1 March of the Bipeds: The Early Years

It is, however, very difficult to establish the precise lines of descent, termed *phylogenies*, for most organisms.

– Ayala FJ and Valentine JW
Evolving: The Theory and Process of Organic Evolution (7)

As understood today, human evolutionary history involves some twenty species of fossil hominins, give or take a few depending on the taxonomic scheme to which one subscribes. In the field of paleoanthropology, taxonomic questions – how to classify fossil species – are famously contentious. As Richard Dawkins comments in the *Ancestor's Tale* (8), there is more than one paleontology book in print entitled "*Bones of Contention*." Names given to species carry implications for how species are related to one another. A species placed in the genus *Homo* for example, is recognized as sharing a more recent common ancestor with modern humans than a species placed in the genus *Australopithecus*.

Resolving species relationships is no straightforward task. That is one reason (among others) why there are so many different points of view about evolutionary relationships among hominin species. Such relationships are summarized in diagrams called *phylogenies* or *phylogenetic trees*. All methods of constructing phylogenies rely on comparing the characteristics of species, from their DNA sequences to their dental features to any aspect of their anatomy and even behavior. The most direct means of genetic comparison is through DNA, but, only in more recent hominins has it thus far been possible to extract adequately preserved DNA (see Chapter 5). For earlier species, the characteristics of teeth and bones must suffice for assessing evolutionary relationships. As noted, teeth figure prominently in such assessments: they are extremely well-preserved in the fossil record and much of the variation in their morphology is due to genes (rather than environment).

There are different ways to assess evolutionary relationships among species. According to the method of *phenetics*,[1] all available traits should be used to construct phylogenies. Species with greater similarity are considered more closely related. This method does not take into account two big problems. The first is the problem of *homoplasy*, when two species have similar traits but not because they inherited them from a common ancestor. One way that homoplasy can occur is when species independently evolve similar solutions to similar problems. The wings of dragonflies and seagulls were not inherited from their common ancestor but evolved independently as adaptations for flight in their separately evolving lineages. Another way homoplasy can occur is through reversal. In this instance, a trait that was present in an ancestor may be lost in some descendant species, but then evolve anew in one or more of them.

The second problem with phenetics is that even for traits that *are* inherited from a common ancestor, so-called *homologous traits*, not all are equal. If you were an alien landing on earth and happened across a dog, a baboon and a human, you might conclude that dogs and baboons share a more recent common ancestor than do baboons and humans. Dogs and baboons walk on all four legs and have very hairy bodies, while humans lack these features. But, these features that baboons and dogs share are *primitive traits* – walking on all four legs evolved in the first vertebrates to walk on land and the presence of hair evolved in the last common ancestor of all mammals. As soon as you looked around a bit more, you'd notice that these characteristics are present in nearly all living mammals. Dogs and baboons share these features not because they are particularly closely related to one another but because their distant mammalian ancestor had these features.

1 The word "phenetics" comes from the Greek root *phainein*, "to show." It is the same root used in the word "phenotype," the observable features of an organism. (9. Tobin A, Dusheck J. *Asking about Life:* Cengage Learning; 2004.)

As you looked a bit further, you'd notice that baboons and humans share multiple traits to the exclusion of dogs and many other non-primate mammals. These traits include stereoscopic vision, nails instead of claws, bony eye sockets, fewer teeth, and larger brains. These characteristics shared by baboons and humans are *derived traits* that were present in their most recent primate common ancestor. Such *shared derived traits* would tell you that there is a branch of the mammalian evolutionary tree that includes baboons and humans but not dogs. Shared derived traits are the basis of a second method of reconstructing phylogenies known as *cladistics*.[2] Most paleoanthropologists prefer the cladistic method because it separates primitive from derived traits (among other advantages).[3]

The product of a cladistic analysis is a *cladogram* – a diagram that shows the branching sequence of a set of species from a hypothetical common ancestor. Strictly speaking, cladistic analyses do not tell you how species are linked to one another in ancestor-descendent lineages and do not have a time dimension. In this way a cladogram differs from other depictions of phylogenetic relationships. Among several and sometimes many possible cladograms that can be created from a set of trait data, those that would necessitate the greatest number of homoplasies are considered to be most improbable. The assumption is that a cladogram requiring a large number of independent evolutionary events to explain similarities among species is less likely than one requiring fewer of them. The most parsimonious cladogram, requiring the fewest homoplasies, is therefore preferred. The principle being applied here is Occam's Razor, that explanations requiring fewer assumptions are more likely to be correct than those requiring more.

