# Introduction to Anthropology: Holistic and Applied Research on Being Human

Indiana University of Pennsylvania

Department of Anthropology

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# MODULE 6: EARLY HOMININ EVOLUTION

## Introduction

It is generally agreed that our earliest human ancestors emerged some 6-7 million years ago (mya) in Africa, which is an unsurprising interpretation as our closest primate relatives—the African Great Apes: chimpanzees, bonobos, and gorillas—presently live there. Of all the primates, African apes are the most like present-day humans (*Homo sapiens*), both morphologically and genetically. This chapter focuses on the early evolution of hominins (from about 7-3 mya), although, one later hominin species is also discussed. Note that the term 'hominin' here refers to the taxon, which is comprised of Homo sapiens and all archaic human species since the initial divergence from the chimpanzee-bonobo line. These archaic hominin species include those that evolved into Homo sapiens, and those who are believed to have gone extinct.

The study of early hominin evolution extends beyond research by examining individual species and their defining traits. These studies are also concerned with a range of methodological issues that impact interpretation. For this reason, this chapter reviews the placement of species along the 'trunk and branches' of the hominin **phylogeny** (or evolutionary family tree), and some of the methods (and their limitations!) that paleoanthropologists rely on in their research.

## Reconstructing the Hominin Phylogeny

A look at how authors of Biological Anthropology textbooks have drawn the phylogeny of human ancestors in the last four decades provides several important insights to the challenging task of understanding our evolutionary ancestry. First, the phylogeny has become increasingly complex over time. There was a time when the evolutionary path leading from the common ancestor of humans and chimpanzees—thought to have lived in Africa between 6 and 7 million years ago—to modern humans was best understood as a straight 'trunk' leading upward through a succession of hominin species; each a distinct biological entity evolving into the next one. The term **anagenesis** is used to represent this process of evolution without branching (see Figure 6.1).

However, the discovery of new species throughout the past decades led paleoanthropologists to recognize the existence of a more complex hominin phylogeny, which consists of multiple side branches emerging from the central trunk with every one of these branches ending at some point in extinction. The exception, of course, are Homo sapiens, which stand as the sole surviving hominin species at the top of the trunk. The resulting 'bush-like' phylogeny incorporates within it both anagenesis (species directly evolving into later ones) and **cladogenesis**; these processes involve the formation of new species through branching from a common ancestral species (see Figure 6.1). The current widespread acceptance of this branching phylogeny as the best representative of hominin evolution has several implications, but the most impactful may be that certain periods in our evolutionary past were marked by the co-existence of two or more hominin species. Further, some of these species may have been aware of or interacted with one another.

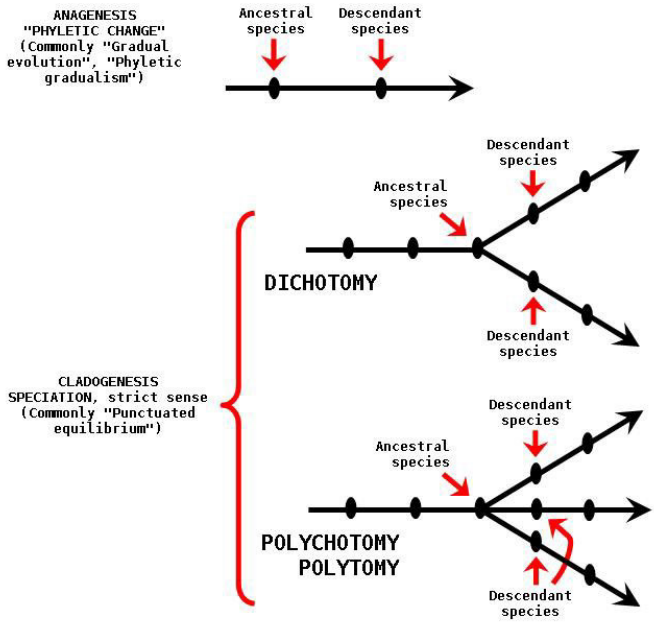



**Figure 6.1.** Example of anagenesis and cladogenesis. Image from Wikimedia Commons.

The second noteworthy feature of hominin phylogenies presented in current textbooks are that they typically differ—sometimes substantially—from one another. A comparison of such phylogenies reveals evolutionary lines branching out at different locations and times. However, question marks pepper many of these diagrams, which indicates that evolutionary links between species remain unsure or unknown. Because the identification of a putative 'oldest human ancestor' has the potential to bring fame and funding to its discoverer, it can be assumed that some of the differences among popular phylogenies reflect different authors' views about the date of a species and its placement along the 'main trunk' leading to Homo sapiens. Having acknowledged this, the main reason for such differences and disagreements about the precise shape of the hominin phylogeny *may* be more prosaic, in that it also reflects the many genuine difficulties associated with the task of reconstructing phylogenies. Considering such limitations, it's no wonder that so many different hominin phylogenies have been—and are still being—proposed.

The following material reviews the main challenges that paleoanthropologists face in reconstructing the phylogeny of hominins. These include the task of distinguishing between species, drawing conclusions from small samples, determining phylogenetic relationships based on shared traits, and dating individual hominin species.

## Distinguishing Between Species

Given access to two sets of unknown fossilized remains and asked to revise the hominin phylogeny based on the evidence, two paleoanthropologists are likely to draw two different phylogenies if one sees the combined remains as representing one species but the other recognizes two. Such differences in interpretation reflects several underlying limitations and viewpoints about the natural world but boils down to the following questions: what is a species? How do we measure and interpret variation within a single species?

The **'Biological species concept'** assumes that species consist of individuals that can mate with one another and produce offspring that are reproductively viable and, therefore, able to produce further offspring. From this perspective, species are reproductively isolated from one another, and the result of a pairing generates differences in offspring including reproductive behavior, anatomy, and physiology. This makes it impossible for individuals from two different species to produce viable offspring. A recent instance of this issue is that of Neandertals and *Homo sapiens*, which were traditionally regarded as two separate species; a distinction reflected in frequent references to *Homo sapiens* and *Homo neanderthalensis* (see Genus Homo module). The finding that Neandertals and Homo sapiens did mate and produce offspring—now evident from the small amount of DNA shared between them—has encouraged some paleoanthropologists to re-assign the two groups to separate subspecies (*Homo sapiens sapiens* and *Homo sapiens neanderthalensis*) within the single Homo sapiens species.

