PALAEOANTHROPOLOGY

Malapa and the genus *Homo*

Two remarkably well-preserved skeletons of the hominin species *Australopithecus sediba*, found at Malapa, South Africa, show an intriguing combination of features, and open up a debate about the origins of the genus *Homo*.

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Following on from the announcement last year by Berger *et al.*[1] of the remains of a newly discovered hominin species, *Australopithecus sediba*, the same group has now published five reports[2–6] in *Science* detailing additional fossils and further analyses. Cave deposits at the Malapa site in South Africa yielded two partial skeletons, which Pickering *et al.*[6] have found to be 1.977 ± 0.002 million years (Myr) old. These skeletons are not only well preserved and remarkably complete, but also show a surprising mix of morphological characters. Given the completeness of the skeletons, the unexpected combination of primitive and derived morphology, and the likelihood that further individuals will be recovered at Malapa, *A. sediba* certainly has the potential to uproot conventional views of human evolution.

Overall, the authors find that *A. sediba* is australopith-like, with a small brain and long arms, and is most similar to its likely ancestor *Australopithecus africanus*, remains of which have been found at several South African sites. However, some aspects of the *A. sediba* skeletons seem to show a closer resemblance to the morphology found in species of the genus *Homo*. These include aspects of the shape of the pelvis[3] and ankle joint[5], as well as the long thumb and short fingers that are characteristic of hands capable of precise manipulation[4]. The authors suggest that these features are phylogenetically shared with *Homo* species, rather than being examples of homoplasy (similar traits that evolved independently in separate lineages), and conclude that *A. sediba* is a plausible candidate ancestor of *Homo*.

Early species of the genus *Homo* — *H. habilis*, *H. rudolfensis* and *H. erectus* — appear in the fossil record about 1.9 Myr ago (Fig. 1). Of these, *H. erectus* stands out because it gave rise to later *Homo* species (including modern humans), dispersed out of Africa, and became extinct less than half a million years ago. *Homo habilis*, or a species similar to it, is commonly considered to have been the ancestor of *H. erectus*, but it is difficult to be sure of this because only a small number of fragmentary fossils older than 1.9 Myr have been attributed to *Homo*, and these could not be attributed definitively to a specific species. The fossil most secure in its affinities and provenance is the approximately 2.35-Myr-old upper jawbone from Hadar, Ethiopia[7], which is more *Homo*-like than that of *A. sediba* and predates the Malapa finds by some 370,000 years. This evidence seems at odds with the idea that *A. sediba* was involved in the first appearance of *Homo*.

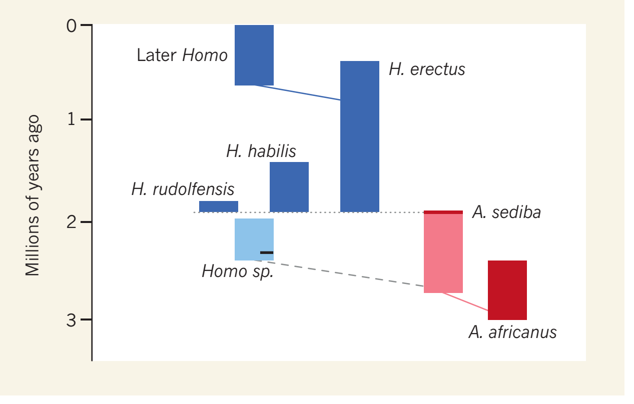

Figure 1 | Temporal distribution of selected hominin species. The bar diagram shows when various hominins (two australopiths, red, and various *Homo* species, blue) appear in the fossil record. The pale blue bar represents fragmentary fossils that are generally thought to come from early *Homo*. Of these, an upper jawbone from Hadar, Ethiopia (black line on the pale blue bar), is well dated at 2.35 million years (Myr) old, and is the most convincingly *Homo*-like. Lines connecting bars indicate hypothetical ancestry between species. The most recent addition to the diagram is *Australopithecus sediba* — two skeletons[2–6] of the hominin found at Malapa, South Africa, are 1.977 ± 0.002 Myr old. Two scenarios have been proposed[1,6] in which *A. sediba* is the ancestor of the genus *Homo*. In the first scenario[1], fossils at Malapa come from a late-surviving population of *A. sediba*, whose earlier representatives (pink bar) were ancestral to *Homo* (dashed line). In the second scenario[6], the *A. sediba* population at Malapa was itself ancestral to early *Homo* (dotted line), which means that fossils pre-dating 2 Myr ago (pale blue) cannot be attributed to *Homo*.

