News & views

Palaeontology

Fossil ape hints at how bipedal walking evolved

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Approximately 11.6-million-year-old fossils reveal an ape with arms suited to hanging in trees but human-like legs, suggesting a form of locomotion that might push back the timeline for when walking on two feet evolved. **See p.489**

Ever since Charles Darwin's work provided the basis for understanding human evolution, there have been long-standing questions regarding when, why and how our early human ancestors begin to walk on two feet. The commitment to terrestrial bipedalism, characterized by skeletal adaptations for walking regularly on two feet, is a defining feature that enables the assignment of fossils to the hominin lineage – which comprises all species more closely related to humans than to chimpanzees (*Pan troglodytes*) or bonobos (*Pan paniscus*), our two closest living relatives. On the basis of fossil findings, some of which are more controversial than others[1,2], the answer to the 'when' question is thought to be between 7 million and 5 million years ago at the end of the Miocene epoch (which lasted from about 23 million to 5 million years ago).

Answering the questions of why and how hominin bipedalism evolved depends a lot on what kind of locomotion was being used before terrestrial bipedalism evolved. Did it evolve from an ancestor that lived mainly in trees, or were these ancestors already walking on all fours on the ground and subsequently evolved to stand up and walk on two feet? On page 489, Böhme *et al.*[3] report the discovery of an ape species called *Danuvius guggenmosi* from the middle of the Miocene. This species moved around in a previously unknown way, which the authors suggest could provide a model for the type of locomotion from which hominin bipedalism evolved.

Questions about the origin of hominin bipedalism and how the last common ancestor of humans, chimpanzees and bonobos might have moved are conventionally addressed using either a top-down or a bottom-up approach (Fig. 1). Darwin[4] and many palaeoanthropologists favoured the top-down approach, examining living primates, particularly the great apes, for clues to how bipedalism evolved[5,6]. African apes – chimpanzees, bonobos and gorillas (of the genus *Gorilla*) – go into the trees to eat, sleep and when they need protection, but spend most of their time on the ground, using their knuckles for walking. Given our close genetic relationship to these apes, and because we also share certain features of our hands and feet with them, some have argued that hominin bipedalism evolved from a knuckle-walking ancestor[5], or a more generalized quadruped lacking knuckle-walking specializations[7], that divided its time between the ground and the trees. By contrast, others have noted that the way that orangutans (of the genus *Pongo*) move bipedally in trees, and the mechanical similarities between how apes use their legs for climbing and how humans use theirs for walking, suggest that bipedalism evolved from an ape ancestor that was previously committed to life in the trees[6,8].

Although logical, this top-down approach is constrained, as Darwin acknowledged[4], to examining evidence from the few remaining living ape species. However, one of the earliest potential hominins for which we have the most fossil evidence – the approximately 4.4-million-year-old *Ardipithecus ramidus* – is argued to be distinctly unlike living great apes in its anatomy, which suggests that the African apes and Asian orangutans we know today are actually quite specialized in their locomotor behaviours compared with their earlier ancestors[7]. Each living ape species is a result of its own long, evolutionary history,

