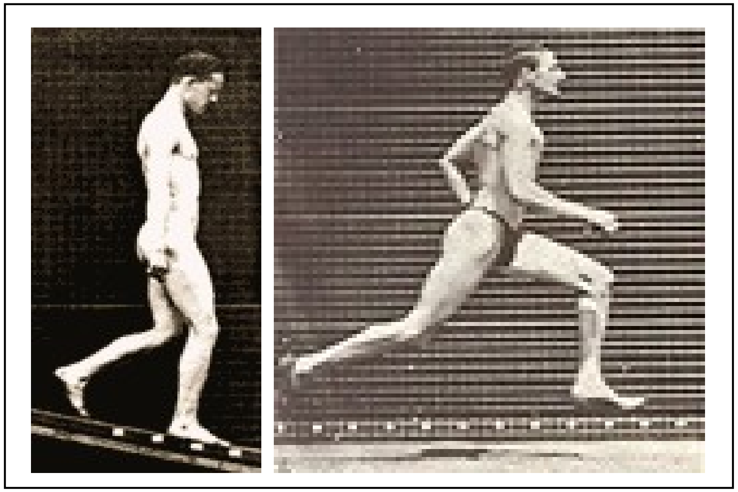
Walking the walk:
evolution of human bipedalism



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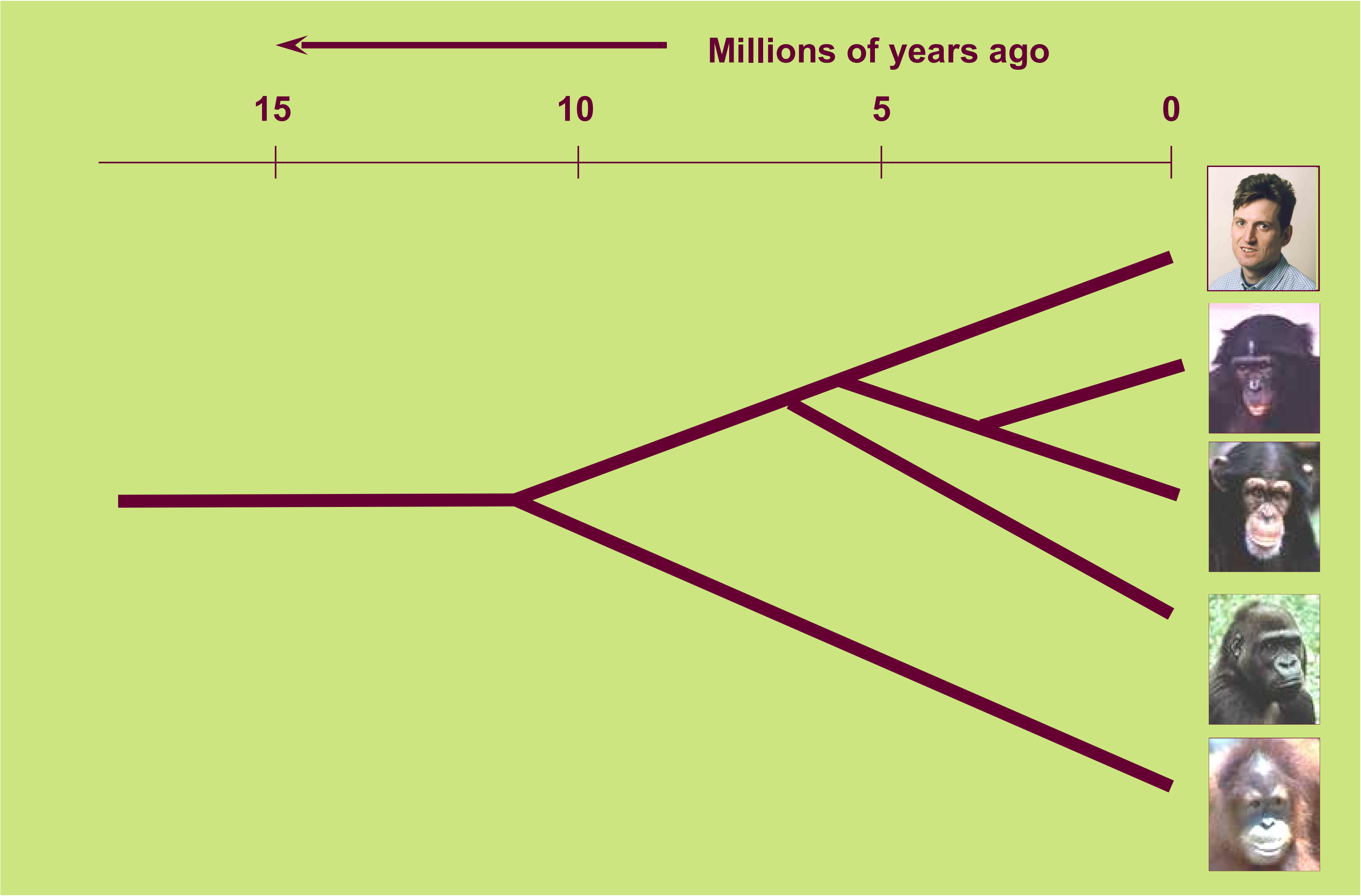
“Human walking is a risky business. Without split-second timing man would fall flat on his face; in fact with each step he takes, he teeters on the edge of catastrophe”

(John Napier)

Bipedal locomotion

Signifies split between human and chimpanzee ancestors

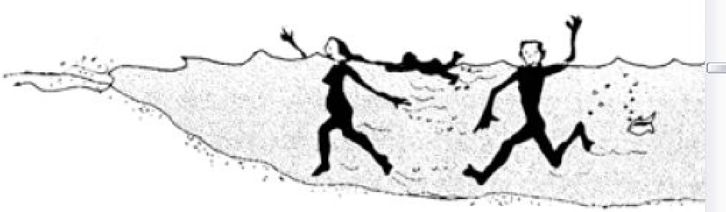


Bipedalism is bad for your health!

- Pulled muscles, slipped discs & rheumatism
- Women's pelvic size unable to keep up with brain size!!!
- Varicose veins
- Calluses/flat feet
- Haemorrhoids !!!!

Why did bipedalism evolve?

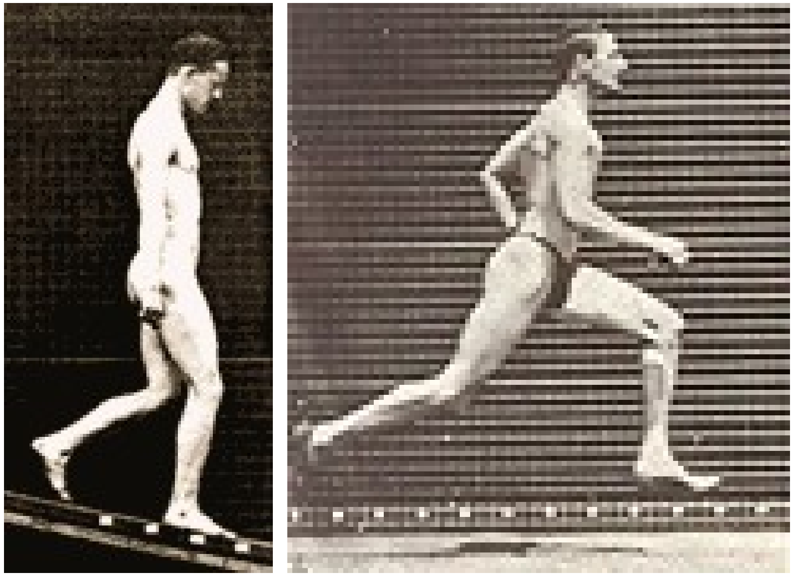
- to allow foraging on the savannah when the sun is overhead, when quadrupeds have to seek shade *(Wheeler, 1984, et seq.)*
- to fulfill the locomotor needs of: scavengers *(Shipman, 1986);* migratory scavengers following ungulate herds *(Sinclair et al., 1986);* endurance hunters *(Spuhter, 1979)* & game stalkers *(Merker, 1984)*
- to make the bipedalist appear taller to intimidate predators and antagonists *(Jablonski & Chaplin, 1993, Thorpe et al, 2002)*
- because there was prolonged flooding and our ancestors were driven out of the remaining forest and into the sea, where there was an abundance of accessible food *(Morgan, 1982 et seq.)*



How did hominins become terrestrial bipeds?

