Lukeino Formation)	"fluvial and shallow lacustrine deposits" Pickford & Senut (2001 p 145) "open woodland" or "denser strands of trees in the vicinity possibly fringing the lake margin and streams that drained into the lake" Pickford & Senut (2001 p 149)	5.6 – 6.3
Ardipithecus ramidus	Middle Awash (Aramis)	Lacustrine silts "Relatively Wooded" Klein (1999 p 185), Wooded Louchart et al. (2009) "these early hominins inhabited riparian environments, likely taking the advantage of water-fed ecosystems developed in a narrow forest corridor bordered by more open woody grasslands, along the banks of palaeorivers" Gani & Gani (2011 p 3)	4.4
	Lothagam, Baringo &Tabarin	*"Lacustrine (lake) sediments and fluvial (river) deposits" Klein (1999 p 173)*	*5.0 – 5.6*
A. r. kadabba		"Relatively wet and wooded environments" (Haile-Selassie 2002)	5.2 – 5.8
Australopithecus anamensis	East Turkana Kanapoi & Allia Bay (Moiti Tuff)	Kanapoi & Allia Bay (Moiti Tuff) Fluvial unit overlain by lacustrine deposits. Fauna suggests: Open woodland or bushland. Klein (1999 p 173)	3.9
Australopithecus afarensis	Hadar (Denen Dora	AL 288, AL 333 Sediments accumulated from streams in a basin periodically flooded by a lake Klein (1999 p 182). "Lakeshore or river floodplain." Leakey et al. (2001 p 439) "Evidence of lake with marshes in the early part of this member but this changes to flood plains and deltas later." "Other reconstructions of habitats for Hadar suggest woodland to treeless savannah." Reed (1997 p 309)	3.2 – 3.18
	Hadar (Sidi Hakoma)	Al 417 "medium to open density woodland" or "riparian" Reed (1997 p 308)	3.4 – 3.2
	Middle Awash (Belohd elie) Maka	Less wooded than aramis	3.8
	Laetoli	Eolian (wind-driven) and air-fall volcanic tuffs. "not located near a water source; no aquatic taxa nor terrestrial mammals indicative of swamp or grassy wetlands." Leakey et al. (2001 p 439) Reed (1997 p 307) "closed to medium density woodland"	3.84 – 3.46
	Feje	Fluviolacustrine (river/lake) deposits	4.1
	Omo (Usno)	Fluvial unit overlain by lacustrine deposits. "Woodland riverine habitat" "there were probably bushland and thicket areas." Reed (1997 p 310)	3.32 – 2.68
	Omo (Shungura B)	"deposits were formed from a perennial river system with occasional riverine flooding which created flood plains." Reed (1997 p 310) "mostly closed woodland with riverine forest and edaphic grasslands." "Other habitat reconstructions include a riverine forest and… a wooded savannah and forest." Reed (1997 p 310)	3.36 – 2.8
	Koobi Fora (Tulu Bor)	Stream sediments overlain by lacustrine deposits. Vulcanism and tectonic movement determined the alternation between lake and river. Klein (1999 p 174) "Scrub woodland region with a flooding river. Wetlands were probably extensive." Reed (1997 p 309)	3.32 - 2.68
	West Turkana (Lower Lomekwi)	Fluvial unit overlain by lacustrine deposits. "Lakeshore or river floodplain." Leakey et al. (2001 p 439)	3.3 – 3.2
Kenyanthropus platyops	West Turkana (Kataboi)	Fluvial unit overlain by lacustrine deposits. Leakey et al. (2001 p 439) "Lakeshore or river floodplain. Relatively well watered and vegetated" and Leakey et al. (2001 p 440) "more vegetated and wetter than Hadar"	3.5 – 3.3

Table 40 Summary of early hominin paleohabitat

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

Proposed research

Finding key fossils is not something that can be planned and the locations where hominin fossils have been searched for to date have tended to be a combination of luck – palaeontologists go back to where fossils have been found previously, and fitting in with the current (largely savannah-based) paradigm – so, east of the rift valley.

This test would nevertheless predict that the earliest dated hominin fossils should be found in paleohabitats conducive to regular, significant wading.

Optimal substrates for a striding gait.

Most authorities would argue, as does this thesis, that modern human anatomy speaks rather clearly of an adaptation to a remarkably efficient form of fully terrestrial bipedalism.

However it seems clear that this efficiency is rather dependent on a specific type of substrate. It is no coincidence that humans have created for themselves an environment filled with pavements, paths, roads and lawns etc., all that are flat, firm and vegetation-free.

