Liste erstellt am 2013-11-10

Literatur

2013-11-12 Paläoklima

Aiello 2001

Leslie C. Aiello & Mark Collard, *Our newest oldest ancestor?* nature **410** (2001), 526–527.

These are exciting times in the study of human origins. But excitement needs to be tempered with caution in assessing the claim of a six-million-year-old direct ancestor of modern humans.
The announcement of Orrorin has caused a considerable stir. The authors also argue that Orrorin is on the direct line leading to modern humans, whereas most of the members of the genus Australopithecus are not.
Most palaeoanthropologists do not recognize a major dichotomy in hominin locomotor ability before the evolution of Homo ergaster, around 1.9 million years ago, and recent analyses of the A. anamensis skeleton suggest that it was much like that of other members of the genus Australopithecus. Senut's claim for more modern walking for Orrorin, linking it with Praeanthropus and Homo, is based on detailed aspects of the anatomy of the upper part of the thigh-bone that are open to alternative explanations.

Beauvilain 2008

Alain Beauvilain, *The contexts of discovery of Australopithecus bahrelghazali (Abel) and of Sahelanthropus tchadensis (Toumaï): unearthed, embedded in sandstone, or surface collected?* South African Journal of Science **104** (2008), 165–168.

The stratigraphic contexts of two important fossil hominid specimens from Chad have been repeatedly reported as being precisely known on the basis of their supposed in situ discovery. It is here demonstrated that neither of the fossils, the holotypes of Australopithecus bahrelghazali and Sahelanthropus tchadensis, was in situ at the time of discovery.

Beauvilain 2009

Alain Beauvilain & Jean-Pierre Watté, *Was Toumaï (Sahelanthropus tchadensis) buried?* Anthropologie **47** (2009), 1–6.

Was Toumaï (Sahelanthropus tchadensis) buried? Photographs taken when the skull of Toumai was discovered establish that the holotype of one of the earliest known hominid species was probably reburied in the recent past. Taphonomic analysis reveals the likelihood of one, perhaps two, burial(s) which seemingly occurred after the introduction of Islam in the region during the 11th century. Two other hominid fossils (a left femur and a mandible) were in the same "grave" along with various mammal remains.
Toumaï | Sahelanthropus | New fossils | Burial | Femur

Begun 2004

David R. Begun, *The Earliest Hominins, Is Less More?* science **303** (2004), 1478–1480.

BRUNET 2002

Michel Brunet et al., *A new hominid from the Upper Miocene of Chad, Central Africa.* nature **418** (2002), 145–151.

Michel Brunet, Franck Guy, David Pilbeam, Hassane Taisso Mackaye, Andossa Likius, Djimdoumalbaye Ahounta, Alain Beauvilain, Cécile Blondel, Hervé Bocherens, Jean-Renaud Boisserie, Louis De Bonis, Yves Coppens, Jean Dejax, Christiane Denys, Philippe Duringer, Véra Eisenmann, Gongdibé Fanone, Pierre Fronty, Denis Geraads, Thomas Lehmann, Fabrice Lihoreau, Antoine Louchart, Adoum Mahamat, Gildas Merceron, Guy Mouchelin, Olga Otero, Pablo Pelaez Campomanes, Marcia Ponce De Leon, Jean-Claude Rage, Michel Sapanet, Mathieu Schuster, Jean Sudre, Pascal Tassy, Xavier Valentin, Patrick Vignaud, Laurent Viriot, Antoine Zazzo & Christoph Zollikofer

The search for the earliest fossil evidence of the human lineage has been concentrated in East Africa. Here we report the discovery of six hominid specimens from Chad, central Africa, 2,500 km from the East African Rift Valley. The fossils include a nearly complete cranium and fragmentary lower jaws. The associated fauna suggest the fossils are between 6 and 7 million years old. The fossils display a unique mosaic of primitive and derived characters, and constitute a new genus and species of hominid. The distance from the Rift Valley, and the great antiquity of the fossils, suggest that the earliest members of the hominid clade were more widely distributed than has been thought, and that the divergence between the human and chimpanzee lineages was earlier than indicated by most molecular studies.

BRUNET 2005

Michel Brunet et al., *New material of the earliest hominid from the Upper Miocene of Chad.* nature **434** (2005), 752–755.

Michel Brunet, Franck Guy, David Pilbeam, Daniel E. Lieberman, Andossa Likius, Hassane T. Mackaye, Marcia S. Ponce de León, Christoph P. E. Zollikofer & Patrick Vignaud

Discoveries in Chad by the Mission Paléoanthropologique Franco-Tchadienne have substantially changed our understanding of early human evolution in Africa. In particular, the TM 266 locality in the Toros-Menalla fossiliferous area yielded a nearly complete cranium (TM 266-01-60-1), a mandible, and several isolated teeth assigned to Sahelanthropus tchadensis3 and biochronologically dated to the late Miocene epoch (about 7 million years ago). Despite the relative completeness of the TM 266 cranium, there has been some controversy about its morphology and its status in the hominid clade. Here we describe new dental and mandibular specimens from three Toros-Menalla (Chad) fossiliferous localities (TM 247, TM 266 and TM 292) of the same age. This new material, including a lower canine consistent with a non-honing C/P3 complex, post-canine teeth with primitive root morphology and intermediate radial enamel thickness, is attributed to S. tchadensis. It expands the hypodigm of the species and provides additional anatomical characters that confirm the morphological differences between S. tchadensis and African apes. S. tchadensis presents several key derived features consistent with its position in the hominid clade close to the last common ancestor of chimpanzees and humans.

