

# Chapter 2

## Why Compare Early Hominins to Baboons?



### 2.1 Introduction

The comparative approach discussed here entails three crucial questions: Why compare early hominins to any living species? Why compare them to baboons in particular? Why are baboons one of the most important primates for this purpose?

Direct evidence for early hominin ecology and behavior comes from the paleo-anthropological record that is provided by archeology and paleontology (e.g., Clarke et al. 2021). This information has been augmented by reference to living species for several reasons (King 2001, 2022). First, because the record only addresses behavior that leaves physical remains, living species contribute to a more rounded interpretation of the past. Second, the living species suggest hypotheses about behavior and ecology where direct evidence is meager or lacking. Third, such evidence is extremely meager for millions of years of earlier hominin evolution. There is no archeological record from this time and the fossils are scarce, sparsely preserved, and highly controversial.

A variety of living species have been compared to early hominins, including social carnivores (Smith et al. 2012) and cetaceans (Yamagiwa and Karczmarski 2014). These are far beyond the scope of this book. In any event our primate relatives have provided most of the comparative material for early hominins, with chimpanzees receiving the most attention (Hopper and Ross 2020; Muller et al. 2017). Chimpanzees (and bonobos) have a unique phylogenetic relationship to hominins (Chap. 1); however, the further evolution of early hominins displays many similarities to the evolution of baboons. These parallels can be summed up as geographic distribution, environmental diversity, arboreal and terrestrial locomotion, medium size relative to other mammals, and sexual dimorphism in body mass.

## 2.2 Environment

As early hominins and baboons evolved, they spread across most of Africa and encountered a wide variety of environments. Both were challenged by long-term aridification.

### 2.2.1 *Environmental Diversity*

“Baboons evolved and radiated in parallel with hominins within a similar landscape and time frame, the savannahs and woodlands of Plio-Pleistocene Africa. It is therefore highly likely that they experienced similar selection pressures and evolutionary processes as hominins” (Fischer and Zinner 2020). By the same token, hominins experienced selection pressures and evolutionary processes similar to those that affected baboons.

Throughout the early paleoecological record, hominins are found in association with evidence for complex habitats with diverse environmental components (Chap. 1). There is widespread agreement among paleoanthropologists that these habitats can be characterized as *mosaic environments*. That is, they consisted of interspersed components that commonly included deciduous tropical woodlands and various more open areas, as well as a substantial body of water (lake, river, or floodplain), at least on a seasonal basis (Andrews 2020). This describes the habitat of *Ardipithecus* and most of the hominins that followed.

There has been some concern about the precise definition of “mosaic” (Reynolds et al. 2015). Some experts have claimed that mosaics are chimeras caused by hydraulic mixing of evidence from different places and levels (White et al. 2009). However, paleoecological reconstructions continue to refer to the mosaic concept (Su and Haile-Selassie 2022) or some equivalent descriptor such as “patchwork” (Magill et al. 2016).

Hominins varied through time and space in the ways that they exploited the mosaics. *Ardipithecus*, the earliest genus generally accepted as hominin, is considered to have been basically a woodland animal despite access to some more open areas (Simpson et al. 2019). *Australopithecus anamensis* apparently continued the open woodland existence (Fig. 2.1). Comparison of their numbers at different sites indicates that they thrived in the mixed environment, as opposed to wetter and more enclosed habitats (Bobe et al. 2020a, b; Manthi et al. 2020). As hominins evolved, they extended the adaptive envelope. Some continued in mosaics like their predecessors (Curran and Haile-Selassie 2016), but in varied temperature regimes (Su and Harrison 2015). Some, including *A. afarensis* and *Kenyanthropus*, seem to have ventured farther into open areas (Martin et al. 2020; Villasenor et al. 2020).

Early *Homo* continued the expansion into diverse environments, as demonstrated by two sites with archeological remains. The environment of one group, at Olduvai Gorge in Tanzania, dated to about 1.84 mya, was heterogeneous woodland.



