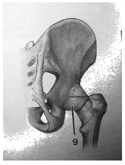
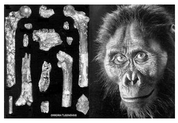
Evolución de la bipedestación: aspectos biomecánicos, energéticos y evidencia del registro fosil



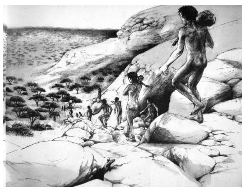


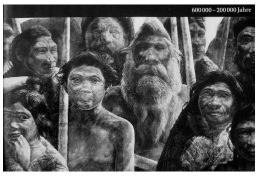
0_ Discusión de hipótesis que proponen causas de bipedestación

1_ Condiciones biomecánicas de bipedestación: Anatomía comparada de antropoides; pelvis + extremidades posteriores

2_ Eficiencia energética de la marcha bípeda

3_ Evidencia del registro fósil: Estados transicionales de marcha bipeda facultativa en homínidos (*Ardipithecus ramidus)*





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GENETICA, ICBM, FACMED + ANTROPOLOGIA FISICA, FACSO; UCHILE
2012

Sitios y recursos (aporte Thomas Püschel)

Liebermann web site

http://www.fas.harvard.edu/~skeleton/PDFList.html

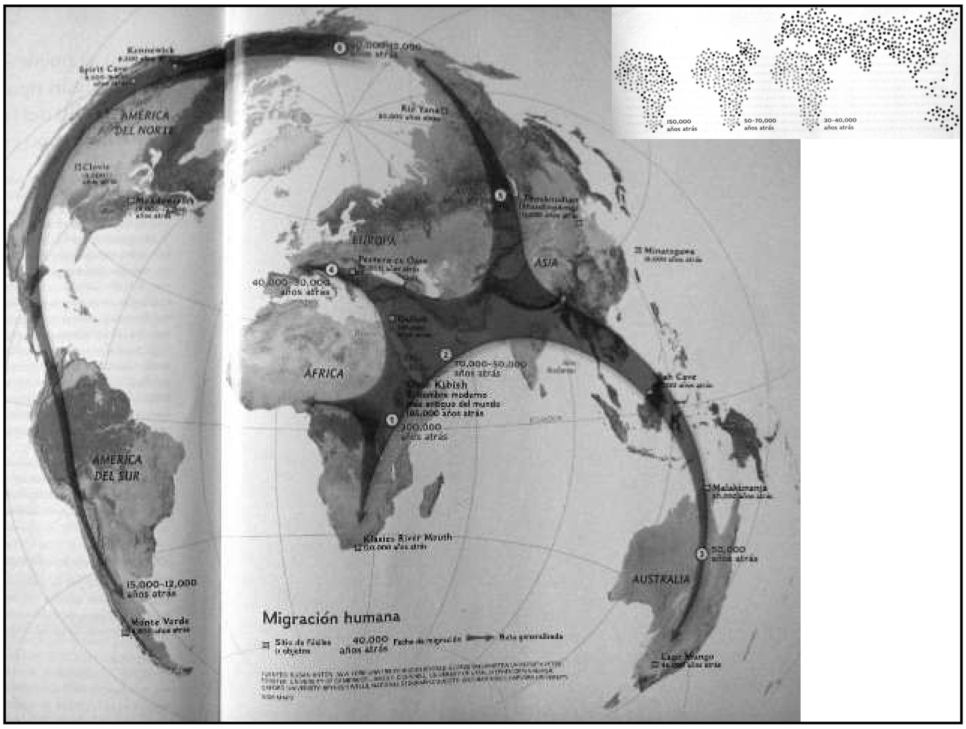
Video sobre caza de persistencia: http://www.youtube.com/watch?v=826HMLoiE_o

Video de Lieberman para Nature: http://www.youtube.com/watch?v=7jrnj-7YKZE

Recursos disponibles en el animal simulation laboratory: http://www.animalsimulation.org/

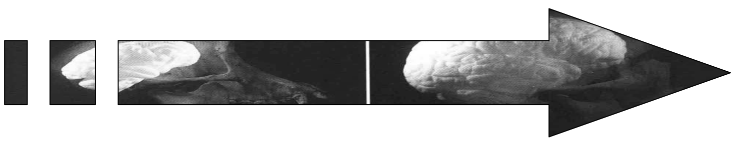
Texto

Aiello, L., Dean, M.C., 1990. *An Introduction to Human Evolutionary Anatomy*. Academic Press, London.



Evolución de la bipedestación: su lugar en la escala de tiempo del linaje homínido

Bipedestación obligada y estación ortógrada	Reducción tamaño dentario	Encefalización	Lenguaje



Novedades evolutivas en el linaje de los homínidos

6-4 My	4-2 My	2 My	200 Ky

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Evolución de la bipedestación: Hipótesis

Hipótesis que buscan entender bipedestación. Todas ellas afirman que es una forma de locomoción exitosa en la evolución, porque:

Es energéticamente más eficiente

Facilita la obtención de alimento

Mejora capacidad de cuidado de las crías

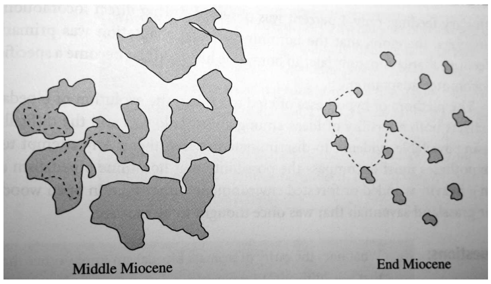
Ayuda a huír de los predadores con mayor rapidez

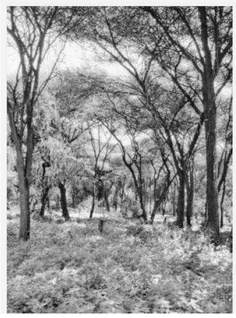
Optimiza las migraciones en manada

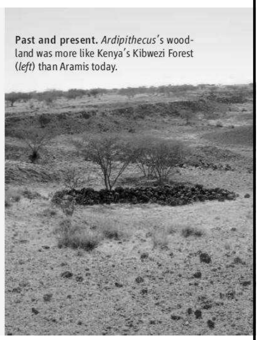
Permite liberación de las manos

Estas hipótesis solo tienen sentido a la luz de los grandes cambio climáticos y ecológicos que ocurren en el Mioceno tardío y Plioceno (5 My)

Ocurre un enfriamiento global con breves período (no más de 15Ky) de desglaciación. La vegetación en Africa se caracterizó por un clima más seco, con aumento significativo de los pastizales dando origen a la actual sabana.