In contrast, the **'Ecological species concept'** first recognizes that a species is adapted to its particular niche (including a specific set of resources), which explains its form and behavior. Importantly, individuals from different

species (in the Ecological sense) may be able to mate and produce offspring, but these 'hybrid' individuals may be uncommon because there is no 'hybrid' environment that exists to which they would be best adapted. Significantly, and somewhat surprisingly, many animal and plant taxa—40% of all mammalian species and more than half of all fern and seed plant species—are not reproductively isolated from one another.

Relying on different definitions of 'species'—in this case, one based on the biological species concept, and the other on the ecological species concept—will undoubtedly result in different, reconstructed phylogenies. In reality, paleoanthropologists are typically unable to determine whether individuals represented by two sets of fossilized partial remains would have been able to reproduce and produce viable offspring. However, the general approach has been to rely on the concept of species as reproductively isolated populations (i.e. the biological species concept), even if it's often near impossible to make that determination. In fact, the best that paleoanthropologists can usually do is rely on an array of basic (and non-genetic) information to determine reproductive isolation. Simply: the likelihood that two individuals represented two different species increases when these two individuals lived at different times and locations and looked 'different enough.' Therefore, a '**phenotypic**' approach may result in different interpretations regarding details and overall shape of the resulting phylogeny.

Another issue frequently encountered by paleoanthropologists when recognizing individuals as belonging to the same or different species is the need to ensure that one does not confuse within-species variation with between-species variation. Common causes of within-variation include phenotypic differences associated with age, health status, and sex. A noteworthy illustration of this issue as it pertains to early hominin evolution is that of the hominin species being characterized by a high degree of sexual dimorphism (anatomical differences between males and females). In such cases, the challenge is to ensure that such dimorphism is not mistaken for between-species variation. While information about the location, depositional context, age, and paleopathological status helps paleoanthropologists determine whether different sets of remains belonged to the same or different species, infrequent and partial remains complicate

the task and disagreements occur. Not surprisingly, differences in interpretations are likely to result in hominin phylogenies that differ from one another in one or more details.

## The Impact of Sample Size

Although the number of hominin remains discovered to date continues increasing at a steady pace, paleoanthropologists remain mindful that the totality of remains available for study may only represent a small proportion of all past hominin species. Naturally, the smaller the proportion of represented species, the more incomplete the phylogeny, and the greater the likelihood of incorrect links between known species. For this reason, the discovery of a new hominin species typically results in some alteration of the current proposed phylogenies, but not necessarily in the clarification of phylogenetic links. As there are likely many species to still be identified and named, such uncertainty is likely to remain for the foreseeable future.

## Determining Phylogenetic Relationships Among Hominin Species Through Shared Traits

The identification of shared traits among species serves as an important tool in the task of reconstructing phylogenies. The challenge for paleoanthropologists is selecting the appropriate type of shared trait, since selecting the 'wrong' shared trait will likely result in a phylogeny that is potentially very different from the 'actual' one. Analogous traits, which are shared through convergent evolution, are a type of trait to be avoided. Thus, while the wings of bats, birds, and flies all solve the problem of flight, they all evolved independently from one another. Placing these three groups in a single taxon because they all have wings would hide the fact that they are evolutionarily distant from one another (in this case representing mammals, birds, and insects). In contrast, homologous traits are shared through common ancestry (see Figure 6.2). Although shared traits of this type are needed in phylogenetic reconstructions, one must (again) carefully use the appropriate type of homologous trait.

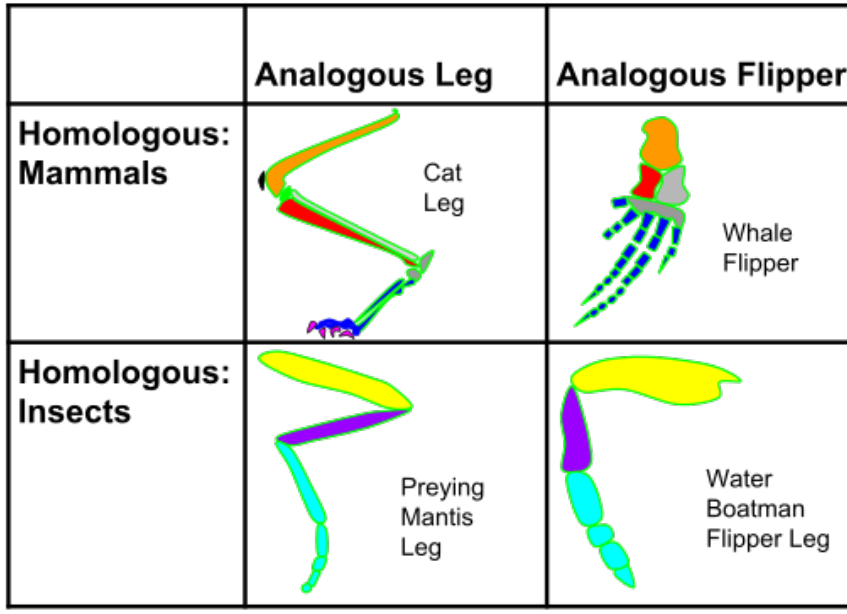
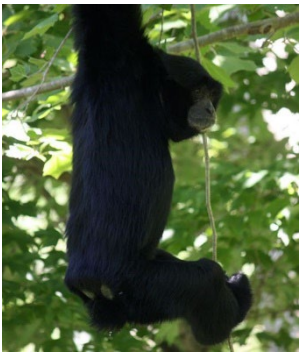



**Figure 6.2.** Comparison of analogous and homologous traits. Image from Wikimedia Commons.

Thus, **homologous ancestral traits**, which appear before the common ancestor of the multiple species whose phylogeny one is trying to reconstruct, should be avoided. For example, relying on the shared trait of eyeballs in primates—a trait that clearly predates the appearance of the first primates—is of no use in trying to understand primate phylogeny (since all primates have eyeballs). In contrast, it is best to rely on **homologous derived traits**, which appear after the common ancestor of the multiple species whose phylogeny one is trying to reconstruct. For example, the presence of a tail in monkeys and its absence in apes permits us to at least distinguish between two types of primates (see Figure 6.3 and Module 5: Primates). Of course, the refinement of any phylogeny into multiple subgroups relies on the identification of large numbers of (shared) homologous derived traits.