A further prediction of this wading hypothesis of bipedal origins, then, is that the scenarios in the natural world where one is most likely to find such optimal places for walking are those right be the water's edge, for example, dried out river beds and the very edge of the water at lakesides or on beaches. It also should be true that the energy efficiency of bipedalism is better on such naturally occurring substrates than elsewhere.

Anecdotal evidence

Humans have built for themselves an environment conducive to facilitating walking. Everywhere where humans might walk, we have laid down pavements, carpets and carefully mown lawns. This is not surprising when one considers the biomechanics of the striding gait. It is simply quicker, safer and easier not to have to keep stepping over things or even to have to keep adjusting one's gait to allow for changes in the floor orientation etc.

Studies done

Various studies (Zarrugh et al. 1974; Pandolph et al. 1976; Zamparo et al. 1992) have measured the cost of walking on different substrates. They found that on substrates that were not ideal, such as soft sand, snow, mud or on inclines, the cost of walking rose significantly (e.g. approximately 80% higher on sand).

A very limited (N = 1) short, unpublished, pilot study was conducted by the author in 2004 to investigate the cost of walking on various substrates. It found that even walking in long grass significantly added to the energetic cost of walking, as compared to a treadmill or perfectly flat, firm, vegetation-free substrates such as pavement and carpets.

Proposed research

That pilot study could easily be extended to test the 3rd phase of the “river apes… coastal people” wading hypotheses by carefully measuring the energy efficiency of striding bipedalism in various, naturally occurring habitats, such as open grassland, woodland, dried out river beds and sandy beaches by the water’s edge, with a large cohort of volunteers. Speed and gait could also be varied.

7.6.2 Testing Other Waterside Hypotheses

It is easy to speculate about human evolution, as it is to think up and write down hypotheses explaining various human traits. Much more challenging, and important, is to do the science that might test them. It is argued here that at least a start has been made by defining and beginning the testing of the wading hypothesis but clearly, to support such a broad reaching waterside hypothesis of human evolution as the River Apes… Coastal People model, a huge amount of science still needs to be done.

Some potentially fruitful avenues of research are now offered based on the major topics covered in Elaine Morgan's books (Morgan 1982, 1997).

The human body hair pattern

The subject of the peculiar (among Primates) human body hair pattern has gained some attention in a number of scientific publications in recent years.

At the moment it appears *de rigeur* to see human nakedness largely as a function of sweat cooling, often specifically in the context of endurance running. Daniel Lieberman's idea is based upon the observation that humans are not only efficient at long distance walking but are also pretty adept and "endurance running" compared to many mammals. He cites examples of African bushmen running down antelopes to the point of exhaustion as evidence for this.

There are some obvious problems with this idea, most notably the one of increased risk of predation. The notion seems to be based on the concept, first espoused by Wheeler (1984), that the big predators of the savannah are not likely to go hunting during the hottest hours of the day but prefer to snooze under the shade of trees. We might not be very fast, but thanks to sweat cooling, we can run for miles, it is argued. Not much thought seems to have been given to what was supposed to happen when the antelope was successfully slayed and dragged back to camp. It is hard to imagine that a pride of lions would rather continue their mid-day sojourn than show some interest in a convenient carcass being dragged across the savannah in front of their eyes. And what about the sweat cooling this idea relies on? Without the invention of handy water carriers, how exactly is it proposed that these brave men (surely young women carrying infants or children would not be doing this) would replenish their ever growing thirst? The point must be made that the best possible place for the evolution of a thermoregulatory strategy based on sweating copious amounts of water has to be in habitats where replenishing water loss can be taken for granted.

Other ideas have been published to explain the peculiar human hair pattern, such as parasite reduction and sexual selection (Pagel and Bodmer 2003).

It is hard to imagine why humans, uniquely among the great apes, could have needed such a completely different strategy to avoid parasites than chimpanzees, or why most humans began to find denuded skin more sexually appealing than bodies covered with hair, but once more, such ideas are hardly incompatible with waterside models.

Sweat cooling, parasite detection and sexual selection are complementary, not contradictory, to waterside models of human evolution which, in addition have a very compelling extra argument that it can be argued, may explain the human hair pattern rather elegantly.

The drag reduction hypothesis.

The hypothesis proposes that the major adaptive cause of the evolution of the human body hair pattern is drag reduction.