BRUNET 2010

Michel Brunet, *Two new Mio-Pliocene Chadian hominids enlighten Charles Darwin's 1871 prediction.* Phil. Trans. Royal Society B **365** (2010), 3315–3321.

The idea of an evolutionary sequence for humans is quite recent. Over the last 150 years, we have discovered unexpected ancestors, numerous close relatives and our deep evolutionary roots in Africa. In the last decade, three Late Miocene hominids have been described, two about 6Ma (Ardipithecus and Orrorin) in East Africa and the third dated to about 7Ma (Sahelanthropus) in Central Africa. The specimens are too few to propose definite relationship to other species, but clearly these belong to a new evolutive grade distinct from Australopithecus and Homo. Moreover, all of them were probably habitual bipeds and lived in woodlands, thus falsifying the savannah hypothesis of human origins. In light of all this recent knowledge, Charles Darwin predicted correctly in 1871 that Africa is the birthplace of humans, chimpanzees and our close relatives.

Keywords: earliest hominids; central Africa; evolutionary grade; woodland origin

Cela-Conde 2003

Camilo J. Cela-Conde & Francisco J. Ayala, *Genera of the human lineage*. PNAS **100** (2003), 7684–7689.

Human fossils dated between 3.5 and nearly 7 million years old discovered during the last 8 years have been assigned to as many as four new genera of the family Hominidae: Ardipithecus, Orrorin, Kenyanthropus, and Sahelanthropus. These specimens are described as having morphological traits that justify placing them in the family Hominidae while creating a new genus for the classification of each. The discovery of these fossils pushed backward by >2 million years the date of the oldest hominids known. Only two or three hominid genera, Australopithecus, Paranthropus, and Homo, had been previously accepted, with Paranthropus considered a subgenus of Australopithecus by some authors. Two questions arise from the classification of the newly discovered fossils: (i) Should each one of these specimens be placed in the family Hominidae? (ii) Are these specimens sufficiently distinct to justify the creation of four new genera? The answers depend, in turn, on the concepts of what is a hominid and how the genus category is defined. These specimens seem to possess a sufficient number of morphological traits to be placed in the Hominidae. However, the nature of the morphological evidence and the adaptation-rooted concept of what a genus is do not justify the establishment of four new genera. We propose a classification that includes four well defined genera: Praeanthropus, Ardipithecus, Australopithecus, and Homo, plus one tentative incertae sedis genus: Sahelanthropus.

Cerling 2010

Thure E. Cerling et al., *Comment on the Paleoenvironment of Ardipithecus ramidus*. science **328** (2010), 1105d.

s328-1105e-Reply.pdf

Thure E. Cerling, Naomi E. Levin, Jay Quade, Jonathan G. Wynn, David L. Fox, John D. Kingston, Richard G. Klein, Francis H. Brown

White and colleagues (Research Articles, 2 October 2009, pp. 65-67 and www.sciencemag.org/ardipithecus) characterized the paleoenvironment of Ardipithecus ramidus at Aramis, Ethiopia, which they described as containing habitats ranging from woodland to forest patches. In contrast, we find the environmental context of Ar. ramidus at Aramis to be represented by what is commonly referred to as tree- or bush-savanna, with 25 % or less woody canopy cover.

Response by Tim D. White, Stanley H. Ambrose, Gen Suwa, Giday WoldeGabriel

Cerling et al. contest our interpretation of the woodland habitat preference of Ardipithecus ramidus. However, their reconstruction of a predominantly open grassy environment with riparian woodlands is inconsistent with the totality of the fossil, geological, and geochemical evidence. In the Middle Awash, Ar. ramidus fossils are confined to the western portion of the sampled Pliocene landscape where the species is associated with woodland to grassy woodland habitat indicators.

CROMPTON 2010

Robin Huw Crompton, William I. Sellers & Susannah K. S. Thorpe, *Arboreality, terrestriality and bipedalism.* Phil. Trans. Royal Society B **365** (2010), 3301–3314.

The full publication of Ardipithecus ramidus has particular importance for the origins of hominin bipedality, and strengthens the growing case for an arboreal origin. Palaeontological techniques however inevitably concentrate on details of fragmentary postcranial bones and can benefit from a whole-animal perspective. This can be provided by field studies of locomotor behaviour, which provide a real-world perspective of adaptive context, against which conclusions drawn from palaeontology and comparative osteology may be assessed and honed. Increasingly sophisticated dynamic modelling techniques, validated against experimental data for living animals, offer a different perspective where evolutionary and virtual ablation experiments, impossible for living mammals, may be run in silico, and these can analyse not only the interactions and behaviour of rigid segments but increasingly the effects of compliance, which are of crucial importance in guiding the evolution of an arboreally derived lineage.

Keywords: bipedalism; biomechanics; evolution; field studies

DESILVA 2009

Jeremy M. DeSilva, *Functional morphology of the ankle and the likelihood of climbing in early hominins.* PNAS **106** (2009), 6567–6572.

Whether early hominins were adept tree climbers is unclear. Although some researchers have argued that bipedality maladapts the hominin skeleton for climbing, others have argued that early hominin fossils display an amalgamation of features consistent with both locomotor strategies. Although chimpanzees have featured prominently in these arguments, there are no published data on the kinematics of climbing in wild chimpanzees. Without these biomechanical data describing how chimpanzees actually climb trees, identifying correlates of climbing in modern ape skeletons is difficult, thereby limiting accurate interpretations of the hominin fossil record. Here, the first kinematic data on vertical climbing in wild chimpanzees are presented. These data are used to identify skeletal correlates of climbing in the ankle joint of the African apes to more accurately interpret hominin distal tibiae and tali. This study finds that chimpanzees engage in an extraordinary range of foot dorsiflexion and inversion during vertical climbing bouts. Two skeletal correlates of modern ape-like vertical climbing are identified in the ankle joint and related to positions of dorsiflexion and foot inversion. A study of the 14 distal tibiae and 15 tali identified and published as hominins from 4.12 to 1.53 million years ago finds that the ankles of early hominins were poorly adapted for modern ape-like vertical climbing bouts. This study concludes that if hominins included tree climbing as part of their locomotor repertoire, then they were performing this activity in a manner decidedly unlike modern chimpanzees.