But, there are problems with cladistics and the parsimony principle.[4] Sometimes there are several equally parsimonious

2 The word "cladistics" comes from the Greek root *clados*, meaning "branch." (9. Ibid.).

3 A third school, "evolutionary systematics," constructs phylogenies on the basis of branching sequences among species as well as on how much species have changed since they shared a common ancestor.

4 A "maximum likelihood" approach can also be used in cladistic analysis. In this statistical technique, a mathematical model of trait evolution is applied to a set of

cladograms. Furthermore, parsimonious solutions may not always be correct ones. It is also sometimes difficult to determine the primitive state for a characteristic. We know that walking on all fours is a primitive state for mammals – this is obvious because the fossil record reveals that four-legged vertebrates predate two-legged ones. If we didn't have the fossil record to help us here, we could look around at a distantly related group – such as reptiles – to figure this out. Walking on four legs is clearly a very old trait if it is shared with reptiles. Distantly related groups, what are called *outgroups*, are used in cladistics to determine the direction of evolutionary change in a trait. But, using outgroups is tricky: whatever species you choose has its own unique evolutionary history and therefore may not always express the primitive condition. So, sometimes you arrive at different answers depending on which species you choose as an outgroup. With these problems, fragmentary remains for some species, and an incomplete fossil record, it is no wonder hominin species relationships are so vigorously debated.

THE EARLIEST HOMININS

Not surprisingly there is debate right from the start in determining exactly which fossil species is the first hominin. From DNA evidence, we know that our closest living relatives among modern primates are chimpanzees and bonobos. The last common ancestor we shared with them existed some 7–12 million years ago, according to a recent estimate[5] (10).

The anatomical similarities of humans to the African apes led Charles Darwin to predict that the fossil hominins would be found on the African continent. In 1924, a young woman named Josephine Salmons, a student at the University of Witwatersrand in South Africa, presented her anatomy professor Raymond Dart with the

species and their traits, and the phylogeny that best fits the data (the most likely one) is produced. This is a newer method that is increasingly being incorporated into hominin studies.

5 Previous estimates had suggested a more recent divergence, around 5–7 million years ago.

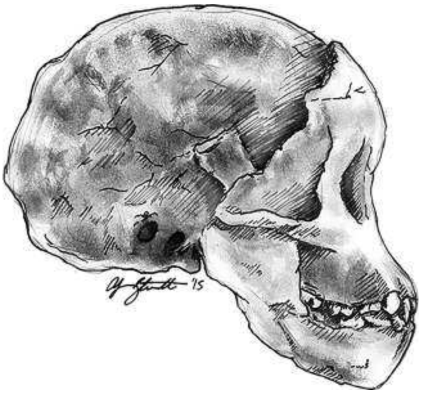

FIGURE 1.1: Artist's rendition of the Taung child. Drawn by Alyssa Starrett.

fossilized skull of a monkey that miners had blasted out of limestone (11). His interest piqued, Dart arranged to have additional fossils brought to him. When he opened one box of fossils, Dart found the remains of an endocast (cast of the interior of the cranium) together with the skeleton of a face cemented to the rock. Dart reportedly used his wife's knitting needles to painstakingly remove the rock (breccia) from the face of what is now known as the Taung Child (12) (Figure 1.1).

From the base of the endocast, Dart could tell that during life the child's head was held on an erect spine. Clearly the creature was bipedal, like humans today. Furthermore, the canine teeth were not the large and pointed variety that the African apes sport; they were far less impressive and similar in shape to those of modern humans. Yet, partly because the Taung Child's brain was small for a similarly-aged modern human and partly because up until this point fossil hominins had been found only in Europe and Asia, few of Dart's contemporaries believed he had found a human ancestor. Subsequent finds from South Africa, as well as the famous Lucy skeleton from Ethiopia dated to 3.2 million years ago, made clear that of our derived human traits, bipedalism arose first. Smaller, less pointed canine teeth than African apes were also present in our early ancestors, but large brains were not.