Evolución de la bipedestación: Robustez de las hipótesis

Hipótesis que buscan entender bipedestación. Todas ellas afirman que es una forma de locomoción exitosa en la evolución, porque:

<u>Es energéticamente más eficiente</u>

Facilita la obtención de alimento

Mejora capacidad de cuidado de las crías

Ayuda a huír de los predadores con mayor rapidez

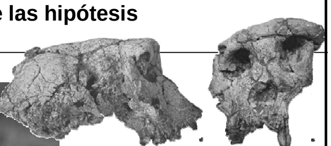
<u>Optimiza las migraciones en manada</u>

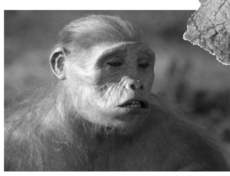
Radiación adaptativa de los artiodáctilos (camélidos, bóvidos, cérvidos, etc), fitófagos, pacedores, con sistemas digestivos y dentición de rumiante, conducta de manada.

Primeros fósiles de homínidos (aprox. 6My): *Sahelanthropus tchadensis* y *Orrorin tugenensis*.

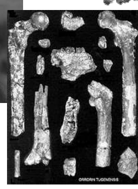
****

La hipótesis adaptacionista que no puede ser contrastada: *Bipedestación como necesidad para liberar las manos*

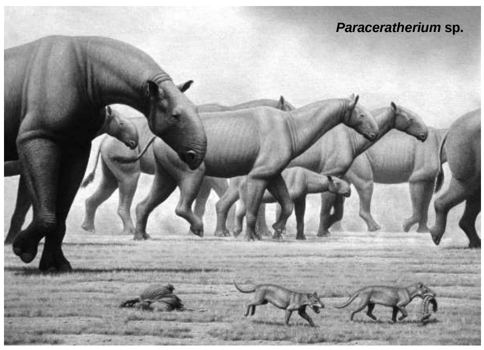




Sahelanthropus tchadensis



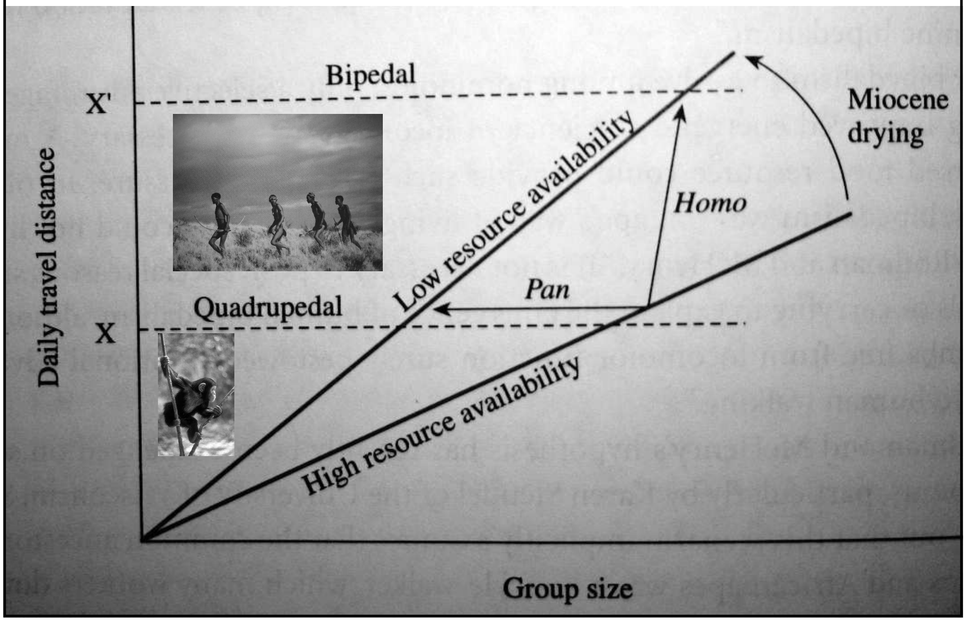
***Orrorin tugenensis*.**



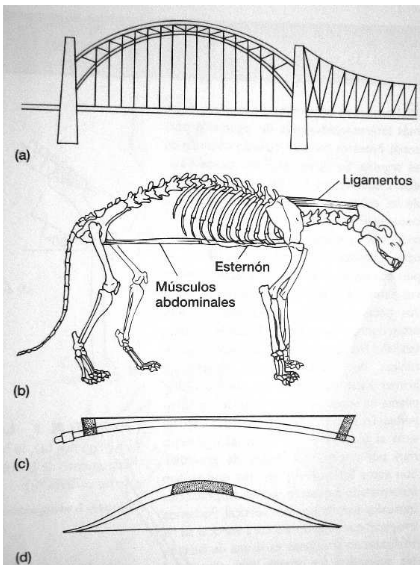
***Paraceratherium* sp.**

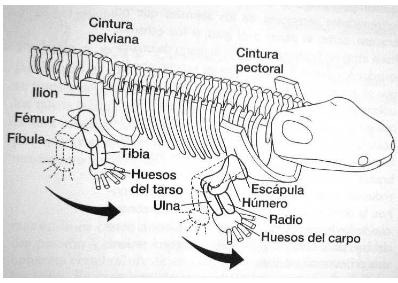
Evolución de la bipedestación: Robustez de las hipótesis

Es energéticamente más eficiente y optimiza migraciones en manadas



Evolución de la bipedestación: Condiciones biomecánicas





Analogías estructurales

Tetrápodo = Puente

Patas = Pilares (Compresión)

Vértebras = vía

Músculos y ligamentos =cadenas (Tensión)

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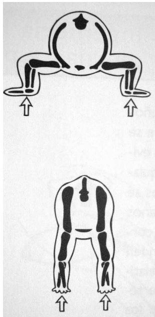
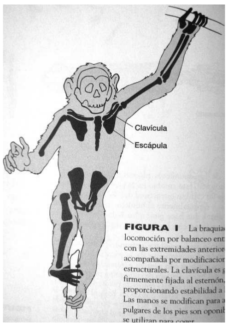
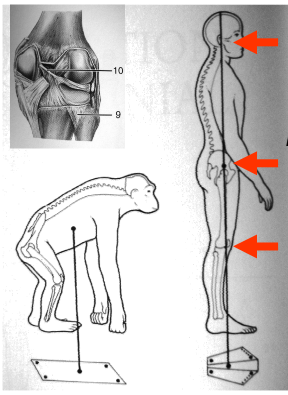
Evolución de la bipedestación: Condiciones biomecánicas



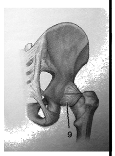


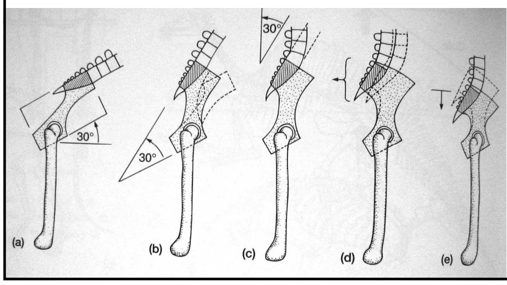


ligamentum ischiofemoralis

ligamentum capitis fibulae posterious

ligamentum meniscofemoralis posterious





Centro de gravedad y musculatura asociada: principales diferencias anatómicas asociadas con posición del foramen magno, presencia de ligamentos pélvicos y fíbulo-femorales

