

Evolution's Bad Girl

Ardi shakes up the fossil record

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Standing tall In this artist's illustration, Ardi stands amid *Ardipithecus ramidus* comrades in once-forested East Africa. Illustration: Jay Matternes © 2009

She's the ultimate evolutionary party crasher. Dubbed Ardi, her partial skeleton was unearthed in Ethiopia near the scattered remains of at least 36 of her comrades. Physical anthropologists had known about the discovery of this long-gone gal for around 15 years, but few expected to see the 4.4-million-year-old hell-raiser that was unveiled in 11 scientific papers in October.

Like a biker chick strutting into a debutante ball, Ardi brazenly flaunts her nonconformity among more-demure members of the human evolutionary family, known as hominids. She boasts a weird pastiche of anatomical adornments, even without tattoos or nose studs. In her prime, she moved slowly, a cool customer whether upright or on all fours. Today, she's the standard bearer for her ancient species, *Ardipithecus ramidus*.

And in true biker-chick fashion, Ardi chews up and spits out conventional thinking about hominid origins, according to a team — led by anthropologist Tim White of the University of California, Berkeley — that unearthed and analyzed her fragile bones ([SN: 10/24/09, p. 9](#)). First, White and his colleagues assert, Ardi's unusual mix of apelike and monkeylike traits demolishes the long-standing assumption that today's chimpanzees provide a reasonable model of either early hominids or the last common ancestor of people and chimps — an ancestor which some scientists suspect could even have been Ardi, if genetics-based estimates of when the split occurred are borne out.

Second, the team concludes, Ardi trashes the idea that knuckle-walking or tree-hanging human ancestors evolved an upright gait to help them motor across wide ancient savannas. Her kind lived in wooded areas and split time between lumbering around on two legs hominid-style and cruising carefully along tree branches on grasping feet and the palms of the hands.

One member of White's team argues for a controversial possibility: that two-legged walking evolved because *Ardipithecus* males had small canine teeth. Many living and fossil male apes

fight for mates by wielding formidable canines, but Ardi's male counterparts had to band together and forage over long distances to obtain mates, his thinking goes.

In a third slap at scientific convention, Ardi fits a scenario in which a few closely related hominid lineages preceded the larger-brained *Homo* genus that emerged around 2.4 million years ago, White says. In contrast, many anthropologists think of hominid evolution as a bush composed of numerous lineages that, for the most part, died out.

Each of Ardi's challenges draws plenty of fire. While lauding the new finds and the painstaking reconstruction of Ardi's bony frame, some critics dismiss White and company's reading of the fossils as incomplete and speculative.

Presentations at the Royal Society of London in October by several members of the Ardi excavation team produced "much sparring," says anthropologist William McGrew of the University of Cambridge in England.

"There's legitimate disagreement," White says. "But Ardi provides a perspective on early hominid evolution that was previously missing. This is a really bizarre primate."

Chimp change

Ardi sports a peculiar skeletal medley that pushes chimps and gorillas out of the evolutionary spotlight, says anthropologist Owen Lovejoy, a member of White's team. Ardi's ancient remains indicate that the last common ancestor of humans and chimps must not have looked much like living chimps, as many researchers have assumed, asserts Lovejoy, of Kent State University in Ohio.

Since a split 8 million years ago or so, chimps and gorillas have evolved along evolutionary paths that eventually produced specialized traits such as knuckle-walking, he says.

In his opinion, Ardi indicates that a human-chimp ancestor had monkeylike limb proportions and feet, a flexible and unchimplike lower back, and an ability to move along tree branches on all fours, rather than swinging chimp-style from branch to branch and hanging by outstretched arms.

"*Ardipithecus*, not living chimps, offers a remarkably good perspective on the last common ancestor," he says. "We can't modify the truth to make chimps more important."

That conclusion leaves some scientists unimpressed. "It's way too early to claim that we know what the last common ancestor looked like without actually finding its fossils," remarks anthropologist Brian Richmond of George Washington University in Washington, D.C.

Richmond holds that Ardi lived several million years after the last common ancestor, plenty of time for her kind to have evolved substantial skeletal changes.

And those changes may not have been as substantial as White's team claims, adds Richmond. Ardi's curved toes, wide big toe and large body correspond pretty well to chimps, in his opinion.