**Fig. 2.1** Contemporary woodland in a baboon habitat. (Photo by Glenn King. Manyara. Tanzania)

Biomarkers in the soil revealed a “patchwork” landscape in which hominins had access to woodland, spring-fed wetland, and adjacent grassland (Magill et al. 2016) or shrubland (Arráiz et al. 2017). A similar mixture of features, including riverine forest, continued down to about 1.3 mya (Dominguez-Rodrigo and Cobo-Sanchez 2017). Roughly contemporaneous with the Olduvai site, hominins lived in open grassland at Kanjera in Kenya (Plummer and Bishop 2016). The soil chemistry associated with archaeological remains provided information about photosynthesis systems, distinguishing grasses from other plants. The values indicate that the plant cover was more than 75% grass (Plummer et al. 2009). Antelope fauna indicate that grassy habitats were well represented throughout the region and not just located around the archeological site.

Baboon occupation of mosaic environments is illustrated by Gorongosa National Park in West Africa, which hosts interspersed forests, woodlands, grasslands, swamps, rivers, and a major lake that fluctuates with seasonal cycles. The park is home to 219 troops that seem to be a mix of chacma baboons and yellow baboons. For paleoanthropologist Rene Bobe, Gorongosa “brings to mind” the vegetation mosaics in which Pliocene and Pleistocene hominins evolved (Bobe et al. 2020a, b).

Probably much like *Ardipithecus*, some baboons live in wooded areas within mixed habitats. In Gombe National Park of Tanzania, for example, they coexist with the chimpanzees made famous by Jane Goodall. The Gombe baboons described by Ransom (1981) lived in a habitat with an abundance of trees, high food density, and streams for drinking water. Baboons studied by Rowell in Uganda (1966) similarly spent most of their time in forest. On the other hand, the grassland habitats that



**Fig. 2.2** Baboon troop foraging in the open. (Photo by Curt Busse. Okavango, Botswana)

hominins eventually occupied are like those in which baboons were originally studied and in which the genus has had great success (Altmann and Altmann 1970; DeVore and Washburn 1963; Fig. 2.2).

Baboons match all of the environments that early hominins occupied, and perhaps more (Table 2.1). The genus has survived in virtually every kind of environment other than the central rainforest and the Sahara Desert (Altmann and Altmann 1970). This includes semidesert habitats in northeastern and southern Africa (Aldrich-Blake et al. 1971; Hamilton 1985; Kummer 1968) and montane habitats comparable to highland sites recently documented for *Australopithecus* (Mbua et al. 2016).

### 2.2.2 *Environmental Changes*

Comparison of hominin and baboon environments is not just a matter of static distribution. Hominins underwent two kinds of major long-term changes in their environment, giving rise to two major themes of explanation for early hominin adaptations: *variability selection* and *aridification* (Maslin et al. 2015). The former focuses on the ability to adjust to continuous or recurring changes in environmental conditions. The latter emphasizes the effects of hotter and drier habitats, varying from sparse woodlands to treeless grasslands. Variability and aridification are not mutually exclusive concepts, especially when applied to different time scales.

**Table 2.1** Baboon environments

	Kinda baboons	Guinea baboons	Hamadryas baboons	Yellow baboons	Chacma baboons	Olive baboons
Rainforest						X
Guinean forest		X				
Dry forest		X				
Secondary forest		X				
Mangrove forest		X		X		
Gallery forest	X	X				X
Miombo woodland	X			X	X	X
Light woodland	X	X			X	X
Dense woodland			X		X	X
Montane forest			X			X
Grass meadow			X			
Swamp					X	X
Bush				X		
Shrub		X				
Scrub					X	X
Savanna		X	X		X	X
Steppe		X		X	X	
Semi-desert			X		X	X
Rocky desert			X			
Coastal			X	X	X	

Environments occupied by the six generally accepted baboon species, derived from descriptions in Mittermeier et al. (2013). Unlikely to be exhaustive

Eastern and southern Africa, the areas that have yielded the greatest quantities of evidence for hominin evolution, have seen “extreme” environmental variability during the last ten million years. This was caused by global climate shifts, local effects such as vulcanism, and lake basin dynamics resulting from such changes (Rocatti and Perez 2019). Hominin evolution began and continued through a period of complex environmental variation. African tropical regions alternated between forest/woodland habitats with high tree density and the expansion of savannas with varying degrees of tree cover. Variations occurred between regions and between localities.

Recognition of these changes led to an important theory of hominin evolution—that environmental variation was more important than any particular type of habitat (Maslin et al. 2015). It was posited that hominins probably underwent “variability selection.” That is, natural selection favored the ability to respond to short-term and long-term environmental fluctuations, rather than adaptation to any particular environment (Potts 2013; Potts and Faith 2015).

