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Hominins, Hominids, and Hominoids

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An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

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CONTENTS

1. HUMANS ARRIVE

1.1. GENERAL INFORMATION AND DATES

- Pleistocene - since 1.8 MYA (million years ago)
- Pliocene - 15 to 1.8 MYA
- Miocene - 25 to 5 MYA; divided into Upper/Late (10 - 5 MYA), Middle (15 - 10 MYA), and Lower/Early (25 - 15 MYA)
- Oligocene - 40 to 25 MYA
- Eocene - 56 to 40 MYA
- Paleocene - 66 to 56 MYA
- Cretaceous - 145 - 66 MYA
- Jurassic - 200 - 145 MYA
- Triassic - up to 200 MYA

- Cenozoic - 66 MYA to present, sub-divided into Paleogene (66 - 22 MYA) and Neogene (22 MYA to present); Paleogene sub-divided into Paleocene, Eocene, and Oligocene; Neogene sub-divided into Miocene, Pliocene, Pleistocene, and Holocene (current? Anthropocene)

- 4 MYA - Australopithecines: small cranial capacity and protruding jaw (like apes), but shorter canine teeth, and walked upright. First specimen discovered was an infant at Taung, South Africa in 1924 by Raymond Dart (Groves 2004a).

- Between 2.5 and 1.5 MYA, key anatomical changes occurred in hominins that were important for Homo sapiens, most particularly brain size increased, hips and thigh bones adapted to bipedalism, and there were changes in teeth (Burenhelt 2004a).

- 5 MYA Antarctic ice sheets grew substantially, while the Arctic equivalent was 2.5 MYA. Thus, two "Ice Ages". The former has been linked to the development of Australopithecines, and the latter to the appearance of the genus Homo (Burenhelt 2004a). Most recent Ice Age epoch (Pleistocene) began about 2.5 MYA with cold periods (glacials) and warm periods (inter-glacials). Most recent glacial 115 000 - 10 000 years ago. The present period is an inter-glacial (Berglund and Bjorck 2004).

- The differences between non-human hominids and early humans include the lack of a mating season (ie: oestrous period), reduction in body hair, and diet of the latter (Burenhelt 2004a).

- Australopithecus africanus ("Nutcrackers"): eat meat or probably not (Rowley-Conwy 2004).

- Homo habilus: scavengers from carnivores or hunters (Rowley-Conwy 2004). "The regular consumption of large mammal carcasses, as evidenced by butchery marks on fossils recovered from Early Stone Age archaeological sites, roughly coincides with the appearance of Homo habilis" (Pante et al 2018 p215). Pante et al (2018) found that opportunism was key in excavations at Olduvai Gorge, Tanzania. In other words, hunting and scavenging.

Two categories of methods of dating fossils (Groves 2004b):

i) Absolute methods are based on the known standardised rate of decay of an element over time (eg: potassium to argon; radiocarbon (C_{14} to nitrogen); uranium to lead).

ii) Relative methods date fossils from the surrounding environment (eg: faunal dating; paleomagnetism (long-term changes in the Earth's magnetic field)).

1.2. HUMAN ORIGINS: ANCESTOR X

Meneganzin et al (2022) observed: "The search for the origin of Homo sapiens [1] has sometimes been defined as

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[1] Technically in biology, the term is speciation.

a 'recipe for frustration' (Foley et al 2016) or an 'unsolvable puzzle' (Batini and Jobling 2011). Indeed, the story of how we emerged as a species is to date ever more complex and no less elusive, as the available data do not seem in many respects to have sufficient resolution to discriminate among alternative scenarios" (p199).

In terms of finding the direct ancestor of Homo sapiens, the picture has changed dramatically in the 21st century, but one possibility is "Ancestor X" (last common ancestor; LCA, both of ourselves and of Homo neanderthalensis. Two populations of Ancestor X became isolated from each other, and the one in Africa around 800 000 years ago evolved into us ("simple single-origin" theory; also called "recent African origin" (RAO) [2]; Meneganzin et al 2022), while the European population became the Neanderthals, so the argument goes (Barras 2022).

Evidence for a single ancestral population in East Africa is based on two sets of evidence - (i) the earliest accepted fully modern human skulls found there, and (ii) mitochondrial DNA (Meneganzin et al 2022). The RAO has support from the allopatric model of speciation (eg: Mayr 1942), which asserts that "speciation is most likely to occur in small, peripheral populations that have geographically separated from the larger parental population. Small populations are majorly susceptible to quick evolutionary changes (by genetic drift or natural selection) as they contain less genetic variation and thus are less stable than larger ones" (Meneganzin et al 2022 pp201-202).

One suggestion for Ancestor X, proposed in the late 20th century, was Homo heidelbergensis, but now this species is viewed as too young. Ancestor X is believed to have existed 800 000 years ago or more (Barras 2022).

Next, Homo antecessor was proposed as Ancestor X (Barras 2022).