GALIK 2004

K. Galik, B. Senut, M. Pickford, D. Gommery, J. Treil, A. J. Kuperavage & R. B. Eckhardt, *External and Internal Morphology of the BAR 1002'00 Orrorin tugenensis Femur.* science **305** (2004), 1450–1453.

s305-1450-Supplement.pdf, s307-0845-Ohman.pdf

Late Miocene fossils from the Lukeino Formation in Kenya's Tugen Hills are assigned to Orrorin tugenensis. Of 20 fossils recovered there to date, 3are proximal femurs. One of these, BAR 1002'00, preserves an intact head connected to the proximal shaft by an elongated neck. Although this fossil is comparable in size to Pan troglodytes, computerized tomography scans of the neck-shaft junction of BAR 1002'00 reveal that the cortex is markedly thinner superiorly than inferiorly, differing from the approximately equal cortical thicknesses observed in extant African apes, approaching the condition in later hominids, and indicating that O. tugenensis was bipedal.

GIBBONS 2009

Ann Gibbons, *A New Kind of Ancestor: Ardipithecus Unveiled.* science **326** (2009), 36–40.

s326-0036-Supplement.flv

The oldest known hominin skeleton reveals the body plan of our very early ancestors and the upright origins of humankind

GUY 2005

Franck Guy et al., *Morphological affinities of the Sahelanthropus tchadensis (Late Miocene hominid from Chad) cranium.* PNAS **102** (2005), 18836–18841.

pnas102-18836-Table2.xls, pnas102-18836-Table3.xls, pnas102-18836-Table4.xls, pnas102-18836-Table5.xls

Franck Guy, Daniel E. Lieberman, David Pilbeam, Marcia Ponce de León, Andossa Likius, Hassane T. Mackaye, Patrick Vignaud, Christoph Zollikofer & Michel Brunet

The recent reconstruction of the Sahelanthropus tchadensis cranium (TM 266-01-60-1) provides an opportunity to examine in detail differences in cranial shape between this earliest-known hominid, African apes, and other hominid taxa. Here we compare the reconstruction of TM 266-01-60-1 with crania of African apes, humans, and several Pliocene hominids. The results not only confirm that TM 266-01-60-1 is a hominid but also reveal a unique mosaic of characters. The TM 266-01-60-1 reconstruction shares many primitive features with chimpanzees but overall is most similar to Australopithecus, particularly in the basicranium. However, TM 266-01-60-1 is distinctive in having the combination of a short subnasal region associated with a vertical upper face that projects substantially in front of the neurocranium. Further research is needed to determine the evolutionary relationships between Sahelanthropus and the known Miocene and Pliocene hominids.

geometric morphometric | 3D reconstruction | Homo | Australopithecus | African apes

HAILE-SELASSIE 2001

Yohannes Haile-Selassie, *Late Miocene hominids from the Middle Awash, Ethiopia.* nature **412** (2001), 178–181.

Molecular studies suggest that the lineages leading to humans and chimpanzees diverged approximately 6.5±5.5 million years (Myr) ago, in the Late Miocene. Hominid fossils from this interval, however, are fragmentary and of uncertain phylogenetic status, age, or both. Here I report new hominid specimens from the Middle Awash area of Ethiopia that date to 5.2±5.8Myr and are associated with a wooded palaeoenvironment. These Late Miocene fossils are assigned to the hominid genus Ardipithecus and represent the earliest de®nitive evidence of the hominid clade. Derived dental characters are shared exclusively with all younger hominids. This indicates that the fossils probably represent a hominid taxon that postdated the divergence of lineages leading to modern chimpanzees and humans. However, the persistence of primitive dental and postcranial characters in these new fossils indicates that Ardipithecus was phylogenetically close to the common ancestor of chimpanzees and humans. These new findings raise additional questions about the claimed hominid status of Orrorin tugenensis, recently described from Kenya and dated to ,6 Myr.

Haile-Selassie 2004

Yohannes Haile-Selassie, Gen Suwa & Tim D. White, *Late Miocene Teeth from Middle Awash, Ethiopia, and Early Hominid Dental Evolution*. science **303** (2004), 1503–1505.

Late Miocene fossil hominid teeth recovered from Ethiopia's Middle Awash are assigned to Ardipithecus kadabba. Their primitive morphology and wear pattern demonstrate that A. kadabba is distinct from Ardipithecus ramidus. These fossils suggest that the last common ancestor of apes and humans had a functionally honing canine–third premolar complex. Comparison with teeth of Sahelanthropus and Orrorin, the two other named late Miocene hominid genera, implies that these putative taxa are very similar to A. kadabba. It is therefore premature to posit extensive late Miocene hominid diversity on the basis of currently available samples.

Hanson 2009

Brooks Hanson, *Light on the Origin of Man*. science **326** (2009), 60–63.

This issue presents 11 papers authored by a diverse international team (see following pages) describing an early hominid species, Ardipithecus ramidus, and its environment. The hominid fossils are 4.4 million years old, within this critical early part of human evolution, and represent 36 or more individuals, including much of the skull, pelvis, lower arms, and feet from one female.

Harrison 2010

Terry Harrison, *Apes Among the Tangled Branches of Human Origins*. science **327** (2010), 532–534.