Though fluctuation was clearly of great importance in hominin evolution, there is reason to think that drying trends and their vegetational consequences played an important role. Early hominins underwent cyclical aridification on local and regional scales and general aridification on a continental scale (Rocatti and Perez 2019). This

resulted in larger areas of grassland within and adjacent to hominin habitats. Genus *Homo* emerged in East Africa at about 2.8 mya during a major drying trend and displayed increasing association with grassland habitats (Plummer and Bishop 2016; Robinson et al. 2017). Hominins adapted to the savannas that expanded and surrounded them over the course of millions of years (Plummer et al. 2009), though some continued to occupy woodland mosaics where such conditions were available (Magill et al. 2016). Hominins did not transition from woodland to savanna; they expanded into the savannas.

Baboons experienced the same kind of long-term Plio-Pleistocene changes as hominins, while taxa closely related to each of them went extinct. Extant baboons undergo short-term challenges comparable to those of early hominins, such as seasonal stress (Chowdhury et al. 2021; Johannes-Boyau et al. 2019). The yellow baboons of Amboseli in Kenya, for example, have survived “environmental change of a type and magnitude typical of ... East African paleoenvironments” (Alberts and Altmann 2007: 282).

Alberts and Altmann (2007) considered baboons in general a “good model” for exploring the consequences of variability selection. Baboons display the responses predicted by the hypotheses. They are flexible in their locomotor system and social systems; they have a large brain in proportion to body size; and they are like humans and unlike most other primates in having adapted to a wide range of environments with little or no seasonality in their reproductive behavior.

Comparison among baboon species and populations can suggest which hominin behaviors could have stayed the same over the long term, and which had to change as they experienced environmental fluctuations and expanded into drier and more open habitats. Baboons, whether we consider one or a few species or the entire genus, are pertinent to the behavior of early hominins in any environment that they encountered.

## 2.3 Positional Behavior

Bipedal locomotion was a crucial adaptation at the beginning of hominin evolution. However, hominins retained considerable ability for arboreal movement for millions of years. Even modern humans can develop great facility in climbing.

### 2.3.1 *Bipedalism and Terrestriality*

*Orrorin* and *Sahelanthropus*, early possible hominins, display some debatable evidence of bipedalism (Boyle and Wood 2017). Stamos and Alemseged (2023) supported the bipedalism inference for these possible hominins, but characterized this aspect of their behavior as “primitive” in form and facultative in the sense that it was

possible but relatively rare. These authors placed the same interpretation on the greater amount of evidence for *Ardipithecus*. Casenave and Kivell (2023) saw evidence for facultative bipedalism in the pelvis and legs of *Ardipithecus*. The rigidity of the midfoot and flexibility at the toes also signaled bipedalism. Prang (2019) viewed the *Ardipithecus* foot as similar to that of African apes, but considered the lengthened midfoot and reduced toes as indicating “propulsive capabilities associated with an early form of bipedalism.”

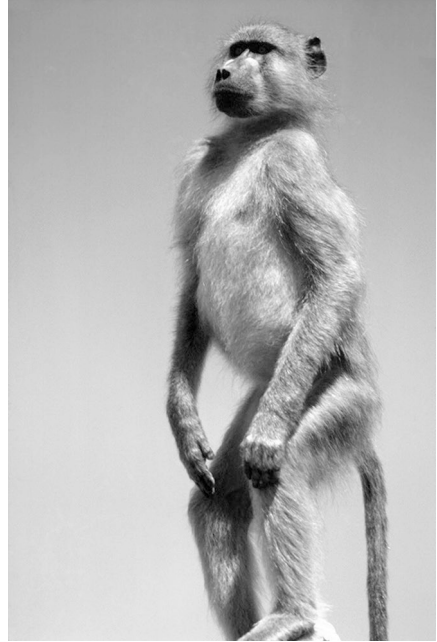
Kozma et al. (2018) compared motion in humans, apes, and other primates to assess the functions of pelvic morphology and hip movement. They concluded that ape pelvises permit enhanced climbing capability, but limitation of hip extension results in a crouched gait. Human pelvises permit a greater degree of hip extension, which greatly improves walking economy, that is, distance traveled in relation to energy consumed. Application of these findings to fossil pelvises led to the conclusion that *Australopithecus afarensis* and *A. africanus* had human-like hip extension and *Ardipithecus* was nearly human-like. They must have spent much of their time moving on the ground.

