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News & views

Palaeontology

Standing up for the earliest bipedal hominins

Daniel E. Lieberman

A leg bone and two arm bones of a hominin from Chad suggest that, seven million years ago, around the time that the human and chimpanzee lineages split, early hominins were bipedal but were also able to climb trees. **See p.94**

What set the human lineage on a separate path from chimpanzees sometime between ten million and six million years ago? The first scientists to study the origins of our species speculated that brain enlargement led the way in driving human evolution. However, nearly a century's worth of fossil discoveries in Africa instead point to the ability to walk on two legs (bipedalism), and perhaps a slightly lower-quality diet compared with that of chimpanzees, as the first distinguishing features of the earliest hominins (species more closely related to humans than to chimpanzees)[1]. Even so, much about the first hominins and why they evolved remains mysterious. Was the last common ancestor of humans and chimpanzees similar to a chimpanzee, a gibbon, a monkey or something completely different? And did bipedalism evolve before, during or after the split between humans and chimpanzees? On page 94, Daver *et al.*[2] present fossil evidence that helps to address some of these questions.

There are almost no fossils unambiguously recognizable as being the immediate ancestors of chimpanzees or the other living African great apes. The best available evidence to address some of the key open questions has instead come from the oldest known hominin species (Fig. 1). These include *Ardipithecus ramidus*, dated to 4.3 million to 4.5 million years ago; *Ardipithecus kadabba*, dated to 5.2 million to 5.8 million years ago; *Orrorin tugenensis*, dated to about 6 million years ago; and, last but not least, *Sahelanthropus tchadensis*, dated to about 7 million years ago. *Sahelanthropus* was previously known from only a partial cranium, a few jaw fragments and some teeth[3]. Daver and colleagues describe three more fossils attributed to *Sahelanthropus*: a partial leg bone (femur) and two arm bones (ulnae), the characteristics of which suggest that this species not only walked on two feet but also climbed trees.

Sahelanthropus was discovered in Chad in 2001, and immediately caused considerable excitement. It was not only about one million years older than any other known hominin species, but was also found 2,500 kilometres away from the closest known hominin fossils in eastern Africa. The cranium of the specimen, nicknamed Toumaï (meaning 'hope of life' in the local Daza language), had a chimpanzee-like brain volume of between approximately 360 and 390 cubic centimetres. Compared with chimpanzees, *Sahelanthropus* has slightly larger molar teeth with thicker enamel, smaller upper canine teeth that don't sharpen themselves against the lower premolar teeth and a slightly flatter face[4] — characteristics that are similar to those of later hominin species.

Perhaps the most exciting feature that Toumaï shares with other hominins is the anatomy of the skull opening (foramen magnum) at the base of the skull where the spine connects and the spinal cord emerges. The foramen magnum of four-legged animals is typically located towards the back of the skull and is oriented