Quadrupedal knucklewalking

Vertical climbing

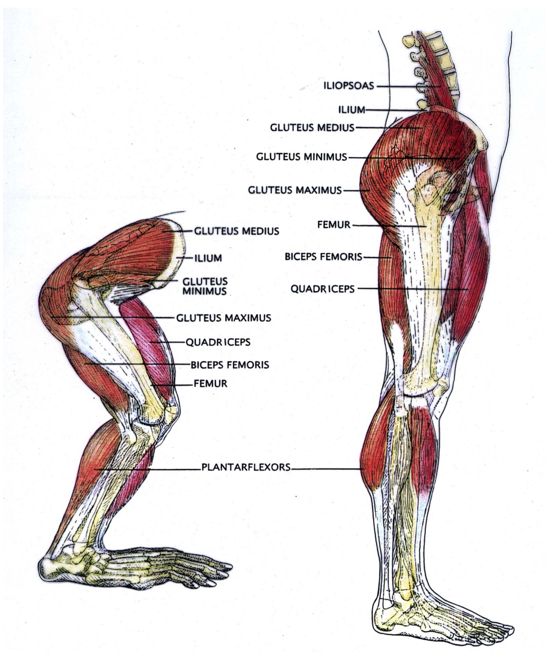


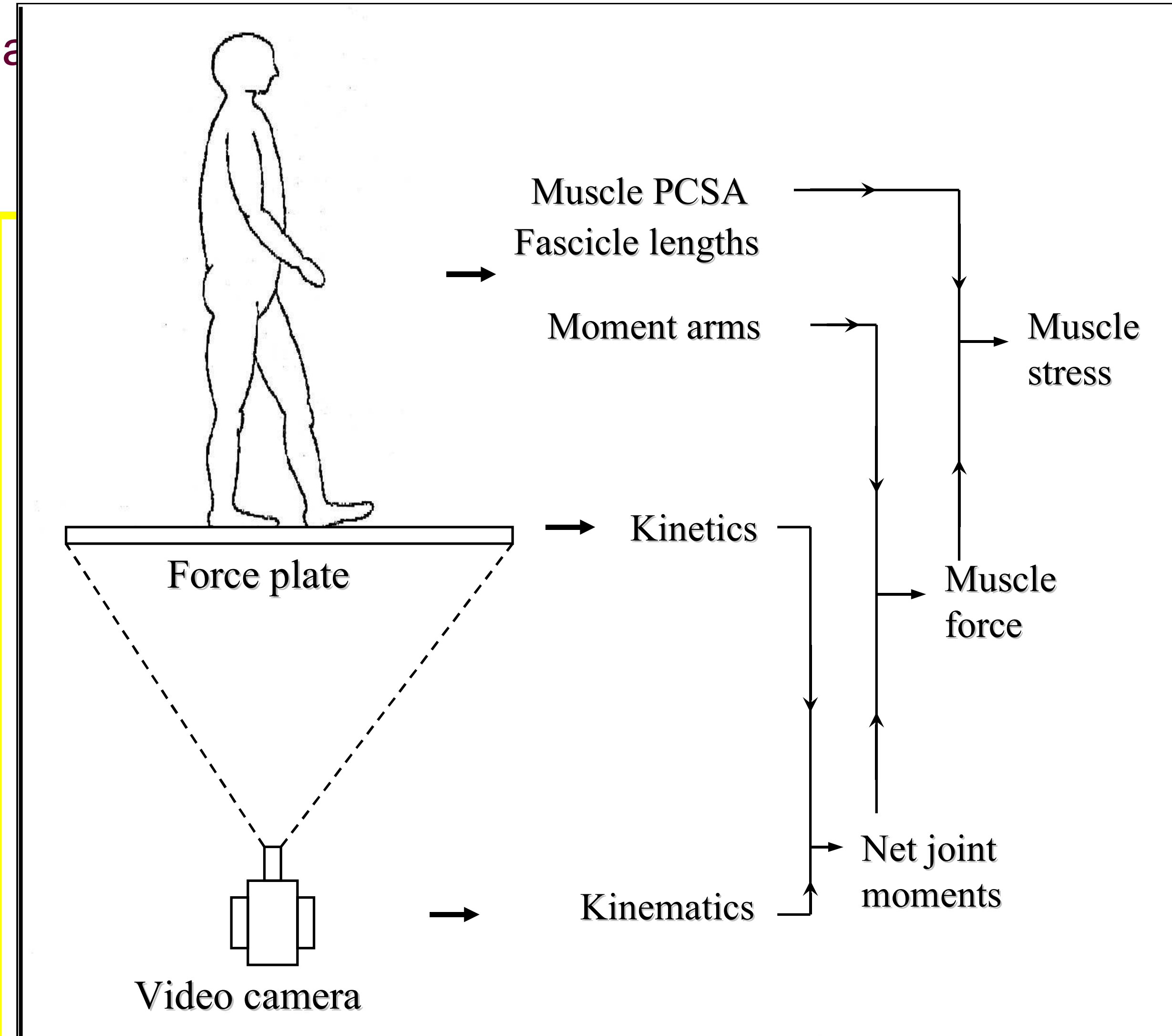
Experimental approach

Multidisciplinary approach:- a
on anatomical features

Structure

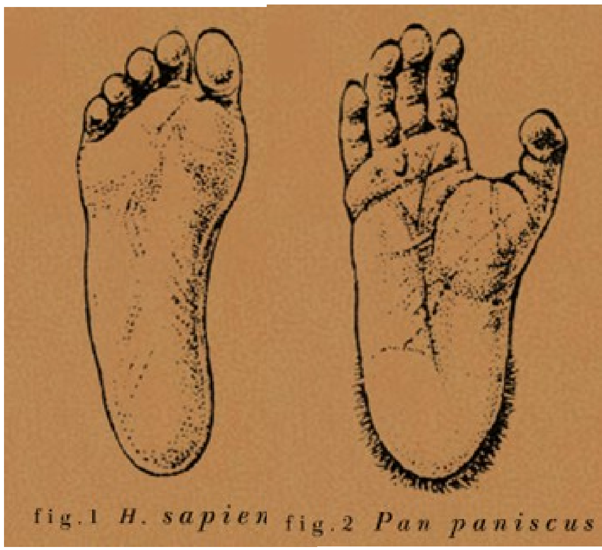
Functional Anatomy

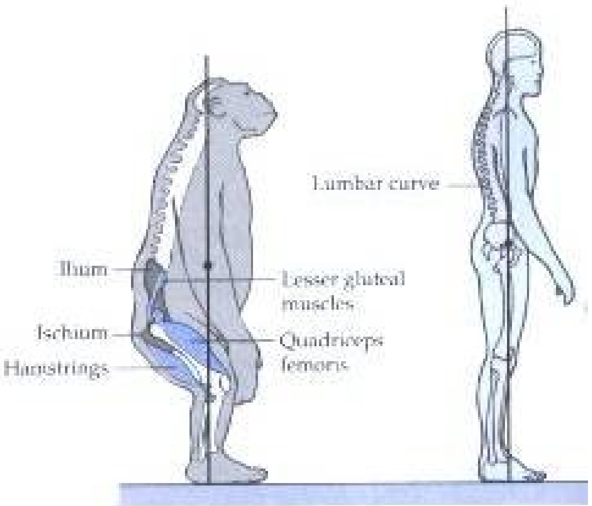


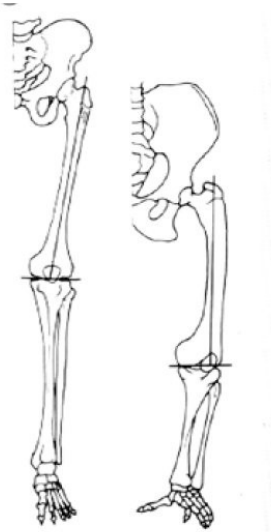


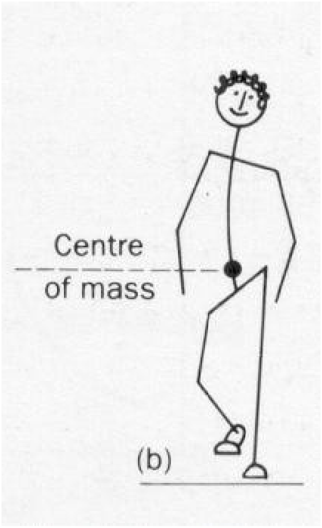
KW hypothesis: Chimpanzee/human bipedalism

- Lockable knees
- Position of CoM: pelvic tilt & valgus angle