Other fossil evidence suggests that hominids came from a climbing and knuckle-walking ape ancestor that was unlike Ardi, Richmond argues.



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Ardi, deconstructed [View larger version](#) | A top-to-bottom look at the skeletal and physical structure of *Ardipithecus Ramidus*. Illustrations: Jay Matternes © 2009

Chimps and other living apes can provide testable ideas about issues such as tool use among early hominids and even the last common ancestor ([SN: 11/21/09, p. 24](#)), McGrew says. “Ardi is an intermediate hominid form, as is Lucy. So what?” he asks.

Questions remain about whether Ardi had the build for regular upright walking — a clear marker of hominid status — or for primarily moving through trees, with occasional two-legged jaunts on the ground, adds anthropologist John Hawks of the University of Wisconsin–Madison.

Consider *Oreopithecus*, an ape that lived on an island near Italy between 9 million and 7 million years ago. This creature possessed a pelvis, legs and feet that supported tree climbing as well as slow and somewhat stilted walking.

“*Oreopithecus* shows that there are alternate pathways to evolving a ground-based skeleton from the ape body plan,” Hawks says.

But *Oreopithecus* differed from Ardi in critical ways, Lovejoy responds, such as having extremely long arms. “Locomotion differed vastly between *Oreopithecus* and Ardi,” he says.

If *Ardipithecus* adopted upright walking in a big way and was a precursor of the human lineage, Hawks posits, “it could be the first hominid or perhaps even the common ancestor of humans and chimps — if we take genetic studies seriously.” DNA analyses suggest that people and chimps split from a common ancestor between 5 million and 4.5 million years ago, around Ardi’s time.

Lovejoy regards those genetic estimates as unreliable. DNA studies rest on doubtful assumptions, he says, such as constant rates of genetic mutation in the human and chimp lineages. Fossil evidence places the human-chimp split at more like 8 million to 10 million years ago, in his view.

Hominid family values

Disputes over Ardi's evolutionary relationships to living and extinct apes seem cordial compared with debate over her sexual relationships and their implications for ancient hominid social life.

This fracas goes back to 1981, when Lovejoy published a paper in *Science* about the sex life of what was, at that time, the earliest known hominid species,

Australopithecus afarensis. The most famous member of that species is Lucy, a 3.2-million-year-old partial female skeleton found at another Ethiopian site in 1974. Lovejoy proposed that Lucy's kind possessed traits consistent with what amounted to a sexual revolution in the ape world ([SN: 6/11/05, p. 379](#)).

In most ape species, males are much larger than females and fight viciously to mate with fertile females, who advertise their availability with swollen red tissue. Females raise offspring on their own.

Lucy's kind upended that arrangement, Lovejoy argued. Males grew only slightly larger than females and had small canines. Adults of both sexes favored long-term relationships as a matter of survival, he theorized. Males supplied food to regular partners with whom they had children, allowing females to spend more time raising their own children.

Monogamy worked, in Lovejoy's view, because female anatomy evolved to mask obvious signs of ovulation that signal sexual readiness to males, instead developing features such as permanently enlarged breasts. Hit-and-run unions stood a good chance of yielding no offspring and thus became unappealing to both sexes.

Lovejoy's evidence for minimal size differences between *A. afarensis* sexes has been sharply criticized. Critics charge that he's underestimated the size disparities.

Detractors add that upright males with diminutive canines could have found plenty of ways to pummel one another in mating battles, even if they had to resort to fisticuffs.

With Ardi in tow, Lovejoy has now elaborated on his argument. A transition to monogamous relationships, expanded child care by mothers and hidden female ovulation first occurred before Lucy, in *Ardipithecus*, he proposes. Ardi's kind displays even smaller sex differences in canine size than Lucy's species. "*Australopithecus* represents a more intense version of what was already evolving in *Ardipithecus*," Lovejoy says.

Cooperation among males later expanded in *A. afarensis*, he posits. Male bands scoured forests and savannas for food and worked together to avoid and defend against predators.

A social puzzle

Ardipithecus canines excavated by White's team validate Lovejoy's scenario, remarks anthropologist Robert Tague of Louisiana State University in Baton Rouge. Male canines are slightly larger than those of females, but all the canines are about the size of female chimps' canines, he says.