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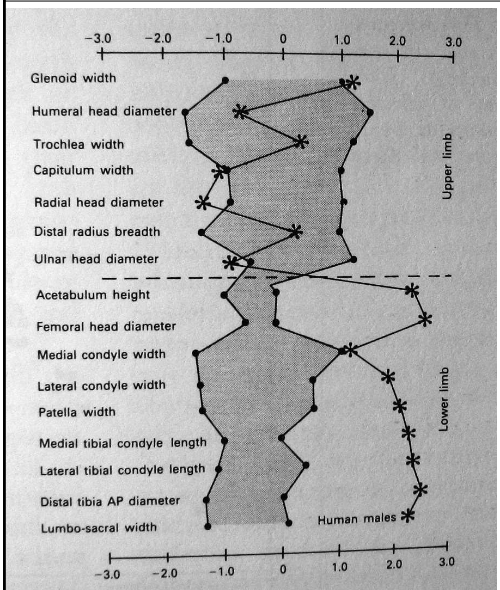
Condiciones biomecánicas de la postura ortógrada y de la marcha bípeda obligada (pelvis + extremidades posteriores)



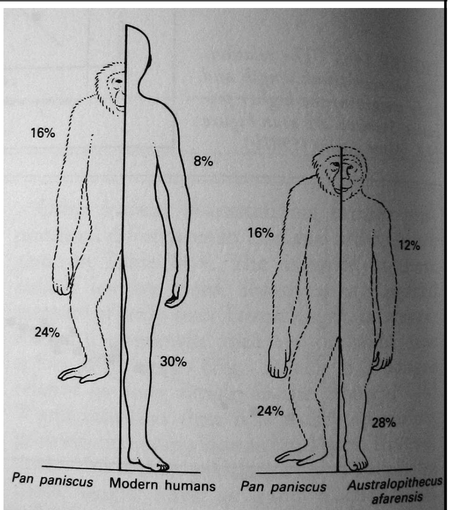
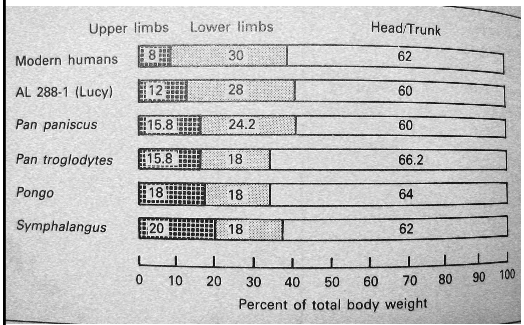
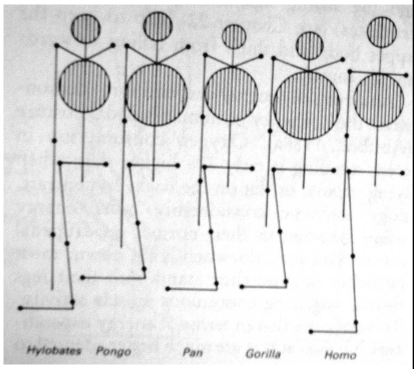


FIGURE 14·13 *Body proportions in modern humans and the pygmy chimpanzee (Pan paniscus) compared to the inferred proportions for 'Lucy'. After Ziblman (1984).*

Condiciones biomecánicas de la postura ortógrada y de la marcha bípeda obligada
(pelvis + extremidades posteriores)

b) Las principales diferencias están en forma, tamaño, y proporción relativa de los huesos del esqueleto apendicular, que dan soporte pero además son palanca biomecánica



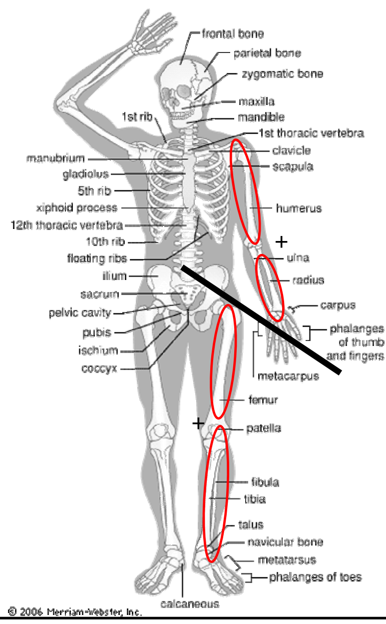


Condiciones biomecánicas de la postura ortógrada y de la marcha bípeda obligada
(pelvis + extremidades posteriores)

TABLE 14·3 Ontogenetic changes in body proportions in humans and the apes. Indices are determined on the basis of external measurements on cadavers and not on the basis of bone lengths. After Schultz (1956).

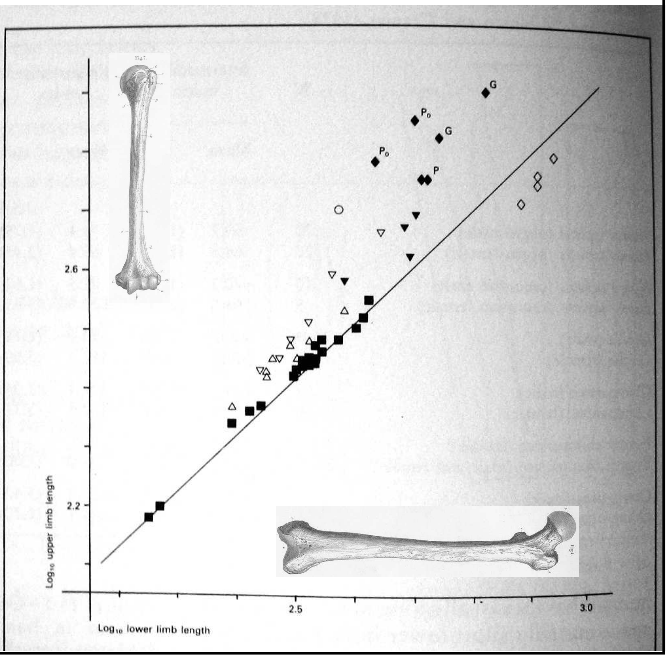
		N	Intermembral index[a]	Crural index[b]	Brachial index[c]
Hylobates	ad	80	165	85	108
Hylobates	nb	2	154	80	96
Symphalangus	ad	9	178	84	107
Symphalangus	nb	2	172	80	93
Pongo	ad	13	172	88	99
Pongo	nb	4	174	84	94
Pan	ad	30	136	83	91
Pan	nb	17	146	83	89
Gorilla	ad	5	138	83	80
Gorilla	nb	2	147	78	83
Homo	ad	25	88	83	76
Homo	nb	20	104	79	80

nb = new born, ad = adult.
[a]Intermembral index = [(total upper limb length × 100)/total lower limb length] where total upper limb length includes the length of the hand and total lower limb length includes the thickness of the sole of the foot.
[b]Crural index = [(leg length × 100)/thigh length] where leg length excludes the foot.
[c]Brachial index = [(forearm length × 100)/upper arm length] where forearm length excludes the length of the hand.