The evolution of apes between 23 and 5 million years ago set the scene for the emergence of the first hominins in Africa.

Lebatard 2008

Anne-Elisabeth Lebatard et al., *Cosmogenic nuclide dating of Sahelanthropus tchadensis and Australopithecus bahrelghazali: Mio-Pliocene hominids from Chad*. PNAS **105** (2008), 3226–3231.

Anne-Elisabeth Lebatard, Didier L. Bourlès, Philippe Duringer, Marc Jolivet, Régis Braucher, Julien Carcaillet, Mathieu Schuster, Nicolas Arnaud, Patrick Monié, Fabrice Lihoreau, Andossa Likius, Hassan Taisso Mackaye, Patrick Vignaud and Michel Brunet

Ages were determined at two hominid localities from the Chad Basin in the Djurab Desert (Northern Chad). In the Koro Toro fossiliferous area, KT 12 locality (16°00'N, 18°53'E) was the site of discovery of Australopithecus bahrelghazali (Abel) and in the Toros-Menalla fossiliferous area, TM 266 locality (16°15'N, 17°29'E) was the site of discovery of Sahelanthropus tchadensis (Toumaï). At both localities, the evolutive degree of the associated fossil mammal assemblages allowed a biochronological estimation of the hominid remains: early Pliocene (3–3.5 Ma) at KT 12 and late Miocene ($\approx$7 Ma) at TM 266. Atmospheric 10Be, a cosmogenic nuclide, was used to quasicontinuously date these sedimentary units. The authigenic 10Be/9Be dating of a pelite relic within the sedimentary level containing Abel yields an age of 3.58 ± 0.27 Ma that points to the contemporaneity of Australopithecus bahrelghazali (Abel) with Australopithecus afarensis (Lucy). The 28 10Be/

9Be ages obtained within the anthracotheriid unit containing Toumaï bracket, by absolute dating, the age of Sahelanthropus tchadensis to lie between 6.8 and 7.2 Ma. This chronological constraint is an important cornerstone both for establishing the earliest stages of hominid evolution and for new calibrations of the molecular clock.
beryllium-10 | absolute dating | hominid site | Abel | Toumaï

LOUCHART 2009

Antoine Louchart, Henry Wesselman, Robert J. Blumenschine, Leslea J. Hlusko, Jackson K. Njau, Michael T. Black, Mesfin Asnake,, *Taphonomic, Avian, and Small-Vertebrate Indicators of Ardipithecus ramidus Habitat.* science **326** (2009), 66–66e4.
s326-0066-Supplement.pdf
Thousands of vertebrate specimens were systematically collected from the stratigraphic interval containing Ardipithecus ramidus. The carcasses of larger mammals were heavily ravaged by carnivores. Nearly 10,000 small-mammal remains appear to be derived primarily from decomposed owl pellets. The rich avifauna includes at least 29 species, mostly nonaquatic forms. Modern analogs of the most abundant birds and of a variety of rodents are associated with mesic woodland environments distant from large water bodies. These findings support inferences from associated geological, isotopic, invertebrate, and large-vertebrate assemblages. The combined results suggest that Ar. ramidus occupied a wooded Pliocene habitat.

LOVEJOY 2009A

C. Owen Lovejoy, Scott W. Simpson, Tim D. White, Berhane Asfaw & Gen Suwa, *Careful Climbing in the Miocene: The Forelimbs of Ardipithecus ramidus and Humans Are Primitive.* science **326** (2009), 70–70e8.
s326-0070-Supplement.pdf
The Ardipithecus ramidus hand and wrist exhibit none of the derived mechanisms that restrict motion in extant great apes and are reminiscent of those of Miocene apes, such as Proconsul. The capitate head is more palmar than in all other known hominoids, permitting extreme midcarpal dorsiflexion. Ar. ramidus and all later hominids lack the carpometacarpal articular and ligamentous specializations of extant apes. Manual proportions are unlike those of any extant ape. Metacarpals 2 through 5 are relatively short, lacking any morphological traits associable with knuckle-walking. Humeral and ulnar characters are primitive and like those of later hominids. The Ar. ramidus forelimb complex implies palmigrady during bridging and careful climbing and exhibits none of the adaptations to vertical climbing, forelimb suspension, and knuckle-walking that are seen in extant African apes.

LOVEJOY 2009B

C. Owen Lovejoy, Gen Suwa, Linda Spurlock, Berhane Asfaw & Tim D. White, *The Pelvis and Femur of Ardipithecus ramidus: The Emergence of Upright Walking.* science **326** (2009), 71–71e6.
s326-0071-Supplement.pdf
The femur and pelvis of Ardipithecus ramidus have characters indicative of both upright bipedal walking and movement in trees. Consequently, bipedality in Ar. ramidus was more primitive than in later Australopithecus. Compared with monkeys and Early Miocene apes such as Proconsul, the ilium in Ar. ramidus is mediolaterally expanded, and its sacroiliac joint is located more posteriorly. These changes are shared with some Middle and Late Miocene apes as well as with African apes

and later hominids. However, in contrast to extant apes, bipedality in Ar. ramidus was facilitated by craniocaudal shortening of the ilium and enhanced lordotic recurvature of the lower spine. Given the predominant absence of derived traits in other skeletal regions of Ar. ramidus, including the forelimb, these adaptations were probably acquired shortly after divergence from our last common ancestor with chimpanzees. They therefore bear little or no functional relationship to the highly derived suspension, vertical climbing, knuckle-walking, and facultative bipedality of extant African apes.