Today there are three contenders for the title of the earliest hominin, stretching back to 6–7 million years ago (Ma) in Africa. They are *Sahelanthropus tchadensis* (from Chad, dated to 6–7 Ma), *Orrorin tugenensis* (from Kenya, dated to 6 Ma) and *Ardipithecus kadabba* (from Ethiopia, dated to 5.2–5.8 Ma (13). The first species of hominin, evolving independently from the lineage that led to chimpanzees, may not have been bipedal. Yet, it is bipedalism that offers the clearest diagnostic clue as to the hominin status of a fossil species. Most of the debate regarding the hominin status of these three species therefore has to do with insufficient or ambiguous evidence of bipedalism (14). The first of these species, *Sahalanthropus tchadensis,* is a case in point: its skull was reconstructed from hundreds of pieces (15), so that details of the cranial base diagnostic of bipedalism have been disputed (16).

Still, the upper canine teeth of *Sahelanthropus tchadensis* are relatively small compared to a chimpanzee's and are worn at the tip as are those of humans today (17). Ape upper canines by contrast wear on the side facing the lower first premolar. Their projecting upper canines sharpen against their conical single-cusped first premolar in a *honing complex* (Figure 1.2). Honing creates wear on the back of the upper canine and front of the lower premolar. Ape lower canines also project beyond the tops of other teeth and are accommodated in the upper jaw by a *diastema* (gap) between the upper canine and incisors. But smaller canines with worn tips don't save the day for *Sahelanthropus* because some quadrupedal fossil ape canine teeth (probably those of females) that came before it in the fossil record appear to have had similarly sized canine teeth with similarly worn tips (16).

There is wider agreement that *Ardipithecus ramidus* (though see [18]), dated to 4.4 million years ago and from the Middle Awash area of Ethiopia (19), is a bona fide hominin. There are 109 specimens of this species, representing at least 36 individuals, including the individual represented by the famous *Ardi* skeleton. Standing 4 feet tall, *Ardi* had a pelvis with several key anatomical adaptations for bipedalism, a small brain, and smaller canines than a chimpanzee's.