**Dusky Leaf Monkey (tail)**



**Siamang (ape; no tail)**

**Figure 6.3.** Example of a homologous derived trait. Monkeys have tails, but apes do not. Image modified from Wikimedia Commons.

In reality, the distinction between the different types of shared traits discussed above—including the identification of homologous derived traits—can be challenging. It is *especially* challenging when dealing with a limited number of partial hominin remains available to the paleoanthropologist that must rely on various, indirect methods. These include:

1. Identifying the presence or absence of a trait in an 'out-group' that is phylogenetically close to the taxon being investigated. For example, the fact that non-primate mammals tend to have tails, which suggests that a tail is an ancestral trait in primates, and the absence of a tail is a derived trait.
2. Determining the chronological order in which different traits appear, as example, in the **stratigraphic record** (see Module 3: Research Methods).
3. Determining the order in which different traits appear or disappear during the embryonic development of living species; an approach often associated with the statement 'ontogeny [development] recapitulates phylogeny'. For example, the fact that a tail is present in the embryonic development of all primates, but subsequently disappears in ape embryos, points to the absence of a tail being a derived trait in primates.

## Dating Hominin Species

Determining the chronological range during which a species lived—from its emergence to its extinction—is essential in any attempt to reconstruct a phylogeny. The challenge faced by paleoanthropologists trying to establish the temporal range of distinct hominin species is of two types: sample size and dating capability.

As the fossil record of any single species is likely to represent only a small proportion of all individuals within that species who ever lived, it is also likely that the earliest dated individual are younger than the time of the species' earliest emergence. In turn, the youngest dated individual is likely older than the time of the species' extinction. This results in a truncated temporal range that ignores the oldest and more recent ends of the range.

Absolute dates of remains obtained through various dating methods—for example radiometric methods such as Potassium-Argon dating (see below)—are typically given with a 'standard deviation' that indicates the statistical likelihood that the actual date falls within a certain range. Combined with the issue discussed above, large standard deviations generated by absolute dating methods, which can happen for various reasons, makes it difficult to date both individual remains *and* the temporal range of the species a whole. This, in turn, complicates the task of determining the phylogenetic relationship among multiple hominin species, especially in when a species' temporal range displays a significant overlap.

## Finding and Studying Hominin Remains

A look at the location of early hominin remains in Africa dating between 7 and 2 mya—the latter being believed as the approximate time that hominins left Africa for the first time—reveals an interesting distribution pattern. Aside from a single location in the present-day country of Chad (north Africa), the remaining hominin remains are concentrated in two regions: east Africa's **Great Rift Valley** region (see Figure 6.4) and southern Africa. This pattern leads us to ask whether early hominins lived in other parts of Africa. The answer is that, while certain regions may have been favored for various environmental or other reasons, the distinctive spatial

pattern is likely the result (a least in part) of other factors. In other words, it is 'difficult to become a fossil', and once **fossilized**, to be 'discovered'; a set of limitations which help account for the large number of remains found in the Great Rift Valley and southern Africa, and the fact that relatively few early hominin remains have been found so far.

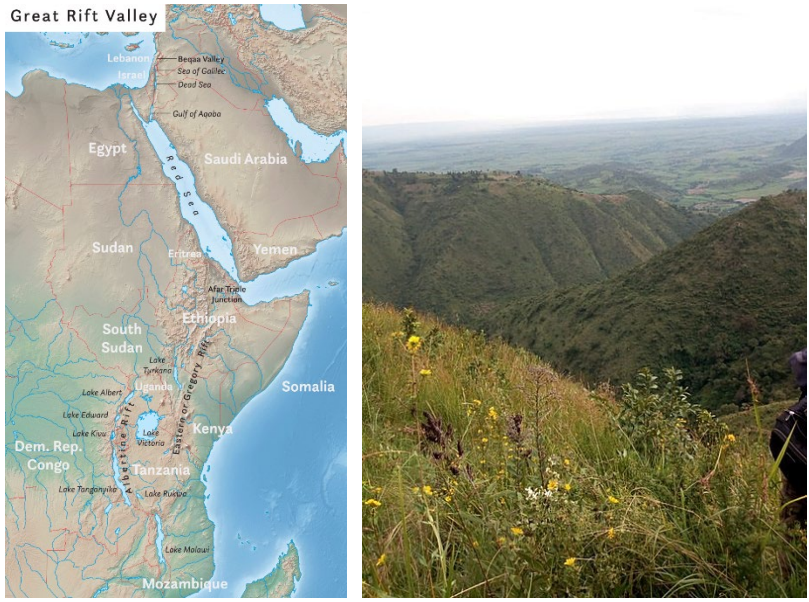



**Figure 6.4.** The Great Rift Valley, map (left) and photograph (right). Image from Wikimedia Commons.

Dead organisms (including hominins) typically do not become fossilized, a process which first requires that the organism be protected from microbial decay, insects and scavenging animals. Such initial protection is more likely when the body is quickly buried by sediments associated with a body of water (e.g. flooding; falling into the water) or by slope runoff. Once buried, the soil conditions also need to be conducive to the preservation of the body by slowing or stopping bacterial and chemical decomposition. Such favorable conditions include low temperatures, dry conditions (e.g. deserts), anaerobic (low / no oxygen levels) conditions (e.g. wetlands), and low soil acidity. Over time, the (often partial) physical remains of the protected and preserved organism become 'fossilized', a process which can take tens of thousands of years and which involves the gradual replacement of the minerals calcium

and phosphorus in bones and teeth by the rock-forming minerals iron and silica present in ground water. Often dating to hundreds of thousands or millions of years ago, hominin fossils therefore appear as durable 'stone-like' copies of past individuals. Of course, the accumulation of sediments above the fossilized remains over such long periods of time results in hominin fossils being locked inside geological strata that are often located deep under the present-day surface. Finding such fossils then becomes the next challenge for palaeanthropologists.

Large numbers of hominin fossils have been found in in the Great Rift Valley, a wide and long geological rift region in East Africa that consists of a series of deep trenches (see Figure 6.4). The area's past and present environment appears to have provided ideal conditions for the fossilization and discovery of hominin fossils. To begin, the region has long been geological active, as evident from its many and frequent volcanoes, geysers and earthquakes. Together, these features have increased the likelihood of hominins being buried under sediments, which in some cases included volcanic tuff (formed from ejected volcanic ash). The other significant factor is that many parts of the Great Rift Valley are presently dry, although prone to heavy downpours during the rainy season. Importantly, these rains result in the erosion of exposed stratified sediments at the edges of the depressions, which in turn occasionally exposes buried hominin fossils. Thus, paleoanthropologists do not – unlike other archaeologists – typically excavate 'downward' from the surface to reach fossils. Instead, they wait for them to emerge from a slope's sedimentary strata. Not surprisingly considering the process by which hominin remains are found, these remains are often highly fragmented. The process of locating, isolating and excavating hominin fossils is often painstaking and can take years and require significant amounts of financial resources.