- Platform arched foot, enlarged big toe in line with other toes

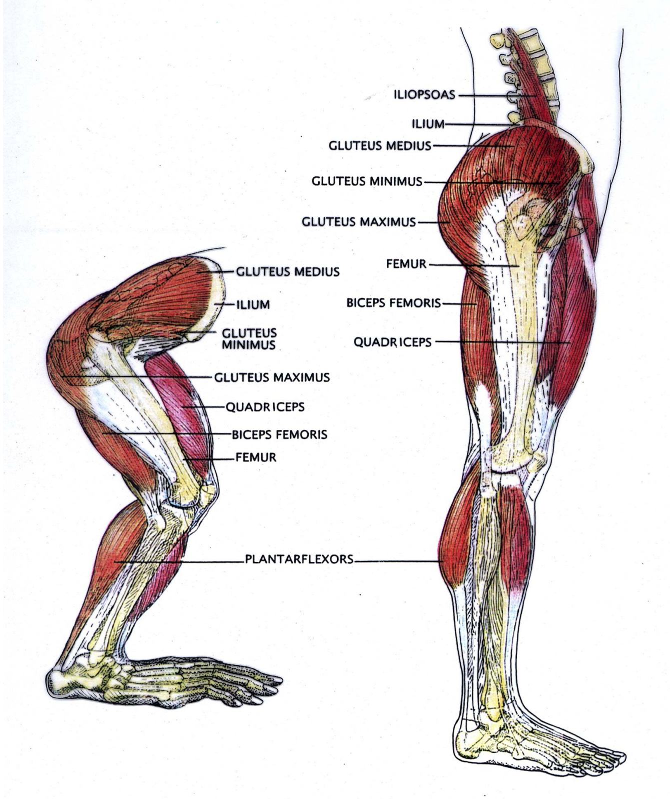








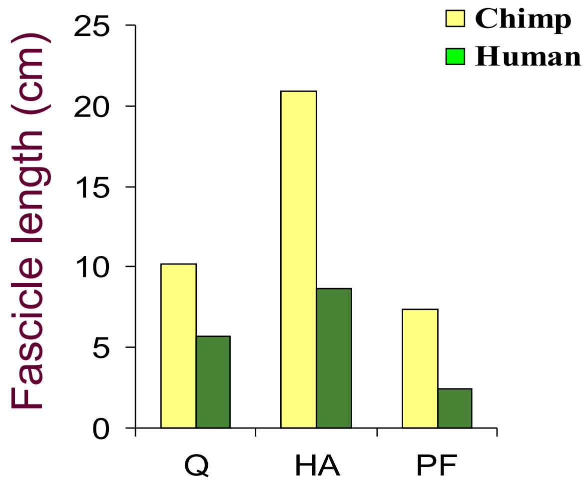
KW hypothesis: Do chimps and humans locomote in a dynamically similar manner?

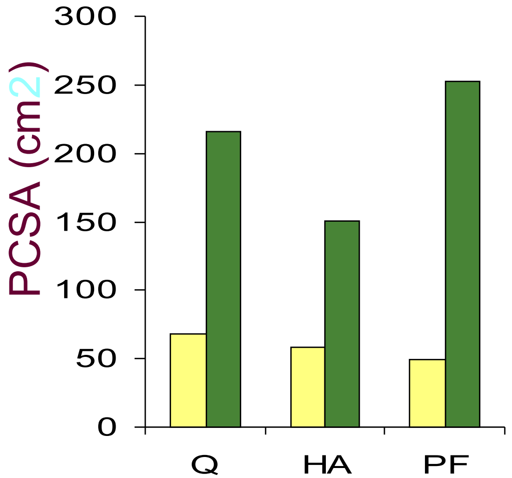


→ are differences in their skeletal structure compensated for by changes in joint geometry or muscle architecture?

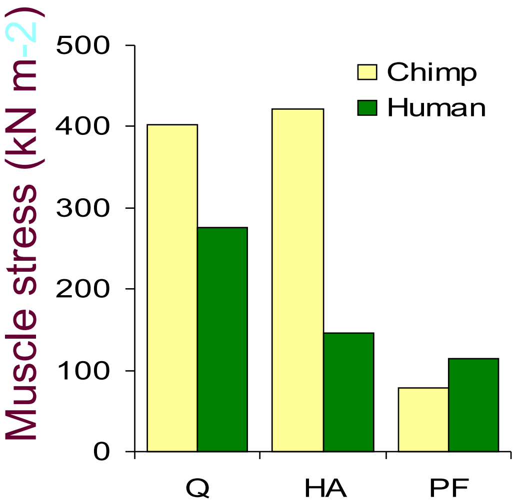
KW hypothesis: Comparison of 50kg chimps and humans

