4.4 MILLION YEARS AGO

The Birth of Bipedalism

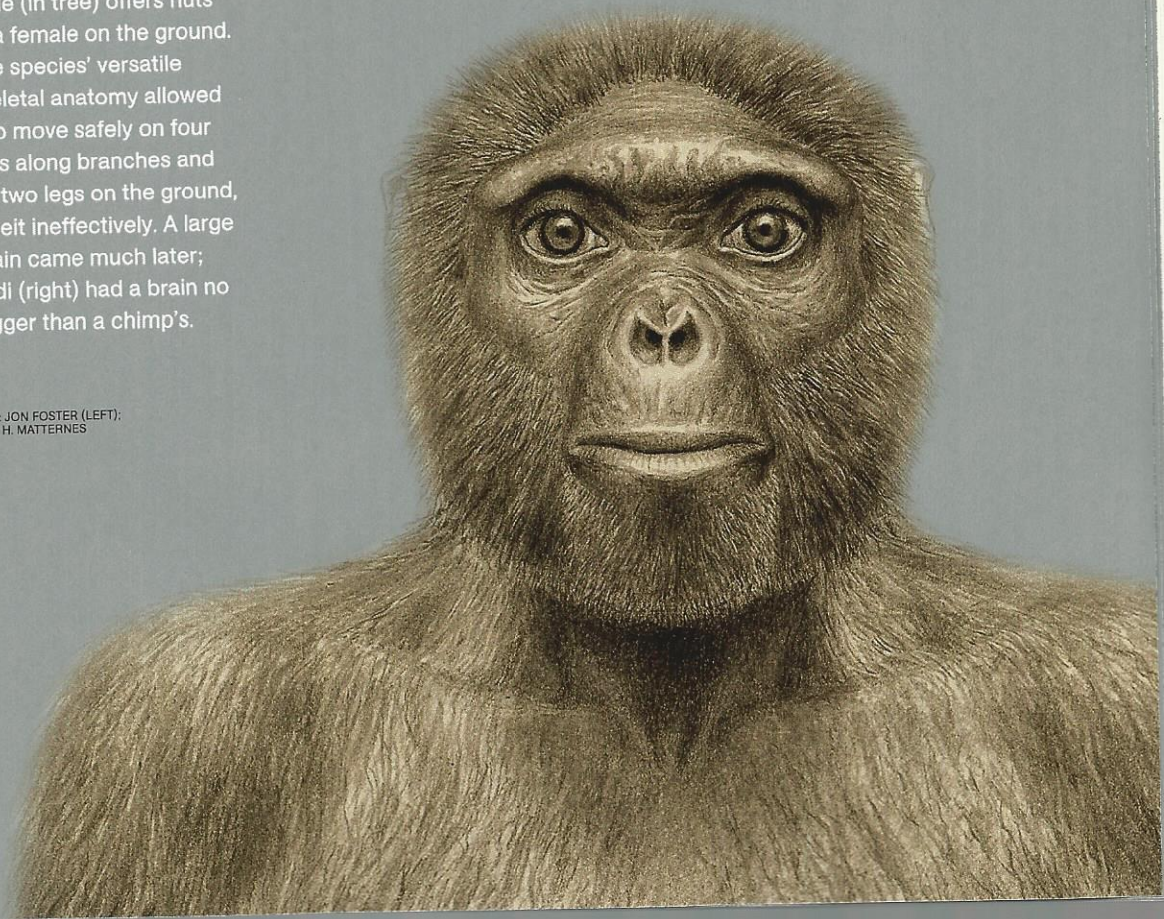
ARAMIS, ETHIOPIA

Owen Lovejoy's first glimpse of the female who would preoccupy him for the next 14 years left him cold. It was 1995, and Lovejoy, a comparative anatomist at Kent State University in Ohio, was getting a privileged peek at the freshly excavated skeleton of *Ardipithecus ramidus* in the National Museum of Ethiopia in Addis Ababa. Some of the bones were badly squashed.

"My first thought was, Why did they bring us over here to look at roadkill?" Lovejoy recalls. "It took about ten minutes to realize that all the important parts were there. My second thought was, Jesus Christ, who could have predicted *this*?"