Condiciones biomecánicas de la postura ortógrada y de la marcha bípeda obligada
(pelvis + extremidades posteriores)

FIGURE 14·6 *The length of the lower limb in relation to the length of the upper limb in higher primates. Males and females of each species plotted separately. (■) = arboreal Old World monkeys; (▼) = baboons; (△) = macaques; (▽) = New World monkeys; (○) = gibbons; (◆) = great apes; (◇) = humans (caucasian and black). Po = orang-utan, P = chimpanzee, G = gorilla. The principal axis line is based on arboreal Old World monkeys. After Aiello (1981b).*



Anatomía comparada de antropoides; pelvis + extremidades posteriores:
Condiciones anatómicas de la postura ortógrada y de la marcha bípeda obligada

Diferencias en estructura de vértebras cervicales

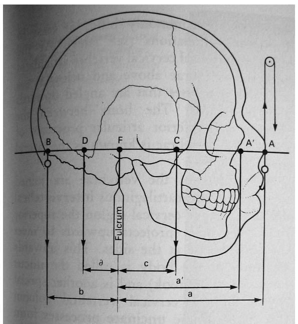


FIGURE 12·3 *Lateral view of a human head (with the skull outlined) mounted on a fulcrum (F) at the midpoint of the occipital condyles. Various lever systems about this axis are illustrated. C is the centre of gravity of the precondylar portion of the head and D is the centre of gravity of the postcondylar portion of the head. A is the most anterior point on the face, A' in the plane of prosthion and B inion. After Schultz (1942).*

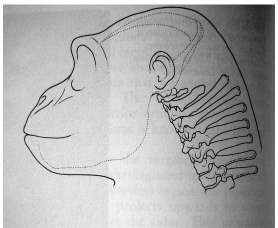


FIGURE 12·8 *The cervical vertebrae of a gorilla (C1 to C7) together with two thoracic vertebrae (T1 and T2) seen in lateral view. After Willoughby (1978).*

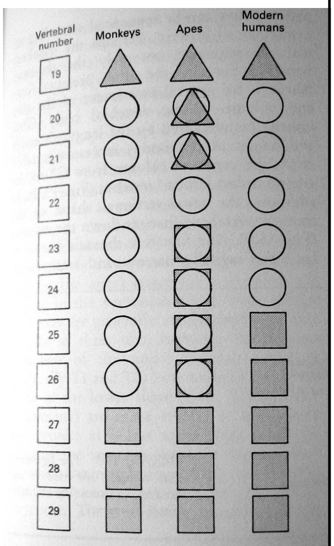


FIGURE 15·6 *The 19th to the 29th vertebrae in monkeys, apes and humans. (△) = Thoracic vertebrae; (○) = lumbar vertebrae; (□) = sacral vertebrae. Superimposed symbols indicate variation within the apes. After Abitbol (1987b).*

1_ Anatomía comparada de antropoides; pelvis + extremidades posteriores:
Condiciones anatómicas de la postura ortógrada y de la marcha bípeda obligada

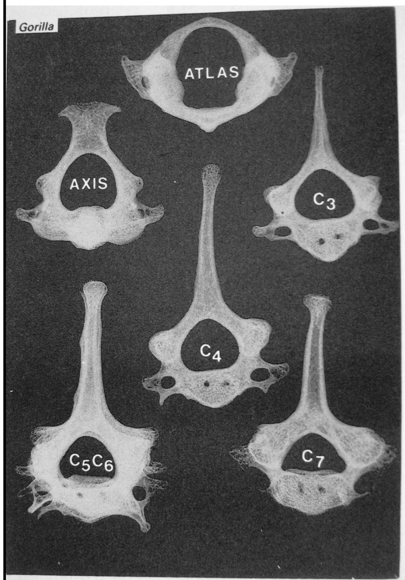
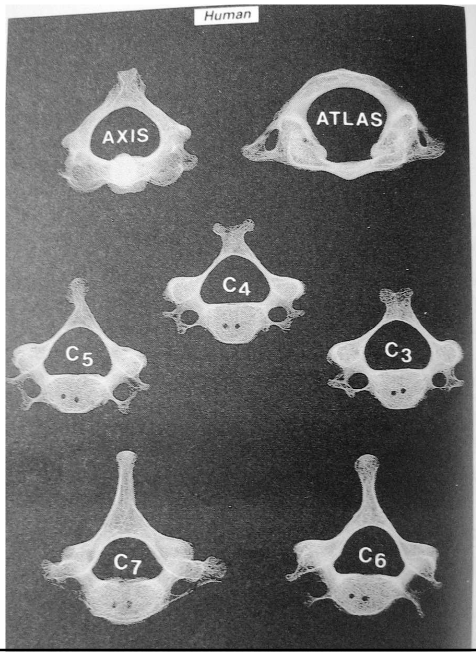
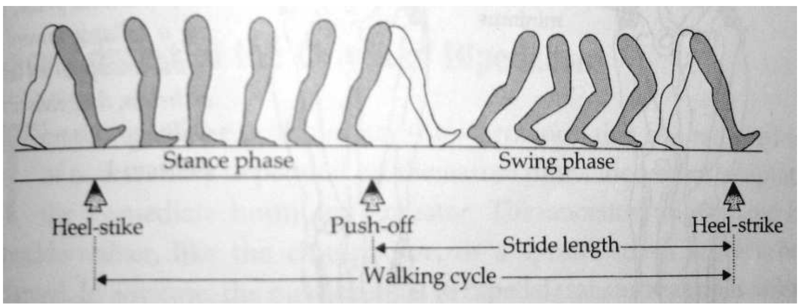


FIGURE 12·9 *Disarticulated cervical vertebrae from a modern human and a female gorilla. Note there is congenital fusion of the gorilla C5 and C6.*



Evolución de la bipedestación: Aspectos energéticos

Pero ¿Cómo lograrlo de manera óptima? ¿Es energéticamente más eficiente la marcha bípeda de H. sapines que la marcha tetrápoda obligada de otros primates?



Evolución de la bipedestación: Aspectos energéticos (Lieberman et al, 2010)

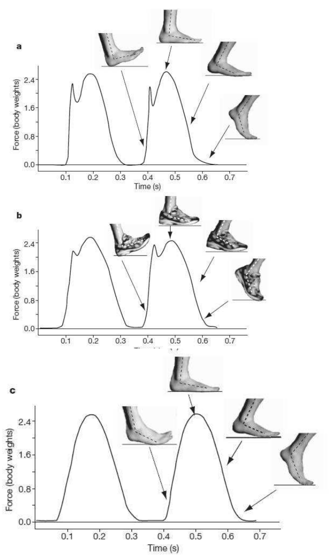
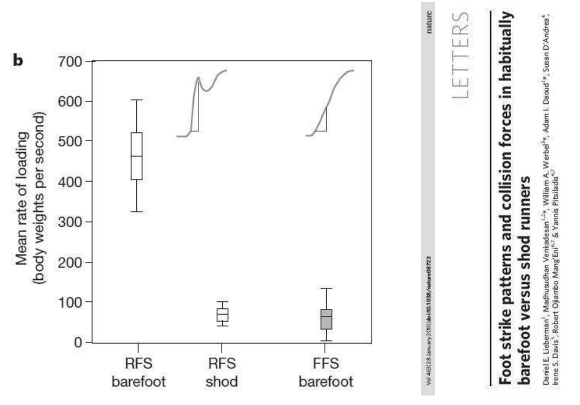


Figure 1 | Vertical ground reaction forces and foot kinematics for three foot strikes at 3.5 m s^{-1} in the same runner. a, RFS during barefoot heel–toe running; **b**, RFS during shod heel–toe running; **c**, FFS during barefoot toe–heel–toe running. Both RFS gaits generate an impact transient, but shoes slow the transient's rate of loading and lower its magnitude. FFS generates no impact transient even in the barefoot condition.