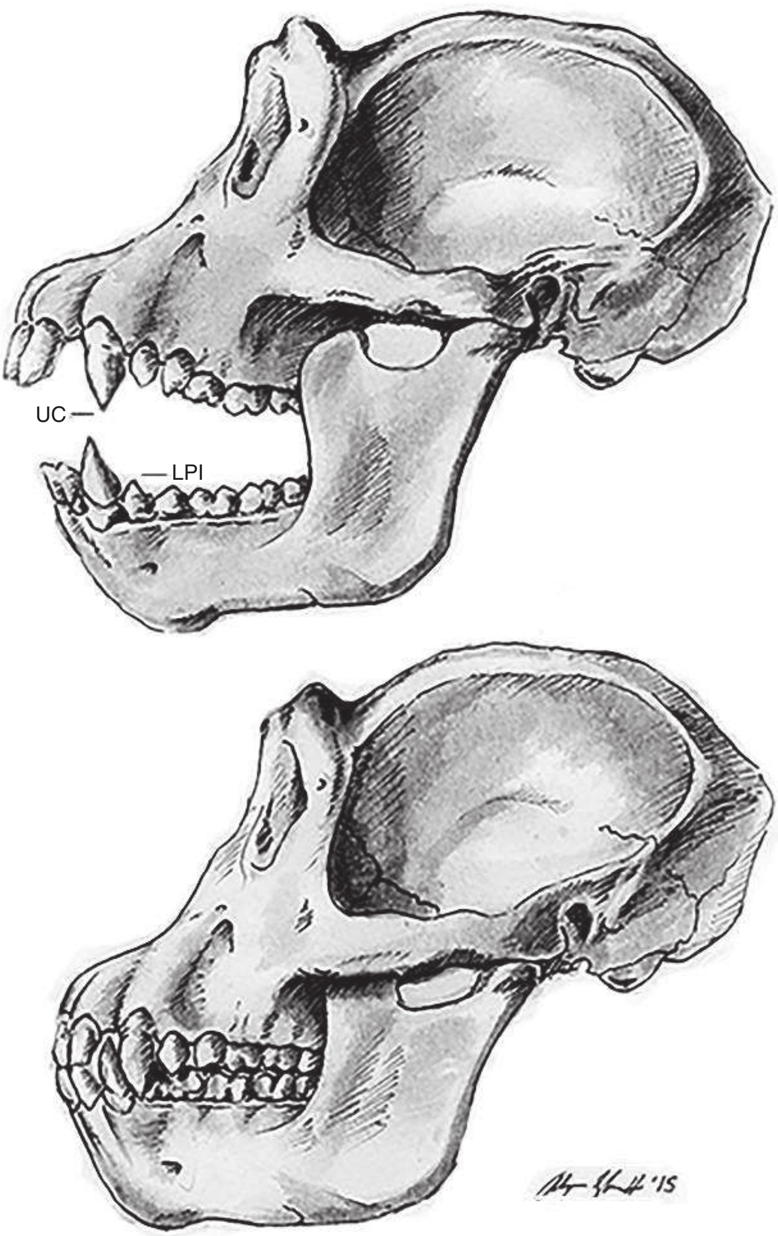

FIGURE 1.2: Chimpanzee skull highlighting UC (upper canine) and LP1 (lower first premolar). The distal edge of the UC hones, through jaw movements, against the mesial side of the LP1. Drawn by Alyssa Starrett.

But, *Ardipithecus's* mode of bipedalism was different from ours. Like an ape's foot, that of Ardi had a divergent big toe (Figure 1.3). Unlike modern humans, then, *Ardipithecus* could not push off the ground with its big toe while walking. Instead, *Ardi* seems to have propelled itself forward by pushing with the middle portion of its foot. *Ardi* also had longer arms (in relation to its legs) than modern humans do and may have combined bipedalism with above-branch climbing and clambering (19).

Whether *Ardipithecus ramidus* was a direct ancestor to modern humans or a member of an extinct side branch is a difficult if not impossible question to answer. After *Ardipithecus ramidus* appeared on earth, many other hominin species evolved, all clearly bipedal. They can be grouped into the genera *Australopithecus, Paranthropus,* and *Homo*. What follows is by no means a full accounting, but an introduction to: the species relevant to Part I of this book, some of their more salient dental attributes, and their possible phylogenetic relationships.

AUSTRALOPITHECUS

With the announcement of the Taung Child in 1925 in the journal *Nature*, Raymond Dart christened a new species: *Australopithecus africanus*. The literal translation of *Australopithecus* is "Southern Ape," reflecting Dart's view that he had found "... an extinct race of apes *intermediate between living anthropoids and man.*" (1925: 195).

The earliest representatives of this genus now known are from East Africa. The first to appear on earth was *Australopithecus anamensis* ranging in time from 4.2 to 3.8 million years ago, and represented by more than fifty dental, cranial, and postcranial specimens (13). Like great apes, *Australopithecus anamensis* had a rectangular *dental arcade* (Figure 1.4), canine teeth with large roots, lower first premolars with only one cusp (or sometimes with an incipient second cusp [20]), but a lower deciduous molar morphology (21) said to be "intermediate" between that of Ar. *ramidus* and *Australopithecus afarensis*.