Over the years, as Ardi's bones were freed from their rock-hard matrix and reconstructed, Lovejoy's astonishment would only grow. It had long been assumed that the further one probed into the human evolutionary past, the more our ancestors would look like our closest living relatives, the chimpanzees. At 4.4 million years, Ardi was over a million years older than the famous Lucy skeleton, which Lovejoy had also analyzed. *Ar. ramidus* didn't look like Lucy—but she didn't look like a chimpanzee either. Instead, she possessed a weird combination of very primitive traits seen before only in monkeys and extinct apes from the Miocene epoch and traits seen only in our own hominid lineage.

Consider Ardi's foot. All later hominids, including Lucy, have a big toe that lines up with the other toes, helping to provide the propulsive force



An *Ardipithecus ramidus* male (in tree) offers nuts to a female on the ground. The species' versatile skeletal anatomy allowed it to move safely on four legs along branches and on two legs on the ground, albeit ineffectively. A large brain came much later; Ardi (right) had a brain no bigger than a chimp's.

ART: JON FOSTER (LEFT);
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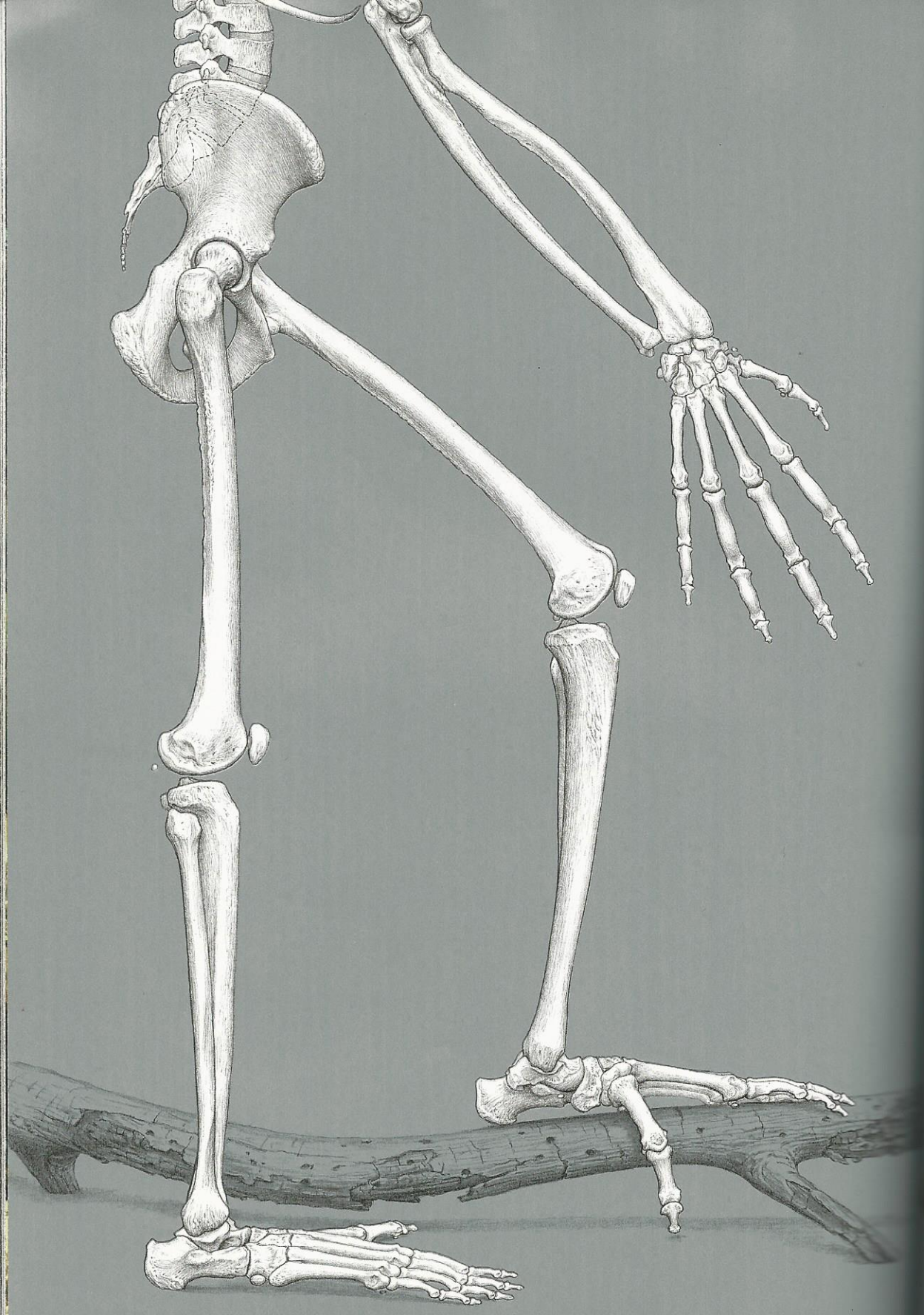

