THE WADING HYPOTHESIS OF HOMINID BIPEDALITY

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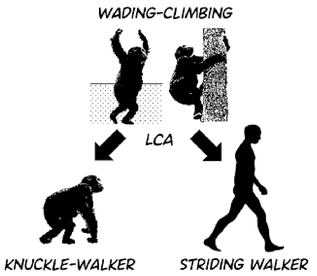
Abstract

There is one, and only one, scenario guaranteed to induce bipedal locomotion in an otherwise quadrupedal extant great ape. Unlike postural bipedalism and bouts of forelimb pre-emption, it will induce it indefinitely, for as long as the conditions prevail. Unlike arboreal bipedalism, this is *unsupported locomotion*, not supported posture. Not only does it not require the use of upper limbs, it actually precludes it. Indeed, it is the only scenario that would theoretically kill a determined quadruped. It is entirely consistent with the palaeohabitats of all the supporting fossil evidence yet found. And yet, despite the occasional brief mention on TV and radio documentaries, the **Wading Hypothesis** appears to have been almost totally ignored by the field of palaeoanthropology for over sixty years. It would appear its historically close association with the so-called "aquatic ape hypothesis" (better labelled "waterside hypotheses of human evolution") has made it somewhat a taboo subject.

A Wading-Climbing Last Common Ancestor?

A wading-climbing locomotor repertoire for the Last common Ancestor (LCA) is an ideal potential precursor to two unique modes of locomotion: knuckle-walking of *Pan* and *Gorilla* and the striding, extended lower limb bipedalism of *Homo.*

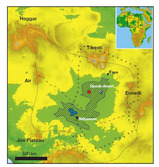


The long-standing assumption that bipedality was a unique human-trait that evolved after the split with the chimpanzee was seriously challenged by the discoveries of *Orrorin* in 2000 and *Sahelanthropus* in 2001 dated at 6 Ma and 7 Ma, respectively.
Molecular evidence suggests the LCA of the *Pan/Homo* lived ca 7-5 Ma suggesting that it could have already exhibited some mode of bipedality, if not our own striding, energy-efficient form.
Other putative bipedal hominids (e.g. *Oreopithecus*, *Danuvius* etc. are even older.)

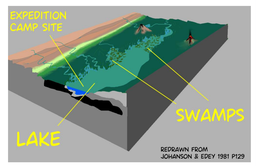
Palaeohabitats

The palaeohabitats of the earliest putative bipedal hominids are consistent with the wading hypothesis. All are associated with swampy, wetland, riverine or other waterside niches or at least were found in lacustrine or fluvial deposits.

Danuvius — Riverine.
Oreopithecus — Swamp.
Sahelanthropus — Lake.
Australopithecus afarensis — Wetland.



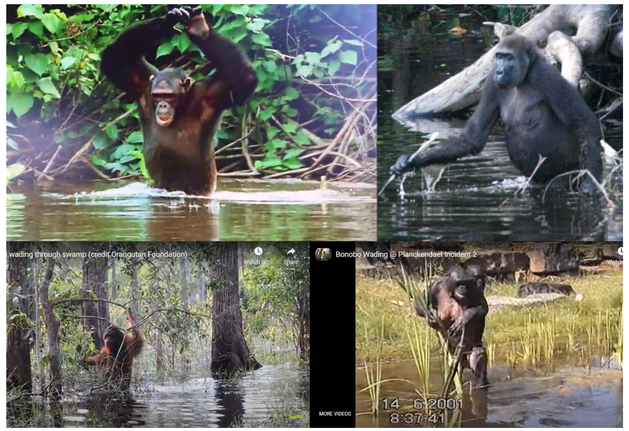
Palaeo Lake Chad (from Vignaud et al 2002)



Hadar

Extant Great Ape Locomotor Repertoire

Until recently there was very little evidence, anecdotal or otherwise, of large primates engaged in bipedal wading behaviour. Elaine Morgan's (1997) four chapters on the subject could only cite stories of wading in the proboscis monkey (*Nasalis larvatus*) to back her arguments up.
However, in the last twenty years there has been a stream of photographic and video evidence repeatedly showing that whereas on land, chimpanzees, bonobos, gorillas and orangutans are largely quadrupedal, they all switch to bipedalism in waist-deep water very predictably.



From top left: Pan troglodytes; Gorilla gorilla; Pongo pygmaeus; Pan paniscus.
BBC Life of Mammals, Breuer et al. 2005, OrangUtan Foundation; Kuliukas 2001.