LOVEJOY 2009C

C. Owen Lovejoy, Bruce Latimer, Gen Suwa, Berhane Asfaw & Tim D. White, *Combining Prehension and Propulsion: The Foot of Ardipithecus ramidus*. science **326** (2009), 72–72e8.

s326-0072-Supplement.pdf

Several elements of the Ardipithecus ramidus foot are preserved, primarily in the ARA-VP-6/500 partial skeleton. The foot has a widely abducent hallux, which was not propulsive during terrestrial bipedality. However, it lacks the highly derived tarsometatarsal laxity and inversion in extant African apes that provide maximum conformity to substrates during vertical climbing. Instead, it exhibits primitive characters that maintain plantar rigidity from foot-flat through toe-off, reminiscent of some Miocene apes and Old World monkeys. Moreover, the action of the fibularis longus muscle was more like its homolog in Old World monkeys than in African apes. Phalangeal lengths were most similar to those of Gorilla. The Ardipithecus gait pattern would thus have been unique among known primates. The last common ancestor of hominids and chimpanzees was therefore a careful climber that retained adaptations to above-branch plantigrady.

LOVEJOY 2009D

C. Owen Lovejoy, *Reexamining Human Origins in Light of Ardipithecus ramidus*. science **326** (2009), 74–74e8.

Referential models based on extant African apes have dominated reconstructions of early human evolution since Darwin’s time. These models visualize fundamental human behaviors as intensifications of behaviors observed in living chimpanzees and/or gorillas (for instance, upright feeding, male dominance displays, tool use, culture, hunting, and warfare). Ardipithecus essentially falsifies such models, because extant apes are highly derived relative to our last common ancestors. Moreover, uniquely derived hominid characters, especially those of locomotion and canine reduction, appear to have emerged shortly after the hominid/chimpanzee divergence. Hence, Ardipithecus provides a new window through which to view our clade’s earliest evolution and its ecological context. Early hominids and extant apes are remarkably divergent in many cardinal characters. We can no longer rely on homologies with African apes for accounts of our origins and must turn instead to general evolutionary theory. A proposed adaptive suite for the emergence of Ardipithecus from the last common ancestor that we shared with chimpanzees accounts for these principal ape/human differences, as well as the marked demographic success and cognitive efflorescence of later Plio-Pleistocene hominids.

LOVEJOY 2009E

C. Owen Lovejoy, Gen Suwa, Scott W. Simpson, Jay H. Matternes & Tim D. White, *The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes*. science **326** (2009), 73, 100–106.

s326-0073-Supplement.pdf

Genomic comparisons have established the chimpanzee and bonobo as our closest living relatives. However, the intricacies of gene regulation and expression caution against the use of these extant apes in deducing the anatomical structure of the last common ancestor that we shared with them. Evidence for this structure must therefore be sought from the fossil record. Until now, that record has provided few relevant data because available fossils were too recent or too incomplete. Evidence from Ardipithecus ramidus now suggests that the last common ancestor lacked the hand, foot, pelvic, vertebral, and limb structures and proportions specialized for suspension, vertical climbing, and knuckle-walking among extant African apes. If this hypothesis is correct, each extant African ape genus must have independently acquired these specializations from more generalized ancestors who still practiced careful arboreal climbing and bridging. African apes and hominids acquired advanced orthogrady in parallel. Hominoid spinal invagination is an embryogenetic mechanism that reoriented the shoulder girdle more laterally. It was unaccompanied by substantial lumbar spine abbreviation, an adaptation restricted to vertical climbing and/or suspension. The specialized locomotor anatomies and behaviors of chimpanzees and gorillas therefore constitute poor models for the origin and evolution of human bipedality.

LOVEJOY 2010

C. Owen Lovejoy & Melanie A. McCollum, *Spinopelvic pathways to bipedality*, *Why no hominids ever relied on a bent-hip–bent-knee gait.* Phil. Trans. Royal Society B **365** (2010), 3289–3299.

Until recently, the last common ancestor of African apes and humans was presumed to resemble living chimpanzees and bonobos. This was frequently extended to their locomotor pattern leading to the presumption that knuckle-walking was a likely ancestral pattern, requiring bipedality to have emerged as a modification of their bent-hip-bent-knee gait used during erect walking. Research on the development and anatomy of the vertebral column, coupled with new revelations from the fossil record (in particular, Ardipithecus ramidus), now demonstrate that these presumptions have been in error. Reassessment of the potential pathway to early hominid bipedality now reveals an entirely novel sequence of likely morphological events leading to the emergence of upright walking.

Keywords: Australopithecus; bipedality; bent-hip–bent-knee; Ardipithecus; human evolution

O'HIGGINS 2007

Paul O'Higgins and Sarah Elton, *Walking on Trees.* science **316** (2007), 1292.

Observations of modern orangutans suggest
that human bipedalism may have evolved in
the trees rather than on the ground.

OHMAN 2005

James C. Ohman, C. Owen Lovejoy, Tim D. White, *Questions About Orrorin Femur.* science **307** (2005), 845.

Given the importance of the Lukeino femur, we urge its discoverers to make available evidence to support their assertions. The required evidence is (i) photographs, measurements, and drawings of its broken neck; (ii) conventional anteroposterior x-rays; and (iii) higher-resolution CT scans obtained with proper femoral orientation. Exceptional claims demand exceptional evidence; the adjustment of previously published data does not suffice.