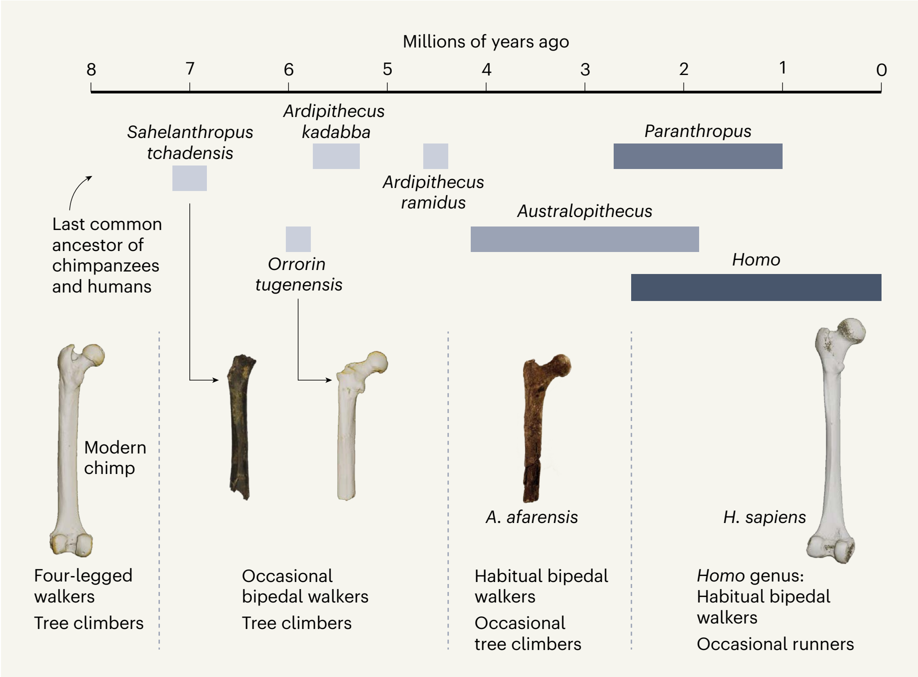

Figure 1 | The evolution of bipedalism. Hominins (species more closely related to humans than to chimpanzees) evolved from an ancestor shared with African great apes (such as chimpanzees and gorillas), which move by walking on four legs and climbing trees. *Sahelanthropus tchadensis* is the oldest known hominin species. It has features that suggest it was an occasional bipedal walker, including leg-bone characteristics (too subtle to see on the scale of this femur image) that Daver *et al.*[2] report. The authors indicate that arm bones (not shown) of this species were adapted for tree climbing. A similar mix of adaptations for occasional bipedal walking and tree climbing characterizes early hominins of the genus *Orrorin* and *Ardipithecus*. Species of the genus *Australopithecus* were comparatively more effective habitual bipedal walkers, but retained adaptations for climbing trees. Species in the genus *Homo* have numerous adaptations for effective bipedal walking and for running, but have lost most adaptations for tree-climbing. Femur images are not shown at their relative scale (images, apart from that of *Australopithecus afarensis,* are from ref. 2; *A. afarensis* image: Daniel E. Lieberman). Note that the *Sahelanthropus* femur is missing joints at the end of the bone, which would have provided insights into how this species moved.

From the archive

Assessing how pollution affects mental health, and praise for a museum's efforts to educate children about science.

50 years ago

Relationships between pollution and health have for long been the subject of debate and study. The effect of air pollution on respiratory diseases, the contribution of poor sanitation to the spread of diseases such as cholera ... have all been discussed in the scientific and popular Press. But what of the effects of pollution on mental health? ... According to a study carried out for the National Institute of Mental Health, such questions have received at best only scant attention, and much more research is required not only on the physiological effects of pollutants on the central nervous system, but also on the mental stresses and strains of living in a degraded environment.

From *Nature* 1 September 1972

100 years ago

The direct educational work accomplished by museums in the United States is a perpetual source of shame to us in this country ... [M]uch is being done in some of our own museums ... but have we anything to compare with what is described in ... the journal of the American Museum of Natural History? ... [T]he American Museum ... has 869 nature-study collections to be lent to any public school in greater New York. There are two motor cars and a motor cycle to deliver slides and collections. Each messenger visits from twenty to forty schools a day. The American Museum is about to erect a special School Service building ... where from three to five thousand children daily may be taken care of properly ... The American Museum has its own Department of Education ... In the same way the Brooklyn Botanical Garden has its Curator of Elementary Education ... [W]hy is it that the Americans have got so far ahead of us on these lines? ... [T]o a large extent it is because Americans are not ashamed of having an ideal and of talking about it. They do not mind saying what they are going to do, and they make the utmost of everything that they have done.

From *Nature* 2 September 1922

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backwards, whereas in *Sahelanthropus* it is positioned near the middle of the skull and is oriented downwards[5]. Combined with the horizontal angle of the back of the skull where the neck muscles attach, a downwards-oriented foramen magnum provides strong evidence that, like bipeds, *Sahelanthropus* balanced its head on a vertical neck[6].

The hominin status of *Sahelanthropus* is controversial. In addition to debates about the geological age of the fossil material, and reservations about the cranium's reconstruction, researchers have speculated that *Sahelanthropus*'s similarities to hominins are just comparable characteristics that evolved independently[7]. This is an important critique, because independent similarities can and do evolve among closely related species, a phenomenon known as convergence. That bipedalism evolved more than once among apes is thought by many to be unlikely, but requires further testing. Hypotheses of bipedalism have previously been questioned[8,9] for extinct species of ape, such as *Oreopithecus* and *Danuvius*.

Some scientists have reserved judgement on whether *Sahelanthropus* was a biped because of the absence of supporting evidence from parts of the body other than the skull, such as the pelvis, femur or feet. And to add to the controversy, such potentially relevant evidence was known to exist but was unavailable to researchers. When the *Sahelanthropus* cranial material was discovered in 2001, a femur and ulna were also retrieved, together with thousands of other fossils. It was not until three years later that the femur was recognized as probably belonging to a hominin by researchers unaffiliated with the team working on *Sahelanthropus*, and an account of the femur's discovery was published[10] in 2009. A subsequent analysis argued that the femur's shape was more similar to that of apes than to that of known bipedal hominins, although this assessment was based on just a few measurements of the femur and on 2D photographs[11].