IT'S NOT ROCKET SCIENCE!

Low Popularity…

Wading models are rarely given much attention in university level texts about the evolution of bipedality. (Kuliukas 2016)….

Popularity of Bipedalism Models in University Level Text Books		
Rank	Model Popularity	% age popularity
1	Carrying	86%
2	Feeding	69%
3	Energy Efficiency	58%
4	Social Behaviour	50%
5	Thermoregulatory	47%
6	Non-wading habitat compulsion	25%
7	Wading habitat compulsion	22%
8	Combination	14%
9	Dietary	3%

… But High Scoring

… but despite their lack of coverage, wading models rank among the highest in terms of an evaluative framework (a kind of marking rubric) designed to assess the strengths of wading models. (see tinyurl.com/BipedalModels for details and a chance to enter rankings.)

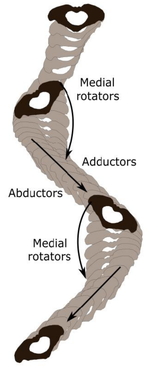
Results

Rank Models | Back to top

Rank	Group	Subgroup	Name	Code	Result
#1	Habitat Compulsion	Wading	"Stow-Apes"	s4.1.1	93%
#2	Habitat Compulsion	Wading	Amphibische Generalistheorie	s4.1.3	86%
#3	Habitat Compulsion	Wading	Wetland foraging	s4.1.2	85%
#4	Habitat Compulsion	Wading	Aquartorweef Model	s4.1.4	81%
#5	Feeding	Postural Feeding	Postural feeding hypothesis	s3.3.1	70%
#6	Locomotor efficiency	Efficiency of movement from tree to tree	Efficiency of movement from tree to tree	s5.1.1	68%
#7	Habitat Compulsion	Arboreal	"Orang-utan-like" hand assisted bipedalism	s4.4.2	65%
#8	Habitat Compulsion	Arboreal	Arboreal "upwardly mobile" hypothesis	s4.4.1	64%
#9	Habitat Compulsion	Arboreal	Descent from arboreal Hylobatian locomotion	s4.4.3	62%
#10	Locomotor efficiency	Slow, long-distance walking	Slow, long-distance walking	s5.1.3	61%
#11	Habitat Compulsion	Wading	Coastal foraging	s4.1.5	61%
#12	Feeding	Terrestrial Gathering	Terrestrial squat feeding on the forest floor	s3.1.2	61%
#13	Forelimb pre-emption (carrying)	Tool Carriage	Tool carriage	s1.5.1	57%
#14	Forelimb pre-emption (carrying)	Tool Carriage	Weapon wielding	s1.5.2	57%
#15	Forelimb pre-emption (carrying)	Unspecified	General freeing of the hands	s1.1.1	57%
#16	Forelimb pre-emption (carrying)	Weapon Throwing	Weapon Throwing	s1.4.1	57%
#17	Forelimb pre-emption (carrying)	Food Carriage	Carrying food back to gallery forest bases	s1.2.1	57%
#18	Feeding	Terrestrial Predation	Stalking	s3.4.1	56%
#19	Forelimb pre-emption (carrying)	Food Carriage	Carrying and scavenging	s1.2.2	56%
#20	Forelimb pre-emption (carrying)	Food Carriage	Display carrying	s1.2.3	56%
#21	Forelimb pre-emption (carrying)	Food Carriage	Migration-carrying hypothesis	s1.2.4	55%
#22	Behaviour	Threat Display (intra-specific)	Intra-specific threat displays	s2.3.1	53%
#23	Feeding	Terrestrial Gathering	Other gathering	s3.1.3	53%
#24	Feeding	Arboreal Predation	Arboreal predation	s3.3.1	53%
#25	Forelimb pre-emption (carrying)	Infant Carriage	Female driven infant carrying	s1.3.1	53%
#26	Habitat Compulsion	Variability Selection Hypothesis	Variability Selection Hypothesis	s4.3.1	52%
#27	Locomotor efficiency	Locomotor de-coupling	Locomotor de-coupling	s5.4.1	51%
#28	Random Genetic Factors	Mutation in vertebral development	"Eco Devo" mutation	s8.1.1	51%
#29	Locomotor efficiency	Endurance Running	Endurance Running	s5.5.1	51%
#30	Combination	Combination of factors	Multi-factorial	s9.1.1	51%
#31	Behaviour	Aggression (inter-specific)	Threat displays directed at other species	s2.2.1	50%
#32	Feeding	Terrestrial Gathering	Seed Eating	s3.1.1	49%
#33	Feeding	Terrestrial Predation	General scavenging/hunting	s3.4.2	49%
#34	Thermoregulatory	Thermoregulatory hypothesis	Thermoregulatory Hypothesis	s6.3.1	48%
#35	Locomotor efficiency	Biomechanical Instability	Biomechanical instability	s5.3.1	46%
#36	Behaviour	Nuptial Gifts	Nuptial Gifts	s2.1.1	44%
#37	Behaviour	Evasion/Vigilance	Sentinel behaviour	s2.4.1	42%
#38	Feeding	Terrestrial Predation	Specific Hunting	s3.4.3	42%
#39	Behaviour	A new "fashion"	Copied Gimmick Idea	s2.6.1	38%
#40	Behaviour	Sexual Display	Phallic Display directed at females	s2.5.1	35%
#41	Habitat Compulsion	Walking in snow/mud	Walking on Snow or mud	s4.2.1	34%
#42	Dietary Factors	Iodine deficiency	Iodine deficiency	s7.1.1	24%