PATTERSON 2006

Nick Patterson, Daniel J. Richter, Sante Gnerre, Eric S. Lander & David Reich, *Genetic evidence for complex speciation of humans and chimpanzees.* nature **441** (2006), 1103–1108.

n441-1103-Supplement.pdf

The genetic divergence time between two species varies substantially across the genome, conveying important information about the timing and process of speciation. Here we develop a framework for studying this variation and apply it to about 20 million base pairs of aligned sequence from humans, chimpanzees, gorillas and more distantly related primates. Human–chimpanzee genetic divergence varies from less than 84 % to more than 147 % of the average, a range of more than 4 million years. Our analysis also shows that human–chimpanzee speciation occurred less than 6.3 million years ago and probably more recently, conflicting with some interpretations of ancient fossils. Most strikingly, chromosome X shows an extremely young genetic divergence time, close to the genome minimum along nearly its entire length. These unexpected features would be explained if the human and chimpanzee lineages initially diverged, then later exchanged genes before separating permanently.

PICKFORD 2001

Martin Pickford & Brigitte Senut, *The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya.* C. R. Acad. Sci. Paris, série II A, Sc. de la Terre et des planètes **332** (2001), 145–152.

Hominid fossils have been recovered from four localities within the Late Miocene Lukeino Formation, Tugen Hills, Kenya. The sediments from which the fossils came consist of fluvial and shallow lacustrine deposits. Some of the specimens are coated in a thin layer of carbonate of organic origin, suggesting deposition and preservation in slightly alkaline water, while others are riddled with superficial cracks indicating exposure at the surface prior to burial. Radioisotopic age determinations from lavas underlying and overlying the Lukeino Formation, and from crystals from the sediments themselves, indicate an age of ca 6 Ma for these hominids.

hominid / Late Miocene / Kenya / stratigraphy / depositional environment

RICHMOND 2008

Brian G. Richmond & William L. Jungers, *Orrorin tugenensis Femoral Morphology and the Evolution of Hominin Bipedalism.* science **319** (2008), 1662–1665.

s319-1662-Supplement.pdf

Bipedalism is a key human adaptation and a defining feature of the hominin clade. Fossil femora discovered in Kenya and attributed to Orrorin tugenensis, at 6 million years ago, purportedly provide the earliest postcranial evidence of hominin bipedalism, but their functional and phylogenetic affinities are controversial. We show that the O. tugenensis femur differs from those of apes and Homo and most strongly resembles those of Australopithecus and Paranthropus, indicating that O. tugenensis was bipedal but is not more closely related to Homo than to Australopithecus. Femoral morphology indicates that O. tugenensis shared distinctive hip biomechanics with australopiths, suggesting that this complex evolved early in human evolution and persisted for almost 4 million years until modifications of the hip appeared in the late Pliocene in early Homo.

SARMIENTO 2010

Esteban E. Sarmiento, *Comment on the Paleobiology and Classification of Ardipithecus ramidus*. science **328** (2010), 1105b.

s328-1105c-Reply.pdf

White and colleagues (Research Articles, 2 October 2009, pp. 64-106 and www.sciencemag.org/ardipithecus) reported Ardipithecus ramidus as an exclusive member of the human lineage post-African ape divergence. However, their analysis of shared-derived characters provides insufficient evidence of an ancestor-descendant relationship and exclusivity to the hominid lineage. Molecular and anatomical studies rather suggest that Ar. ramidus predates the human/African ape divergence.

Reply by Tim D. White, Gen Suwa, C. Owen Lovejoy

We assigned Ardipithecus to the Hominidae based on numerous dental, cranial, and postcranial characters. Sarmiento argues that these characters are not exclusive to hominids, contending that Ardipithecus is too old to be cladistically hominid. His alternative phylogeny, however, is unlikely because it requires tortuous, nonparsimonious evolutionary pathways.

SENUT 2001

Brigitte Senut, Martin Pickford, Dominique Gommery, Pierre Mein, Kiptalam Cheboi & Yves Coppens, *First hominid from the Miocene (Lukeino Formation, Kenya)*. C. R. Acad. Sci. Paris, série II A, Sc. de la Terre et des planètes **332** (2001), 137–144.

Remains of an early hominid have been recovered from four localities in the Lukeino Formation, Tugen Hills, Kenya, in sediments aged ca 6 Ma. 13 fossils are known,belonging to at least five individuals. The femora indicate that the Lukeino hominid was a biped when on the ground, whilst its humerus and manual phalanx show that it possessed some arboreal adaptations. The upper central incisor is large and robust, the upper canine is large for a hominid and retains a narrow and shallow anterior groove, the lower fourth premolar is ape-like, with offset roots and oblique crown, and the molars are relatively small, with thick enamel. A new genus and species is erected for the remains.

Hominoidea / Hominidae / Tugen Hills / Upper Miocene / Kenya

STORCH 2013

Volker Storch, Ulrich Welsch & Michael Wink, *Evolutionsbiologie*. (Berlin ^{3}2013).

SUWA 2009A

Gen Suwa, Berhane Asfaw, Reiko T. Kono, Daisuke Kubo, C. Owen Lovejoy & Tim D. White, *The Ardipithecus ramidus Skull and Its Implications for Hominid Origins*. science **326** (2009), 68–68e7.

s326-0068-Supplement.pdf

The highly fragmented and distorted skull of the adult skeleton ARA-VP-6/500 includes most of the dentition and preserves substantial parts of the face, vault, and base. Anatomical comparisons and micro-computed tomography-based analysis of this and other remains reveal pre-Australopithecus hominid craniofacial morphology and structure. The Ardipithecus ramidus skull exhibits a small endocranial capacity (300 to 350 cubic centimeters), small cranial size relative to body size, considerable midfacial projection, and a lack of modern African ape-like extreme lower facial prognathism. Its short posterior cranial base differs from that of both Pan troglodytes and P. paniscus. Ar. ramidus lacks the broad, anteriorly situated zygomaxillary facial skeleton developed in later Australopithecus. This combination of features is apparently shared by Sahelanthropus, showing that the Mio-Pliocene hominid cranium differed substantially from those of both extant apes and Australopithecus.