An entirely different view is that Homo sapiens emerged as a "meta-population" (ie: in several geographical areas) with "sub-populations" rather than from a single region in Africa. This idea has been called "African multi-regionalism" (eg: Aiello 1993) or "pan-African evolution" (multi-regional models; MRE) (Barras 2022) [3]. In very basic terms, there is no single Ancestor X, but ancestors (ie: "sub-populations that contributed

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[2] Other terms include the "Noah's ark hypothesis" or "replacement theory" (Burenhelt 2004b).

[3] Other terms include the "candelabra model" or "regional community theory" (Burenhelt 2004b).

some DNA to our species"; Barras 2022 p48) [4].

The challenge of Pan-Africanism includes discoveries and dating of finds at Jebel Irhoud (Morocco) (eg: Hublin et al 2017), which suggested "the monophyletic group that would eventually lead to H. sapiens, but it is not yet itself H.sapiens. The findings are sometimes too hastily referred to as 'the oldest Homo sapiens fossils' or 'modern human fossils' not only by media coverage, but also in scholarly publications" (Meneganzin et al 2022 p202).

Fossils in Asia have been underplayed for various reasons, compared to African ones, but "it has become increasingly clear that Asia is another hotbed of human evolution" (Barras 2022 p49). For example, Homo longi (or "Dragon Man") based on fossils found in China (Barras 2022).

The arguments revolve around traits that are viewed as unique (or specific) to Homo sapiens. Menganzin et al (2022) noted eight traits in the literature (eg: narrow pelvis; high and rounded neurocranium; prolonged post-natal growth period).

"Mosaic evolution" suggests that at the beginning of speciation "a new species do not appear as a fully assembled package within a single evolutionary trajectory: novelties can arise at separate intervals (ie: evolving at different rates and times) throughout hominin evolution, in an asynchronous fashion" (Meneganzin et al 2022 p203) [5].

"The fact that small portions of the present genome of H.sapiens are of Eurasian 'archaic' origin (ie: introgressions (appendix 1A) from Neanderthals, Denisovans and other deeply divergent lineages) rejects the strictest versions of RAO — that is, a full replacement scenario — although this does not provide support to the intercontinental and long-standing gene flow claimed by MRE" (Meneganzin et al 2022 p200).

Placing themselves in the middle of the debate, Meneganzin et al (2022) argued that "the emergence of H.sapiens should be understood as a multi-phase process.

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[4] Scerri et al (2018) asserted that the data "consistent with the view that our species originated and diversified within strongly sub-divided (ie: structured) populations, probably living across Africa, that were connected by sporadic gene flow" (quoted in Meneganzin et al 2022).

[5] Mosaic evolution "can refer to (i) different traits within the same lineage evolving quasi-independently at different rates and times; (ii) different domains of evolutionary change and novelties changing at different times and with different evolutionary trajectories across hominin phylogeny; (iii) the evolution of a complex trait (eg:, language) consisting of various sub-traits with distinct evolutionary histories" (Meneganzin et al 2022 p210).

Within this framework, we argue that from the initial conditions represented by an ancestral meta-population (ie: the putative LCA), characterised by demographic complexity, morphological variability and shifting structure, a more derived form — that is, a 'crown node' [Hennig 1969 quoted in Meneganzin et al 2022] - likely emerged locally. This would have later expanded across Africa, interbreeding with populations of the LCA, as well as in Eurasia, where there is evidence of gene flow among H.sapiens and its sister taxa" (p204). This can be called an "extended single-African origin" view.

1.3. COGNITIVE ABILITIES

"Whether and how cognitive abilities of modern humans might differ from those of extinct archaic humans such as Neanderthals remains a matter of debate. Discovery of artefacts and art of presumably Neanderthal derivation fuels the debate. Cognitive abilities reside primarily in the neocortex, the largest and most recently evolved part of the brain, which is present only in mammals. The evolutionary expansion of the neocortex and the concomitant increase in neuron production are considered to be a basis for the increase in cognitive abilities that occurred during human evolution" (Pinson et al 2022 p1).

The cranial volume of modern humans and Neanderthals were similar, suggesting similar brain and neocortex size, but this does not mean similar cognitive abilities. Pinson et al (2022) argued that one particular gene variant in humans (transkeletolase-like 1; TKTL1) generated more neocortical neurons, particularly in the frontal lobe. This gene is important in the developing foetal brain (at 13-16 weeks post-conception). Research with knockout mice and ferrets, and human brain tissue supported this view (Pinson et al 2022).

Talking more generally, Bertrand et al (2021) stated: "What ecological and evolutionary factors affect brain size in mammals? Studies have assessed the impact of various ecologies and behaviours — such as diet, locomotion, habitat, and activity pattern — on relative brain size in various mammalian groups. There is evidence that relatively larger brains are associated with diets involving more complex foraging strategies (vs folivorous diets (leaf-eating herbivores)), diurnal (vs nocturnal) activity pattern, life in complex environments like forests (vs more open habitats), and arboreal or climbing locomotion (vs fossorial or digging)" (p1).