It assumes:

- The base human body hair pattern is that of a pre-adolescent child, so as to preclude the undoubted phenomenon of body hair for sexual signalling which is also the source of much variation between human populations.
- That the primary mode of locomotion in water was swimming at the surface, often with face down (e.g. looking in coastal shallows for shellfish).
- The part of the body most likely to be covered with hair (apart from the eyebrows) is that which is most likely to be above the surface of the water. The part least to be covered with hair is that most likely to be subject to drag forces in water.

Exceptions to this could also be explained by the movement of water across the skin. Eyebrows help to deflect water from entering the eyes when the head is raised out of the water. Body hairs on limbs (for example the forearm) are patterned and orientated in a way to aid propulsion through water.

Testing the hypothesis

A series of experiments have already been conducted, by exercise physiologists, on elite swimmers to show that there are some interesting correlations between human body hair and drag whilst swimming.

Sharp et al. (1988) and Sharp & Costil (1989) showed there was a significant gain in swimming speed when male swimmers shaved off body hair. Most notably, they found a significant reduction (approximately 9%) in deceleration in passive push off trials where the subjects were told merely to push of from the side of the pool and glide, rather than swim. This would appear to be best explained by a reduction in drag. However, other studies by a German group (Krüger et al. 2000) reported somewhat contradictory findings. They found some increase in speed from shaving off body hair in swimmers but concluded that as both males and females exhibited similar levels of speed gain, the reason was not likely to be drag reduction from hair loss but, perhaps, a kind of ‘placebo’ effect from the sensation of having shaved one’s skin.

Clearly neither of these studies adequately tests the hypothesis. Neither study attempt to quantify the amount of body hair removed or to consider the possibility that removing body hair from some parts of the body (e.g. the forearm) might actually hinder swimming speeds. Neither study specifically looked at variation within humans in this regard, and the Krüger et al. study only considered speed and did no passive push off trials.

What might shed more light on this could be a series of experiments along the following lines:

- Volunteers selected with a wide range of degree body hair. Ideally, very hairy male volunteers should be sought, as well relatively denuded children.
- A series of passive push off trials would be conducted where the volunteer pushes off from the side of the pool and then stays motionless to record deceleration in water.
- A series of trials should be done where speed and energy consumption are recorded for different swimming strokes – e.g. breast stroke and front crawl.
- The volunteers then undergo body hair shaving in a variety of ways, some full, some partial. Of particular interest would be the effect of specifically shaving, or not, the hairs

on the forelimbs and lower leg. Each time, an estimate of the number, average length and mass of body hair removed would be recorded.

- The trails would be repeated immediately after shaving and again, at regular intervals as body hair regrew.

The hypothesis would predict that passive push off deceleration should reduce proportionately to the amount of body hair removed, when scaled with body size.

It would further predict that some swimming strokes benefit from certain pattern of body hair, for example on the forearm.

Dip-sweat cooling hypothesis

Another body-hair related waterside hypothesis is the "dip-sweat" cooling hypothesis. As discussed earlier this is often seen as a contradictory idea contra to the so-called "aquatic ape hypothesis" and indeed, if one is postulating mermaid-like convergences with manatees, it is absolutely contradictory.

Of course, no such thing is being postulated here. The idea, remember is that human ancestors lived in waterside habitats more than chimp ancestors and waded, swam, dived and procured food from such habitats more than they did and as a result of some (perhaps only slight) selection from such behaviour, our remarkable phenotypic divergence can be explained.

Here, sweat cooling is deliberately being claimed as a waterside hypothesis as it rather blatantly depends on very dependable sources of drinking water to replenish that lost through evaporative sweat cooling.

The "dip sweat" cooling hypothesis.

The hypothesis proposes that the major adaptive cause of the evolution of human sweat cooling is as an adjunct (or proxy) to going for a dip.

It assumes:

- The most efficient and rapid way for a human to cool down is simply to jump in water and cool down.
- When coming out of water again, the wet skin provides a mechanism of evaporative cooling for a length of time that is consistent with the onset of sweating.
- To replenish water lost by such sweating, an equal amount of fresh (or very slightly brackish) water needs to be regularly and reliably consumed.

Testing the hypothesis

Several predictions of this hypothesis could be scientifically tested.

Namely:

a) The amount of body heat loss resulting from evaporative sweat cooling is small compared to that resulting from immersion in water.

b) The wetting of skin with water resulting from such immersion would still provide greater thermoregulatory benefit than that resulting from sweat cooling.

c) The onset of the sweat cooling response approximates to the time it takes for skin made wet from immersion in water to become dry.

infant adiposity for floatation hypothesis

One of the most important early observations behind the original “aquatic ape hypothesis” of Alister Hardy was that of Wood Jones, who commented that the subcutaneous fat layer on human beings was unlike most mammals, where the skin tends to peel away during a dissection, leaving the fat next to the viscera. When Hardy read that, he had his ‘eureka’ moment as he was experienced in dissecting aquatic mammals where he had observed a similar phenomenon.

