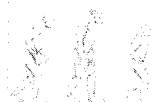


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Australopithecus garhi: A New-Found Link?

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INTRODUCTION

The human line separated from the chimpanzee line some 5 million years ago or a little more, according to dates derived from molecular "clocks". The earlier members of the human lineage, all of them entirely African, are lumped together as "australopithecines", named for the genus *Australopithecus* but including other genera too. Later members are placed together in the genus *Homo*.

Australopithecines have small cranial capacities (about 350 to 550 cc), large faces, jaws and cheek teeth, and the arrangement of the teeth in the jaws (dental arcade) tends to be rectangular. Where the postcranial skeleton is known, the ribcage is funnel-shaped (narrow at the top, expanding downwards), the hipbones are very wide and flaring, and the legs are short (leg:arm ratio intermediate between chimpanzee and human). The feet are basically bipedal and resemble humans, but the phalanges (toe-bones) are more curved. Fossils of the genus *Homo* have larger cranial capacities (510 cc upward), usually smaller faces, jaws and cheek teeth, and the dental arcades are parabolic. Except in the most primitive members the ribcage, where known, is barrel-shaped, the hipbones do not flare as much and are more curved, the legs are long, and the feet are fully modern.

can be separated from other Great Apes as a tribe, Hominini, so fossils on the human side of the divide are "hominins". Anthropologists as a crew are always about 10 years behind other biologists, so it will probably be quite a while yet before textbooks of human evolution stop using "hominids" in the old sense.

THE AUSTRALOPITHECINES

Among the australopithecines, the earliest member is *Ardipithecus ramidus*, which is about 4.4 million years (Ma) old and presents a quite distinct set of traits. The other distinctive clade represents the "robust" or "nutcracker", *Paranthropus* species, a distinct lineage which can be traced through a million and a half years from 2.5 to about 1 Ma. The others are for the moment (for want of a decent cladistic model, really) lumped into the genus *Australopithecus*, which contains — or did until early this year — at least 4 species:

1. *Australopithecus anamensis*, 3.9 to 4.1 Ma, from Kanapoi and Allia Bay, Lake Turkana district, northwestern Kenya. Though only recently described, this species is represented by quite a range of remains.
2. *Australopithecus babrelghazali*, about the same age as *A. anamensis*. This species is recovered from Koro Toro in Chad and represents the only australopithecine known from western Africa. *A. babrelghazali* is known so far only by a single jaw.
3. *Australopithecus afarensis* is well known from Fejej in Ethiopia; about 4 Ma, Laetoli in Tanzania, 3.5 to 3.75 Ma; and Hadar in Ethiopia, 3.3 to 2.9 Ma. These sites cover a wide area in space and time, and not everyone is convinced that they all belong to a single species. Laetoli has over 20 fossil individuals (mainly jaws and teeth), and some important fossil footprints, while the extremely rich deposits at Hadar include a collection called "The First Family" and the very famous partial skeleton "Lucy".
4. *Australopithecus africanus*, the earliest described species, from South Africa; it has long been known from the sites of Taung, Sterkfontein and Makapansgat, and new exca-

Table 1: Brief Comparison of *Australopithecus* with early *Homo* fossils¹

	<i>A. afarensis</i>	<i>A. africanus</i>	<i>A. garhi</i>	Early <i>Homo</i>
Molar & premolar size	moderate	moderate to large	huge	moderate
Anterior upper premolar	asymmetrical	more oval	more oval	more oval
Tooth enamel thickness	fairly thick	thick	thick	thick
Dental arcade shape	rectangular converges backward	rectangular diverges posteriorly	rectangular diverges	parabolic diverges
Anterior depth of palate	shallow	varies	shallow	deep
Diastema in upper jaw	common	absent	present	rare
Anterior pillars on face	no	yes	no	no
Prognathism	strong	usually strong	strong	reduced
Supraorbital structure	thin bar	thin bar	thin bar	torus
Cranial capacity	343-500	428-ca 515	450	510-752

¹Table based on Asfaw and others, 1999.

As a typical bang-up-to-the-minute biologist, I adopt a cladistic attitude to taxonomy: a family or genus is an evolutionary lineage. I place humans, chimpanzees, gorillas and orangutans together in the family Hominidae; so "hominid", a term still all too often used to mean "in the human line", actually refers to other living Great Apes too. At most, humans

vations have recently begun at other sites in the Sterkfontein Valley (Drimolen and Gladysvale). Until very recently no absolute ages for these South African sites seemed possible, but they were dated by comparing their mammal faunas with those from sites in East Africa that could be dated. These comparisons suggested dates of 2.5 to 3 Ma. Very recently, attempts have been made to apply Electron Spin Resonance dating to them, and the results so far seem consistent with the faunal inferences.