Putative Gait for Australopithecines

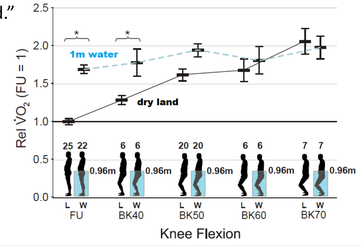
The platypelloid pelvis of *Australopithecus afarensis* (AL 288-1 or "Lucy") has rarely been studied from the point of view of a putative gait. Clearly, many characteristics indicate a kind of bipedality but as it's so unlike the modern human form it begs the question – what mode of locomotion could they have been engaged in? As it's not intermediate between that of *Pan/Gorilla* and *Homo*, it seems to suggest it's bipedality was not a vestige of climbing, but something completely different.
A 3D geometric morphometric analysis of the pelvic shape from the point of view of relative load arms of the main muscle blocks showed that Lucy's pelvis was adapted to more powerful abduction/adduction and rotation of the hip, consistent with a putative side-side, wading gait. (Kuliukas 2016)



Energy Efficiency

It is very unlikely that very first hominid terrestrial bipeds were preadapted to walking as efficiently as later *Homo* palaeospecies seem to have been. Scenarios should therefore be considered where the cost of bipedal locomotion in a hominid not yet anatomically adapted to doing so efficiently might have been "cushioned."

A study of human volunteers engaged in bipedal wading in different depths of shallow water and walking on dry land, with varying hip and knee flexion, showed that in water 1m deep the cost differential of bipedal locomotion with a 50^0 hip flexion was reduced from 55% to 19% and eliminated completely at 70^0. (Kuliukas 2016.)



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HISTORY


Max Westenhöfer (1942)
"The shape of the human foot, broadening towards the front, could indicate a paludine habitat..."


Alister Hardy (1960)
"I imagine him wading, at first perhaps still crouching almost on all fours groping about in the water, digging for shell fish...

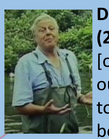

Carl Sauer (1962)
"A riparian location is indicated for his [early hominid] earliest living."


Elaine Morgan (1972, 1982, 1990, 1991, 1993, 1994, 1995, 1997, 2002, 2008, 2011)
"Professor Hardy wrote that wading in water would explain not only our erect walk…" (1972)
1 Chapter on bipedalism (1980)
2 Chapters (1990) & 4 Chapters (1997).
41 years promoting the wading hypothesis and other waterside hypotheses of human evolution.


Carsten Niemitz (2000, 2002, 2004, 2007, 2008, 2010)
Amphibische Generalisten-theorie (2002).


Algis Kuliukas (2000, 2002, 2008, 2011 2013, 2016, 2018)
MSc (UCL, 2000)
PhD UWA (2016)
12 Papers, 3 Book Chapters. Biography of Elaine Morgan (2020).


Marc Verhaegen (2002)
Aquarboreal Ancestors? Verhaegen, Puech, Munro 2002).


David Attenborough (2002)
[on wading] "… when our distant ancestors took a step away from being apes and a step towards humanity."
Life of Mammals Documentary.


Richard Wrangham (2005, 2009, 2021)
"Delta Hypothesis" (2005)
"That's what we come from... a water-walking wading ape."
H_2O Documentary E2 (2021).

1940 1945 1950 1955 1960 1965 1970 1975 1980 1985 1990 1995 2000 2005 2010 2015 2020