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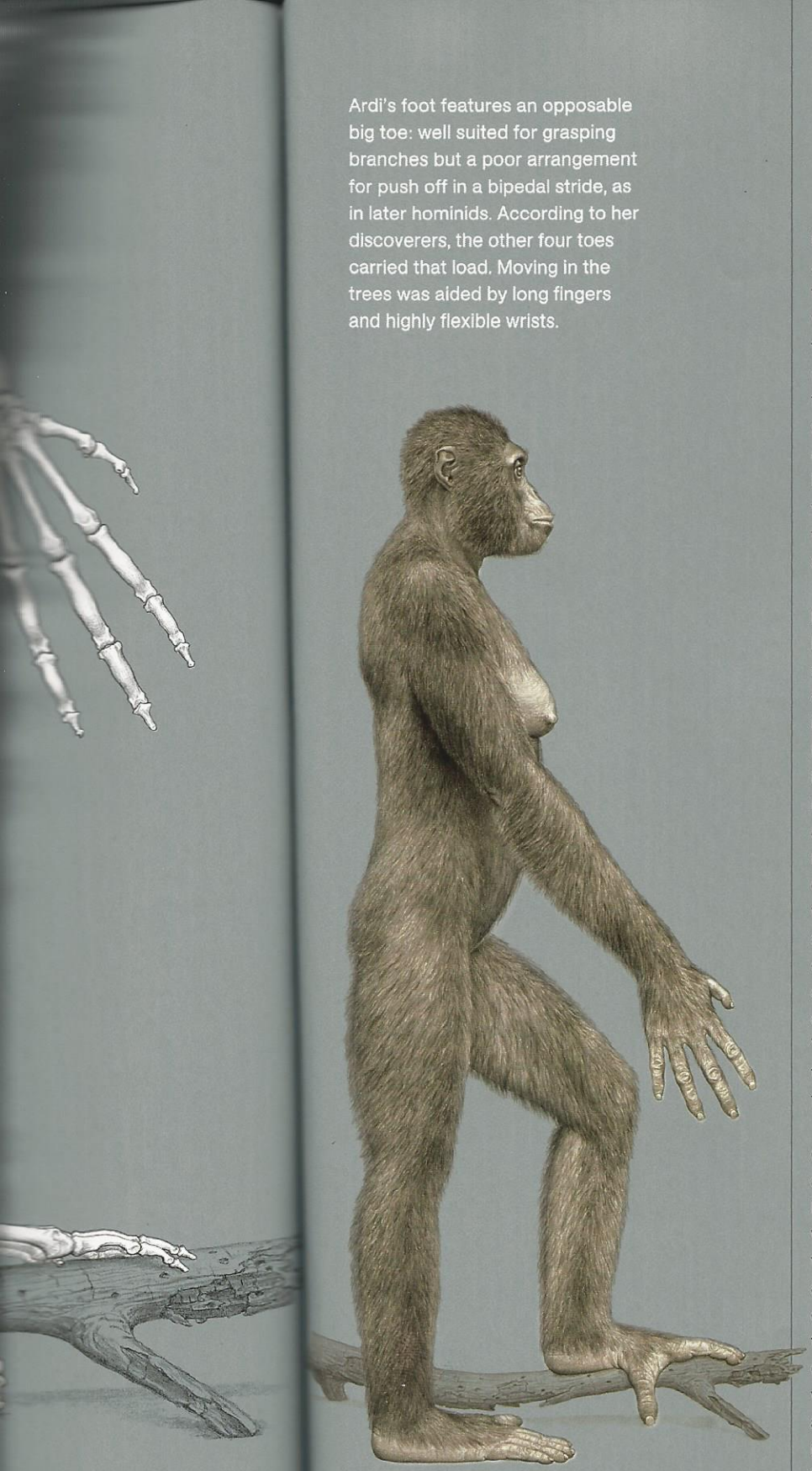

Ardi's foot features an opposable big toe: well suited for grasping branches but a poor arrangement for push off in a bipedal stride, as in later hominids. According to her discoverers, the other four toes carried that load. Moving in the trees was aided by long fingers and highly flexible wrists.

in upright walking, long the hallmark of our lineage. Ardi's big toe instead splayed out to the side, like those of apes—the better to grasp on to limbs when clambering about in the trees. Yet Ardi's foot also contains a small bone called the os peroneum—retained in the hominid lineage from ancient apes and monkeys but almost never seen in chimps and gorillas—that keeps the bottom of the foot more rigid. Lovejoy and his colleagues believe that this rigidity enabled *Ar. ramidus* to walk upright on the ground, using its four aligned toes to provide the levering "toe off" that propels a bipedal stride.

