From forelimbs to two legs

Mark Collard and Leslie C. Aiello

A reanalysis of the wrist bones of early human fossils provides the first good evidence that humans evolved from ancestors who 'knuckle-walked', as chimps and gorillas do today.

Most people think that palaeoanthropologists spend their lives in exotic places prospecting for fossils. Not so — researchers working on human evolution generally spend most of their time in the laboratory seeking new ways of testing ideas about the existing fossil record. At least as many advances in our understanding of human evolution have come from reanalyses of familiar fossils as from the discovery of new ones. The study described by Richmond and Strait on page 382 of this issue[1] is an excellent case in point.

Richmond and Strait reanalysed several well-known early hominid fossils, including the famous skeleton known as Lucy. Comparing the wrists of these fossils with the wrists of modern humans and several other primate species, Richmond and Strait found that two of our earliest fossil relatives, *Australopithecus afarensis* and *Australopithecus anamensis*, exhibit characteristics of the wrist that are seen today only in the African apes. These features are thought to be associated with knuckle-walking, an unusual mode of quadrupedal locomotion in which the fingers are bent and weight is supported on the backs of the second of the three rows of finger bones. In contrast, the wrists of the other early hominid species in their sample, *Australopithecus africanus* and *Paranthropus robustus*, are like those of modern humans in that they lack the putative knuckle-walking characteristics (Fig. 1).

Richmond and Strait's study is significant for several reasons. First, it bears on the long-standing debate over the evolutionary history — the 'phylogenetic' relationships — of modern humans (*Homo*), chimpanzees (*Pan*) and gorillas (*Gorilla*). Genetic analyses overwhelmingly indicate that chimpanzees and humans are more closely related to one another than either is to gorillas[2]. Until the study by Richmond and Strait, however, the anatomical evidence largely ran counter to this conclusion. Many palaeoanthropologists took the knuckle-walking characters of *Pan* and *Gorilla* to be 'shared derived' characters which showed that the two groups of African ape were each other's closest relative[3].

The anatomical evidence could be reconciled with the molecular evidence in only two ways. Some researchers thought that the knuckle-walking characters exhibited by *Pan* (Fig. 2, overleaf) and *Gorilla* were independently derived or 'convergent' characters, resulting from natural selection under similar environmental and ecological conditions[4]. This perspective implied that the knuckle-walking characters are of no phylogenetic significance. Others argued that the knuckle-walking characters were present in the common ancestor of *Pan*, *Gorilla* and *Homo*, and were simply lost in the lineage leading to *Homo*[5]. According to this view, the knuckle-walking characters of *Pan* and *Gorilla* are 'primitive' features, which, like convergent characters, tell us nothing about phylogeny. Richmond and Strait's results offer strong support for the idea that knuckle-walking characters were present in the common ancestor of modern humans and the African apes, and provide grounds for reconciliation between the molecular and anatomical evidence.