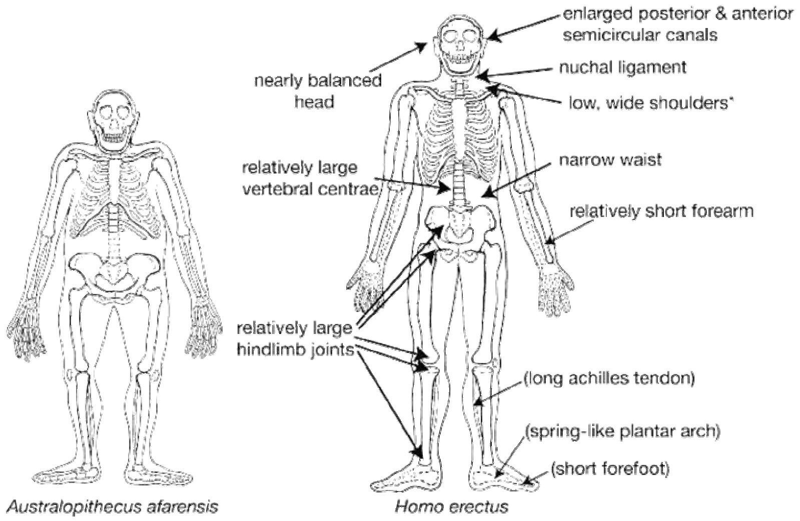
Differences between RFS and FFS running make sense from an evolutionary perspective. If endurance running was an important behaviour before the invention of modern shoes, then natural selection is expected to have operated to lower the risk of injury and discomfort when barefoot or in minimal footwear. Most shod runners today land on their heels almost exclusively. In contrast, runners who cannot or prefer not to use cushioned shoes with elevated heels often avoid RFS landings and thus experience lower impact transients than do most shod runners today, even on very stiff surfaces (Fig. 2). Early

Evolución de la bipedestación: Aspectos energéticos (Lieberman et al, 2009)

Importancia evolutiva de los caracteres derivados en *H. erectus*, ausentes en *A. afarensis*

Aumento en la eficiencia locomotora y de resistencia en la carrera,

Capacidad de termoregulación en condiciones de climas secos calientes y áridos



Evolución de la bipedestación: Aspectos energéticos (Lieberman et al, 2006)

El centro de gravedad cambia y se desplaza hacia delante durante la carrera, aumentando al energía potencial acumulada con cada nuevo salto

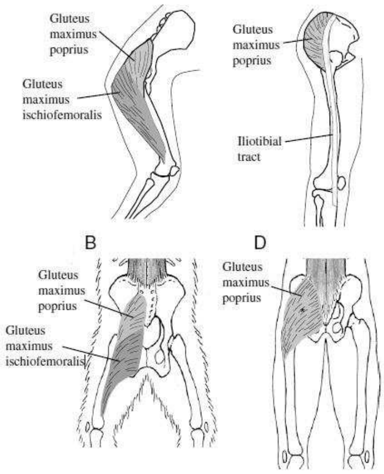
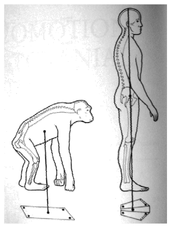
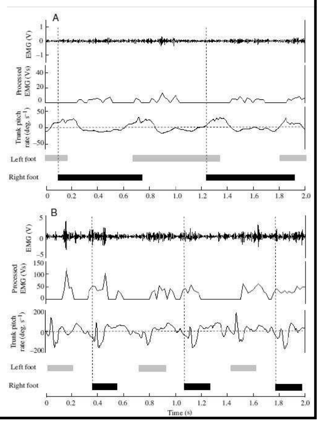


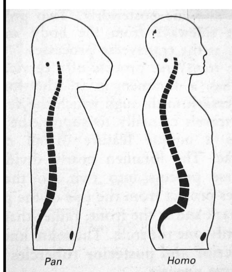
Fig. 1. Comparison of gluteus maximus anatomy in *Pan troglodytes* (A,B) and *Homo sapiens* (C,D). Note that the gluteus maximus in *Pan* has a cranial component, the gluteus maximus proprius (GMP), and a caudal component, the gluteus maximus ischiofemoralis (GMIF); humans have just the GMP, but it functions primarily like the ape GMIF. The GMP in humans is much thicker and larger than either portion of the GM in apes. The asterisk indicates the approximate location of GM electrodes used in this study.

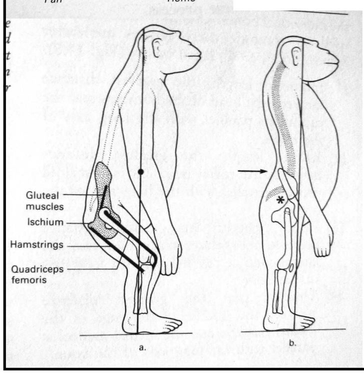


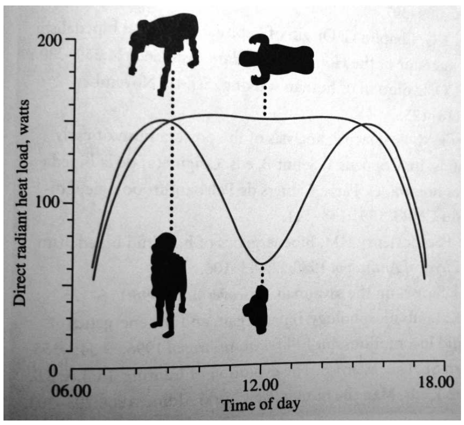


Evolución de la bipedestación: Aspectos energéticos (Aiello & Dean, 1990)