Suwa 2009b

Gen Suwa, Reiko T. Kono, Scott W. Simpson, Berhane Asfaw, C. Owen Lovejoy & Tim D. White, *Paleobiological Implications of the Ardipithecus ramidus Dentition*. science **326** (2009), 69, 94–99.

s326-0069-Supplement.pdf

The Middle Awash Ardipithecus ramidus sample comprises over 145 teeth, including associated maxillary and mandibular sets. These help reveal the earliest stages of human evolution. Ar. ramidus lacks the postcanine megadontia of Australopithecus. Its molars have thinner enamel and are functionally less durable than those of Australopithecus but lack the derived Pan pattern of thin occlusal enamel associated with ripe-fruit frugivory. The Ar. ramidus dental morphology and wear pattern are consistent with a partially terrestrial, omnivorous/frugivorous niche. Analyses show that the ARA-
VP-6/500 skeleton is female and that Ar. ramidus was nearly monomorphic in canine size and shape. The canine/lower third premolar complex indicates a reduction of canine size and honing capacity early in hominid evolution, possibly driven by selection targeted on the male upper canine.

Thorpe 2007

S. K. S. Thorpe, R. L. Holder & R. H. Crompton, *Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches*. science **316** (2007), 1328–1331.

s316-1328-Supplement.pdf, s316-1328-Supplement1.mov, s316-1328-Supplement2.mov, s316-1328-Supplement3.mov

Human bipedalism is commonly thought to have evolved from a quadrupedal terrestrial precursor, yet some recent paleontological evidence suggests that adaptations for bipedalism arose in an arboreal context. However, the adaptive benefit of arboreal bipedalism has been unknown. Here we show that it allows the most arboreal great ape, the orangutan, to access supports too flexible to be negotiated otherwise. Orangutans react to branch flexibility like humans running on springy tracks, by increasing knee and hip extension, whereas all other primates do the reverse. Human bipedalism is thus less an innovation than an exploitation of a locomotor behavior retained from the common great ape ancestor.

Vignaud 2002

Patrick Vignaud et al., *Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad*. nature **418** (2002), 152–155.

Patrick Vignaud, Philippe Duringer, Hassane Taïsso Mackaye, Andossa Likius, Cécile Blondel, Jean-Renaud Boisserie, Louis de Bonis, Véra Eisenmann, Marie-Esther Etienne, Denis Geraads, Franck Guy, Thomas Lehmann, Fabrice Lihoreau, Nieves Lopez-Martinez, Cécile Mourer-Chauvire, Olga Otero, Jean-Claude Rage, Mathieu Schuster, Laurent Viriot, Antoine Zazzo & Michel Brunet

All six known specimens of the early hominid Sahelanthropus tchadensis come from Toros-Menalla site 266 (TM 266), a single locality in the Djurab Desert, northern Chad, central Africa. Here we present a preliminary analysis of the palaeontological and palaeoecological context of these finds. The rich fauna from TM 266 includes a significant aquatic component such as fish, crocodiles and amphibious mammals, alongside animals associated with gallery forest and savannah, such as primates, rodents, elephants, equids and bovids. The fauna suggests a biochronological age between 6 and 7 million years. Taken together with the sedimentological evidence, the fauna suggests that S. tchadensis lived close to a lake, but not far from a sandy desert, perhaps the oldest record of desert conditions in the Neogene of northern central Africa.

White 1994

Tim D. White, Gen Suwa & Berhane Asfaw, *Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia.* nature **371** (1994), 306–312.

Seventeen hominoid fossils recovered from Pliocene strata at Aramis, Middle Awash, Ethiopia make up a series comprising dental, cranial and postcranial specimens dated to around 4.4 million years ago. When compared with Australopithecus afarensis and with modern and fossil apes the Aramis fossil hominids are recognized as a new species of Australopithecus-A. ramidus sp. nov. The antiquity and primitive morphology of A. ramidus suggests that it represents a long-sought potential root species for the Hominidae.

White 2009a

Tim D. White, Berhane Asfaw, Yonas Beyene, Yohannes Haile-Selassie, C. Owen Lovejoy, Gen Suwa & Giday WoldeGabriel, *Ardipithecus ramidus and the Paleobiology of Early Hominids.* science **326** (2009), 64, 76–86.

s326-0064-Supplement1.pdf, s326-0064-Supplement2.xls, s328-1105b-Sarmiento.pdf, s328-1105c-Reply.pdf

Hominid fossils predating the emergence of Australopithecus have been sparse and fragmentary. The evolution of our lineage after the last common ancestor we shared with chimpanzees has therefore remained unclear. Ardipithecus ramidus, recovered in ecologically and temporally resolved contexts in Ethiopia’s Afar Rift, now illuminates earlier hominid paleobiology and aspects of extant African ape evolution. More than 110 specimens recovered from 4.4-million-year-old sediments include a partial skeleton with much of the skull, hands, feet, limbs, and pelvis. This hominid combined arboreal palmigrade clambering and careful climbing with a form of terrestrial bipedality more primitive than that of Australopithecus. Ar. ramidus had a reduced canine/ premolar complex and a little-derived cranial morphology and consumed a predominantly C3 plant-based diet (plants using the C3 photosynthetic pathway). Its ecological habitat appears to have been largely woodland-focused. Ar. ramidus lacks any characters typical of suspension, vertical climbing, or knuckle-walking. Ar. ramidus indicates that despite the genetic similarities of living humans and chimpanzees, the ancestor we last shared probably differed substantially from any extant African ape. Hominids and extant African apes have each become highly specialized through very different evolutionary pathways. This evidence also illuminates the origins of orthograde, bipedality, ecology, diet, and social behavior in earliest Hominidae and helps to define the basal hominid adaptation, thereby accentuating the derived nature of Australopithecus.