Much has been written about this subject and several critics have pointed out problems with the fundamental idea it pertains to – that the subcutaneous fat layer may be indicative of a convergence with aquatic mammals and may have served the similar role of thermoregulation in water in the past.

Suffice it to say that they key objection by one of the chief critics, Caroline Pond, (Pond 1991) is that the distribution of body fat in humans and apes is not all that different and is quite dissimilar to that of true aquatic mammals.

The counter argument to this has been well rehearsed here by now. If humans were never as aquatic as Sirenia and the like, one should not expect any convergent evolution, in terms of our body fat, with them. If the argument is simply that human populations lived in waterside habitats more than chimpanzee habitats and were exposed to a higher risk of drowning than they did, what would we expect then?

Pond makes great play on the idea that humans and chimpanzees have a similar distribution of subcutaneous fat and suggests that the only difference of note, between men and women, may be explained by sexual selection but, oddly, she ignores the even bigger difference – between human and chimpanzee infants in this regard – something that cannot possibly be explained in that way.

The infant adiposity for floatation hypothesis.

The hypothesis proposes that the major adaptive cause of the evolution of infant adiposity is as a buoyancy aid to help parents more successfully enact rescues in near-drowning situations.

It assumes:

- A major inherited, not environmental, difference between humans and chimpanzees is that human infants develop significantly higher levels (about 35% compared to around 5%) of body fat before birth and for the first 6-9 months afterwards.
- As fat floats, increased adiposity will make infants more likely to float. Chimpanzee infants are more likely to sink being less fat.
- The distribution of infant fat is consistent with helping the baby float face up. Fat pads on cheeks, wrists and knees (compared to relatively thin subcutaneous fat layers on the back, for example) make it easier for the infant to twist to a face up position and make that orientation more stable.

Testing the hypothesis

The above assumptions all need to be tested experimentally. The hypothesis, obviously, would predict that they would all be supported.

Clearly to test such an hypothesis would pose serious ethical problems but there are likely to be a number of entirely ethical avenues of research which could test this hypothesis to a degree.

CT scans of human and chimpanzee infants can be carefully compared. CT scans produce a vast array of “voxels” from which high definition density estimates can be accurately predicted. 3D modelling of such data could be generated and tested.

Evidence of near-drowning incidents could be collated and analysed to see if there is any correlation between adiposity and the likelihood of drowning.

Voluntary breath control (speech pre-requisite) swimming adaptation hypothesis

Probably the most consequential difference between human beings and our chimpanzee cousins is our ability to speak. Chimpanzees and their close cousins, the bonobos, have been successfully trained to learn a remarkably complex vocabulary of symbolic language through images and sounds, indicating that their brains, like ours, are capable of deciphering complex patterns into quite abstract meanings. Remarkably little progress has been made, however, in getting them to speak back.

It would appear that there is a fundamental physical impediment that prevents great apes from speaking to us and it seems rather logical that this could have its source in basic breath control. Clearly, breathing control and speech must have co-evolved to some degree but these feedback loop “solutions” do beg a simple question: What could have started the loop in the first place? Waterside hypotheses are clearly useful here because they posit a rather obvious early need for fine breath control, long before speech was needed: Again, for swimming and diving.

Every time one swims across a stretch of water, one is making many tiny conscious and subconscious decisions about breathing that are obviously critical to life. The timing of every single breath is clearly of vital importance and it stands to reason that if early human ancestors had regularly swam then they would have inherited a complex respiratory mechanism which included fine breath control, the perfect exaptation for speech.

The voluntary breath control speech precursor hypothesis.

The hypothesis proposes that the original benefit of human voluntary breath control was as an adaptation to swimming and diving. It assumes:

- Human voluntary breath control is innate and quite different from that in chimpanzees.
- The centres of the brain involved with breath control are also involved in speech and that chimpanzees lack these centres, or at least have very different ones.

Testing the hypothesis

Some predictions made by this hypothesis could be scientifically tested:

a) The time intervals of inspiration and expiration during swimming have characteristics which correlate with those during speech. During silent rest, humans tend to take approximately 2.5 seconds to both inhale and exhale. During speech, the inhalation time drops to less than half a second and the exhalation, during speech, is prolonged to 5-10 seconds. It is predicted that whilst swimming this pattern is exaggerated, providing a clear cut exaptation for breathing during speech.

b) Physiological differences in the regions of the brain concerned with voluntary breath control will markedly differ between humans and chimpanzees.