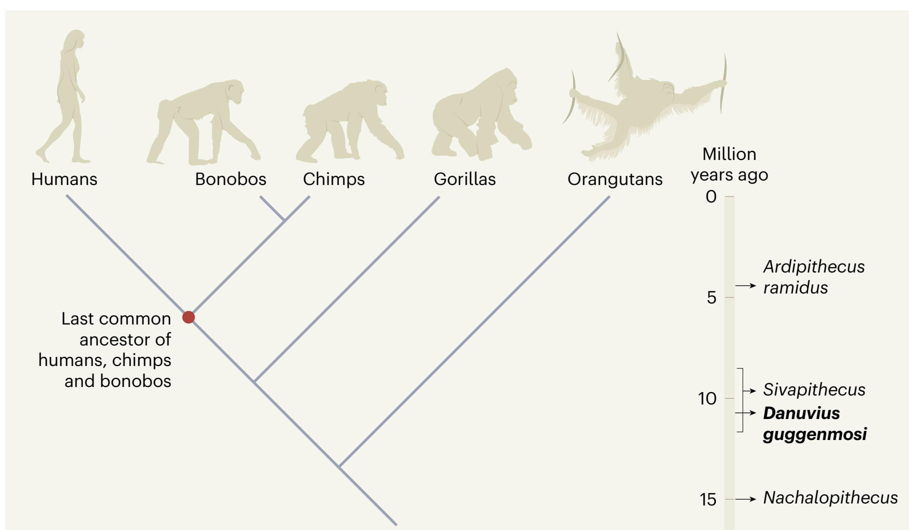


Figure 1 | The evolution of bipedalism. In the branch of the evolutionary tree that splits from our last common ancestor with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), humans and our extinct hominin relatives have a skeleton adapted for regular walking on the ground using two feet. A top-down approach to assessing how our early ancestors might have evolved bipedalism focuses on possible modes of ancestral locomotion by considering how living great apes move around. For example, African apes – chimps, bonobos and gorillas (of the genus *Gorilla*) – use knuckle-walking more frequently on the ground than in trees, and these apes and orangutans (of the genus *Pongo*) also climb and use suspensory locomotion in trees. However, fossils of the ancient potential hominin *Ardipithecus ramidus* suggest that living apes might have evolved quite specialized locomotion compared with their earlier ancestors. A bottom-up approach focuses instead on ancient ape fossils that pre-date our last common ancestor, such as those of the genus *Nacholapithecus* or *Sivapithecus*. However, the clues uncovered from such fossils can be difficult to interpret. Böhme *et al.*[3] present fossils of a previously unknown ape called *Danuvius guggenmosi*, which the authors suggest provides a good model for the type of locomotion from which bipedalism might have evolved. The branch-point timings shown are approximate.

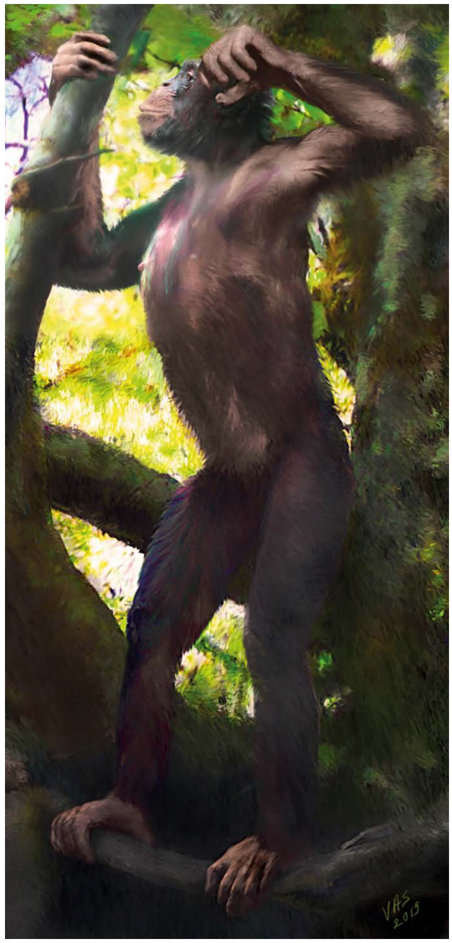
and, in the case of African apes, one that we often forget because there is so little fossil evidence of it. This absence of fossil information to reveal how African apes evolved makes questions about the nature of our common ancestor even trickier to answer.

Other palaeoanthropologists address the question of bipedal origins from a bottom-up approach instead, looking to the approximately 30 genera of fossil apes that have been identified from the Miocene of Africa, Asia and Europe as potential models for what our last common ancestor might have looked like[2,7,9]. However, these apes show a hotchpotch of skeletal adaptations, with features found in combinations that are unlike anything we see in living primates, and that often leave us guessing about how these animals moved around and how much time they spent in trees or on the ground.