Diferencias en costo energético de la postura ortógrada

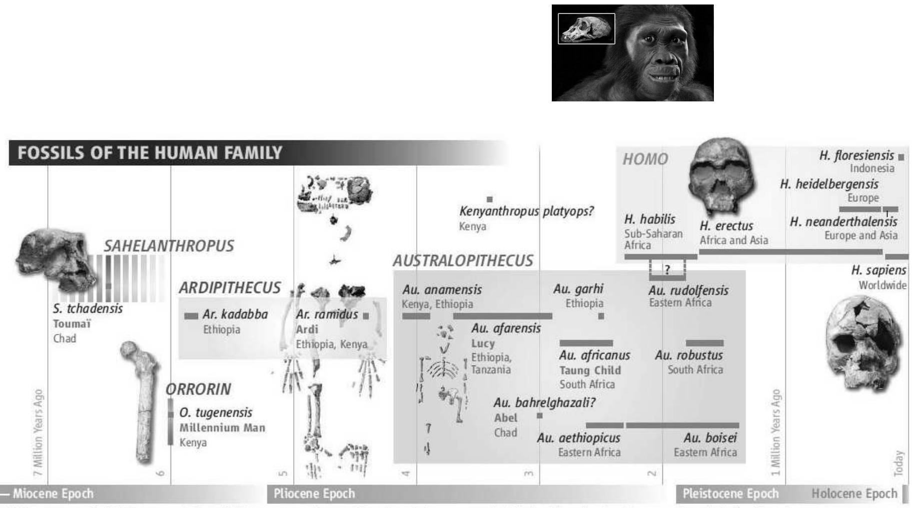






La postura ortógrada es energéticamente eficiente en *Homo sapiens*: sólo 7% de diferencia en gasto energético de pie que acostado

Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009



Filling a gap. *Ardipithecus* provides a link between earlier and later hominins, as seen in this timeline showing important hominin fossils and taxa.

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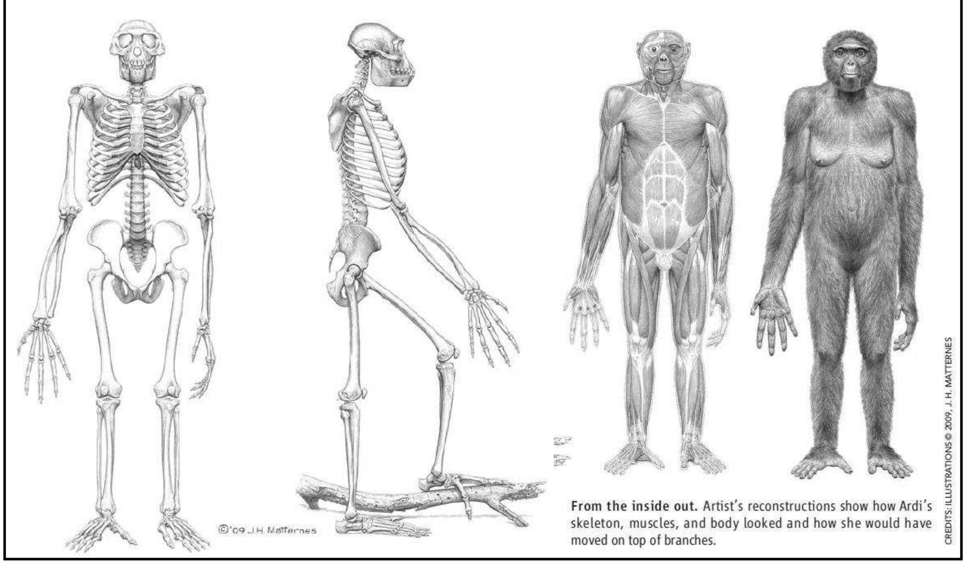
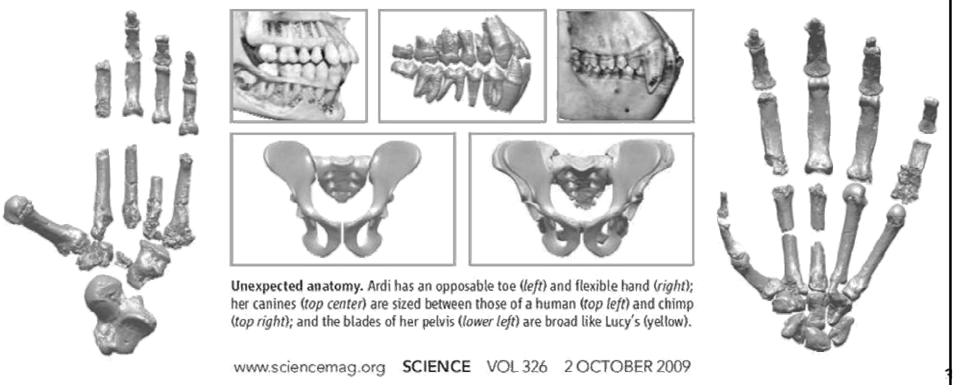
Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009



From the inside out. Artist's reconstructions show how Ardi's skeleton, muscles, and body looked and how she would have moved on top of branches.

Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009

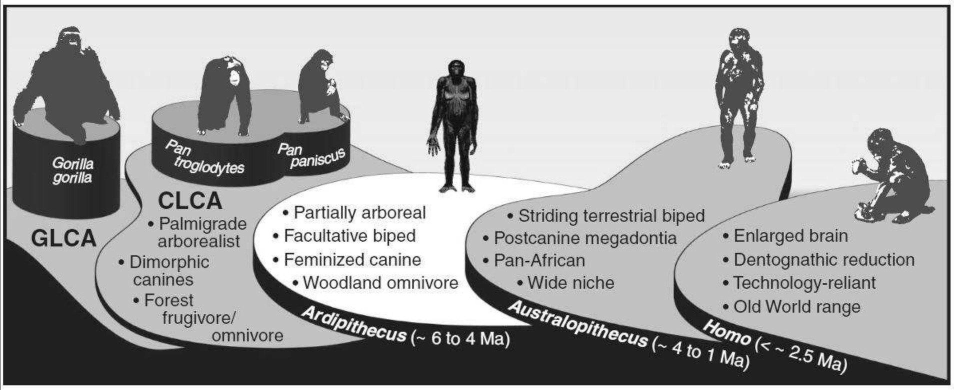


Manos: *Ardipithecus ramidus* (izq), *Homo sapiens* (der)

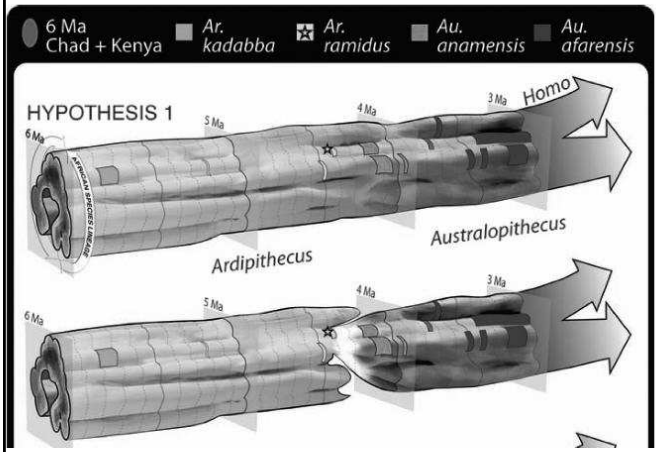
Caninos: *H. sapiens* (izq), *A. ramidus* (centro), Pan troglodytes (der)

Pelvis: *A. ramidus* (izq), *A. afarensis* sobrepuesta (en amarillo)