Fascicle lengths
& PCSAs





Muscle stresses for chimp
bipedal walk & human run



Humans ⇨ Large forces over a small range of movement

Chimps ⇨ Smaller forces over a greater range of movement

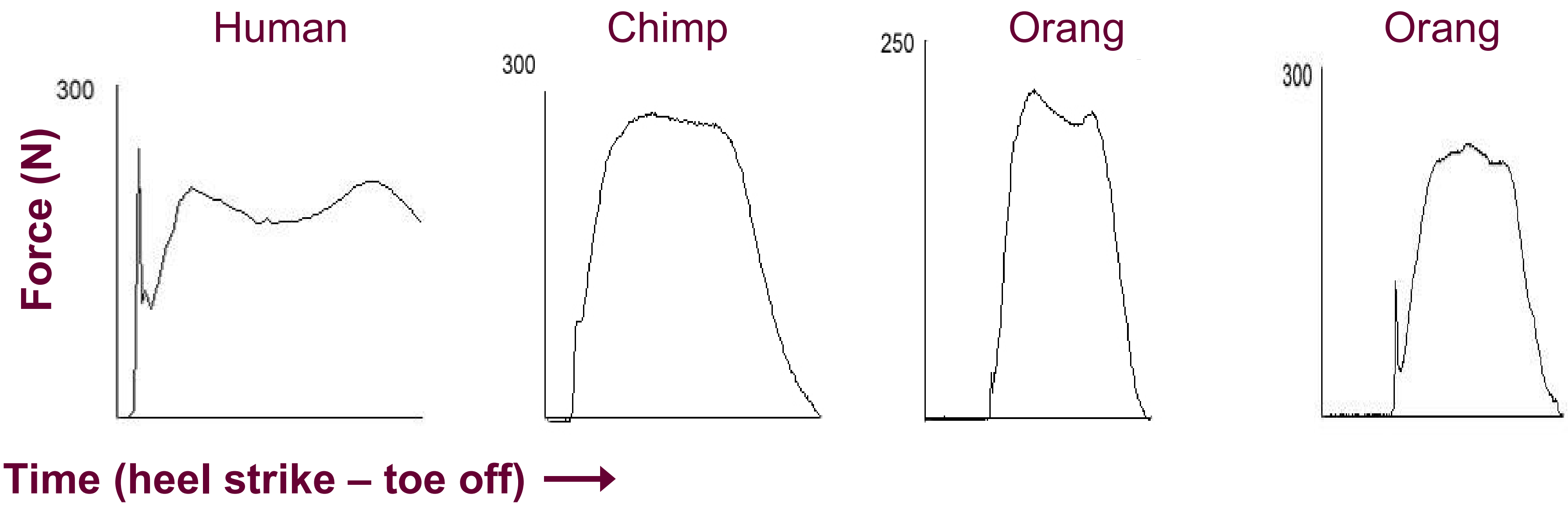
Chimps ⇨ exert greater muscle stresses in slow walk than human in run because of BHBK posture

Q: Quadriceps, HA: Hamstrings & Adductors, PF: Plantar Flexors

(Thorpe et al., 1999 *J. Ex. Biol.*)

KW hypothesis: Biomechanics

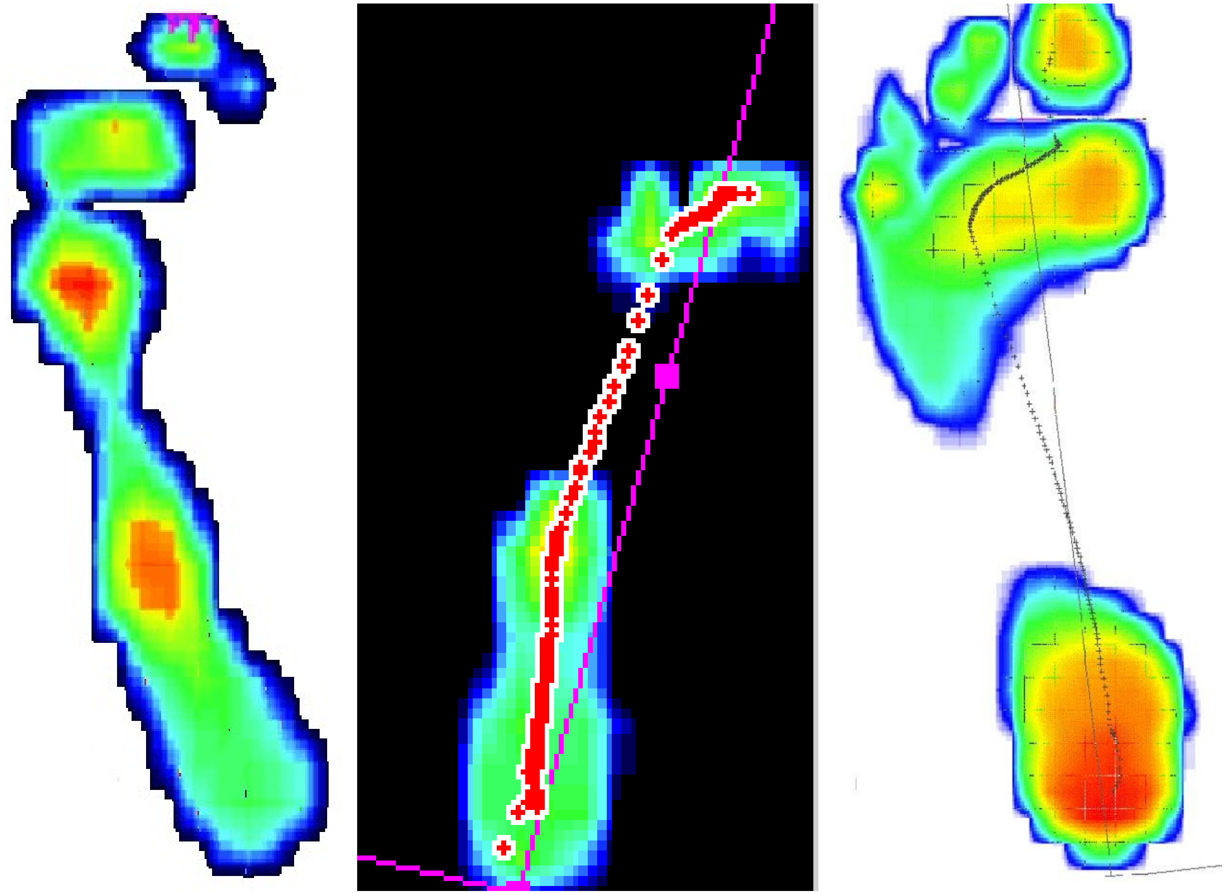
- Human-like foot function favoured by KW, (weight shifts anteriorly, encouraging **heel-down posture** during foot contact, & **contact along the whole length of the foot**
- Orangutan adaptations for grasping favour elevated heel postures (Gebo, 1992)



(Crompton et al., 2003, *Cour Forsch Senckenberg*)