For example, a genus of fossil ape called *Nacholapithecus* had a monkey-like body but unusually large forelimbs and long toes, whereas another ape genus, *Sivapithecus*, had an orangutan-like face, an ape-like shoulder, and a monkey-like elbow and pelvis[10,11]. Such characteristics suggest odd combinations of arboreal suspension (hanging from tree branches), quadrupedal movements and body postures that are difficult to imagine today, and which make it hard to interpret these creatures' probable locomotion patterns[10].

Böhme and colleagues add to this amazing Miocene diversity by presenting approximately 11.6-million-year-old fossils of *D. guggenmosi*. The authors interpret the shape of the *D. guggenmosi* fossils as indicating a type of previously unknown movement that they term extended limb clambering, which combines adaptations of both suspension in the trees and bipedal locomotion. This makes it a good possible model of locomotion for the last common ancestor.

The teeth of *D. guggenmosi* identify it as belonging to a group of fossil ape species called dryopithecins that have been found from the mid- to late Miocene in Europe and that some consider to be ancestral to African apes[9]. Living African ape species inhabit the equatorial region of Africa, but, during certain times of the Miocene, many ancestral great apes were living throughout Europe and Asia and migrating both to and out of Africa. Some researchers suggest that the dryopithecins show features found in chimps and gorillas today and therefore make good candidates for the ancestors of living African apes[9]. The *D. guggenmosi* skeleton is unique compared with other dryopithecin specimens, both in its preservation of two, almost complete, limb bones — an ulna (a forearm bone) and a tibia (a leg bone) — and in the combination of characteristics it displays. Böhme *et al.* focus their attention on a baboon-sized and probably



VELIZAR SIMEONOVSKI

Figure 2 | *Danuvius guggenmosi*. Böhme and colleagues instructed the artist Velizar Simeonovski to make an illustration of what this species might have looked like.

male partial skeleton. As well as the ulna and tibia, the skeleton includes some vertebrae, a partial thigh bone (femur), and hand and foot bones.

The length of the ulna relative to the tibia shows that the forearm of *D. guggenmosi* was long relative to the leg, similar to a bonobo's

"The newly discovered ape species might have walked flat-footed on branches."

form. Combined with a flexible elbow and hand bones indicating a powerful, grasping thumb and curved fingers, the forelimb has the telltale signs of arboreal suspension found in all living great apes.

However, the lower limb of *D. guggenmosi* tells a different story, and one that is more reminiscent of human lower limbs than of those of other great apes. The shape of the joints of the femur and tibia suggests the use of extended (upright) hip and knee postures that differ from the bent hips and knees that living African apes use when they occasionally walk bipedally on the ground or in trees. The top of the tibia is reinforced, and the ankle joint is stable, properties that are adaptations for resisting the higher load placed on the lower leg when moving on two limbs instead of four. But the foot has a long, robust big toe that would be good for grasping, suggesting that *D. guggenmosi* might have walked flat-footed on branches (Fig. 2). Whether or not it regularly walked bipedally on the ground is less clear.

Together, the mosaic features of *D. guggenmosi* arguably provide the best model yet of what a common ancestor of humans and African apes might have looked like. It offers something for everyone: the forelimbs suited to life in the trees that all living apes, including humans, still have; lower limbs suited to extended postures like those used by orangutans during bipedalism in the trees[8]; and further specialization of such features of the lower limbs in humans to enable habitual terrestrial bipedalism.

If it is accepted that the locomotor behaviours observed in living great apes and humans evolved from an ancestor that used extended limb clambering, this would answer the question of what kind of early locomotion underlies our bipedal origins. And that would get us closer to answering why and how our human ancestors became less dependent on life in the trees and fully embraced two-footed terrestrial locomotion. Until more fossil evidence of how African apes evolved is found, a bottom-up approach from the Miocene is probably our best means of deciphering the evolution of one of our most defining human features.

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