Bertrand et al (2021) analysed a number of anatomical differences in 38 rodent species (living and extinct). Species living in trees (arboreality) have greater relative overall brain size and neocortex size compared to other habits. Arboreality was important in the evolution of brain size and neocortex size in squirrels, while fossoriality (living underground) had an opposing effect.

1.4. GENERALIST VS SPECIALIST

"Conventional wisdom" for Paranthropus becoming extinct while Homo continued was that "early Homo was a highly flexible ecological generalist, whereas Paranthropus was an ecological specialist... This led to the development of evolutionary narratives in which the flexibility of Homo underpinned its long-term success, whereas the narrower niche of Paranthropus rendered it incapable of coping with climatic change through the Pleistocene, ultimately leading to its demise" (O'Brien et al 2023 p1). Others (eg: Wood and Strait 2004) have argued that both genera were ecological generalists.

O'Brien et al (2023) analysed mammalian fossil data for the last fifty years in East Africa (in particular East Turkana in Kenya) covering 2 - 1.4 million years ago to understand the diets of Paranthropus boisei and early Homo in the context of the specialist vs generalist debate. Evidence supported the "characterisation of P.boisei as an ecological specialist relative to the more generalist Homo" (p1). Specialist here refers to eating plants (and particular plants) only, while a generalist eats what is available ((wider range of) plants and meat; also called omnivores).

1.5. HOMININS IN MIOCENE

Tracing back the evolution of humans, more widely hominins (humans and their ancestors), and hominid (ancestors of primates and apes) species involves very long time periods [6] [7]. For example, the Middle to Late Miocene period (12.5 to 9.6 million years ago), and only

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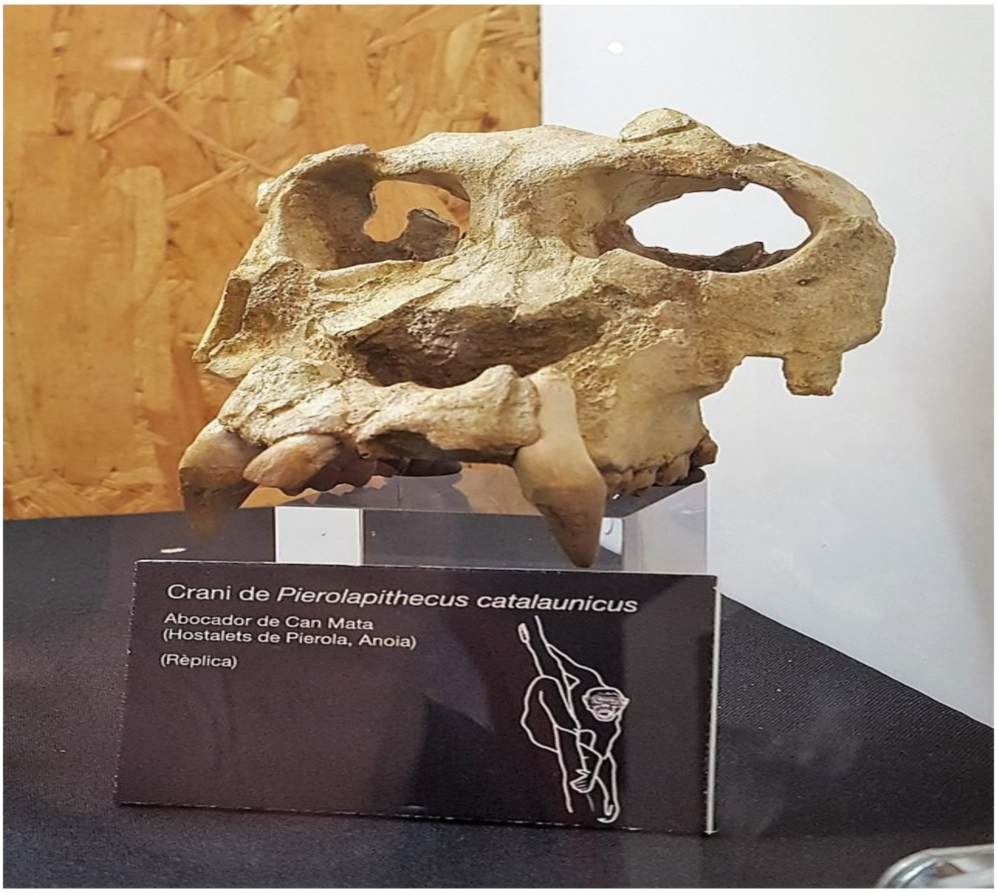
[6] Hominoidea (or hominoids) is a super-family including humans and apes (extinct and living), which was established about 20 million years ago. There is also Hominidae, which covers humans, chimpanzees, gorillas, and orang-utans, but not gibbons (which are a separate group) (Groves 2004a).

[7] Also around at the time: Early Miocene - genus Proconsul and Middle Miocene - Kenyapithecus.

a limited amount of fossil finds exist (eg: Valles-Penedes Basin, North-East Iberian peninsula) (Zanolli et al 2023).