“Although Lovejoy’s theory is widely cited and presented in almost all biological anthropology textbooks, it is also widely rejected,” Tague acknowledges.

And for good reason, argues J. Michael Plavcan of the University of Arkansas in Fayetteville. Using a different statistical approach, he estimates that Lucy was actually considerably smaller than her male cohorts.

To portray early hominids as a peaceful, monogamous crowd “is phenomenally speculative,” Plavcan says. Although large-bodied primate males with fanglike canines usually fight over mates, minimal sex differences can result in any of a variety of mating arrangements, he contends.

What’s more, *Ardipithecus ramidus* fossils do display size differences between the sexes sufficient to assume that males mated with several females, as in many other primates with size disparities, McGrew remarks.

“Lovejoy’s social hypothesis is an interesting just-so story,” Richmond asserts. “He’s winning the competition for the title of the Rudyard Kipling of paleoanthropology.”

Primatologist Frans de Waal of Emory University in Atlanta doesn’t dismiss Lovejoy’s social hypothesis but faults him for comparing Ardi’s kind with common chimps while ignoring pygmy chimps, or bonobos. Bonobos have small canines relative to common chimps, a largely peaceful social life and a fondness for sexual activity.

“It’s high time for a new look at the bonobo,” de Waal wrote in a published commentary shortly after the Ardi papers appeared in *Science*. “What if we descend not from a blustering chimplike ancestor but from a gentle, empathic, bonobo-like ape?”

That’s doubtful, since bonobos differ in some critical ways from Ardi’s kind, Lovejoy responds. In particular, he says, bonobo males display moderately larger canines and body sizes than females.

“*Ardipithecus ramidus* preserves some of the ancestral characteristics of the last common ancestor [of humans and chimps] with much greater fidelity than does any living African ape,” Lovejoy says.

Not-so-bushy evolution

If Ardi cuts a singular figure that sets her apart from living apes, she also bolsters an argument for cutting back the expanding number of proposed early hominid lineages, White says. Since 1994, fossil discoveries have led to reports of four new genera from eastern Africa and Chad: 7-million to 6-million-year-old *Sahelanthropus* ([SN: 7/13/02, p. 19](#)), 6-million-year-old *Orrorin* ([SN: 7/14/01, p. 20](#)), 3.5-million-year-old *Kenyanthropus* ([SN: 3/24/01, p. 180](#)) and *Ardipithecus*, including fragmentary remains of 5.8-million to 5.2-million-year-old *Ardipithecus kadabba*.

White's team folds *Sahelanthropus*, known only from skull remains, and *Orrorin*, known from fossil teeth and leg-bone pieces, into the better-described *Ardipithecus* genus.

"*Ardipithecus* may represent a long period of stasis in hominid evolution," Lovejoy says.

From about 6 million to 4.2 million years ago, he proposes, *Ardipithecus* evolved as a set of separate hominid groups in East Africa that interbred enough to maintain biological unity.

After that, Ardi's kind possibly evolved into the first *Australopithecus* species. Or, one *Ardipithecus* group may have settled in an isolated area where it alone evolved into *Australopithecus*. It's also possible that *Australopithecus* derived from a hominid lineage that researchers haven't found, relegating *Ardipithecus* to an evolutionary side branch.

Anthropologists, in particular those who have excavated and named other early hominid genera, have not jumped on the *Ardipithecus* bandwagon. Proponents of bushy hominid evolution, such as Richmond, rely on computerized models that divvy up species by distinguishing between shared and distinctive skeletal traits across fossil sets, an approach that White and Lovejoy have criticized ([SN: 11/25/00, p. 346](#)).

"More time is needed to study Ardi and compare her to living primates," Hawks says. "White's team had 15 years to study this skeleton that the rest of us saw for the first time in October."

Complaints have circulated in anthropological circles over the past decade that White has inappropriately kept outside investigators from studying Ardi's remains. White vehemently denies those charges, saying that he has abided by Ethiopian law by publishing an initial description of the finds before making them available for others to study.

Researchers can now examine casts of the *Ardipithecus* fossils or, in certain cases, the fragile bones themselves, White says.

"These finds are phenomenally important and will keep many of us busy for years to come," says anthropologist Carol Ward of the University of Missouri in Columbia.

In other words, the evolutionary shindig that Ardi crashed has just started. The night is young. Party hearty, Ardi.