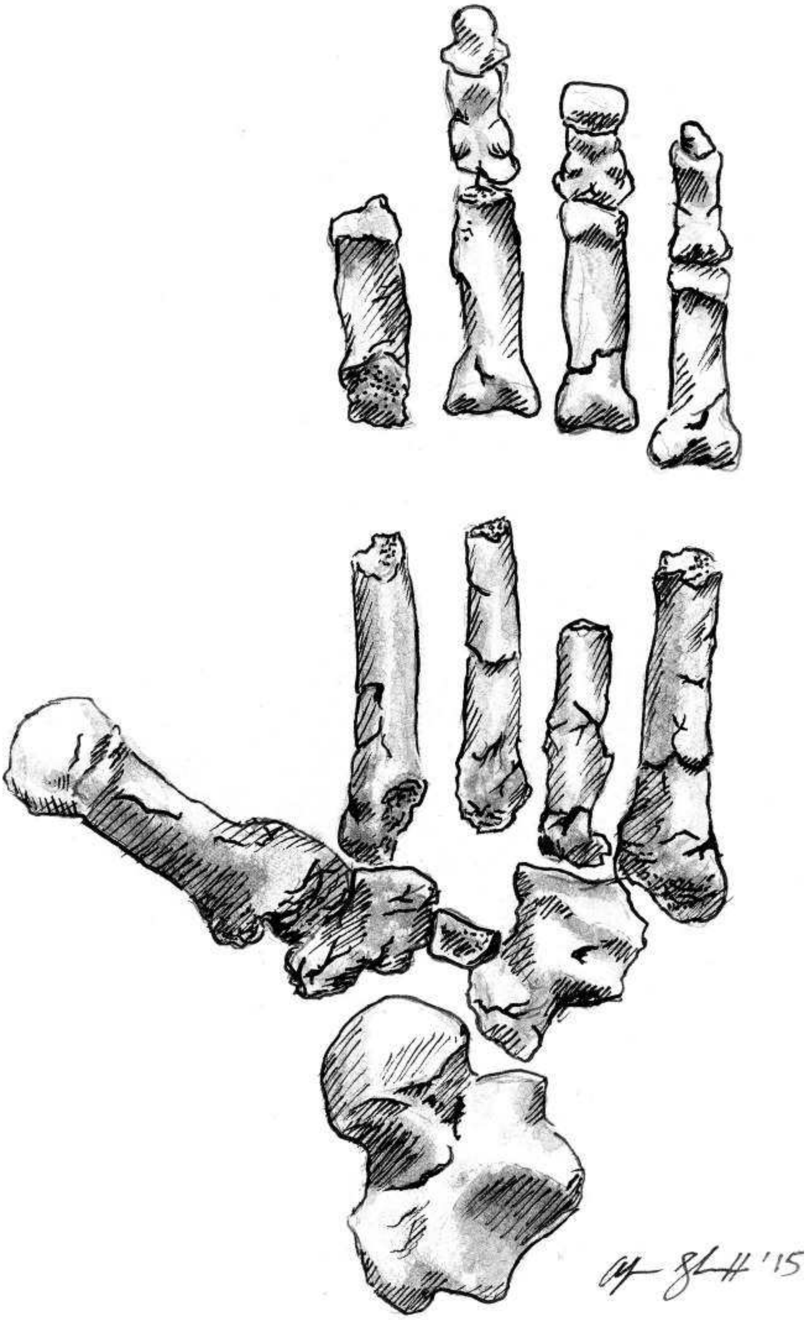

FIGURE 1.3: *Ardipithecus ramidus* foot. Redrawn by Alyssa Starrett from Figure 1a in Lovejoy CO, Latimer B, Suwa G, Berhane A, White TD, Combining prehension and propulsion: the foot of Ardipithecus ramidus. *Science*. 2009;326:72e2. Reprinted with permission from AAAS.

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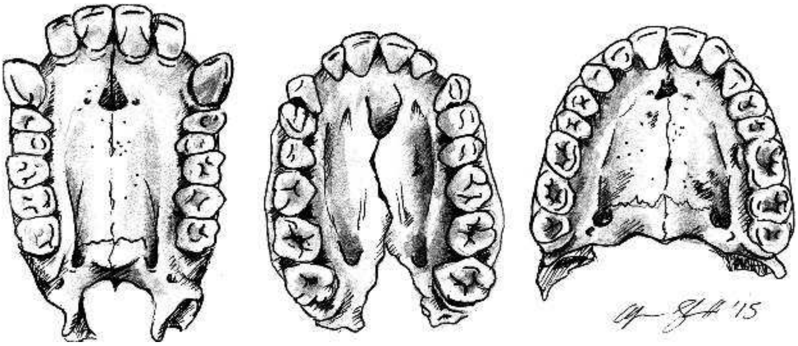

FIGURE 1.4: Artist's rendition of the dental arcades of a chimpanzee (left), *Australopithecus afarensis* (center) and a modern human (right). Drawn by Alyssa Starrett.

Au. afarensis, first appearing in the fossil record around 3.7 million years ago (22) was the next Ethiopian hominin in time, and likely evolved from *Au. anamensis* (23, 24). In 1974, Donald Johanson and his team discovered the famous Lucy, the nearly complete skeleton of an *Australopithecus afarensis* individual, whom President Barack Obama had the pleasure of "meeting" during his 2015 visit to Ethiopia. Small-brained and bipedal, but with long arms, Lucy stood about 3.5 feet tall, yet she was clearly an adult when she died as her wisdom teeth had already erupted and begun to wear. Since 1974, *Australopithecus afarensis* has become one of the most well-known early hominin species, with hundreds of remains from multiple sites along the East African Rift Valley (15). Like Ardi, Lucy also had long arms, and may have spent time in the trees (15). But with the big toe now in line with the other toes, Lucy's kind could "toe-off" while walking (15).

In *Au. afarensis*, as in *Au. anamensis*, the shape of the dental arcade (Figure 1.4) is somewhat rectangular, more like that found in Miocene and modern apes (although this is more true of *Au. anamensis* than of *Au. afarensis*). Both species had projecting jaws with large front teeth and nearly parallel-sided molar rows that created this rectangular form. Both also had more thickly enameled teeth than