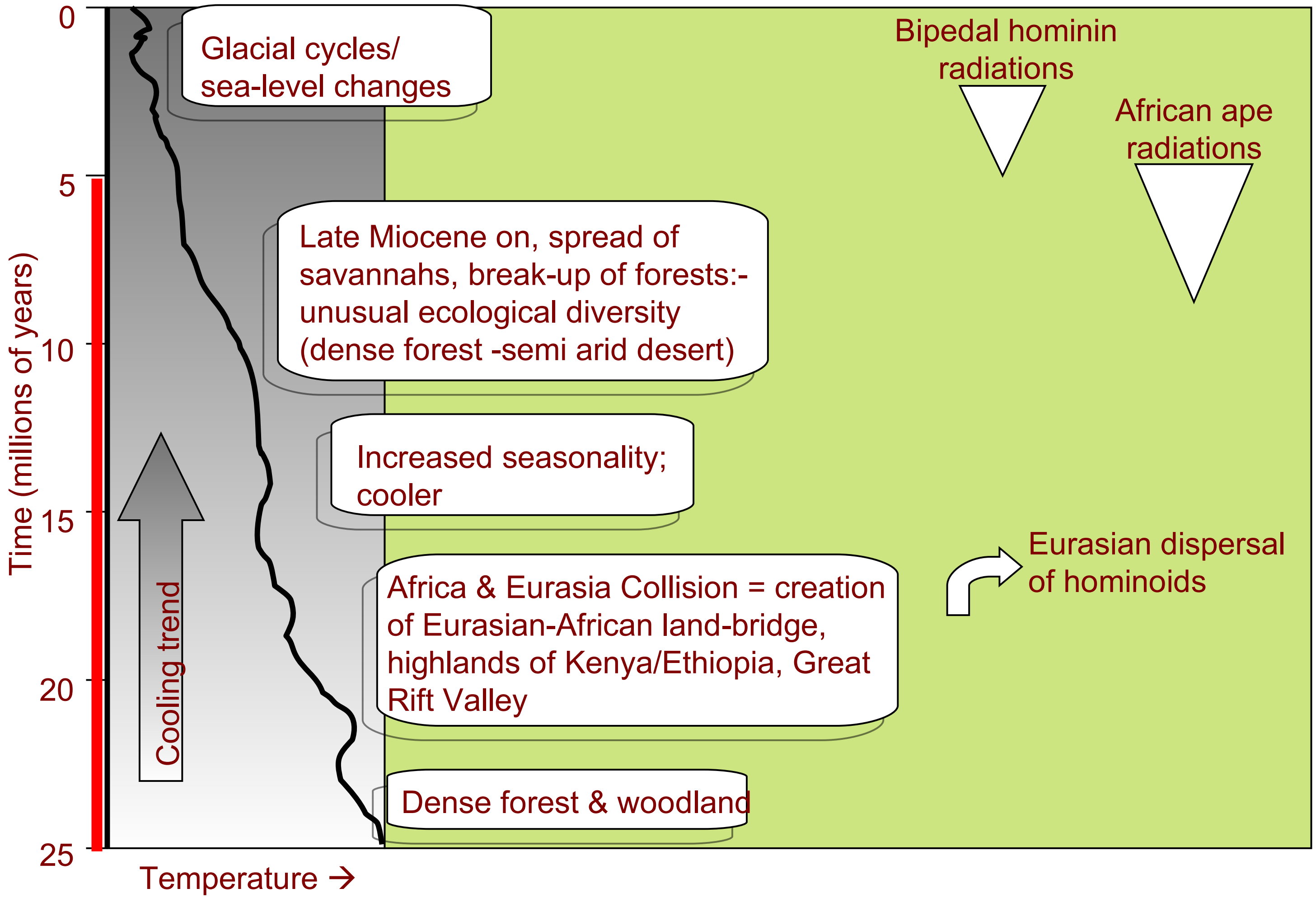
KW hypothesis: contact along whole length of the foot

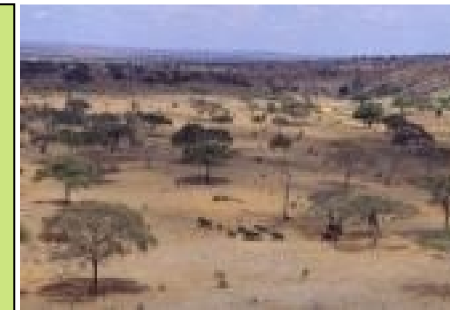
Bonobo Orangutan Human



(Crompton et al., 2003, *Cour Forsch Senckenberg*)

Recent ecological evidence





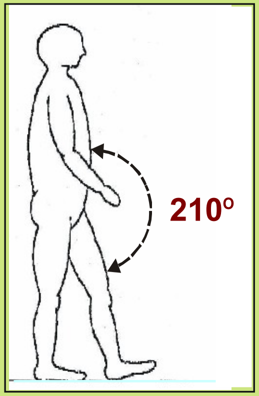
- Deforestation : local and alternated with reclosure (Kingdon, 2004)
- Bipedalism evolved in a forested, not savannah habitat
- *Homo*: associated with more open environments

Vertical climbing: kinematics

Crux of vertical climbing hypothesis: ape vertical climbing kinematics = more similar to human bipedalism than is ape bipedalism

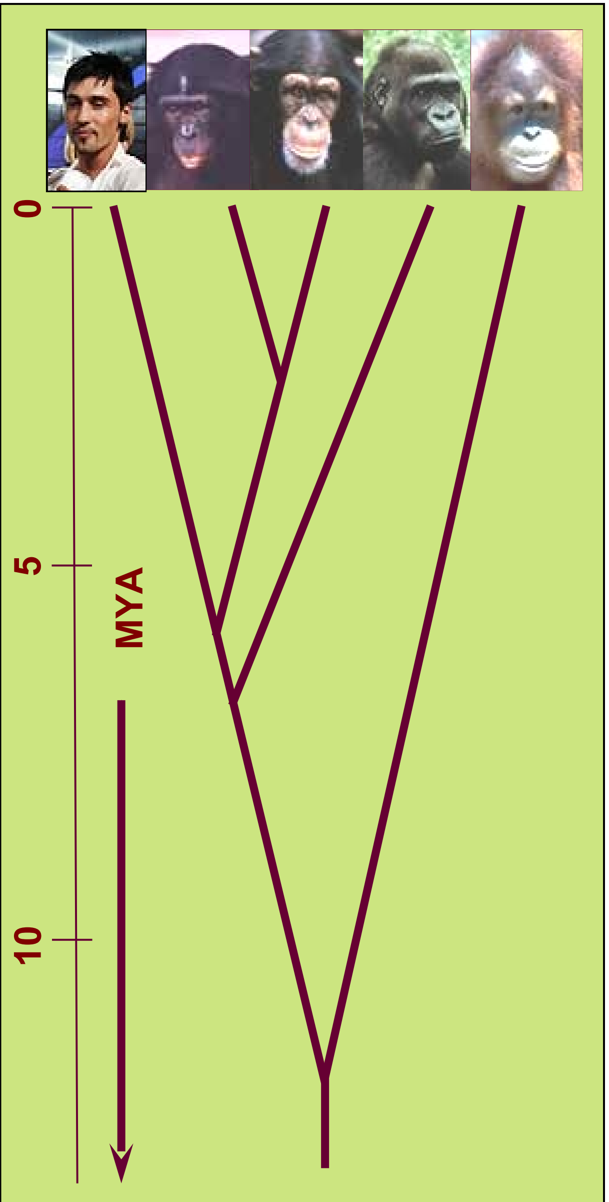
Maximum Hip Joint Excursions

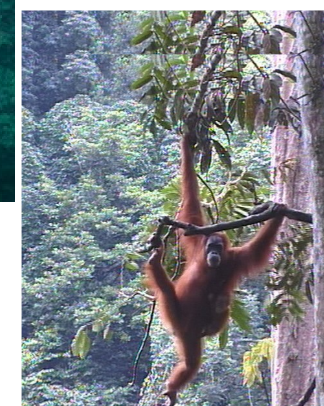
	Bipedalism	Vertical climb
	125 º	85-155 º
	193 º	120-133 º
	215 º	120 - 140 º