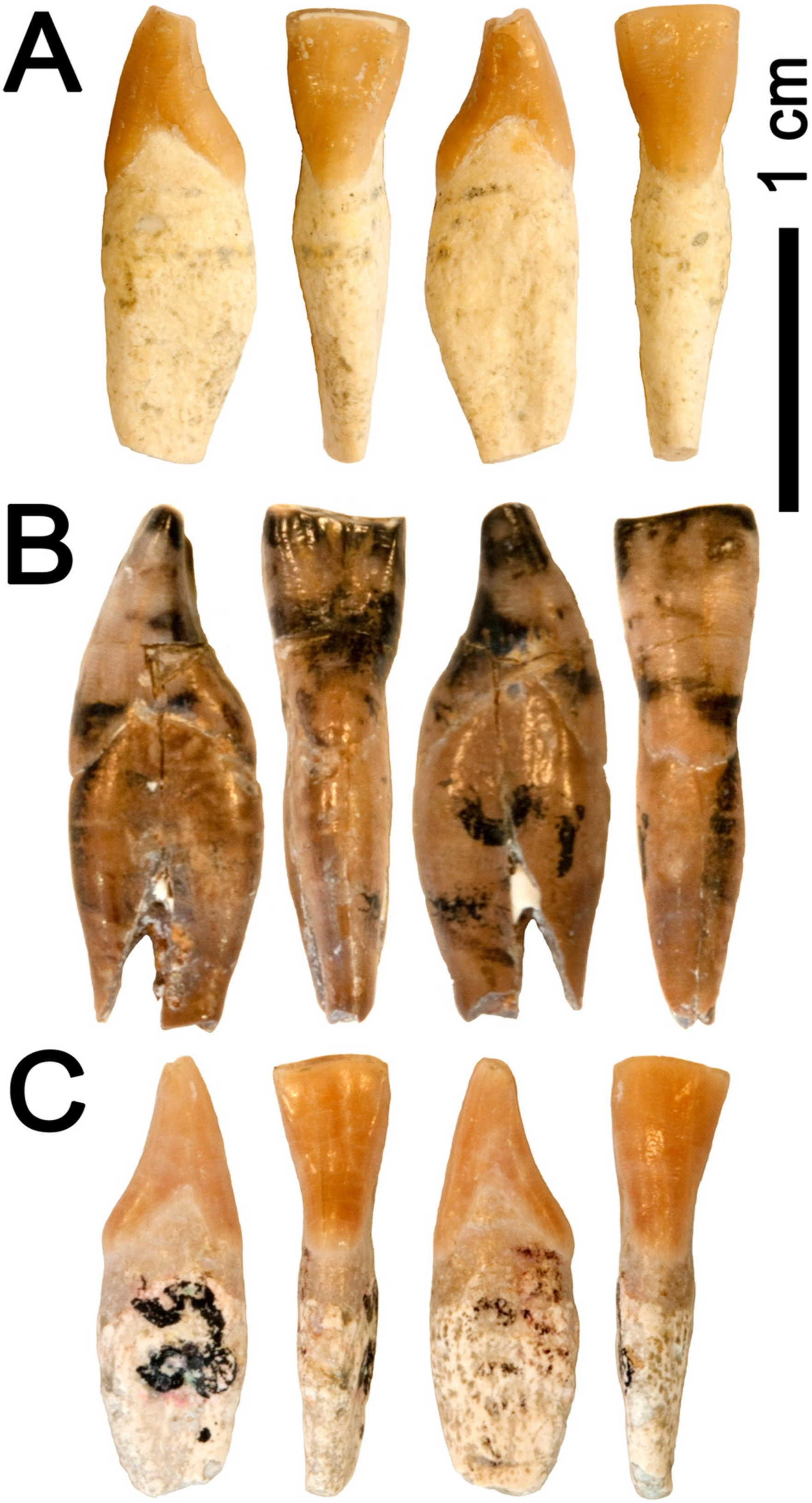
At this site several hominid species have been found - Pierolapithecus catalaunicus (figure 1.1), Anioapithecus brevirostris, Dryopithecus fontani, Hispanopithecus laietanus (figure 1.2), and Hispanopithecus crusafonti - as well as "disputed" remains attributed as "Sivapithecus" occidentalis (Zanolli et al 2023).

How these different species relate together in terms taxonomy is debated. Put simply, they are all part of a single genus or from separate genera. Consensus tends towards the latter (Zanolli et al 2023). The focus of the debate is teeth (molars - eg: shape; enamel thickness; positioning on mouth and skull) because these tend to be the best (and/or only) remains found.



(Source: Nosobema lyricum (taken in 2017); public domain)

Figure 1.1 - Model of skull of Pierolapithecus catalaunicus in Miquel Crusafont Catalan Institute of Palaeontology, Barcelona.



(Source: Alba et al 2012 figure 5)

Figure 1.2 - Lower incisors of Hispanopithecus laietanus.