Since baboons are quadrupeds, the analogy with hominins in this case is primarily functional/ecological rather than anatomical/behavioral. Both taxa adapted to extensive activity on the ground. Baboons differ from most other primates in this regard, although there is a parallel with chimpanzees. The behavioral implications are profound, including foraging patterns (Chaps. 4 and 5) and responses to predators (Chap. 6).

It may also be significant that baboons are capable of limited bipedal posture and locomotion (Fig. 2.3). The reasons for this behavior in baboons might be pertinent to the origin of bipedal evolution in hominins, during a time long before *Ardipithecus*. Baboons may stand erect to gather food (Fig. 2.4) and they may walk or run bipedally to carry food. Early hominins might also have used erect posture to gather food and might have carried food to avoid competition with each other or danger from predators. Increased selection pressure along these lines could have favored anatomical changes.

On the premise that infant primates have a more diverse locomotor repertoire than adults, Druelle et al. (2017) theorized that locomotor development is a source of variation subject to natural selection. They observed six infant baboons at two different stages of development. During the same stage of development, the infants improved significantly in coordination between the hind limbs in spontaneous bipedal walking and in interlimb coordination in quadrupedal walking. The researchers hypothesized that neural networks underlying quadrupedal locomotion might also be employed to perform occasional bipedal walking. They inferred that a secondary locomotor mode experienced during infancy, as a byproduct of locomotor development, may lead to evolutionary innovation under appropriate selective pressures. Thus, a baboon analogy suggests an evolutionary pathway from quadrupedalism to bipedalism for hominins.

**Fig. 2.3** Young chacma baboon in bipedal stance. (Photo by Curt Busse. Okavango, Botswana)



**Fig. 2.4** Foraging chacma baboon stands bipedally to reach for tree branch. (Photo by Glenn King. On the road near Mkhuzi, South Africa)



### 2.3.2 Arboreality

While evolving bipedal capability for ground locomotion, hominins probably retained considerable ability for arboreal behavior. There is wide agreement on this point, but some debate as to what form(s) of behavior were involved. Table 2.1 summarizes some of the evidence and interpretations. Two obvious categories are vertical climbing and suspension. Selby and Lovejoy (2017) added the concept of clambering. Based on comparative evidence from gorillas and some New World monkeys, clambering was described as cautious movement through trees that makes equal use of all four limbs. All of these modes of locomotion have been attributed to *Ardipithecus*. The evidence from various species of *Australopithecus* suggests that substantial arboreal activity continued, but the balance between effective climbing and bipedal movement on the ground was shifting.

Some scientists have argued that arboreal traits in hominins later than *Ardipithecus* were relicts with no functional significance, because those hominins had become obligate or near-obligate terrestrial bipeds (e.g., Lovejoy 2009). Stamos and Alemseged (2023) responded that the system of postcranial traits in *Australopithecus* seems to have been relatively stable over the course of about two million years, contrasting with significant changes in craniodental morphology. They argued that the stability of climbing morphology in *A. afarensis* over such a long period is consistent with stabilizing natural selection, which indicates that arboreal behavior contributed to the fitness of these early hominins. Paradoxically, one case of individual fitness loss also provides evidence for arboreality in *A. afarensis*: perimortem fractures throughout the skeleton of “Lucy” are consistent with a vertical fall from a tree (Kappelman et al. 2016).

After a review, Casenave and Kivell (2023) concluded that *A. afarensis*, *A. prometheus*, and *A. sediba* present suites of anatomical features that differ from one another and suggest (subtly for some features and dramatically for others) that locomotor biomechanics were different for each taxon. Whatever the details, however, these and other hominins seem to have retained arboreal features for millions of years (although it is not clear just how frequent and significant arboreal behaviors were in any particular species) (Casenave and Kivell 2023).

Baboons are comparable to this varied hominin pattern of positional behavior. Although spending much of the day on the ground, they are agile in trees and on cliffs. These are the places where they find relative safety when confronted with predators during the day and when sleeping at night (Chap. 6). The fact that baboons often climb cliffs for sleeping, at least in some habitats, suggests that the term “arboreality” should be used loosely in relation to early hominins and perhaps replaced by a term such as *scando-terrestrial* (Chap. 1).