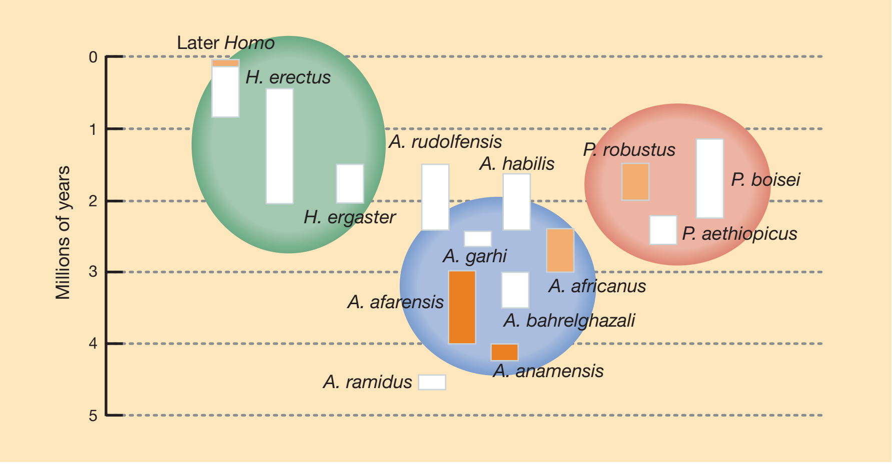

Figure 1 **Approximate time ranges of known hominid species. Those species shown in the red circle are robust 'australopithecines' belonging to the genus *Paranthropus* and represent an evolutionary dead-end. Those in the blue circle belong to the genus *Australopithecus*, and those in the green circle are of the genus *Homo*. There is no consensus over the precise phylogeny linking these species. Richmond and Strait[1] have recognized knuckle-walking features in the wrists of those species indicated by dark orange colouring; species indicated in light orange do not have these features. Evidence for the presence or absence of such features in the other species is either non-existent or not yet analysed.**

The second point of significance in the new study[1] relates to the phylogenetic relationship between *A. afarensis* and *A. africanus*. For many years, palaeoanthropologists thought that *A. afarensis* was the ancestor of *A. africanus* and the later hominids because its skull has more chimpanzee-like features than that of *A. africanus*. In 1995, however, the discovery at Sterkfontein, South Africa, of a collection of foot bones from a single *A. africanus* individual[6] complicated the picture. Unexpectedly, the bones indicated that the foot of *A. africanus* was more ape-like than the foot of its putative ancestor *A. afarensis*. This finding was supported by analyses of a newly discovered shin bone from Sterkfontein, which suggested that the lower leg of *A. africanus* was more ape-like than that of *A. afarensis*[7]. It was also supported by an assessment of hominid joint sizes, from which it seemed that *A. africanus* had more ape-like limb proportions than *A. afarensis*[8].

So it looked like the skulls of these species were telling one story (that *A. afarensis* was the ancestor of *A. africanus* and the later hominids), and their limbs were telling another (that either *A. afarensis* was a side-branch in human evolution and *A. africanus* was the ancestor of the later hominids, or vice versa). The work by Richmond and Strait further complicates the picture: it suggests that *A. afarensis* retained some knuckle-walking features, whereas *A. africanus* did not. It is no longer a case of the skull pointing to one set of phylogenetic relationships, and the postcranial skeleton — everything but the skull — to another. Rather, different parts of the postcranium may not support the same phylogenetic hypothesis.

The third notable aspect of Richmond and Strait's study concerns the interpretation

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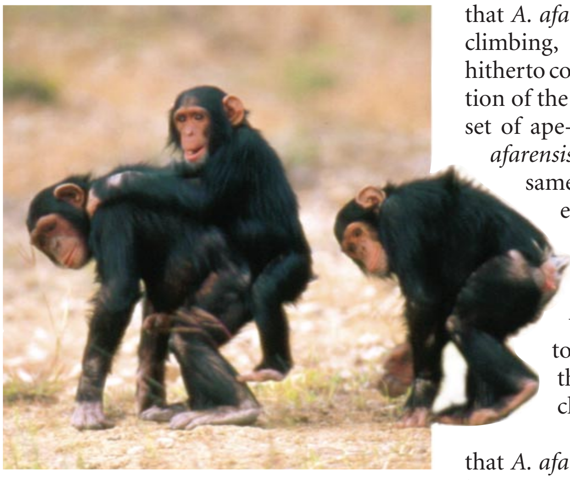

Figure 2 **The common ancestor of modern humans and African apes, including gorillas, bonobos and chimps (pictured), may have used a form of locomotion called 'knuckle-walking' when on the ground.**

of fossil morphology in terms of function, especially locomotion. Ever since Lucy was discovered in the late 1970s, there has been debate about the locomotor repertoire of *A. afarensis*, the species to which she is assigned.

The basic facts are not in dispute. *A. afarensis* has a combination of traits that is not seen among living primates. In some respects, *A. afarensis* is quite human-like (for instance in the foot structure, non-opposable big toe, and pelvis shape). In others, it is quite ape-like (relatively long and curved fingers, relatively long arms, and funnel-shaped chest).

What can be made of these features? For some researchers, the ape-like characteristics of *A. afarensis* are non-functional retentions from the common ancestor of hominids and the African apes. Here, emphasis is put on the human-like characteristics, and *A. afarensis* is seen as a hominid that walked on two legs and got about in no other way[9]. For others, the ape-like traits are functionally important, and *A. afarensis* is interpreted as using a 'mixed' locomotor repertoire, in which a form of terrestrial bipedalism was combined with an ability to move around effectively in trees[10].