1.6. APPENDIX 1A - ARCHAIC INTROGRESSION

Introgression is the process of passing genes from one species to another, usually by interbreeding. In the case of archaic introgression, it is interbreeding between different hominins. Modern genetic techniques allow the study of ancient DNA to understand this process.

Modern humans arrived in Europe around 45 000 - 49 000 years ago, and overlapped with Neanderthals there for about 5000 years, which allowed time for interbreeding (Sumer et al 2024).

Sumer et al (2024) analysed data from six humans from a site at Ranis, Germany. An estimate of about eighty generations since the Neanderthal interbreeding was made [8], and this dated it to 45 000 to 49 000 years ago. Previous estimates varied between 41 000 and 65 000 years ago (Sumer et al 2024).

Iasi et al (2024) analysed the genomic data from 59 ancient humans living between 45 000 and 2200 years ago, and 275 present-day individuals. Interbreeding with Neanderthals was dated between 50 500 and 43 500 years ago.

Skov et al (2023) analysed X chromosomes from living human males around the world (from a database), and found that individuals with "long-standing African ancestry" have DNA with a mix of genetic material from many different ancestors, whereas in individuals without recent African ancestry, there is less diversity suggesting a single ancestor (Le Page 2022).

1.6.1. Circadian Genes

"Anatomically modern humans" (AMHs) who left Africa approximately 70 000 years ago were exposed to diverse environments which shaped biology and behaviour. In Europe and Asia (Eurasia) AMHs were faced with greater seasonal variation in temperature and daylight length (photoperiod) than in Africa (closer to the equator). This was the pressure for the evolution of circadian adaptation. Also other hominins (eg: Neanderthals) were already living at higher latitudes, and AMHs interbred with them (as around 2% of present-day human DNA comes

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[8] A generation is estimated at about 30 years.

from archaic ancestry [9]) (Velazquez-Arcelay et al 2023).

Velazquez-Arcelay et al (2023) investigated the circadian genes (ie: those that control processes related to the body clock). In total, 1136 variants in circadian genes and related biology were found by the researchers' analysis of DNA from various hominins (eg: Neanderthals [10], Denisovans [11], AMHs, present-day humans) available on genome databases. Sixteen genes in particular were likely key in the divergence between present-day humans and archaic hominins in this area [12]. One behaviour in particular was interesting - "morningness" (a preference for earlier hours in the daytime; called "larks" in everyday language) - increased in humans compared to other hominins.

The advantage of this behaviour is that light in the morning resets the circadian rhythms, and this could be useful when photoperiods are greatly shortened (as in winter) or greatly extended (as in summer) (Velazquez-Arcelay et al 2023).

In terms of evaluating their research, Velazquez-Arcelay et al (2023) admitted that "given the complexity of circadian biology, there is no gold standard set of circadian genes. We focus on the core clock genes and a broader set of expert-curated genes relevant to circadian systems, but it is certainly possible that other genes with circadian effects are not considered" (p11).

1.6.2. Natural Selection in Action

Analysing ancient DNA has shown natural selection at work (eg: genes involved in the production of vitamin D and Bronze Age Britons).

Mathieson and Terhorst (2022) found seven regions of the genome showing selection when comparing DNA from 529 ancient Britons from 4500 before present and 98 present-day individuals in the UK Biobank. The genes related to increased vitamin D and calcium, and the upshot of lighter skin.

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[9] East Asians show approximately 20% more Neanderthal ancestry than West Eurasians (Iasi et al 2024).

[10] Sequencing of the Neanderthal genome reported first by Green et al (2010) (appendix 1B).

[11] Genome sequencing by Meyer et al (2012), for example.

[12] Studies have "identified that the distribution of Neanderthal ancestry is not uniform across the genome: Some regions are significantly depleted of Neanderthal ancestry (referred to as 'archaic deserts'), whereas other regions contain Neanderthal variants at unusually high frequencies, possibly because they harbour beneficial mutations ('candidates of adaptive introgression'). The evolutionary forces, for example, genetic drift or natural selection, that have shaped these patterns are still not fully understood" (Iasi et al 2024 p1).

Early Britons (eg: "Cheddar Man"; 10 000 before present) had darker skin, but obtained vitamin D from eating oily fish. When Britons started crop farming, the risk of vitamin D deficiency rose, and so selection pressures for increased calcium consumption as in milk drinking throughout life (Marshall 2022). "Virtually everything in the body requires vitamin D", Nina Jablonski pointed out, "so it isn't surprising that a shortage provoked rapid evolution" (Marshall 2022 p8).

But Mathieson and Terhorst (2022) admitted, "the strength of selection on individual loci [gene locations] varied substantially over time, suggesting that cultural or environmental factors moderated the genetic response" (p2057).

1.7. APPENDIX 1B - NEANDERTHAL GENES

Extensive genetic information has been extracted from skeletal remains of at least eighteen Neanderthals from fourteen archaeological sites (Skov et al 2022). Neanderthals occupied Western Eurasia from 430 000 years ago to their extinction 40 000 years ago, and there were "multiple distinct Neanderthal populations over time and space" (Skov et al 2022 p519).