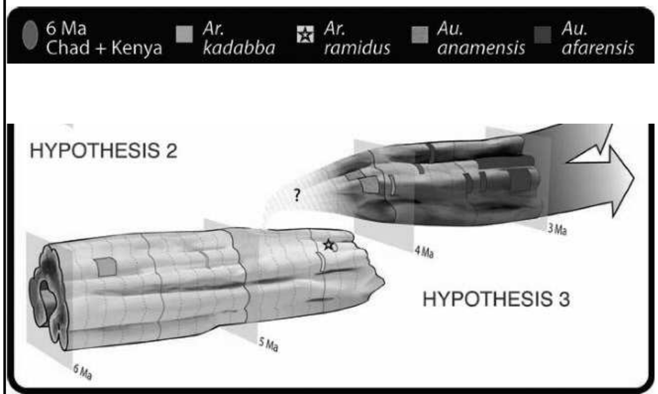
2_ Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009



Evolution of hominids and African apes since the gorilla/chimp+human (GLCA) and chimp/human (CLCA) last common ancestors. Pedestals on the left show separate lineages leading to the extant apes (gorilla, and chimp and bonobo); text indicates key differences among adaptive plateaus occupied by the three hominid genera.

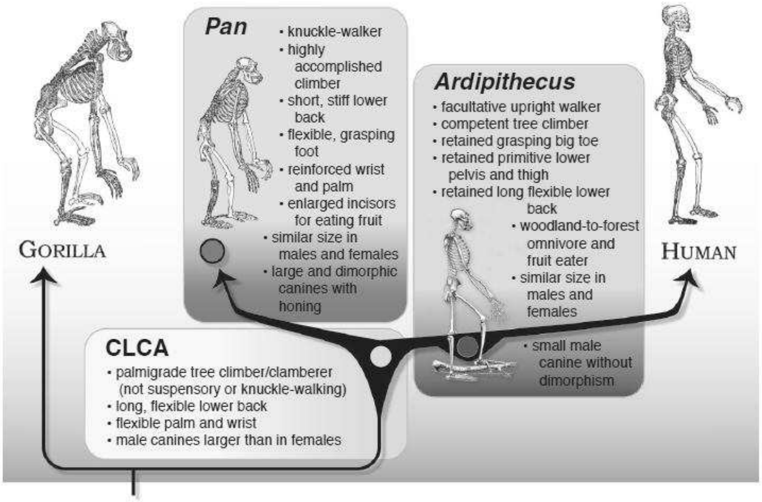


Hypothesis 1 interprets all known evidence to represent a species lineage evolving phyletically across its entire range. Hypothesis 2 depicts the same evidence in an *Ardipithecus*-to-*Australopithecus* transition (speciation) occurring between ~4.5 and ~4.2 Ma in a regional (or local) group of populations that might have included either or both the Afar and Turkana rifts.



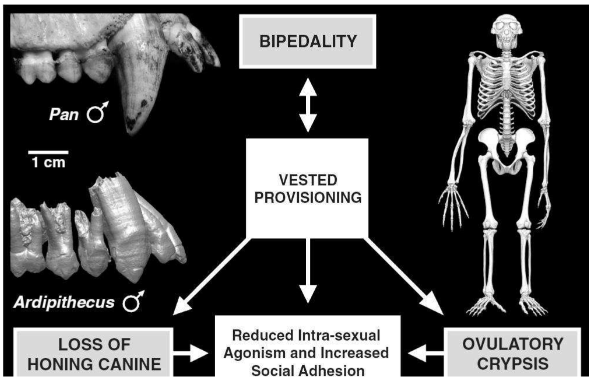
Hypothesis 3 accommodates the same evidence to an alternative, much earlier peripheral allopatric "rectangular" speciation model (cladogenesis through microevolution accumulated in a peripheral isolate population, becoming reproductively separated). Other possibilities exist, but at the present time, none of these hypotheses can be falsified based on the available evidence. To choose among them will require more fossil evidence, including well-documented transitions in multiple geographic locales. See the text [and (7)] for details.

2_ Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009



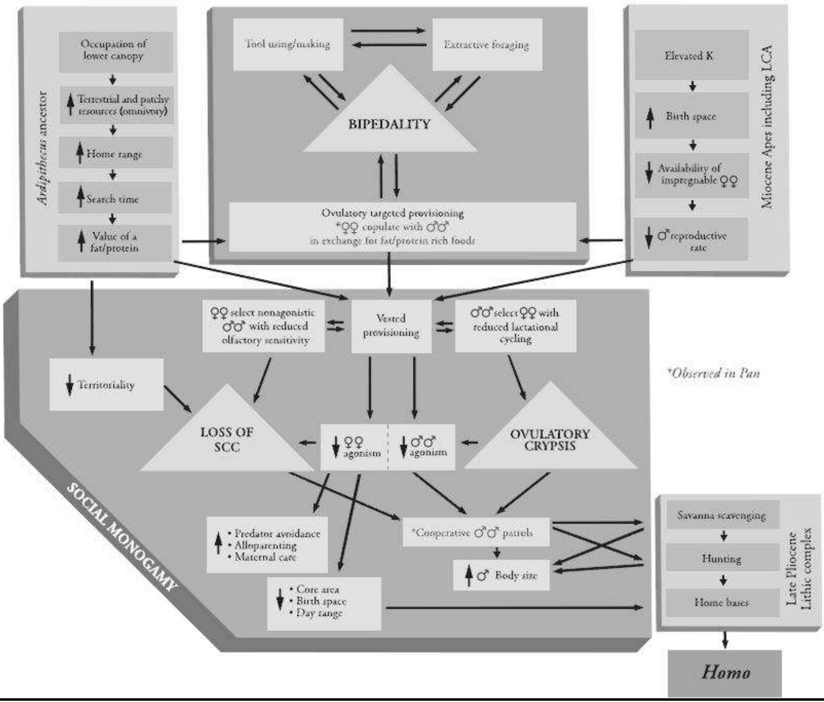
Cladogram adding *Ar. ramidus* to images of gorilla, chimpanzee, and human, taken from the frontispiece of *Evidence as to Man's Place in Nature*, by Thomas H. Huxley (London, 1863) (with the positions of *Gorilla* and *Pan* reversed to reflect current genetic data). Numerous details of the *Ar. ramidus* skeleton confirm that extant African apes do not much resemble our last common ancestor(s) with them.

2_ Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009



Breakthrough adaptations can transform life-history by deviating from typical reproductive strategy. Early hominids show feminized male canines (left) and primitive bipedality (right). These suggest that females preferred nonaggressive males who gained reproductive success by obtaining copulation in exchange for valuable foods (vested provisioning). Success would depend on copulatory frequency with mates whose fertility remained cryptic (e.g., absence of cycling in mammary size). The result would be reduced agonism in unrelated females, and cooperative expansion of day ranges among equally cooperative males, eventually leading to exploitation of new habitats. Credit: Illustration of Ar. ramidus: copyright J. H. Matternes.