As mentioned earlier, the southern part of Africa has also yielded several important hominin fossils, although the setting within which such discoveries have been made is very different from that encountered by paleoanthropologists working in the Great Rift Valley region. Most important, many of southern Africa's hominin fossils have been found in limestone caves, with the remains encased in a calcium carbonate matrix. In this case, preservation was possible because the hominin individuals ended

up in the limestone caves or depressions, either because they died there or, according to some paleoanthropologists, because they were dropped into such spaces from trees by leopards who had previously preyed on them. The later discovery of the fossils would then have to wait until the cave mouth was found or when new openings into ancient karst (limestone) formations appeared as a result of erosion – limestone is relatively soluble in rainwater. What about the rest of Africa? Why haven't hominin fossils been found outside southern Africa's karst regions and the Great Rift Valley? As mentioned earlier, different factors may have played a role. Thus, hominins who lived in Africa's more humid and forested areas were likely quickly exposed to humidity, insects, animals, and ultimately decay. This helps explain why fossils are rarely found in tropical forests. On the other hand, factors having more to do with the visibility and exposure of fossilized remains would have played a role in other regions of Africa.

As discussed above, the dating of hominin remains is an essential task in the reconstruction of the hominin phylogeny. Even as the various dating methods employed by paleoanthropologists present several challenges in regard to both **accuracy** (i.e. how close a measurement is to the true value) and **precision** (i.e. how close measurements of the same item are to one another), scientific advances over the past decades have played a central role in helping scientists sort out the chronology of different hominin individuals and the species they belong to. As suggested by the label, **'relative' dating methods** focus on determining the relative age (i.e. older vs younger) of remains, which is carried out through a range of methods, including (among others): their position in a stratigraphic sequence; fluorine dating (based on the accumulation over time of fluorine in animal and human bones); and the use of index fossils (which are known to belong to specific time ranges and found at multiple locations). Of course, reconstructing the hominin phylogeny is ultimately dependent on 'absolute' dates, which are (more or less) accurate age determinations in years.

**Absolute dating methods** include a range of techniques, of which **radiometric methods** are the most widely used (see research methods module). Such techniques are based on the known radioactive decay rate of different elemental isotopes, such as **Carbon 14** (which decays to Nitrogen 14: half-life of 5730 years) and **Potassium 40** (which decays to

Argon 40: half-life of 1.25 billion years). Importantly, these two radiometric dating methods differ in their specific practical uses. Thus, radiocarbon dating is used to date once-living organisms and plants (whose levels of Carbon 14 begin to decrease after death), although the method only extends back to about 50,000 years ago, by which time there is too little Carbon 14 left to measure. In contrast, due to the very long half-life of Potassium 40, the Potassium-Argon method is most useful in (volcanic) sediments that are older than about 100,000 years old. Moreover, the technique, which dates the age of sediments rather than the fossilized skeletons themselves, has proven especially useful in dating volcanic strata, such as those lying below and above hominin remains in the Great Rift Valley (which saw elevated levels of volcanic activity in the past).

Scientific techniques have also proven essential in the reconstruction of past environmental conditions and hominin diet. The most direct approach employed by paleontologists consists of identifying the fossilized animal and plant remains associated with hominins. A parallel technique involves the determination of Carbon 13 and 12 ratios present in the animal bones and the soils. Importantly, C3 plants (trees, nuts, bushes and cool-season grasses in wet, wooded environments) use a different carbon pathway than C4 plants (grasses and sedges in open grasslands / tropical savannas). This results in different Carbon 13 to 12 ratios between the two carbon pathways and allows paleoanthropologists to reconstruct the environment in which early hominins lived. One interesting illustration of how the method has been used to adjust some of our views concerns the commonly held notion that early hominins first evolved in a savanna setting associated with the development of bipedalism (see below).

Recent paleoenvironmental research has in fact shown that the earliest hominins lived in open woodland settings, including near lakes. In regard to diet, interpretations have traditionally been based on tooth and jaw morphology. For example, the large jaws and molars of several early hominin species has led to the view that much of their diet consisted of (hard) nuts and seeds. However, recent studies of Carbon 13 and 12 isotopes in tooth enamel has shown that at least in the case of one later hominin species with a very large jaw and molars, C4 plants (i.e. tropical grasses) played a large role in the diet, rather than the C3 plants (i.e. nuts and seeds) initially believed to

be the focus of its diet. Whether this reassessment of diet also applies to earlier hominins remains to be seen.

## The appearance, characteristics and evolution of early Hominins

During the 19th century, Charles Darwin put forward a model meant to account for the earliest stages of hominin evolution. His **'Hunting hypothesis'** relied on the identification of important and obvious differences between apes and humans, as well as the belief that the transition from ancestral ape to early hominins had involved a shift from life in the trees to life on the ground. The model links several developments in important ways. Crucial initial steps included the emergence of language and a resultant large brain, which itself was thought to be essential for the production of tools and weapons. Along a parallel (but later) track, the emergence of **bipedalism** from quadrupedalism – as early hominins left the forest for more open spaces - would have freed the hands to make and carry tools and weapons, which in turn weakened the selective pressure on large canines, while also supporting the development of hunting. A number of complementary or competing hypotheses were proposed by later paleoanthropologists. For example, Peter Rodman and Henry McHenry's **'Patchy Forest Hypothesis'** presented bipedalism as being a more efficient mode of locomotion (than moving on four legs) in more open environments, where forests were fragmented, and food resources 'patchy' / scattered. Owen Lovejoy's **'Provisioning hypothesis'** proposed that the early emergence of bipedalism (and the freeing of hominin hands) would have permitted males to bring food to ('provision') females and their offspring, which in turn resulted in their increased reproductive fitness, the development of pair-bonding, and the protection and support of offspring.