Using the genetic information, Skov et al (2022) attempted to describe the social organisation of Neanderthals (ie: the size and composition of groups). In particular, Y-chromosome and mitochondrial DNA from thirteen individuals at two sites in southern Siberia (Russia) were analysed.

At one of the sites (Chagyrskaya cave), for example, a first-degree relationship was found between two individuals. First-degree relatives (in terms of genetically) are biological parent-child, or brother-sister. Other information about the two individuals led to the conclusion of father-daughter. Close relationships like this also told that the individuals were contemporaneous rather than bones of different periods in the same place. While, for instance, at the other site (Okladnikov cave), two individuals were genetically unrelated to each other.

Put these and other information together, the researchers suggested a community size of 20 individuals, and a scenario of female-based migration between communities.

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2. EATING, HUNTING, AND TOOLS

2.1. NEANDERTHAL AND HUMAN DIETS

"The transition from a primarily vegetarian diet to regular mammalian resource consumption has been suggested to have driven increased brain size, increased stature, and reduced gut size within the genus Homo. However, evidence suggests that habitual animal resource consumption was not exclusive to the genus Homo, with earlier hominin taxa (eg: australopithecines) also regularly exploiting such resources" (Ludecke et al 2025 p309).

Finding evidence, particularly for the latter, is not an easy task. Stone tool production and evidence of animal butchery (eg: cut marks on bones), for example, suggest meat consumption as early as two million years ago by Paranthropus, maybe even earlier (Ludecke et al 2025).

Another line of evidence is elemental composition (ie: elements in fossils that signal animal meat consumption - eg: nitrogen). "Nitrogen (N) stable isotope ratios have long been used to reconstruct different aspects of an organism's diet. Metabolic reactions in the body generally result in a series of ^{15}N-depleted N byproducts (eg: ammonium, urea, and uric acid). The elimination of these metabolites in urine, faeces, and sweat results in an increase in the ^{15}N/^{14}N of the organism with respect to their diet. Therefore, the ratio of ^{15}N to ^{14}N... is widely used as a trophic indicator in modern ecosystems" (Ludecke et al 2025 p309).

Ludecke et al (2025) analysed teeth from seven

Australopithecus specimens found in South Africa for animal-based organic nitrogen and carbonate carbon isotopes. The conclusion was a plant-based diet for these hominins. But the researchers pointed out that the "data do not preclude occasional consumption of meat or other animal resources, similar to that observed in some modern non-hominin primates, including capuchins (Cebus or Sapajus), baboons (Papio), and chimpanzees and bonobos (Pan). In these primates, meat typically accounts for a small proportion of total energy and protein intake" (Ludecke et al 2025 pp311-312).

The "eventual replacement" of Neanderthals by anatomically modern humans (AMHs) may have been due to differences in diet (eg: Neanderthals did not hunt small prey like rabbits, birds and fish). Put simply, Neanderthals were more rigid in their diet than AMHs, though this is disputed (Jones and Carvalho 2023).

It could be that the differences were due to the availability of foods (eg: changes in numbers of mammals 50 - 40 000 years ago). The study of archaeofauna (and archaeozoology) is the method used here, as in data available on the Iberian Peninsula for the Middle and early Upper Paleolithic period (60 - 30 000 years ago) (Jones and Carvalho 2023).

The analysis by Jones and Carvalho (2023) from 59 archaeological sites (in modern-day Spain and Portugal) found similarities in the meat diet (based on animal bones at sites, for instance) between Neanderthals and AMHs.

2.1.1. Homo Erectus

Dmanisi in Georgia is an important site for evidence of Homo erectus outside of Africa. But also for information about behaviour of this hominin. For example, a skull of an aged individual with a single tooth suggesting "such strong social ties that others had cared for this disabled individual for years, obtaining soft food or processing food into mush so that he could eat" (Shipman 2022 p14).

Carbone et al (1999) mapped diet and body size in a range of carnivores. Small carnivores can survive from eating insects, and some plants and fruits. But carnivores weighing over 20 kg cannot survive on such a diet. They need 70% or more meat in their diet, which is derived from prey larger than themselves. This is known as a hyper-carnivorous strategy, and is associated mostly with pack hunters (Shipman 2022).

Homo erectus shows similarities and differences to hyper-carnivores. Similarities include the larger body size, and possible pack-hunting. But not the dental adaptations seen in extinct Canidae, for example (Van Valkenburgh et al 1999). However, this could be overcome by cutting tool use. "It is not only legs, claws, and teeth that gave hyper-carnivores an advantage. Bonding among individuals, communication skills, and living in close-knit packs may have conferred an edge among hunting species" (Shipman 2022 p18).

2.1.2. Cooking

Richard Wrangham (eg: 2009) hypothesised that hominins started cooking around two million years ago. in the search for the "invention of cooking", an earthen oven has been dated to 780 000 years ago (which predates Homo sapiens). Even further back, traces of ash and burned bones have been dated as one million years ago, and evidence of roasting meat at 1.5 million years ago (Marshall 2022).