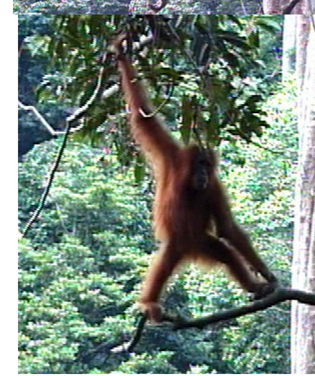


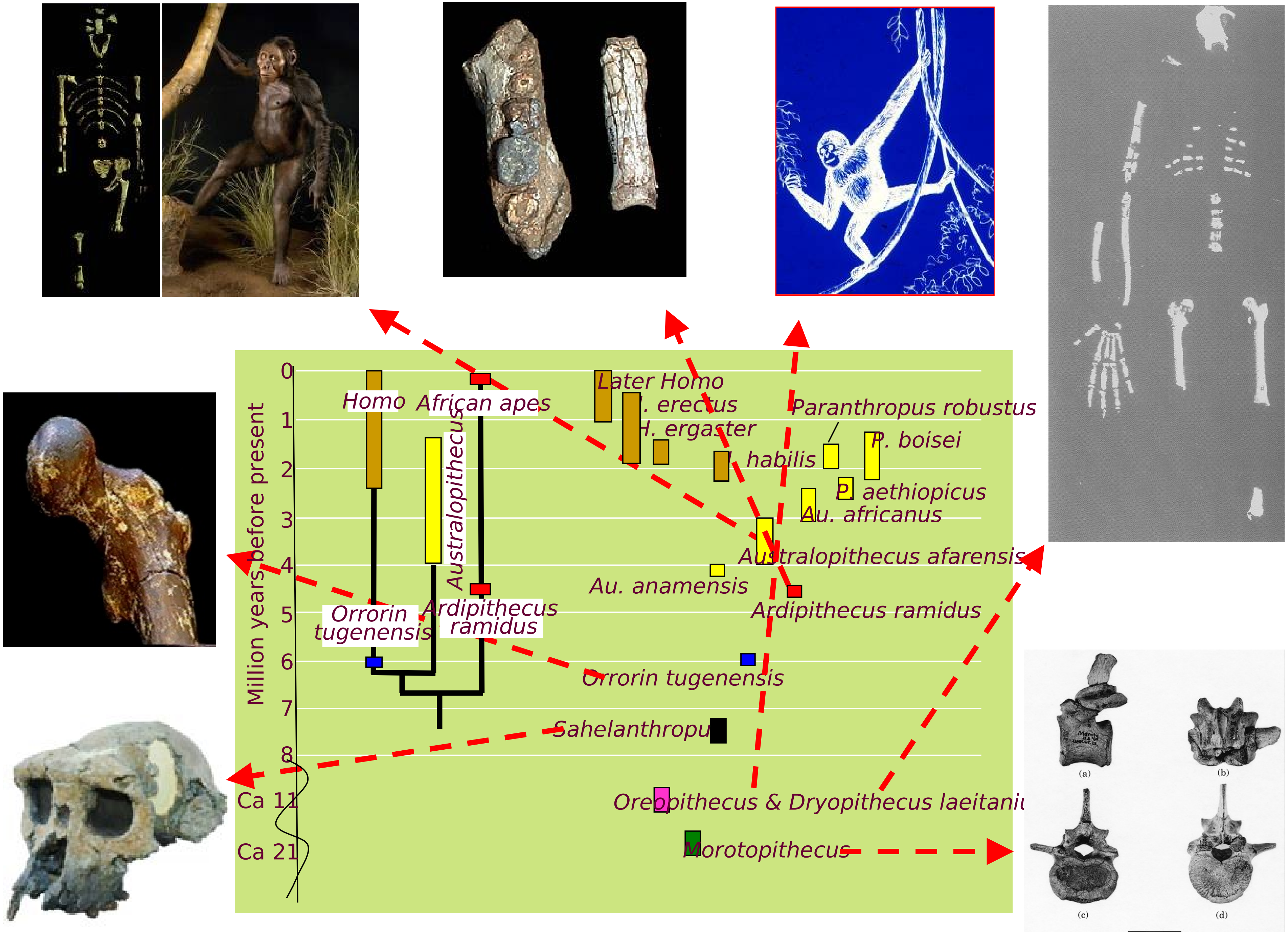
(Crompton and Thorpe, *Science*, 2007)

Recent fossil evidence: Great ape orthogrady









Million years before present
0
1
2
3
4
5
6
7
8
Ca 11
Ca 21
Homo
African apes
Australopithecus
Orrorin tugenensis
Ardipithecus ramidus
Later Homo
. erectus
H. ergaster
. habilis
Paranthropus robustus
P. boisei
P. aethiopicus
Au. africanus
Australopithecus afarensis
Au. anamensis
Ardipithecus ramidus
Orrorin tugenensis
Sahelanthropu
Oreopithecus & Dryopithecus laeitani
Morotopithecus
(a)
(b)
(c)
(d)

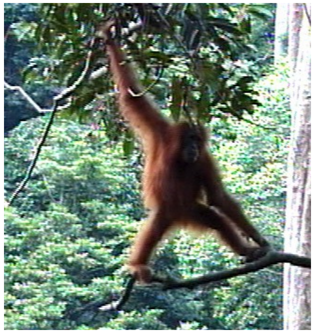
Terminal branch niche

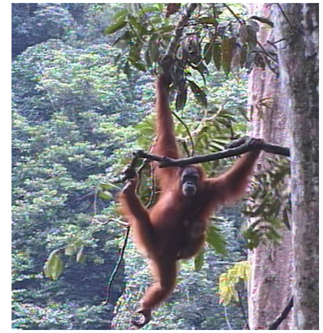
→ **How does arboreal bipedalism benefit large-bodied apes?**

- Major problem → branches taper towards ends
- Narrowest gaps between adjacent tree crowns and tastiest fruits are in the terminal branch niche

→ **Bipedal locomotion might confer significant selective advantages on arboreal apes because long prehensile toes can grip multiple small branches and maximize stability, while freeing one/both hands for balance & weight transfer**

Role of bipedalism in orangutan gait






Variables:

- locomotion (bipedal, quadrupedal, orthograde suspend)
- number of supports used (1, >1)
- support diameter (<4cm; ≥4-<10cm; ≥10-<20cm; ≥20 cm)

Loglinear model expressions	**(χ2/DF)**
Number of supports* support diameter	85.99
Locomotion*number of supports	18.06
Locomotion*support diameter	15.50

Likelihood ratio χ2: 8.91, DF: 6, P:0.18.