The ulna found in 2001 and another discovered in 2003 were subsequently recognized as being those of hominins. Given all of this uncertainty and controversy, Daver and colleagues' analysis of the *Sahelanthropus* femur and ulnae is of considerable interest. But don't expect a full resolution just yet, because the femur consists mostly of a shaft that doesn't have the joints at either end (Fig. 1) that would provide most of the information needed to infer *Sahelanthropus*'s posture and how it walked.

Nevertheless, the authors have squeezed as much information as possible from the fossil data, focusing on features that they suggest are consistent with bipedalism. First, as is characteristic of bipedal hominins, the base of the femur's neck seems to be oriented slightly towards the front of the body and is flattened. The upper part of the femur is also slightly flattened, and the sites at which the gluteal muscles insert are fairly robust and human-like. In addition, the cross-sectional shape of the femur at several locations falls within the range expected for hominins. This feature is indicative of a femur that shows resistance to the sideways-bending forces that are characteristic of those encountered by bipedal hominins.

The researchers also point to traces of a bony ridge called a calcar femorale, a region of dense bone thought to buttress the upper femur from the forces produced by walking upright. However, this feature is not necessarily diagnostic of bipedalism[12].

Whatever you might think about the femur, the ulnae are unquestionably chimpanzee-like and are clearly well adapted to climbing trees. In addition to being short, the bones have highly curved shafts, indicating the presence of powerful forearm muscles that could flex the elbow during climbing. The elbow joints are also ape-like, with a shape that would be able to cope with high forces while flexed – a position typical for tree climbing that is mechanically challenging.

The *Sahelanthropus* femur doesn't have 'smoking-gun' traces of bipedalism, but it looks more like that of a bipedal hominin than that of a quadrupedal ape. When considered in conjunction with the orientation of the foramen magnum, which is compatible only with bipedalism, it seems reasonable to infer that *Sahelanthropus* was some type of biped and that, like later hominins such as *A. ramidus*, it was also well adapted to climbing trees. A few million years after *Sahelanthropus* and *Ardipithecus*, another genus of hominin – *Australopithecus* – evolved to be highly effective walkers while retaining many adaptations necessary for climbing trees. It was in only the human genus, *Homo*, that hominins lost the adaptations needed for moving through the trees as they became runners. That said, we know little else about the gait of *Sahelanthropus*. A mixed repertoire of walking and climbing makes sense given that *Sahelanthropus* lived near a lake with woodland adjacent to it.

It bears repeating that, apart from bipedalism and slightly more hominin-like teeth and face, many *Sahelanthropus* features are similar to those of a chimpanzee. This resemblance makes sense if the last common ancestor of humans and chimpanzees was chimpanzee-like[1] and *Sahelanthropus* evolved very soon after humans and chimpanzees diverged. But these and other inferences are sure to remain the subject of much debate, especially until more fossils are found to fill the evolutionary record, not just of humans, but also of chimpanzees.

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Biophysics

A phase transition for chromosome transmission

Kazuhiro Maeshima

An analysis of chromosomes during mitotic cell division reveals that DNA and associated histone proteins condense through a process called phase transition, which helps them to resist the pushing forces involved in mitosis. **See p.183**

The faithful transmission of matching copies of DNA from a dividing mother cell to its two daughters requires the DNA to be tightly compacted. This process is fundamental to the mitotic cell divisions needed for an organism's development and maintenance, but the underlying physical principles of chromosome compaction remain unclear. Schneider *et al.*[1] provide evidence on page 183 that a key aspect of accurate chromosome transmission is condensation into a more solid-like state through a process called phase transition.

The packaging of DNA into the condensed, rod-like shape characteristic of mitotic chromosomes involves multiple levels of organization. On a local scale, negatively charged DNA is wrapped around positively charged histone proteins to form bead-like structures called nucleosomes that are linked by DNA 'strings' – this irregularly folded, beads-on-a-string structure is known as chromatin[2]. Long tails on the histones, enriched with positive charges, bind to nearby nucleosomes and mediate nucleosome–nucleosome contacts, thus compacting the chromosomes. On a larger scale, a ring-like protein complex called condensin forms an axis around which chromatin packs in loops to form a compact, rod-like shape[3].