The indications are that the early hominins were as diverse as any other group of large mammals. Among all the diversity, however, there must have been some actual ancestors and, human nature being what it is, everyone is obsessed with trying to deduce which, if any, of the fossil species might have filled this role. About all we can say so far about the ancestral possibilities of *A anamensis* is that it is in the right place at the right time and has no specialized bits of anatomy that would *exclude* it from having been an ancestor. *A afarensis* seems pretty primitive all around, but of course is more derived in the human direction than *A anamensis*. So, a plausible sequence begins to emerge. But what of *A africanus*?

Opinions have been rather divided about *Australopithecus africanus*. It is later in time than *A afarensis* and earlier than the first *Homo*, *H habilis*, so it fills the time gap; but it has seemed to be in the wrong place. Maybe our ancestors evolved in East Africa, moved south, and then later moved back again to become *Homo* (though of course they may have existed in East Africa too but we just haven't found any yet). But the differences from *A afarensis* to *H habilis* seem mostly to be pointing in the wrong direction. On the one hand *A africanus* had a larger cranial capacity on average, the lower premolars were wider (in *A afarensis* they were often narrow and fairly apelike), and the dental arcade sometimes tended to be more parabolic. On the other hand it had larger, broader molars and premolars but somewhat smaller front teeth, and a heavily built-up facial skeleton with what one specialist, Yoel Rak, has called "anterior pillars" — prominent bony thickenings alongside the snout and nasal aperture. If *A africanus* was ancestral to *Homo*, these last features would have been developed then lost again — a transition we try to avoid in deriving ancestor-descendant lineages.

EARLY HOMO

Well-preserved specimens of *Homo* appear at around 2 Ma in East Africa, mainly at Olduvai Gorge (Tanzania), where *Homo habilis* occurs, and at Koobi Fora (Kenya), where 2 species are present, a *habilis*-like species and the larger *Homo rudolfensis*. Both, especially *H rudolfensis*, have large molars, but the premolars are less expanded than in *A africanus*. The cranial capacity is 510-680 cc in *H habilis* and

about 750 in *H rudolfensis*. The postcranial skeleton in *H habilis*, at least, is every bit as primitive as in australopithecines (it is "well known" that the legs are even relatively shorter than in "Lucy", but Asfaw and others [1999] point out that the evidence actually will not sustain this conclusion; this was shown earlier by Korey [1990]). A couple of hundred thousand years after these 2 early *Homo* species appeared, the first more modern-looking species, *Homo ergaster* with its long legs, shortened forearms, short face, prominent nose and beetle-brows, and a cranial capacity over 800 cc, appears in the record and is well on the way to becoming us.

The early *Homo*-bearing beds also have stone tools. Chimpanzees modify grass stems, branches and other perishable material, and they use stones to crack nuts but do not modify the stone. Presumably australopithecines did at least as well as chimpanzees, but not until *Homo* are there signs that stone was deliberately modified to form tools.

Where, then, did *Homo* spring from? There has been a big gap in the record before 2 Ma — back to 2.5, if we think that *A africanus* was the ancestral stock; or to 2.9 if we reject *A africanus* and take it back to *A afarensis*. (A related question, where did *Paranthropus* spring from, has now gone some way to being answered by the discovery, in the mid-80s, of "the Black Skull", from 2.5-ma deposits at Lomekwi, west of Lake Turkana. This specimen is beautifully intermediate between *A afarensis* and the later (1-2 Ma) *Paranthropus* specimens we find at Koobi Fora, Olduvai and so on.

Until this year, there were just a few suggestive scraps:

1. A jaw from deposits of 2.3-2.5 Ma at Uraha, in Malawi. This has extremely large teeth and a characteristic U-shape, and has been ascribed to *Homo rudolfensis*.
2. A maxilla from 2.3-ma levels at Hadar. This is very clearly *Homo*, less prognathous ("snouty") than an australopithecine, with a fairly parabolic dental arcade and no anterior pillars. Its smaller teeth resemble *Homo habilis*. From the same level come stone tools.
3. A temporal bone fragment, mainly the glenoid fossa (where the jaw fits into the skull), from 2.4 Ma deposits at Chemeron in Kenya. The glenoid fossa is deep and *Homo*- (rather than *Australopithecus*-) like. It appears to be placed further under the braincase suggesting that the brain had expanded above and out over the side of the joint.
4. Finally, a basicranial specimen (Sts 19) from Sterkfontein, found in amongst the *Australopithecus africanus* remains, has quite a number of *Homo*-like details of the form of the ear region, all of which distin-

The indications are that the early hominins were as diverse as any other group of large mammals.

guish it from any australopithecine. In comparable parts, in fact, it is quite like the Chemeron temporal.