As evident from the above brief review of models concerned with the emergence and early evolution of hominins, bipedalism is believed to have played a crucial role in this process. In light of its centrality and the fact that humans are the only habitual bipeds in the Primate Order, it is therefore not surprising that the identification, development and 'benefits' (from a reproductive fitness perspective) of bipedalism has remained a topic of interest in paleoanthropology. Many theories have been put forward and pointed to several possible advantages – some of these mentioned above –

of bipedalism:

1. The ability to see further, as when standing over tall grass.
2. The freeing of hands to transport food, for example to females and children.
3. The freeing of hands for tool and weapon manufacture and use.
4. The greater efficiency of long-distance running.
5. Keeping cool in warm climates, associated with reduced exposure to solar radiation and lower temperatures at the head level.

But bipedalism also likely had 'disadvantages' ('costs' from a reproductive fitness perspective), although an evolutionary perspective centered on natural selection proposes that its benefits would have outweighed the costs. These possible costs included:

1. Greater visual exposure to predators, for example as hominins could now be seen standing above tall grass.
2. Reduced speed (compared to quadrupedalism) over short distances.
3. Back injuries caused by lifting and carrying heavy objects.
4. Stress on the circulatory system associated with the difficulty of moving blood upward, for example from the legs to the heart.
5. Reduced mobility resulting from injury to one foot.

The broad interest in the role and timing of early bipedalism in hominin evolution has been supported by knowledge of its representation in the fossilized remains of hominins. Fortunately, many parts of the skeleton can be used in such an assessment, such that even partial remains can be helpful in determining the presence or absence of bipedalism. Beginning with the head and moving downward through the body, such evidence includes the following:

1. A centrally located foramen magnum (the large hole at the base of the skull through which the spinal cord passes), in contrast to more posteriorly located foramina magna in quadrupeds.
2. An S-shaped spinal column whose vertebrae increase in size as one moves downward, in contrast to curved spinal columns with vertebrae of similar sizes in other primates. The S-shape facilitates bipedalism by keeping the head centered above the pelvis, while the

larger (lower) vertebrae help support the weight of the body.
3. A bowl-shaped pelvis with a shorter ilium.
4. A longer femoral neck, which fits into the acetabulum (socket) of the pelvis.
5. Inward-angled knees.
6. Robust ankle bones.
7. A foot arch, which acts as a 'spring' to counteract the weight of the body pressing down on the feet.
8. Forward-pointing toes, which facilitate forward bipedal movement. This contrasts with apes, whose opposable toes are used in climbing and grasping.

While certain components of the early hominin evolutionary models presented above remain popular, paleoanthropological research over the past decades has forced a re-evaluation of many of their details. This has involved not only the chronological re-ordering of different morphological and behavioral features, but also the identification of new ones. Thus, it is now generally accepted that bipedalism – long thought to be a defining feature of humanity - emerged in association with the earliest stages of hominin evolution (but see below). Another early hominin trait is the absence of a honing chewing complex, in contrast to apes, whose chewing complex is characterized by larger canines, a diastema (space) between the upper incisors and canines (where the lower canine fits), and a sharpened ('honed') back edge of the upper canine caused by rubbing with the front edge of the lower premolar. Furthermore, the thicker enamel of many early hominin species is associated with their proposed reliance on a diet the requires the grinding and crushing of seeds and nuts, in contrast to the thinner enamel of apes, which tend to eat more fruit and whose consumption of plants involves the slicing of leaves with their sharpened ('honed') canines. On-going research has revealed developments in other crucial traits that have called into question the details of some of the earlier models of hominin evolution. These include:

1. A significant increase in brain size beginning only around 2 mya.
2. The appearance of stone tools at about 3.3 mya, although (now-decayed) tools made of organic materials may have been used earlier.
3. The possible development of language and hunting after 3 mya.

## Prominent Early Hominin Species

In comparison to the period from the emergence of the genus *Homo* (between 2 and 3 mya) to that of *Homo sapiens* about 200,000 years ago, the fossil record of the first four million years (7 – 3 mya) of hominin evolution is relatively sparse, with much uncertainty remaining about the shape of early hominin phylogeny. The fossilized remains of the few species identified so far for this period do nevertheless point to several overarching trends. Brain size is limited and shows only a modest increase over the course of this early period (see above), while bipedalism – or at least some ability for bipedal locomotion – appears to have been present from the beginning. Simple stone tools appear at the end of the period (around 3.3 mya). Importantly, there is as yet no evidence for the presence of early hominins outside Africa prior to 2 mya. The following review of four well-known early hominin species (including one which postdates 3 mya) is meant to illustrate some of the traits and trends mentioned above, while also underscoring the fact the fact that individual species do not always fall neatly along a path of gradual morphological development from early to later species. This is best illustrated by the identification of assumed ancestral and derived traits co-existing in single species, a finding that also points to the possibility that some of these species may in fact represent 'side branches' that went extinct and never evolved into the more recent ancestors of modern humans.


**Video 6.1. Check out the video by The American Museum of Natural History presenting 7 million years of human evolution.**

## *Sahelanthropus tchadensis* ('Toumai')

First discovered in 2001 in northern Chad's Sahel desert, the remains of *Sahelanthropus tchadensis* include skull fragments and a femur representing several individuals. Of these, a single deformed skull (nicknamed Toumai) has drawn the most attention and serves to define the species (Figure 6.5). A generally accepted date is 6 to 7 mya, making Toumai the oldest hominin known so far, although some would argue that it preceded the 'chimpanzee-

human last common ancestor' (CHLCA) or even that it represents an early representative of a separate ape line. The species' 'primitive' traits include its small brain (about 350cc, which is similar to that of a chimpanzee) and a U-shaped dental arcade (present in apes and early hominins). In contrast, several 'derived' traits have been identified, such as small canines, the absence of a honing chewing complex, as well as a more centrally foramen magnum, the latter of which has been interpreted by many (including the discoverers of Toumai) as evidence of bipedalism. However, recent research on a femur which had been put aside in the species' original description has suggested that Toumai was not bipedal, a finding which may be in keeping with the foramen magnum, whose placement and angle make it difficult to determine locomotion. Along with the presence of other interesting features such as (non-human) large brow ridges and a somewhat (human-like) 'flatter' face, the uncertainty about the species' locomotion and chronology complicates its placement in the phylogeny of early hominins. Importantly, research on the fossilized remains of several animal species found close to Toumai has determined that it lived in a forest near a lake.