White 2009b

Tim D. White et al., *Macrovertebrate Paleontology and the Pliocene Habitat of Ardipithecus ramidus.* science **326** (2009), 67, 87–93.

s326-0067-Supplement.pdf, s328-1105d-Cerling.pdf, s328-1105e-Reply.pdf

Tim D. White, Stanley H. Ambrose, Gen Suwa, Denise F. Su, David DeGusta, Raymond L. Bernor, Jean-Renaud Boisserie, Michel Brunet, Eric Delson, Stephen Frost, Nuria Garcia, Ioannis X. Giaourtsakis, Yohannes Haile-Selassie, F. Clark Howell, Thomas Lehmann, Andossa Likius, Cesur Pehlevan, Haruo Saegusa, Gina Semprebon, Mark Teaford, Elisabeth Vrba
A diverse assemblage of large mammals is spatially and stratigraphically associated with Ardipithecus ramidus at Aramis. The most common species are tragelaphine antelope and colobine monkeys. Analyses of their postcranial remains situate them in a closed habitat. Assessment of dental mesowear, microwear, and stable isotopes from these and a wider range of abundant associated larger mammals indicates that the local habitat at Aramis was predominantly woodland. The Ar. ramidus enamel isotope values indicate a minimal C4 vegetation component in its diet (plants using the C4 photosynthetic pathway), which is consistent with predominantly forest/woodland feeding. Although the Early Pliocene Afar included a range of environments, and the local environment at Aramis and its vicinity ranged from forests to wooded grasslands, the integration of available physical and biological evidence establishes Ar. ramidus as a denizen of the closed habitats along this continuum.

WoldeGabriel 2009

Giday WoldeGabriel et al., *The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of Ardipithecus ramidus.* science **326** (2009), 65–65e5.
s326-0065-Supplement.pdf
Giday WoldeGabriel, Stanley H. Ambrose, Doris Barboni, Raymonde Bonnefille, Laurent Bremond, Brian Currie, David DeGusta, William K. Hart, Alison M. Murray, Paul R. Renne, M. C. Jolly-Saad, Kathlyn M. Stewart & Tim D. White
Sediments containing Ardipithecus ramidus were deposited 4.4 million years ago on an alluvial floodplain in Ethiopia's western Afar rift. The Lower Aramis Member hominid-bearing unit, now exposed across a >9-
kilometer structural arc, is sandwiched between two volcanic tuffs that have nearly identical 40Ar/39Ar ages. Geological data presented here, along with floral, invertebrate, and vertebrate paleontological and taphonomic evidence associated with the hominids, suggest that they occupied a wooded biotope over the western three-fourths of the paleotransect. Phytoliths and oxygen and carbon stable isotopes of pedogenic carbonates provide evidence of humid cool woodlands with a grassy substrate.

Wolpoff 2002

Milford H. Wolpoff, Brigitte Senut, Martin Pickford & John Hawks, *Sahelanthropus or 'Sahelpithecus'?* nature **419** (2002), 581–582.
Because the face is orthognathic rather than prognathic and the anterior teeth are small, posture is the only credible explanation of this nuchal anatomy. It is evident that Sahelanthropus did not habitually hold its head in an upright position over the spine and was not an obligate biped. This contrast with all known hominids is itself sufficient to exclude Sahelanthropus from the hominid clade as we currently understand it.
We believe that Sahelanthropus was an ape living in an environment that was later inhabited by australopithecines and, like them, it adapted with a powerful masticatory complex. A penecontemporary primate with a perfect and well-developed postcranial adaptation to obligate bipedalism6 is more likely to have been an early hominid.

WOOD 2002

Bernard Wood, *Hominid revelations from Chad*. nature **418** (2002), 133–135.

The story of human origins in Africa takes a twist with the description of a 6–7-million-year-old cranium from Chad. The discovery hints at the likely diversity of early hominids.

WOOD 2011

Bernard Wood & Terry Harrison, *The evolutionary context of the first hominins*. nature **470** (2011), 347–352.

The relationships among the living apes and modern humans have effectively been resolved, but it is much more difficult to locate fossil apes on the tree of life because shared skeletal morphology does not always mean shared recent evolutionary history. Sorting fossil taxa into those that belong on the branch of the tree of life that leads to modern humans from those that belong on other closely related branches is a considerable challenge.

ZOLLIKOFER 2005

Christoph P. E. Zollikofer et al., *Virtual cranial reconstruction of Sahelanthropus tchadensis*. nature **434** (2005), 755–759.

Christoph P. E. Zollikofer, Marcia S. Ponce de León, Daniel E. Lieberman, Franck Guy, David Pilbeam, Andossa Likius, Hassane T. Mackaye, Patrick Vignaud & Michel Brunet

Previous research in Chad at the Toros-Menalla 266 fossiliferous locality (about 7 million years old) uncovered a nearly complete cranium (TM 266-01-60-1), three mandibular fragments and several isolated teeth attributed to Sahelanthropus tchadensis. Of this material, the cranium is especially important for testing hypotheses about the systematics and behavioural characteristics of this species, but is partly distorted from fracturing, displacement and plastic deformation. Here we present a detailed virtual reconstruction of the TM 266 cranium that corrects these distortions. The reconstruction confirms that S. tchadensis is a hominid and is not more closely related to the African great apes. Analysis of the basicranium further indicates that S. tchadensis might have been an upright biped, suggesting that bipedalism was present in the earliest known hominids, and probably arose soon after the divergence of the chimpanzee and human lineages.