Separating these tightly packaged mitotic chromosomes into daughter cells involves two opposing forces. First, fibres called microtubules pull the two sister chromosomes apart. Second, other microtubules make contact with the chromosome arms and push them in the opposite direction through a 'polar ejection' force (Fig. 1a)[4]. These two forces first align chromosomes around the centre of the cell and then accurately divide them into two daughters. Condensins are known to confer the mechanical stability needed for chromosomes to remain intact despite being pulled[5]. Do they also confer mechanical resistance to the polar ejection force, or is another factor involved?

Schneider *et al.* first showed that chromosomes remained resistant to the polar ejection force even when condensin was depleted (Fig. 1b). The authors confirmed that, as previously observed[6], the mitotic-chromatin density (an indicator of compaction state) was similar in condensin-depleted and control cells. However, they also found that chromosomes in the condensin-depleted cells adopted abnormal shapes.

The authors therefore investigated another possible factor – 'deacetylation' of the histone tail. Acetyl groups can modify histones, changing the physical properties of local chromatin through loss of positive charges in histone tails and so loss of nucleosome–nucleosome contacts. Histone tails are deacetylated in mitotic chromosomes[7], leading to a greater increase in nucleosome–nucleosome contacts and subsequent global chromatin compaction. Could this deacetylation explain how mechanical resistance to polar ejection forces is obtained?

Schneider *et al.* treated human cells with a drug called trichostatin A (TSA), which inhibits the histone deacetylase enzymes that remove acetyl groups from histones. As expected, TSA treatment led to histone-tail hyperacetylation,

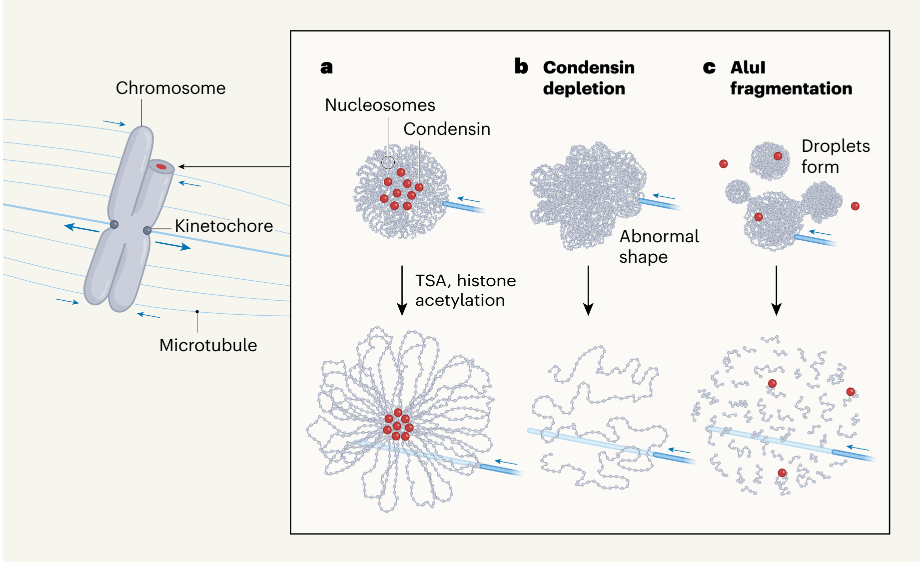

Figure 1 | Resisting pushing forces during mitotic cell division. a, Chromosomes undergoing mitosis form a rod-like shape, with an axis of condensin protein at the centre, surrounded by nucleosomes (bead-like complexes of DNA wrapped around histone proteins). Fibres called microtubules attach to kinetochore structures to pull halves of the chromosome to opposite poles of the dividing cell, and other microtubules push the chromosome arms in the opposite direction (the polar ejection force). Proper chromosome separation requires that the chromosome arms resist the polar ejection force, preventing microtubules from penetrating them. Schneider *et al.*[1] show that an absence of acetyl groups on histone tails is key to this resistance. Treatment with the drug trichostatin A (TSA), which induces histone acetylation, leads to puncturing of the chromosome surface by microtubules. **b**, When condensin was depleted, chromosomes adopted an abnormal shape, but resisted the polar ejection force until treated with TSA. **c**, When DNA was fragmented using an enzyme called AluI, round bodies formed and fused to one another like liquid droplets. A stiff surface still prevented microtubules from penetrating the round bodies, but TSA treatment dissolved these bodies.