Richmond and Strait add a twist to this debate. They propose that the knuckle-walking features of *A. afarensis* are non-functional retentions from the common ancestor of hominids and African apes. This seems an entirely reasonable position, given that *A. afarensis* shows many traits that are thought to be associated with bipedal locomotion. The alternative idea — that *A. afarensis* combined knuckle-walking, bipedalism and climbing — is somewhat counterintuitive, because it implies the use of two entirely different modes of terrestrial locomotion.

By the same token, however, Richmond and Strait's argument undermines the idea that *A. afarensis* combined bipedalism with climbing, which many researchers have hitherto considered to be the best interpretation of the evidence. Can we assert that one set of ape-like characters indicates that *A. afarensis* was an able climber, while at the same time arguing that another, equally good, set of ape-like characters is indicative of nothing except the phylogenetic history of *A. afarensis*? If the knuckle-walking characters are considered to be primitive retentions, must not the same hold for the other ape-like characters?

Are our only choices to accept that *A. afarensis* was a striding biped with a large number of non-functional primitive retentions, or to have to take seriously the counterintuitive idea that the locomotor repertoire of *A. afarensis* included forms of bipedalism, climbing and knuckle-walking?

It is difficult to predict how palaeoanthropologists will react to Richmond and Strait's study. But one thing is certain. It will encourage many researchers to reconsider their assumptions about the phylogenetic and functional implications of bone shape and size in the primates, and most especially in the early hominids. ■

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Quantum optics

Tricks with a single photon

Peter Zoller

Laser light can trap atoms. But can the light field of a single photon hold an atom in free space? Because it was the development of the laser as an intense light source that made optical trapping and cooling of atoms practical, this seems to be an essentially impossible task. But now a group from the Max-Planck Institute for Quantum Optics in Munich headed by G. Rempe reports an experiment[1] (on page 365 of this issue) in which a single photon stored in a microcavity produces an optical force sufficient to trap an atom. Together with the related experiments on trapping and cooling of single atoms in optical cavities by H. J. Kimble's group at Caltech[2], these recent advances mark a new generation of cavity quantum electrodynamics (QED) experiments[1–5]. Such work opens up exciting new avenues for basic research in quantum physics with single atoms and photons, and suggests fascinating future applications in quantum information processing.

When a laser beam is focused, an atom can experience an optical force so that it is attracted to the centre of the light focus. The same concept underlies 'optical tweezers', which are used to manipulate much more macroscopic particles than atoms with light fields. For intense laser beams, the optical force can be strong enough to overcome gravity. The stronger the light beam, the deeper is the optical potential that holds the atom. In addition, for an atom to remain bound in the laser focus, its thermal energy must be sufficiently small that it cannot escape. In fact, the atoms must be extremely cold in comparison with gases at room

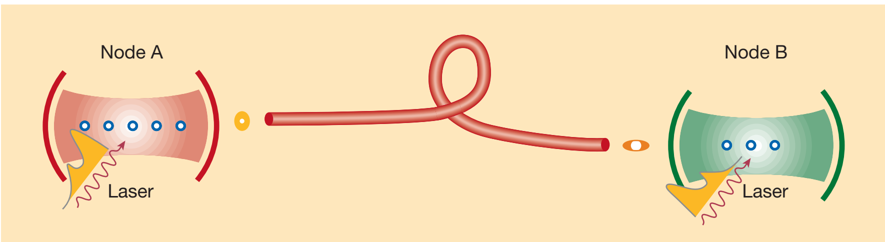

Figure 1 **A quantum network based on cavity quantum electrodynamics (QED). Quantum communication channels connect the spatially separated nodes. Each node is a quantum processor that stores and processes quantum information locally. Atoms in the cavity provide the quantum memory, laser pulses play the role of quantum gates by exchanging cavity photons, and the cavities themselves become optical interconnects with a fibre linking the cavities. Exchange of information between the nodes of the network is accomplished by way of quantum channels. New techniques to confine atoms within optical cavities[1–3] bring such quantum networks closer to reality.**