Lovejoy, CO (2009) Authors' Summary: Reexamining Human Origins in Light of Ardipithecus ramidus Science 2 October 2009: vol. 326 no. 5949 pp. 74-74e8



2_ Estados transicionales de marcha bipeda facultativa en homínidos; *Ardipithecus ramidus: Science*, October 2th, 2009

Table S3
Hindlimb, forelimb, Mc4, and manual phalangeal lengths and indexes normalized by body mass vicar in fossil and extant anthropoids, and by body mass in extant anthropoids

Taxon	Intermem. Index	Forelimb/ Normalizer§	Hindlimb/ Normalizer§	Phalanx‖/ Normalizer§	Mc4/ Normalizer§	Forelimb/ Mass$^{(.33)}$§	Hindlimb/ Mass$^{(.33)}$§	Phalanx‖/ Mass$^{(.33)}$§	Mc4/ Mass$^{(.33)}$§
Ar. ramidus	89-91†	31.2	34.6	2.4	3.5	143.1‡	154.7–157.7‡	10.9‡	16.1‡
Au. afarensis	87-89†	34.7	38-40†			147.0‡	165.6–168.0‡		
Proconsul	86.9¶								
OWM	88	36.4 (2.8)	40.1 (2.7)	2.4 (.33)	4.4 (.32)	151.1 (15.6)	173.0 (17.6)	10.5 (1.6)	18.3 (2.4)
NWM	100	43.2 (4.5)	42.8 (3.7)	3.5 (.23)	5.0 (.88)	173.2 (30.6)	178.9 (28.2)	14.5 (2.3)	20.0 (4.8)
Homo	69*	27.8 (1.4)	39.6 (2.0)	1.7 (.08)	2.9 (.20)	134.9	193.7	8.4	13.9
Pan	106*	34.3 (1.8)	32.6 (1.9)	2.7 (.17)	4.8 (.27)	159.9	147.3	12.3	22.2
Gorilla	114*	34.0 (2.2)	29.3 (1.6)	2.2 (.12)	4.1 (.24)	152.1	132.7	9.6	18.2
Pongo	138	42.5 (3.0)	30.1 (2.1)	3.5 (.24)	5.8 (.34)	191.9	139.5	15.9	26.3
Hylobates	130	62.0	47.9	4.6	7.2	278.1	218.2	19.7	31.1

*Hominoid taxa differ from one another by t-test at P < .0001

Table 1. The assembly of shared derived characters among early hominid taxa.

Craniomandibular characters	**Chimp/human LCA (INFERRED)**	***Ar. kadabba/Sa. tchadensis/ O. tugenensis***	***Ar. ramidus***	***Au. anamensis***	***Au. afarensis***
TMJ articular eminence	flat	flat	flat	TMJ with defined eminence	TMJ with defined eminence
Mandible corpus breadth	indeterminate	mandibular corpus broad	mandibular corpus broad	mandibular corpus broad	mandibular corpus broad
Mental foramen	indeterminate	circum mid-corpus ht	circum mid-corpus ht	circum mid-corpus ht	secondarily lowered
Mandibular lateral prominence	weak	weak	weak	intermediate	lateral prominence developed
Ramus root/ extramolar sulcus	root posterior, sulcus narrow	root posterior, sulcus narrow	root posterior, sulcus narrow	intermediate	ramus root anterior and wide extramolar sulcus
Symphyseal inclination	strong	strong	strong	strong	bulbous (Laet.) to vertical (AL, M
Basion position	slightly posterior	anterior	anterior	indeterminate	anterior
Cranial base flexion	moderate midsagittal flexion, orbital kyphosis minimal	advanced?	advanced	indeterminate	advanced
Midfacial breadth	not extreme	not extreme	not extreme	indeterminate	midfacial breadth greater
Zygomatic root	zygomatic root c. M1	zygomatic root c. M1	zygomatic root c. M1	zygomatic root more anterior	zygomatic root more anterior
Incisor/lower canine step	present	indeterminate	present	absent	absent
Postcranial characters	**Chimp/human LCA (INFERRED)**	***Ar. kadabba/Sa. tchadensis/ O. tugenensis***	***Ar. ramidus***	***Au. anamensis***	***Au. afarensis***
Iliac isthmus	superoinferiorly long	indeterminate	short	indeterminate	short
Pubic symphysis outline	superioinferiorly long	indeterminate	short	indeterminate	short
Ilium/iliac isthmus orientation	coronal	indeterminate	sagittal	indeterminate	sagittal
Iliac breadth	moderately broad	indeterminate	slightly broadened	indeterminate	further broadened with expanded sciatic notch
Anterior inferior iliac spine	not developed	indeterminate	strong, formed by separate ossification center	indeterminate	strong, formed by separate ossification center
Pubic ramus	mediolaterally short	indeterminate	mediolaterally short	indeterminate	elongated
Ischium	long	indeterminate	long	indeterminate	abbreviated
Ischial tuberosity	not angulated	indeterminate	not angulated (INFERRED)	indeterminate	angulated
Greater sciatic notch	not developed	indeterminate	weak	indeterminate	well-developed
Femoral hypotrochanteric fossa	lacks true fossa	lacks true fossa	lacks true fossa	intermediate?	true fossa
Third trochanter and gluteal ridge	strong/rugose 3rd trochanter leading to laterally placed gluteal line	strong/rugose 3rd trochanter leading to laterally placed gluteal line	3rd trochanter weaker but same pattern	3rd trochanter weaker but same pattern	3rd trochanter localized, gluteal line angles medially
Femoral linea aspera	widely spaced med and lat lips	widely spaced med and lat lips	widely spaced med and lat lips	widely spaced med and lat lips	usually true linea aspera
Femoral neck cortical distribution	superior cortex relatively thick	superior cortex relatively thick	indeterminate	indeterminate	superior cortex relatively thin
Hallux	fully abductable, no dorsal doming	indeterminate	fully abductable, no dorsal doming	indeterminate	permanent adduction of hallux, dorsal doming
Second metatarsal	not robust	indeterminate	shaft and base robust	indeterminate	secondary gracilization
Metatarsal heads (rays 2–5)	limited dorsal doming	indeterminate	dorsally domed (Mt3 known)	indeterminate	dorsally domed
Proximal foot phalangeal cant	proximal orientation	indeterminate	upwardly canted	indeterminate	upwardly canted orientation
Trapezoid	mediolaterally narrow	indeterminate	mediolaterally narrow	indeterminate	broader
Capitate	head located palmarly	indeterminate	head located palmarly	head dorsalized and broader	head dorsalized and broader
Metacarpal heads	moderate dorsal constriction	indeterminate	weak, but constriction still seen	indeterminate	constriction lacking
Metacarpal distal end	moderate/strong proximal collateral ligament facets	indeterminate	intermediate?	indeterminate	weak collateral ligament grooves
Skeletal size dimorphism	weak	indeterminate	weak	indeterminate	moderate
Megadontia relative to body size	weak	indeterminate	weak	expressed (INFERRED)	distinct

← LCA → ← Hominid clade

Key: Primitive condition | Intermediate derived condition | Derived condition