It is intriguing that Pavia’s (2020) reconstruction of a South African hominin paleoenvironment included a possible cliff at the edge of an open grassland. Baboon behavior suggests the speculation that this provided local early *Homo* with a refuge, especially for sleeping at night. Chacma baboons in South Africa frequently use such cliffs for sleep. (Table 2.2)

**Table 2.2** Arboreal features in early hominins

<b><i>Ardipithecus</i></b>
<b>Anatomical features</b>
Long forelimbs (Selby and Lovejoy 2017)
Long phalanges on hands and feet (Selby and Lovejoy 2017)
Long, curved manual and pedal phalanges (Stamos and Alemseged 2023)
Ape-like hip extension (Kozma et al. 2018)
Origin of hamstring muscles and related features of pelvis (Selby and Lovejoy 2017)
<b>Locomotor interpretations</b>
Suspensory behavior and vertical climbing (Prang et al. 2021)
Vertical climbing (Kozma et al. 2018)
Greater arboreal efficiency than <i>Australopithecus</i> (Stamos and Alemseged 2023)
Clambering (Simpson et al. 2019; Selby and Lovejoy 2017)
<b><i>Australopithecus</i> (various species)</b>
Humerus with mixture of orangutan-like and monkey-like features: significant amount of suspensory behavior (Arias-Martorell 2018) and climbing (Melillo et al. 2021).
Hip extension different from <i>Ardipithecus</i> : reduced power in climbing (Kozma et al. 2018)
ape-like features in cochlea and semicircular canals: sense of balance needed for some arboreality (Beaudet et al. 2019)
Atlas bone (the first cervical vertebra) with “substantial similarities” to same feature in living apes.
Consistent with greater head mobility than in modern humans
Three-dimensional visual field adapted to arboreal behavior, especially vertical climbing.

## 2.4 Body Mass

Body size, usually considered in terms of weight or mass, is a basic feature of animals that affects almost every aspect of their biology, including (for example) locomotion, diet, energy requirements, social organization, and life history (Jungers et al. 2016; Grabowski and Jungers 2017). Variation in research methods has produced uncertainty as to the body mass of various early hominins (Grabowski et al. 2015; Ruff et al. 2020; Will et al. 2017). Differing approaches use different fossil bones as reference points. Material from the legs is preferable because they are weight-bearing. Commonly used are the talus from the ankle and the head of the femur, but these are not always available. No matter which fossil bones are used, extant models are necessary to formulate equations that relate bones to the mass of a living body. The usual models, chimpanzees and humans, can lead to significantly different results. The equations themselves represent differing mathematical approaches that can yield significantly different results.

The weights for hominin species presented in the first chapter (Table 1.1) were drawn from a survey of research available to Boyle and Wood (2017), with the intention of providing a comprehensive result as a basis for further discussion. More recent studies, summarized in Table 2.3, have more limited coverage. It is

immediately apparent that the results from Jungers et al. (2016) and Will et al. (2017) are in close agreement with each other and with Boyle and Wood (2017). They suggest a range roughly 25–65 kg for early hominins. Ruff et al. (2020) produced outliers for several taxa by analyzing humeri rather than lower limb bones. However, the analysis of one individual by Simpson et al. (2019) obtained estimates ranging from about 50 to 63 kg from the femur and about 56 kg from the talus.

Recent discoveries have expanded the sample of *A. anamensis* to 74 individuals, including the first known postcranial remains of a small individual (Ward et al. 2020). Based on limb bones (humerus, radius, tibia, capitata, manual phalanx) and dental evidence, the largest individuals of this species were about the same size as the largest members of *A. afarensis*, that is, up to about 70 kg. The figures for *Homo habilis* fall within the loose parameters established for *Australopithecus*.

In relation to any of the varied assessments of hominin body mass, baboons are on the whole significantly smaller. The weight of most baboons falls into the range of 15–35 kilograms (Fischer et al. 2019). There is an overlap at the lower end, but the largest early hominins seem to have been twice the size of the largest extant baboons.

Aside from the overlap, there are reasons to regard early hominins and baboons as comparable in size. First, despite the differences between them, baboons and early hominins are medium-sized mammals. This makes for similar relations to other mammals. For two simple examples, both the hominins and the baboons were/are capable of killing hares for food and susceptible to being killed and eaten by leopards (Chaps. 5 and 6). Another reason for comparison is that both the hominins and baboons are large enough to cope with some of the same problems, such as making successful defenses against leopards.