Ardi's pelvis also bears witness to a primitive primate caught in the act of becoming human. The human pelvis has undergone a major overhaul to adapt it for upright walking—a locomotor juggling act requiring one limb or the other to be suspended in the air while the other pushes forward. As far back as Lucy, 3.2 million years ago, our hip bones had become broader and shorter to enlarge attachment areas for gluteal muscles that stabilize the supporting hip joint. In contrast, chimp pelvises are narrow and long and provide more rigid support for climbing but force chimps to lurch side to side when walking upright. Ardi's upper pelvis is short and broad and shows other features rarely seen except in hominids, such as a protrusion on the inside edge of the pelvis where bone was added during development to bolster support for a bipedal stride. Yet the lower pelvis is thoroughly apelike, with attachments for massive hind-limb muscles needed for effective climbing.

Then there is Ardi's surprising hand. Living African apes have long fingers and palms adapted to arboreal climbing and strong, stiff joints in their hands to support their weight on their knuckles when they walk on the ground. Since this knuckle-walking adaptation is seen not only in chimps but also in gorillas, which separated from our lineage even farther in the past, it has long been thought that it represents the primitive condition that our own ancestors passed through on their way to walking upright. Ardi's hand utterly confounds that assumption. Though her fingers are long, her palm is short and very flexible. This would have allowed her to walk on her palms on top of tree limbs, more

Lovejoy has a provocative answer to Jungers's question: sex. Lovejoy views the origins of bipedalism as the consequence of an epochal shift in social behavior. A key part of his theory is not something gained in our lineage but something lost: those daggerlike male canine teeth of apes, so effective as weapons against other males vying for mating opportunities. Males of virtually all living and extinct apes have large, pointed canines that sharpen by honing against their lower teeth. Hominid male canines are much smaller, more like a female's. Canines from 21 individuals were found in the *Ar. ramidus* sediments of the Middle Awash, presumably both male and female. All share the hominid pattern.

Instead of gaining access to females through conflict with other males, in Lovejoy's view, a male *Ar. ramidus* would supply a targeted female and her offspring with high-fat, high-protein foods, gaining her sexual favors exclusively in return—a reproductive strategy that ensured the children he was providing for were his own. This would require, however, that the male's hands be freed from their role in quadrupedal locomotion so they could carry back the food. Bipedality may have been a poor way for *Ar. ramidus* to get around, but through its contribution to the "sex for food" contract, it would have been an excellent way to bear more offspring. And in evolution, of course, more offspring is the name of the game.

Whatever the reason for Ardi's incipient bipedality—if that's what it was—a mere 200,000 years later Lucy's genus, *Australopithecus*, appeared in the same region—fully bipedal, like all the hominids that would follow. Did primitive, splay-toed *Ar. ramidus* undergo some accelerated change in those 200,000 years and emerge as the ancestor of all later hominids? Or was it a relict species that carried its quaint mosaic of primitive and advanced traits with it into extinction?

"These finds are incredibly important, and given the state of preservation of the bones, what the discoverers did was nothing short of heroic," says Jungers. "But this is just the beginning of the story." —*Jamie Shreeve*