The Uraha mandible and Hadar maxilla are early *Homo*, there is no disagreement about this. The Chemeron temporal and Sts 19 are much more controversial. Even if we narrow it down to just the first two, we come to the interesting conclusion that by 2.3 Ma two species already seem to be in existence, the same two species that we find in the 2 Ma deposits at Koobi Fora.

ENTER THE BOURI HOMININ — OR SHOULD THAT BE HOMININS?

And now, and now... hot off the presses ... a paper by Asfaw and others (*Nature* 1999 Apr 23; 284:629-5) describes a new species which they think "is descended from *Australopithecus afarensis* and is a candidate ancestor for early *Homo*." The new species is *Australopithecus garhi* from Bouri, on the Middle Awash River in Ethiopia. The age is 2.5 Ma, and the remains are associated with large antelope remains with cut-marks on them, apparently from stone tools. The primitive stone tools themselves were found not at Bouri itself but at the nearby, contemporaneous site of Gona.

The type specimen of *Australopithecus garhi* is a partial cranium. From nearby sites, and perhaps belonging to the same species or perhaps not, come several postcranial bones including a partial skeleton, a fragment of a second cranium, and 2 mandibles (one

what is astounding about the specimen are the huge premolars and molars. The canine, for example, is larger than any other hominin, the anterior premolar is larger than any except for some specimens of *Paranthropus boisei* (the East African "nutcracker" species), and the second molar is larger than any *Homo*, though within the range of *A africanus*.

About the mandible, Asfaw and colleagues say little, except that its morphology would be compatible with belonging to the same species. The stone tools might have been made by *A garhi*, or they might not. As for the postcranial bones, the authors are careful to explain, they too need not belong to the same species. There could be one species that left its head in the deposits and another that left its postcranial skeleton there (and of course either or neither of them might have made the stone tools). But for what it is worth, and it is worth a good deal, Asfaw and colleagues give a brief description and an interesting diagram of the limb bone proportions. The femur-to-humerus ratio was like *Homo ergaster* and modern humans (long femur, short "Lucy"-sized humerus), but the forearm (radius and ulna)-to-humerus ratio was long like a chimpanzee or, for that matter, like "Lucy".

What are we to make of it? One, 2 or 3 species? What we have is

- a skull (to which the name *Australopithecus garhi* belongs), resembling *A afarensis* but more derived; possessing features shared by *A africanus* and *Homo*, and without the apparently unique specializations of *A africanus*;
- limb bones intermediate in proportion between *A afarensis* and *H ergaster*; and
- the earliest stone tools so far discovered.

On balance, the evidence favors the single-species interpretation, but until we find associated parts we must be cautious, especially because of those vast teeth. It has been argued by McHenry, Tobias and others that megadontia (big-toothedness) is the primitive condition so that the teeth of early *Homo* ought to get smaller. Indeed, we do observe a decrease in tooth size in the emerging hominins, except for these specimens from Bouri. That the putative ancestor of *Homo* (based on derived condition of skull and limb bones) had the biggest teeth of the lot — that was entirely unexpected!

Suppose *Australopithecus garhi* made the tools and was the ancestor of *Homo*. Where do the 4 early *Homo* specimens presumed older than 2 Ma fit in? The Bouri cranium lacks a base, so that prevents direct comparisons with both Sts 19 and the Chemeron temporal. Asfaw and colleagues do not describe the Bouri-region mandibles, so that (for the moment) excludes comparisons with Uraha. But the Hadar maxilla is definitely different from the one found at Bouri. In fact, it could be lost among the Olduvai maxillae, more than 300 000 years later. So, if *A garhi* is ancestral to *Homo*, either there was a rapid change in maxillary morphology in the intervening 200 000 years, or else

Table 2: Body Proportions^a of Some Important Fossils Compared With Modern Humans and the Most Humanlike Ape (the Bonobo or "Pygmy Chimpanzee").