Finally, baboons are among the very few primates that approach the size of the hominins and also occupy a comparable range of environments. Chimpanzees and orangutans are better size matches for early hominins. However, orangutans live largely arboreal lives in the tropical forests of Southeast Asia. Chimpanzees are

**Table 2.3** Recent body mass estimates of hominin taxa

Taxon	Jungers et al. (2016)	Will et al. (2017)	Simpson et al. (2019)	Ruff et al. (2020)*
<i>Ardipithecus</i>	32 ( $N = 1$ )	32 ( $N = 1$ )	50–63	50, 45 ( $N = 1$ )
<i>A. anamensis</i>	46 ( $N = 1$ )	–	–	68, 55 ( $N = 1$ )
<i>A. afarensis</i>	41 (25–64)	40 (25–64)	–	30–75
<i>A. africanus</i>	31 (23–43)	31 (23–43)	–	40–60
<i>A. sediba</i>	26 (23–29)	27 (23–30)	–	40–41
<i>H. habilis</i>	34 (27–38)	48 (38–65)	–	–
<i>H. ergaster</i>	49 (29–64)	51 (32–68)	–	52–53

These are recent estimates that were not used in Table 1.1. Fewer taxa have been reexamined. The results overlap with the earlier work, but provide higher figures for all taxa except *Homo ergaster*.

\*All studies reference lower limbs, except for the use of humeri by Ruff et al. (2020). All measurements in kilograms, rounded to the nearest whole number. Mean given first, followed by range in parentheses, except where  $N = 1$ . *Australopithecus africanus* includes *A. "prometheus"*

more like hominins and baboons in that they are largely terrestrial African primates that live in a wide range of environments. Nevertheless, they have not penetrated the full range of environments occupied by baboons and have had limited success in the more demanding ones. The maximum size of male mandrill monkeys is similar to orangutans and they are more terrestrial; however, they are largely limited to the tropical forests of Africa.

## 2.5 Sexual Dimorphism

Like most monkeys and apes, early hominins were sexually dimorphic in body mass. In some hominin species, the degree of sexual dimorphism in this trait may have approached that of baboons. Sexual dimorphism in the size of the canine teeth is also important in many primate species, including baboons. In contrast, sexual dimorphism in the canine teeth seems to have been unimportant in early hominins.

### 2.5.1 *Sexual Dimorphism in Body Mass*

Establishing the range of weight variation within a species is bound up with disputes about sexual dimorphism. One way to interpret a wide range of variation within a group of related fossils is that males and females are significantly different in size (gorillas are a familiar living example of such a species). Alternatively, the material in question may represent more than one species; this interpretation requires that other markers of species distinction be present.

Sex difference in early hominin size is the subject of a long-running and intense debate because sexual dimorphism has important social and ecological implications (Cassini 2020; Plavcan 2018). One common explanation is aggressive competition among males for mates, which in turn has implications for social organization. An important alternative is niche partitioning between males and females for access to resources, especially food, which alleviates conflict. A long-standing hypothesis that combines ecological and social factors is that males defend females and young against predators (Washburn and DeVore 1961). Whatever hypotheses are favored, there is general agreement that the issue of sexual dimorphism in size is important.

There is considerable disagreement about the degree of dimorphism in early hominins. Some researchers have concluded that early hominins in general were little different from modern humans in sexual dimorphism. Reno and Lovejoy (2015) argued that small sample sizes had exaggerated previous results and that their analysis of *A. afarensis* fossils demonstrated moderate dimorphism on the order of chimpanzees and living humans (see also Reno et al. 2010). They suggested that other studies indicated similar results for several other early hominin species.

However, numerous studies using various criteria have concluded that sexual dimorphism in early hominins was significantly greater than in modern humans and

that our ancestors did not approach the modern condition until after the genus *Homo* had appeared. Recent discoveries of *A. anamensis* fossils seem to support the sexual dimorphism interpretation. A partial tibia, undoubtedly from an adult, is only 75% of the size of previously known one. Other than size, the fossils exhibit similar morphology, indicating membership in the same species. A similar range of variation exists between some of the largest and smallest *A. afarensis* tibias. Together with the dental data, the fossil sample suggests a similarly wide range of body sizes in these two *Australopithecus* species, possibly due to similar levels of sexual dimorphism (Ward et al. 2020). Using fossil footprints to reconstruct foot size and comparative data to infer body mass, Villmoare et al. (2019) concluded that *A. afarensis* sexual dimorphism was comparable to that of gorillas, that is, males about twice the size of females (see also Kimbel and Deleuzene 2009; Masao et al. 2016).