In their original publication[1], Berger *et al.* suggested that *A. sediba* could have originated much earlier than the time to which the remains were dated, with the Malapa sample representing a late-surviving population (Fig. 1). However, in their latest report[6], the authors go further by concluding that even *A. sediba* fossils as late as those preserved at Malapa could have been the ancestor of *Homo*. As a logical corollary, they also contest the *Homo* affinities of any fossil older than 2.0 Myr old. What's more, the authors hint at the possibility that *A. sediba* itself, rather than a species such as *H. habilis* or *H. rudolfensis*, was ancestral to *H. erectus*. It will, however, be difficult to uphold the suggestion that the extensive evolutionary change required could have occurred in the time available (a maximum of 80,000 years) if *A. sediba* at Malapa gave rise to *Homo* species. Moreover, the idea that no fossil older than 2.0 Myr is legitimately attributable to *Homo* is highly debatable — the arguments provided in the paper are insufficiently specific to be conclusive, particularly with respect to the Hadar jawbone.

Another question is whether the authors' morphological analyses[1–6] do indeed suggest that *A. sediba* has closer evolutionary links with *H. erectus* than do *H. habilis* or *H. rudolfensis*. The answer seems to be no, mainly because the required comparisons either were not made or cannot be made in the absence of fossil evidence. For example, the morphology of the entire postcranial skeleton of *H. rudolfensis* is unknown, as is that of the pelvis of *H. habilis*, and very few hand and foot bones of *H. erectus* have been recovered, which means that none of these bones can be compared with those of *A. sediba*. Conversely, several brain endocasts — casts of the inside of fossil braincases — of species of early *Homo* are available[8], but the authors compared[2] their endocast of *A. sediba* only with those of modern humans and chimpanzees, and with two *A. africanus* fossils.

The rear and base of the *A. sediba*

cranium are not preserved, which is unfortunate as these areas are highly diagnostic of *H. erectus*. However, Berger *et al.*[1] have argued that the two species share two characteristic features in other parts of the cranium that are not present in *H. habilis* or *H. rudolfensis*. One feature is a slightly swollen area under the eye socket, but neither the definition nor the expression of this character in hominins is well established. The other feature is the amount of constriction of the braincase relative to the breadth of the face: both *A. sediba* and *H. erectus* show less constriction than other early hominin species.

At first sight, this shared characteristic does seem to be convincing evidence supporting a link between *A. sediba* and *H. erectus*. However, the constriction of an individual's braincase changes significantly, late in development; Berger and colleagues[1] studied a juvenile *A. sediba* that would have developed greater constriction had it lived to adulthood. Furthermore, early *H. erectus* shows greater constriction than do geologically later forms, and in this respect is similar to *H. habilis*. When all of these factors are taken into account, the exclusive grouping of *A. sediba* with *H. erectus* no longer seems clear.

Taken together, the published evidence[1–6] indicates that *A. sediba* is a late australopith that has several intriguing *Homo*-like features. If these features do indeed associate *A. sediba* with the emergence of *Homo*, rather than reflecting homoplasy, then it seems that the scenario in which the Malapa specimens represent a late surviving population[1] is the most plausible explanation for Berger and colleagues' findings.

Many reviews of palaeontological research end with the statement that it would be highly desirable to recover more fossils. In this case, however, the Malapa team has already done that. The interpretation of their findings may be a matter of debate, but they have undoubtedly added a spectacular and thought-provoking sample to the hominin fossil record. This achievement represents a major contribution to the study of human evolution in all its complexity. ■

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1. Berger, L. R. *et al. Science* **328,** 195–204 (2010).
2. Carlson, K. J. *et al. Science* **333,** 1402–1407 (2011).
3. Kibii, J. M. *et al. Science* **333,** 1407–1411 (2011).
4. Kivell, T. L. *et al. Science* **333,** 1411–1417 (2011).
5. Zipfel, B. *et al. Science* **333,** 1417–1420 (2011).
6. Pickering, R. *et al. Science* **333,** 1421–1423 (2011).
7. Kimbel, W. H., Johanson, D. C. & Rak, Y. *Am. J. Phys. Anthropol.* **103,** 235–262 (1997).
8. Holloway, R. L., Broadfield, D. C. & Yuan, M. S. *The Human Fossil Record* Vol. 3 (Wiley, 2004).