2.1.3. Miscellaneous

In understanding the diet of hominins, as well as analysis of carbon isotopes in teeth, assumptions are made about the environment from fossil faunal and floral assemblages (called paleo-environmental reconstruction) (Negash and Barr 2023).

Negash and Barr (2023), using data from the modern world, showed how assumptions about the animals present in a certain landscape (eg: woodland vs grassland) need caution.

African papionin monkeys, which includes baboons, geladas, mandrills, and mangabeys, are used as a model for hominin evolution. For example, Robinson (1954) hypothesised "foraging similarities between modern savanna-dwelling papionins and Plio-Pleistocene hominins based on previously documented ante-mortem enamel chipping similarities between Papio ursinus [Chacma baboons] and Paranthropus robustus" (Fannin et al 2023 p2).

Fannin et al (2023) developed this work with a diverse set of African papionin species. The chipping of teeth in the baboon species was found to be greater than seen in the hominin taxa (Australopithecus and Paranthropus) (eg: 20% vs 10% of teeth). "Plio-Pleistocene hominins appear to have effectively mitigated enamel chipping relative to modern dietary analogues living in similar habitats, a testament to the durability and strength of their post-canine teeth, the adaptability and flexibility of the hominin clade, and their expanding array of adaptive strategies" (Fannin et al 2023 p11).

2.1.4. Cannibalism

There is evidence from bones that cannibalism was practised by human ancestors (eg: Gough's Cave, England, 14 700 years ago) (Marshall 2024).

The behaviour may have been more common among hominins than at first thought, and for reasons of funerary ritual (eg: Marsh and Bello 2023) as much as hunger (Marshall 2024).

In understanding this behaviour there is a negative association linked to cannibalism, including its use as a justification in Western colonial times (eg: "civilising" the "cannibal native"). A reaction to this attitude came in Arens (1979), who argued that there was no evidence of cannibalism ever (Marshall 2024). But archaeological evidence has refuted this view (eg: Villa et al 1986).

About one-fifth of Neanderthal sites in Europe show evidence of cannibalism, and similarly for early humans. But there is much variability between periods and cultures (Marshall 2024).

Going back further, Homo antecessor at one site in Spain (1.2 - 0.8 MYA) is "convincingly a case of cannibalism" (Silvia Bello in Marshall 2024), and a single hominin leg bone from Kenya dated 1.45 MYA (Pobiner et al 2023). though the latter is disputed (Marshall 2024).

Eating humans does not yield that many calories compared to other animals. One estimate of 144 000 calories from a typical Stone Age adult compared to 3.6 million calories just from the muscles of a mammoth (Marshall 2024).

2.2. HUNTING HOMININS

2.2.1. Bear Exploitation by Early Humans in Europe

Mammals caught by early humans were not just to eat as cut marks on the bones suggest skinning to use the hide. Bears are a particular example as their skins have "high insulating properties and might have played a role in the adaptations of Middle Pleistocene hominins to the cold and harsh winter conditions of Northwestern Europe" (Verheijen et al 2023 p1) {approximately 30 000 years ago] [13].

Members of the cave bear and brown bear lineage were common in Europe at this time as many bones have been found at cave sites, for example, over the years. In the early 20th century, the "cave bear cult" theory was proposed (Bachler 1921 quoted in Verheijen et al 2023). "The accumulation of large masses of cave bear remains, sometimes found in peculiar constellations in cave sites where stone artifacts were also discovered, led to the interpretation that cave bears were actively hunted and worshipped as part of a cult. Even at the time, the theory was already contested and the accumulations were explained as a taphonomic phenomenon... [14], leading some authors to be sceptical of cave bear hunting under any circumstances..." (Verheijen et al 2023 p2). More recent research shows bear exploitation for use of meat, skins, marrow, and bones at cave sites (eg: Romandini et al 2018).

Open-air sites are not as well studied. But Verheijen et al (2023) reported evidence of bear exploitation from a site at Schoningen in Germany as seen in the cut marks on the bones. The researchers interpreted the "finds as evidence for bear hunting and primary access since bear skins are best extracted shortly after the animal's death. The very thin cut marks found on the Schoningen specimens indicate delicate butchering and show similarities in butchery patterns to bears from other Paleolithic sites" (Verheijen et al 2023 p1). There is similar evidence from open-air sites at Boxgrove (UK) and Bilzingsleben (Germany) (Verheijen et al 2023).

Verheijen et al (2023) explained the importance of the finds: "One of the main obstacles for hominins to overcome in Northwestern Europe, even during interglacial conditions, was maintaining their body temperature. Year-round occupation without major seasonal migration implies that hominins were able to cope with these severe conditions and endure wind chill, low temperatures,

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[13] More generally there is a debate around when hominins started eating meat. Hominin-made cut marks on animal bones up to one million years ago have been found at a limited number of archaeological sites (eg: Olduvai (Tanzania), La Boella (Spain), Dmanisi (Georgia)) (Yravedra et al 2024).