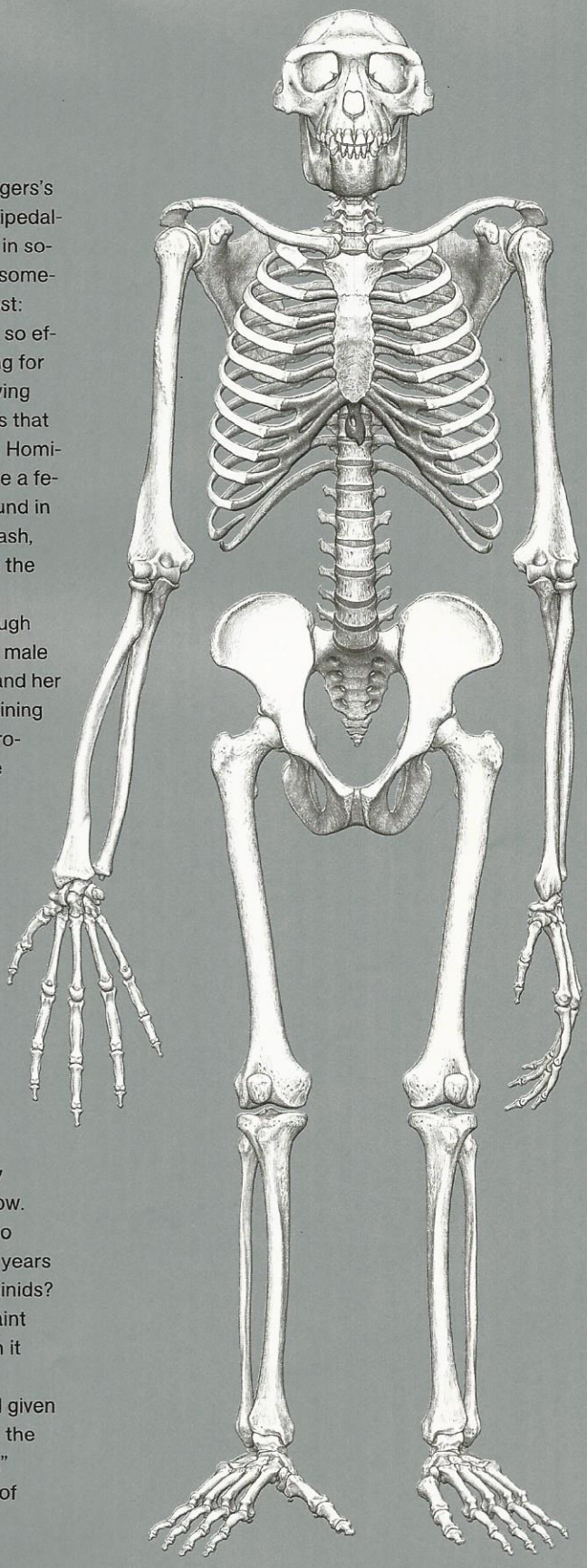

PHOTO: DAVID L. BRILL. ART: © J. H. MATTERNES

Owen Lovejoy (in white shirt) confers with Bruce Latimer about Ardi's pelvis and hips, which would have enabled both bipedal walking and powerful climbing in the trees. In an artist's reconstruction (far right), Ardi's lower lumbar vertebrae are not attached by ligaments to her hip blades (as they are in modern apes). This primitive skeletal arrangement was inherited from ancient apes and repurposed in hominids for upright walking.

like a monkey than any living ape, as well as hold on to branches well behind her head as she moved along limbs.

Combined with the other very primitive traits in *Ar. ramidus,* this monkey-like hand holds enormous repercussions for understanding our origins. If Ardi's discoverers are right, our ancestors never passed through a chimp-like, knuckle-walking phase on their way to walking upright. To argue that they did so would require that very early in our lineage we developed a chimp-like tool kit of adaptations—and then lost them all again and reverted to the primitive condition by the time *Ar. ramidus* was walking around. This is highly unlikely.

Still, given all the extremely primitive traits, some researchers argue that *Ar. ramidus* isn't really a hominid in the first place. Terry Harrison of New York University, for instance, points out that there was a tremendous diversity of ape species throughout most of Africa and Eurasia in the Miocene epoch, between 23 and 5 million years ago. "Perhaps it was just one of those apes running around, rather than the one that gave rise to hominins," says Harrison. In response, Lovejoy points to more than two dozen distinct traits that link *Ar. ramidus* exclusively to later hominids—which, if what Harrison postulates is right, would all have somehow ended up together by coincidence in an extinct ape that had nothing to do with us.

Even if *Ar. ramidus* is a hominid, was it really bipedal? Before Ardi was found, such a question would have been unthinkable. Among higher primates, only hominids are bipedal, ergo all hominids must be bipedal. But people assumed all hominids must have enlarged brains too—until the first little-brained australopithecine was found in 1924. Many scientists simply don't see how Ardi would have gotten around very well on two feet, especially with that widely divergent big toe.

"That ain't the foot of a biped!" comments William Jungers, an evolutionary morphologist at Stony Brook University. "Ardi has one of the most divergent big toes you can imagine. How did she get up in the trees without vertically climbing the trunks? Did she fly up there?" Why, asks Jungers, would an animal fully adapted to quadrupedal movement in trees elect to walk bipedally on the ground?