(Thorpe et al,2007, *Science*)

Locomotion*no. of supports

	No. supports		Total
	1	>1	
Quadrupedalism	69.2 (41.5) *1.9*	30.8 (28.9) *-2.5*	(36.6)
Bipedalism	29.1 (6.0) *-4.7*	70.9 (22.9) *5.4*	(12.6)
Orthograde suspension	63.1 (52.5) *0.6*	36.9 (48.2) *-0.7*	(50.9)
Total	61.1	38.9	

1 Entries are row % and (column %)

2 Values in italics denote standardized cell residuals (negative values indicate frequency is lower than expected).

(Thorpe et al,2007, *Science*)

Locomotion*no. of supports

	No. supports		Total
	1	>1	
Quadrupedalism	69.2 (41.5) *1.9*	30.8 (28.9) *-2.5* ↓	(36.6)
Bipedalism	29.1 (6.0) *-4.7* ↓	70.9 (22.9) *5.4* ↑	(12.6)
Orthograde suspension	63.1 (52.5) *0.6*	36.9 (48.2) *-0.7*	(50.9)
Total	61.1	38.9	

1 Entries are row % and (column %)

2 Values in italics denote standardized cell residuals (negative values indicate frequency is lower than expected).

(Thorpe et al,2007, *Science*)

Locomotion*diameter

Support diameter (cm)	Quadrupedalism	Bipedalism	Orthograde suspension	Total
<4	16.3 (7.0) *-4.1* ↓	22.4 (28.2) *3.4* ↑	61.2 (19.0) *1.8*	(15.8)
4-10	20.4 (18.2) *-4.7* ↓	12.5 (32.5) *0*	67.1 (43.0) *4.0* ↑	(32.6)
10-20	51.4 (32.0) *3.6* ↑	6.1 (11.1) *-2.6* ↓	42.5 (19.0) *-1.7*	(22.7)
>20	80.2 (27.3) *7.8* ↑	4.3 (4.3) *-2.5* ↓	15.5 (3.8) *-5.3* ↓	(12.4)
<4, 4-10	28.7 (8.5) *-1.3*	19.8 (17.1) *2.1* ↑	51.5 (11.0) *0.1*	(10.8)
4-10, 10-20	52.5 (6.2) *1.7*	5.0 (1.7) *-1.3*	42.5 (3.6) *-0.7*	(4.3)
<4, 10-20	25.0 (0.9) *-0.7*	50.0 (5.1) *3.7* ↑	25.0 (0.6) *-1.3*	(1.3)
Total	-36.6	-12.6	-50.9	

(Thorpe et al,2007, *Science*)

Hand-assisted arboreal bipedality

- Prehensile feet exert a torque that resists the toppling moment, grip multiple supports
- Leaves long forelimbs free for feeding/weight transfer/stability
- Benefits:
  - Effective gap crossing techniques → reduce energetic costs of travel
  - Safe access to fruit in terminal branches → increases nutritional intake

→ Hand-assisted locomotor bipedality, adopted under these strong selective pressures, seems the most likely evolutionary precursor of straight-limbed human walking

(Thorpe et al,2007, *Science*)

A tantalising fact…..

>90% of orangutan bipedalism utilizes extended hindlimbs

- Contrasts with flexed-limb gait of other monkeys and apes
- But, straight-limbed bipedality is characteristic of normal modern human walking (reduces joint moments & enables energy-savings by pendulum motion)
- Straight-limbed bipedality in orangutans must reduce required joint-moments
- Enable other energy-savings ????

(Thorpe et al,2007, *Science*)

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  - The Leverhulme Trust
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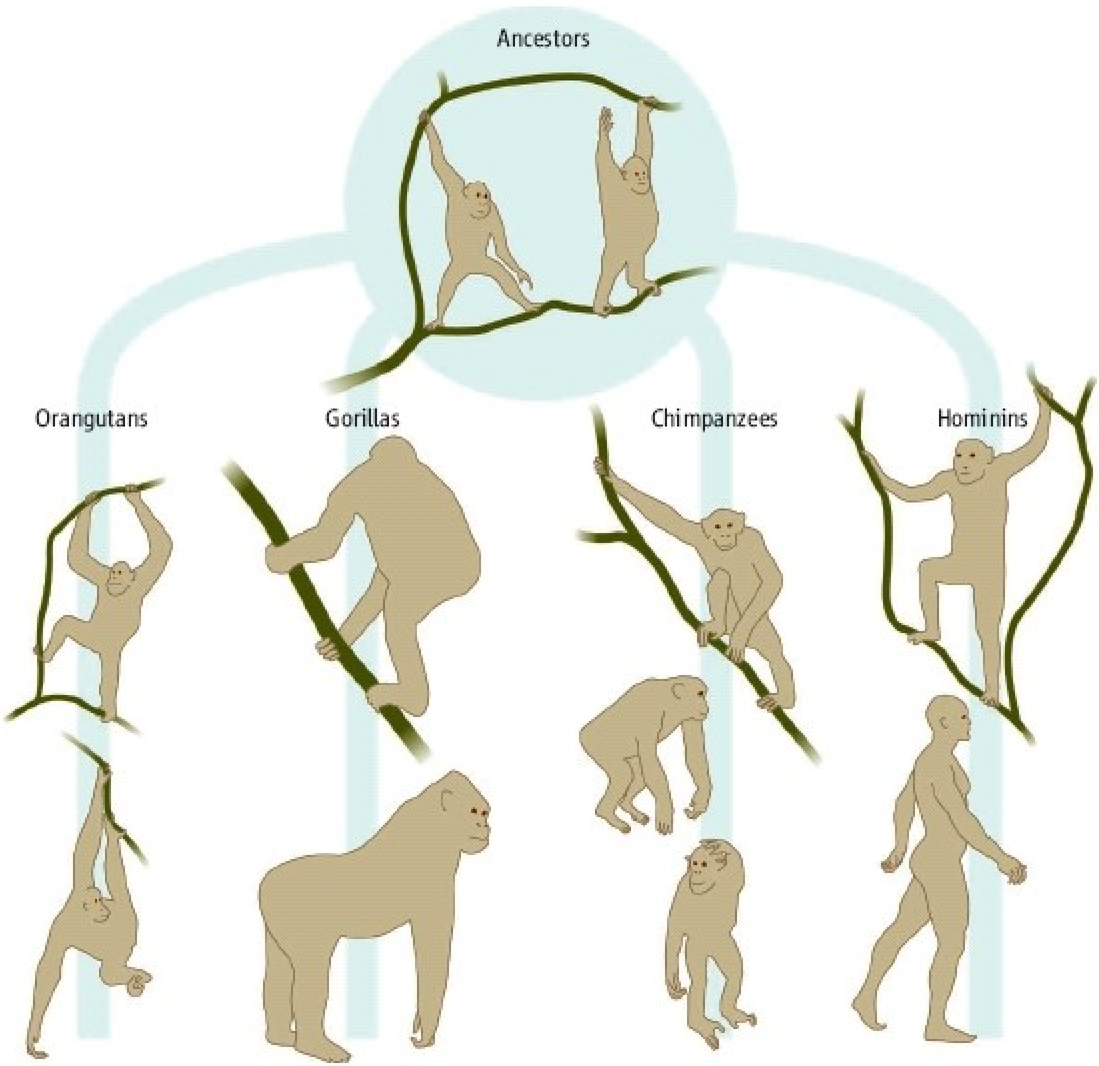
  - LSB Leakey Foundation
  - University of Cape Town
  - NERC