## *Ardipithecus ramidus* ('Ardi')

Dating to about 4.4. mya, this species was identified and named during the 1990's by a team working in the Afar region of Ethiopia (see Figure 6.5). Although the remains of several individuals were found, one – nicknamed 'Ardi' – has achieved some fame as a result of its well-preserved skeleton. It is believed that Ardi was a 4-foot-tall female weighing about 110 lbs. Ardi's skeleton presents a mosaic of both ancestral and derived features. The former include a small (300-350 cc) brain (similar in size to that of a chimpanzee), long arms, curved fingers and an opposable toe (see below). In contrast, several 'modern' traits associated with hominins have been identified: small canines (suggesting reduced sexual dimorphism and male aggression), a non-honing chewing complex, and a dentition associated with an omnivorous diet not dependent on fibrous or hard food. The thickness of the tooth enamel lies between that of living apes (thick) and later hominins (thin). One especially interesting issue concerns Ardi's likely bipedalism. Although indicated by various traits (e.g. Ardi's foramen magnum, pelvis, knees, and rigid feet), other traits instead suggest arboreal locomotion, such as her opposable / grasping toes, long arms, and curved fingers. Together, these

findings point to the likelihood that Ardi walked bipedally when on the ground and moved quadrupedally (on her palms) in the trees by grasping branches. Importantly, the fossilized plant and animals remains associated with the species' remains indicate that Ardi lived in a forest, rather than in an open savannah / grassland, the latter being the setting proposed by Darwin as the home of the earliest human ancestors (whose bipedalism was explained by the need to travel between stands of trees).

## *Australopithecus afarensis* ('Lucy')

Dated to 3.2 mya, **'Lucy'** is a well-known early hominin female (see Figure 6.5) whose remains were discovered during the 1970's in the Afar region of Ethiopia (not far from where Ardi was found). In keeping with the fact that the earliest hominins were small-brained and small-bodied bipeds, Lucy is believed to have been 3.5 feet tall, although we also note that her brain – at 430 cc – was slightly larger than that of earlier hominins. Lucy's species present clear evidence of a more developed capacity for bipedalism, as indicated by all of the diagnostic traits mentioned earlier. Interestingly, however, other traits point to the likelihood that individuals of Lucy's species also had climbing abilities and spent time in trees. These include their long curved fingers, as well as the shape of their shoulder joint. Also noteworthy is the high degree of sexual dimorphism in *Australopithecus afarensis*, with males said to have been 5 – 5.5. feet tall. Importantly, this has led some paleoanthropologists to suggest that, as with other primate species with high levels of sexual dimorphism, this was not a sexually monogamous species, an interpretation which itself questions the previously mentioned view that the emergence of bipedalism in early hominins was associated with pair-binding.

Found in Tanzania and dated to 3.7 mya (by potassium-argon dating and stratigraphy), the **Laetoli footprints** (Figure 6.6) are usually associated with *Australopithecus afarensis*. The footprints were formed by three bipedal individuals walking nearly 88 ft (27 m) in wet volcanic ash. The dried ash preserved the footprints, which were then covered by subsequent volcanic eruptions. More than 70 individual prints have been documented, allowing researchers to document the anatomy and gait of these individuals. The footprints, which are the oldest known early hominin footprints, clearly indicate bipedal locomotion and demonstrate that these individuals moved

like modern humans, walking on their heels and exhibiting forward-pointing big toes. Additionally, the feet are small, as is the distance between each footprint, suggesting a short stride and short individuals. The three individuals associated with the footprints are estimated to have been between 4.1 and 5 feet tall.

## *Paranthropus boisei*

Dating to 2.5 - 1.2 mya, Paranthropus boisei likely overlapped temporally with other hominin species (see Figure 6.5). 'Nutcracker Man', with its robust skull and developed musculature, is the best-known fossil of this little-known species. Most prominent are its large teeth, robust jaw, and pronounced sagittal crest on the top of the skull (where large chewing muscles were attached). While paleoanthropologists traditionally believed – on the basis of these anatomical features – that Paranthropus' diet consisted mainly of tough foods such as hard-shelled nuts and seeds, more recent isotopic analyses have revealed that Paranthropus also consumed grass. Importantly, its contemporaneity with hominin species that shared more derived traits with modern humans suggests to some that Paranthropus was not an ancestor of more recent hominins and that it in fact went extinct. Theories proposed to account for its extinction include the species' overspecialized diet (and thus inability to adapt to changing conditions) and possible predation by other larger-brained hominins.


**Figure 6.5.** Examples of early hominin fossils. Images from Wikimedia Commons**.**

**Figure 6.6.** Section of the 3.7-million-year-old Laetoli Footprints. Image from Wikimedia Commons.

## Summary

Understanding hominin evolution and the development of modern humans is a complicated undertaking that is limited by the size and condition of the known fossil record, the types of traits and definitions used in interpretations, and current analytical capabilities. While bipedalism has been identified as an important homologous derived trait and defining feature of humanity, it remains difficult to determine when and where the shift from temporary to full-time bipedalism occurred. Furthermore, researchers are still debating which of the known fossilized hominin species (if any) were the direct ancestors of modern humans. The task of writing the human phylogeny continues with new data and improved analytical techniques contributing to its on-going refinement.

## Review Questions

- **T/F.** Hominin evolution is best described as an anagenesis process.

- **T/F.** Defining a "species" is complicated in paleoarchaeological contexts, and researchers may refer to the "biological" or "ecological" species.

- **T/F.** Homologous traits are best for phylogenetic reconstructions.

- **T/F.** Evidence for bipedalism can be found on many bones on the body, including the skull, hips, legs, and ankles.

- **T/F.** Sahelanthropus is the oldest known hominin, dating to 6-7 mya.

## Discussion Questions:

- What is a phylogeny, and why do researchers disagree about how to construct the early human phylogeny?

- Explain three traits that lend to the difficulty of explaining hominin evolution.

- Why are homologous derived traits more appropriate than homologous ancestral traits in understanding hominin evolution?