Reconstruction of hominin sex differences in body mass by Grabowski et al. (2015) suggested a steady decline in size dimorphism from *A. afarensis* to *H. erectus* and ultimately to *H. sapiens*. In their study of fossil footprints, Villmoare et al. (2019) concluded that sexual dimorphism was significantly reduced in *H. erectus* compared to earlier hominins, but was still greater than in modern humans. The drastically changing environmental and social circumstances of early hominins may well have selected for a drastic reduction in sexual dimorphism. Interpretation may be complicated further by variation across the fossil record. *Ardipithecus* seems to show minimal size dimorphism while dimorphism in *Australopithecus* species varies from “modest to strong” (Plavcan 2018).

Sexual dimorphism in body mass seems to have been substantial for at least some early hominin species. In some cases, this feature may have reached the point of males being twice the size of females. If this is correct, then baboons may be a better match for early hominins than are chimpanzees. Chimpanzee sexual dimorphism approximates that of modern humans while the rate of male/female mass in baboons varies from 1.55 to 2.20 among the six species (Fischer et al. 2019; see also Table 2.3). Variation among baboons is significant and seems to be related to important aspects of behavior (Petersdorf et al. 2019). Comparison among baboons species may contribute to an understanding of variations among hominins.

### 2.5.2 Sexual Dimorphism in Canine Teeth

Sexual dimorphism in the canine teeth is a vital difference between baboons and hominins because canine size has profound implications for ecology and social behavior. Suwa et al. (2021) emphasized the idea that reduction of the canine teeth “indicates a profound behavioral shift associated with comparatively weak levels of male aggression.” The phenomenon also raises questions about the ability of early hominins to protect themselves against predators.

In brief, a reduction in canine size can be interpreted as a reduction in fighting ability. However, an alternative to large canine teeth for fighting is the use of *extra-somatic* (non-anatomical) weapons, that is, artifacts. This point will be explored

further in relation to predator defense (Chap. 6). For now, the main implication is that large canine teeth do not eliminate baboons from consideration as models for early hominin ecology and behavior.

## 2.6 Summary and Discussion

Paleoanthropology provides direct evidence for the ecology and behavior of early hominins. However, it is limited to phenomena that leave physical remains. Living species augment this record. They also provide hypotheses pertaining to gaps in the record and to the long period before hominin behavior began to provide archeological remains.

The main rationale for comparison of early hominins with baboons is provided by several major functional similarities. First of all, both taxa are unusual among primates in their wide distribution across diverse habitats from woodlands to hot grasslands and cold highlands. As they spread across these habitats, both taxa adapted to drastic cycles of climate change with great flexibility in their physiology and behavior. Of very broad significance, flexibility in positional behavior allowed hominins and baboons to travel on the ground during most of each day while retaining the ability to climb trees and cliffs when necessary, especially for safer sleeping.

Body mass is a somewhat more problematic point of comparison. Early hominins were significantly larger than baboons, with a possible range of 25–75 kg. However, the baboon range of 15–35 kg overlaps with early hominins. Both taxa are medium sized compared to mammals in general and are relatively large compared to most other primates. Although a few other primates match the hominins in size more closely than do baboons, none of these species come close to occupying the range of environments shared by hominins and baboons. Baboons can suggest answers to questions about crucial features of hominin life, such as subsistence and danger, in any environment that the hominins encountered.

A controversial aspect of body mass is the degree of difference between males and females in a species. This sexual dimorphism varies across baboon species but is relatively large in all of them. Most analyses of early hominin fossils have concluded that sexual dimorphism in body size was substantial, perhaps even as great as in baboons. If this is correct, then baboons may provide better perspectives on a variety of issues than less dimorphic species such as chimpanzees. Size dimorphism decreased during the course of hominin evolution. Variation among baboon species in this characteristic may provide clues about the social and/or ecological factors involved.

A crucial difference between early hominins and baboons is the size and shape of the canine teeth. The canines of both sexes in hominins were hardly different from incisors in size and shape. In baboons, the canines in both sexes are long and sharp and this is especially the case in males. One interpretation is that canine reduction in hominins accompanied a reduction in aggressive behavior. An alternative is that hominins came to rely on extrasomatic weapons at an early date.

## References

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