	Brachial index: ^b		Humerofemoral index: ^c	
	Radius as % of humerus	Humerus as % of femur	Radius as % of humerus	Humerus as % of femur
<i>Pan paniscus</i> (Bonobo)	91.9	97.8 ± 2.1	91.9	97.8 ± 2.1
<i>A. afarensis</i> ("Lucy" skeleton)	90.7	84.6 ± 2.8	90.7	84.6 ± 2.8
Bouri (perhaps <i>A. garhi</i>)	97.9	ca. 70.4	97.9	ca. 70.4
<i>H. habilis</i> (OH 62)	179.5-93.2]	[94.3 ± 7.7]	179.5-93.2]	[94.3 ± 7.7]
<i>Homo sapiens</i> (African)	79.6 ± 2.5	73.3 ± 1.7	79.6 ± 2.5	73.3 ± 1.7

^a ± means, for living forms, the sample standard deviation; for individual fossils, the standard deviation of the estimate. See especially Korey (1990), who shows how the *Homo habilis* data have been grossly overinterpreted.

^b The brachial index calculates the length of the forearm as a proportion of the upper arm.

^c The humerofemoral index calculates the relative lengths of the arms and legs by comparing the upper arm to the thigh.

fairly complete). The specific name, *garhi*, means "surprise" in the Afar language, and a bit surprising it is, too. It is basically australopithecine, with a small cranial capacity (450 cc), rectangular or slightly diverging dental arcade, and very prognathous face. It lacks the anterior pillars of *Australopithecus africanus*, and it even has a gap (diastema) between the lateral incisor and the canine, a primitive feature seen in *A afarensis* but not in *A africanus*. From the photos, it looks very like *A afarensis*, but the authors point out some more "advanced" features like the premolar shape and the more anteriorly placed malar (cheekbone) root. Like many australopithecines, including some *A afarensis*, it has a sagittal crest for anchoring large temporal (chewing) muscles. But

the Bouri specimen is a late survivor of its species. We must not exclude a speeding-up of evolutionary rates, nor must we fall into the trap of assuming anagenesis (evolution without branching).

It's an exciting time to be alive if you're interested in human evolution. New countries are getting onto the paleoanthropological map: India, Syria, Eritrea, Chad, Malawi, and Portugal. Every new fossil fulfills certain expectations but opens up a whole barrel of new research questions. Fossil discoveries are matched by new discoveries of just how human our nearest living relatives are. And the press is avid for them all, as well it might be. Keep on your (bipedal) toes; if you miss this week's reports you might already be out-of-date.

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The De-riving Force of Cladogenesis

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Cladogenesis is the term used to describe the branching off of new taxa. These branches — or *clades* — are based on several criteria which make the descendants along a particular branch different from their ancestors and from related taxa on other branches. Each new branch exhibits a combination of novel characteristics which are unique to that branch mixed with some "familial" characteristics which this branch shares with its evolutionary ancestors. Although certain novel traits may be diagnostic for members of an evolving lineage, it is often the *combination* of unique and shared characteristics which defines new branches.

The basis of constructing a good cladogram is the ability to identify the characteristics of the ancestral population and those of the descendants. Characteristics found among the ancestors and shared by most or all members of related taxa are referred to as *primitive*. In cladistic studies this word is understood as "original" or "primal" and not as "crude" or "simple". In order to avoid confusion, some writers refer to these traits as *conservative* or simply *ancestral*. Shared, conservative traits link the members of related branches to a common ancestor.

On the other hand, characteristics that are found in various evolutionary branches which differ from those of the ancestors are considered *derived*. In many cases these derived characteristics are changes to the structure or function of widely-shared ancestral characteristics. Derived traits distinguish the members of one evolutionary branch from the members of another branch.

A cladogram is based on these combinations of ancestral and derived characteristics in related species by organizing and diagramming the pattern and sequence in which they could have arisen. There are two fundamental principles that we follow in building cladograms. First, a cladogram is based on an ordered or sequenced pattern of traits. The goal is to produce the most *parsimonious* cladogram — one that proceeds from the ancestor's to the descendant's profile with the fewest backward or sideward steps. In a sense, we want a cladogram in which evolution need invent a characteristic only once in an evolving lineage.

Second, we want a *monophyletic* cladogram. Each evolutionary branch must contain all descendants of a common ancestor. One of the chief criticisms against the "classical" taxonomy which places humans on one branch and the great apes (African apes and the orang utan) on another is that fails on the criterion of monophyly. Based on fossil data, comparative anatomy, and molecular biology, humans share a more recent common ancestor with African apes than either group does with orangs, and so humans should not occupy a separate branch.

Fossil data help to refine cladistic analysis by providing information about the sequence or order in which certain derived traits emerged. Cladistic analysis helps to resolve the "problem" of the so-called "missing links" or the intermediate specimens, because it does not require that fossil species *evolve into* any related species which emerge later. Instead, it represents the evolutionary history of an evolving lineage in terms of a collection of characteristics which can be passed along to descendant populations — or not!