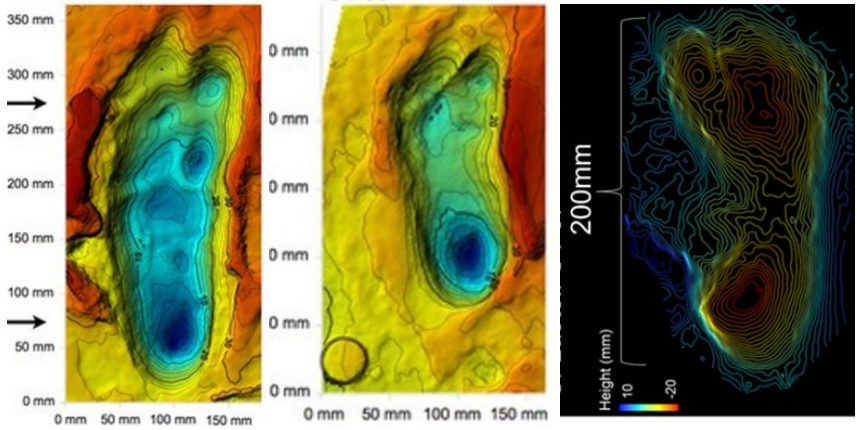
- Describe three skeletal traits that researchers use to interpret locomotion patterns in early hominin species.

## Activities

1. **Laetoli Footprints:** Reconstructing Individuals and Behaviors from Archaeological Remains

- Students can work individually or in groups. Add extra rows to the table for group work.
- How do paleoanthropologists learn about hominins from something like preserved footprints? In this exercise, you will learn about the relationship between foot length and height, as well as walking strides.
    a. Students first report or measure their height. Then, they measure their foot length (in inches) to see the relationship between foot length and height using the generic formula [(foot length*100)/15]. Students compare the estimated height to their reported/measured height and discuss the relationship and accuracy between foot length and height. Next, they measure the Laetoli footprint. In the images below, footprints are in mm and must be converted to inches. Students use the same formula to estimate the height of *A. afarensis*. Then, they discuss whether *A. afarensis* individuals were taller or shorter than the students (Most don't notice that the "tall" footprint is made of multiple footprints! You can see the big toe imprint inside the footprint).

| Name | Self-Reported Height (inches) | Foot Length (inches) | Estimated Height (inches) |
|---|---|---|---|
| **G2/3-26** | X | | |
| **G1-35** | X | | |
| **G1-37** | X | | |




| G2/3-26 | G1-35 | G1-37 |
|---|---|---|

**The G2/3-26 and G1-35 figures are modified from Masao et al. 2016; G1-37 figure is modified from Wikimedia Commons. See the original sources for higher-resolution images.**

b. Next, the instructor marks a 10m distance in the hallway or outside. Students count how many steps it takes to walk 10m at their average walking pace by taking the average of 3-4 walks. Then, they divide their average steps by 10m to determine average step distance per meter (i.e., 10/# steps per 10m). The Laetoli footprints below include average step distance (convert mm to m), and students compare the step distance between themselves and A. afarensis to understand pace of these shorter individuals.
c. Based on the images and the student's participation, discuss what else might be interpreted from footprints (e.g., stature, pace, biological sex, weight placement on the foot, etc.).

| Name | Average Steps per 10 m | Average step distance (m) |
|---|---|---|
| A. afarensis | X | |

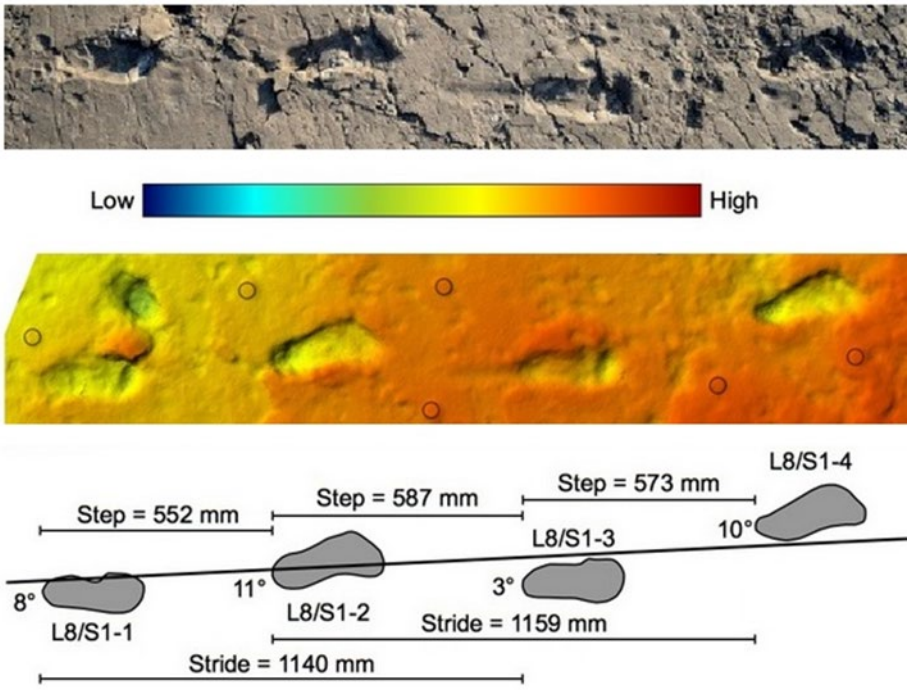
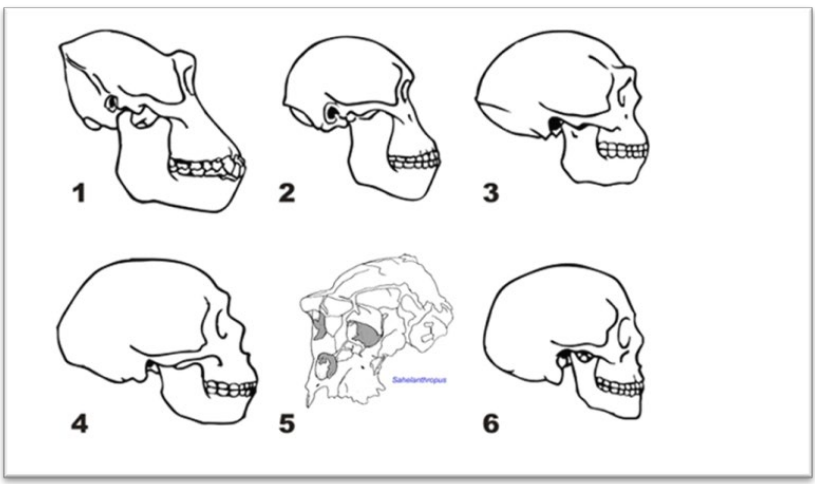