Diverse phenotypic changes predicted from waterside selection

Langdon (1997 p 481 - 487) paraded 26 anatomical human features that Morgan had claimed were evidence of a more aquatic past. They were given equal weighting even though Morgan had given far more attention to some than others. The feature she gave most attention to was the subject of this thesis: wading in shallow water. Morgan wrote a paper on the subject (Morgan

1993) and four chapters on the subject in her penultimate book on the "aquatic ape" (Morgan 1997) but Langdon dismissed the idea in just four sentences (Langdon 1997 p481).

It is asserted that this thesis shows that such a summary dismissal of the wading hypothesis by Langdon was not justified and that if objective reasoning is applied and more science is done, the idea may well prove to be the best idea on hominin bipedal origins.

Similarly, for four or five other ideas in Morgan's books, outlined above, are surely deserving of a more serious scientific response than they have been afforded to date.

Putting all of this together into some kind of context, Langdon's intention appears to have been to draw ridicule on the diversity of the claims made by Morgan. Vaginal depth, breasts, loss of estrus, hymen are, for example, listed alongside and given as much consideration as, the wading idea. But behind the parody lies a serious point: If human ancestors had lived in waterside habitats and, although remaining largely terrestrial, regularly waded, swam and dived for food, what would one expect? If one is not postulating a convergence with cetaceans or sirenians but simply a differential in the regime of selection compared to our great ape ancestors, isn't such a seemingly diverse set of peculiar traits entirely predictable?

It is the assertion of this thesis that this is exactly what one should expect.

7.7. Concluding remarks

It is time to conclude this whole thesis and offer some final thoughts.

A significant review of the scientific literature on the subject hominin bipedal origins has shown that very few of the many papers have attempted a comprehensive meta-analysis of the different ideas that have been published on the matter, before promoting any new idea. Even fewer, if any, have attempted to objectively assess them and identify areas of strength and weakness against which the new idea can be compared. Uniquely, I believe, this thesis has attempted to do this and has found that wading hypotheses of hominin bipedal origins have been significantly under-represented in the literature, compared to other ideas which are, at best, no better and many much weaker overall. The reason for this under-representation has been identified as its unfortunate association with a mislabelled and largely misunderstood set of ideas about human evolution called "the aquatic ape hypothesis".

The intention of this thesis was to show that if one looks at the subject objectively, there is no justification for rejecting the wading hypothesis merely because of such an association. Clearly much of the thinking behind these ideas remains speculation, but speculation and curiosity are the fuel on which science burns. Converting idle speculation into rigorous hypotheses, whose predictions can be scientifically tested is the real challenge and I hope anyone reading this will appreciate the efforts some have made to start the process even though, obviously, there is a huge amount of work that remains on the "to do" list.

It is undoubtedly a daunting prospect to consider just how much science remains to be done in this area. The fact that there remains largely a void in the scientific literature investigating these waterside hypotheses of human evolution, provides a huge opportunity for anyone with an open mind and exciting research prospects in the near future.

Personally, I hope others will be inspired, like I have, to take the subject more seriously than before.

Last word to Elaine

Talking of inspiration, I must end by recording my debt of gratitude to my main inspirer, a little Welsh woman from Mountain Ash, an old mining village in the valleys north of Cardiff, who opened my eyes to this fascinating idea and the quite bizarre, and very disappointing, response to it by most experts in anthropology.

I want the last words of this thesis to be hers. They are some of the first I read from her on the subject in 1998. I think they're as relevant today as when they were written.

> *"The Question*
>
> *It is generally agreed that around eight or nine million years ago there lived in the forests of Africa an animal known to anthropologists as the last common ancestor (l.c.a.) The descendants of the l. c. a. split into different lineages and their extant survivors are gorillas, chimpanzees, bonobos and humans. Of these, humans differ more markedly from the African apes than the apes differ from one another. There are numerous and striking physical differences, and at least some of them began to appear either at the time when the human lineage diverged from the other apes, or very shortly afterwards. It would seem reasonable to conclude that something must have happened to our ancestors which did not happen to the ancestors of the other apes.*
>
> *The question at issue is simply: WHAT HAPPENED?"*
>
> *Elaine Morgan (1997 p 3)*
>
> *(Elaine Morgan died in July 2013, aged 92)*

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