Evolution of locomotor diversity in the great apes



Common ancestor: Generalised orthogrady

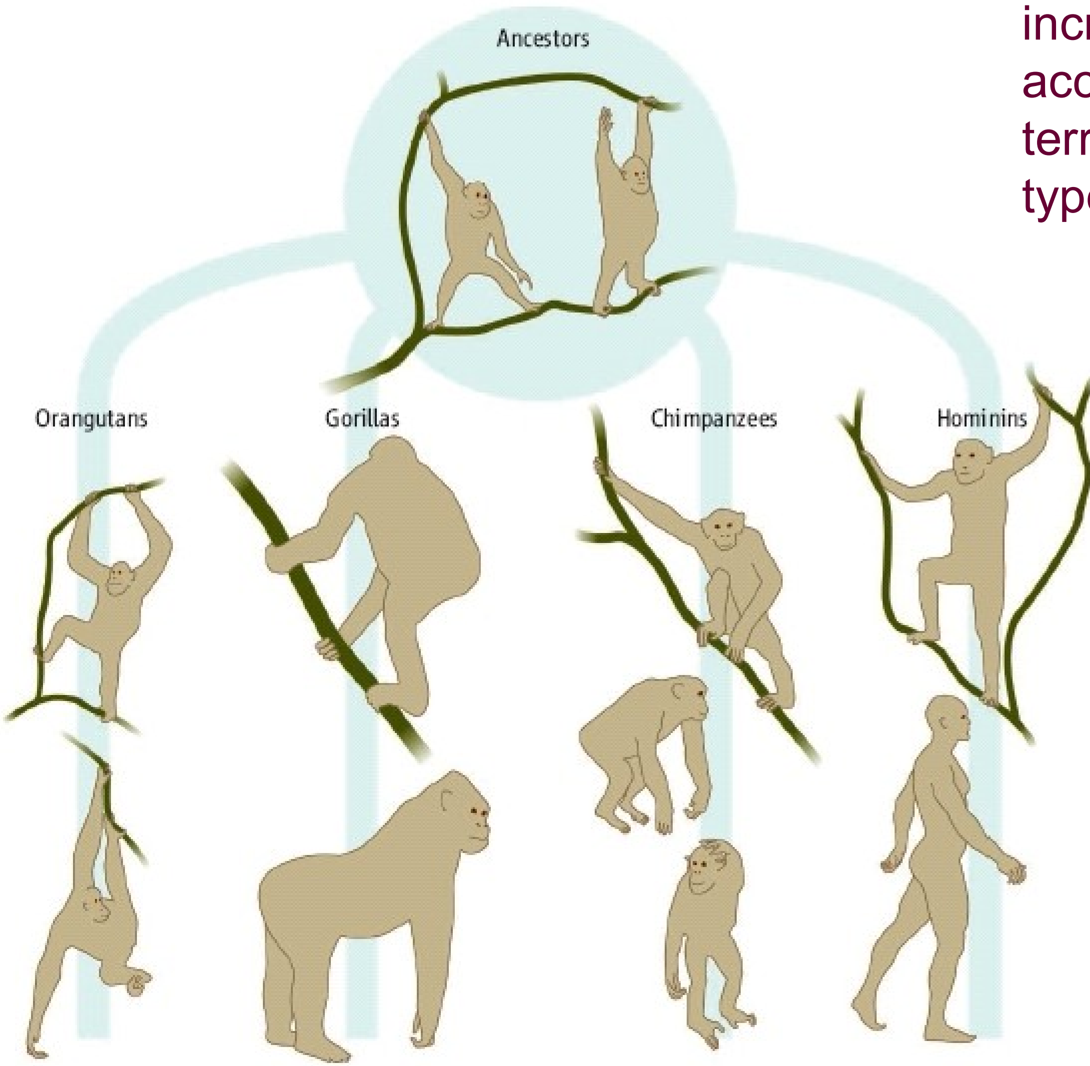
SE Asia: orangutan ancestors became more specialised for/restricted to arboreality

Africa: forest fragmentation alternated with reclosure

Hominins retained existing adaptations for straight-legged bipedalism, sacrificed canopy access to exploit savanna for rapid bipedalism.

(Thorpe et al,2007, *Science*)

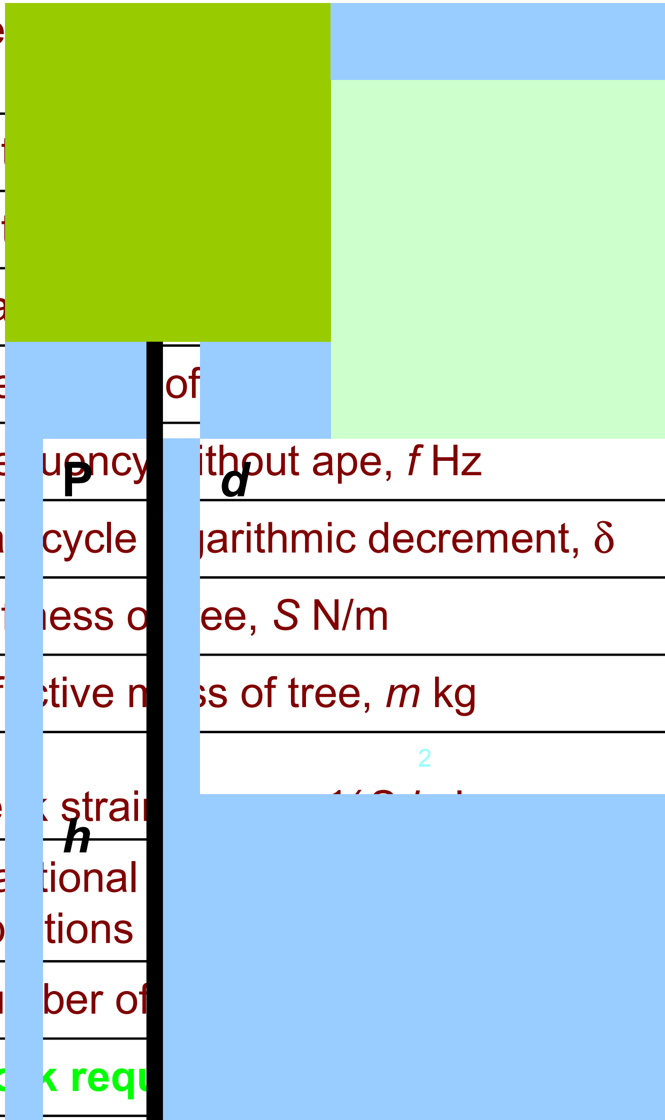
Evolution of locomotor diversity in the great apes



Chimps and gorilla ancestors → increased height-range/freq. of VC to access to canopy fruits and fallback terrestrial foods – (different times/forest types)

VC kinematics = similar to knuckle-walking → knuckle-walking selected as the least inefficient locomotion for terrestrial crossing between trees, but compromised existing adaptations for stiff-legged arboreal bipedality

Cost of gap crossing in orangutans



De	Rehabilitant Mother	Rehabilitant Mother & infant	Wild Sub-adult male
Est	40	43	55
Est	7.2	7.1	7.9
Ma	0.61	0.58	1.46
Fre of	0.49	0.51	0.37
Fre uency ithout ape, *f* Hz	0.88	0.89	(0.88)
Ha cycle garithmic decrement, δ	0.073	(0.073)*	(0.073)
Sti ness o ee, *S* N/m	550	657	361
Eff ctive n ss of tree, *m* kg	18.0	21.0	11.8
Pe k strai	102	111	385
Fra tional s vib tions	0.08	0.08	0.06
Nu ber of	3.5	4.5	4.5
Wo k requ	**0.12**	**0.13**	**0.44**
Work for a jump, kJ **Work to climb to height *h*, kJ**	**0.25** **2.8**	**0.25** **3.0**	**1.31** **4.3**