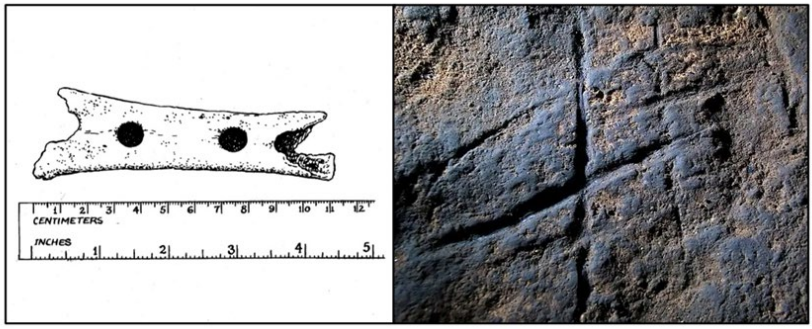

**Image from Wikimedia Commons. See the original source for higher-resolution image.**

2. **Skulls:** Using the image below, answer the following questions:



- Which skull is NOT a hominid (i.e., it is a Great Ape instead)?
- Which skull is the oldest known common ancestor to humans (and why is it a bit controversial)?
- Which hominin had the largest brain?
- Which hominin had large molars for breaking down fibrous tubers?
- Which hominin has no chin?
- Which hominin(s) have robust brow ridges?

3. **Neanderthals on Trial:** The artifacts below are both attributed to Neanderthals. The artifact on the left, dated between 43,000-82,000 years old, was discovered in a cave in western Slovenia called Divjak Babe I. It is believed to be from the thighbone of a juvenile cave bear. The artifact on the right was found in Gorham Cave, on the coast of Gibralter. Humorously dubbed "tic tac toe," it is at least 39,000 years old and incised into the limestone cave wall. What do you think these objects were? What might they have been used for? What level of confidence do you have in your conclusion? What else could they be? What other information would you want to feel more confident in your interpretations?



## Key Terms

**Absolute Dating methods:** Methods used to determine the chronological age of a specimen based on a specific time scale or calendar, such as radiometric dating.

**Accuracy:** How close a measurement is to the true value.

**Anagenesis**: Species directly evolving into later ones, without branching.

**Analogous traits**: Traits shared through convergent evolution.

**Ardipithecus:** A genus of extinct hominine. Ardipithecus ramidus is a species dating to 4.4 mya in Ethiopia, most commonly represented by the skeleton of 'Ardi'.

**Biological Species Concept**: A species consists of individuals that can produce viable offspring.

**Carbon 14:** A radioactive isotope that decays into Nitrogen 14 with a half-life of 5730 years.

**Cladogenesis**: The formation of new species through branching from a common ancestral species.

**Ecological Species Concept**: Species are adapted to particular niches, but they may be able to produce viable offspring with individuals from other ecological niches.

**Fossilization**: A process where the calcium and phosphorus content of organic remains are gradually replaced by iron silica, resulting in 'stone-like' remains.

**Great Rift Valley:** A location in east Africa where numerous hominin fossils have been found.

**Homologous ancestral traits:** Traits that appear before the common ancestor of a phylogenetic group.

**Homologous derived traits:** Traits that appear after the common ancestor of a phylogenetic group.

**Homologous traits:** Traits shared through common ancestry.

**Hunting Hypothesis:** Darwin's theory about hominin evolution, based on the belief that the transition from ancestral ape to early hominins involved a shift away from arboreal lifestyles.

**Australopithecus:** A genus of extinct hominins, primates closely related to modern humans. Australopithecus afarensis dates to around 3.2 mya in Ethiopia, most commonly represented by the skeleton of 'Lucy.'

**Laetoli Footprints:** A set of about 70 of the oldest early human footprints from three individuals discovered in norther Tanzania, trailing 88ft (27m), and representing bipedal locomotion. The footprints are typically associated with the Australopithecus afarensis as fossils were found in the same stratigraphic layers.

**Lucy:** A 40% complete skeleton of an Australopithecus afarensis, discovered in Ethiopia. Lucy's species present clear evidence of a more developed capacity for bipedalism.

**Paranthropus:** A genus of extinct hominin. Paranthropus aethiopicus dates to about 2.5 mya from East Africa, and while little is known about this genus, the "Black Skull" is one of the best-known fossils of this species.

**Patchy Forest Hypothesis:** A theory that suggests bipedalism was more efficient than quadrupedalism for collecting resources in inconsistent environments.

**Phenotypic approach**: Creating phylogenies based on shared basic (and non-ge
etic) traits.

**Phylogeny**: Evolutionary family tree.

**Potassium 40:** A radioactive isotope that decays into Argon 40 with a half-life of 1.25 billion years.

**Precision:** How close measurements of the same item are to each other.

**Provisioning Hypothesis:** A theory that suggests bipedalism allowed males to provide better for females and their offspring.

**Radiometric methods:** Techniques based on the known radioactive decay of elemental isotopes to calculate the absolute age of an item.

**Relative Dating methods:** Focus on determining the relative age (e.g., older versus younger) of objects, using methods including their position in a stratigraphic sequence, fluorine dating, and the use of index fossils.

**Sahelanthropus:** An extinct species of hominin. Sahelanthropus tchadensis dates to around 6 to 7 mya from Chad and is most commonly represented by the deformed skull nicknamed 'Toumai,'

**Stratigraphy:** Analysis of the superimposed layers at an archaeological site, may be used to determine relative dating among artifacts and features in a site.

**Subspecies**: A subdivision of a species, associated with geographic distribution.

## Suggested Readings

Ayala FJ, Cela-Conde CJ. 2017. *Processes in Human Evolution: The Journey from Early Hominins to Neanderthals and Modern Humans.* Oxford University Press.

Boyd R, Silk JB. 2020. *How Humans Evolved*, 9th ed., W. W. Norton & Company.

DeSilva J. 2021. *First Steps: How Walking Upright Made us Human.* HarperCollins Publishers.

Stringer C. 2013. *Lone Survivors: How We Came to be the Only Humans on Earth.* St. Martin's, Griffin.

Tattersall I. 2013. *Masters of the Planet: The Search for Our Human Origins.* St. Martins, Griffin.

## Videos

American Museum of Natural History. 2018. Seven Million Years of Human Evolution. Electronic document, https://www.youtube.com/watch?v=DZv8VyIQ7YU&t=3s, accessed 14 February 2022.