[14] The process of decay and fossilisation.

reduced daylight hours, and snow cover... Although some physical adaptations of Middle Pleistocene hominins might have allowed them to better cope with these harsh conditions..., cultural solutions such as pyrotechnology, shelter, and increased insulation through clothing... were probably also required for survival. Direct evidence for such cultural solutions in the Middle Pleistocene record of Eurasia is scarce and often disputed. Nonetheless, there are several indications that the technology necessary to produce simple clothing... was already present. This type of simple clothing probably constituted of animal skins that were wrapped around the body without elaborate tailoring. Carnivore pelts, and especially bear pelts have high insulating properties..., which would make them very suitable for constructing simple clothing and/or bedding" (p10).

2.2.2. Neanderthal Hunting

Straight-tusked elephants have been described as the largest terrestrial mammal of the Pleistocene period, and were twice as large as living African elephants (Gaudzinski-Windheuser et al 2023). These animals existed between 800 and 100 000 years ago, and would have have contacted with western Eurasian hominins, particularly Neanderthals. Their skeletal remains have been found at hominin sites (Gaudzinski-Windheuser et al 2023). But were these the remains of scavenged (ie: died a natural death) or hunted animals?

Gaudzinski-Windheuser et al (2023) argued for the latter based on their analysis of bones at the Neumark-Nord site in Germany. Bones of over seventy elephants were found during excavations between 1985 and 1996 (over 3100 individual remains; some virtually complete skeletons; two individuals with partially preserved gut contents). Dating of the site is based on pollen, and "pollen assemblage zones" (PAZs) in time have been used.

Forty-four "bone complexes" were particularly studied by Gaudzinski-Windheuser et al (2023), and they showed "traces of anthropogenic modification of elephant carcasses" (p6) (eg: cut marks showing butchering).

"Butchering of elephants yields large packages of protein-rich meat. Other macro-nutrient food resources must have been a welcome and necessary supplement to balance the daily dietary needs of Neanderthals. Particularly noteworthy at Neumark-Nord is the focus on fatty tissues, for example, visible in the frequent and meticulous exploitation of the large fatty weightsupporting foot cushions, as indicated by the cut mark distribution data. These foot cushions are a well-known repository of adipose tissue in present-day elephants and, together with the trunk, form a highly prized body part for consumption by recent indigenous elephant hunters. They are also quite resistant to fast degradation processes and spoiling and are a rich source of nutritionally valuable n-3 long-chain polyunsaturated fatty acids" (Gaudzinski-Windheuser et al 2023 p10).

The nature of the butchering marks suggested fresh carcasses, which in turn suggested hunting. Hunting and processing of such large animals would have meant teamwork from a group of hunters, but "required little technological sophistication, with hunting strategies mostly aimed at limiting the mobility of prey, eg: by digging pits or driving them into mud traps, and killing them with wooden thrusting spears" (Gaudzinski-Windheuser et al 2023 p10).

Butchering an animal with a body mass of ten metric tons would take time and require co-operation with the basic stone tools. Gaudzinski-Windheuser et al (2023) estimated 3-5 days for 25 individuals to skin, strip the meat from bones, and dry or smoke the meat. There would be a lot of meat, which "either imply a large group of consumers and/or the presence of cultural means to preserve food and to store products over a significant period" (Gaudzinski-Windheuser et al 2023 pp10-11).

Gaudzinski-Windheuser et al (2023) concluded that hominins in the "Last Interglacial" period (or MIS 5e {Marine Isotope Stage]) (130 - 115 000 years ago) were "systematically and regularly targeting" (p11) straight-tusked elephants.

2.2.3. Female Hunters

"The notion of separate subsistence roles for females and males in forager societies has been a long-standing paradigm for a wide range of social science disciplines, as well as in the public sphere, and include influential texts such as 'Man the Hunter' [Lee and DeVore 1968], and 'Woman the Gatherer' [Dahlberg 1983]... Such assumed sex-specific gender roles in subsistence activities are commonly construed with additional gendered traits such as human men being less emotional and more aggressive, while human women tend to demonstrate more nurturing behaviour and a focused interest in children" (Anderson et al 2023 p1).

This sexual division of labour is challenged by archaeological evidence. For example, a 9000 year old burial in Peru of an adult female with hunting toolkit as found buried with men elsewhere (Anderson et al 2023). Haas et al's (2020) review of burials in the Americas from the Late Pleistocene to the Early Holocene period (around 100 000 years ago) found eleven such cases. "By using a probability analysis of all twenty-seven sites which had evidence of big-game hunting, Haas et al [2020] determined that females made up a 'non-trivial' amount of big-game hunters across the Americas. In fact, their analysis suggested that females represented up to fifty percent of big game hunters from the Americas pre-historically" (Anderson et al 2023 p2). Weapons have also been found in female burials (eg: Viking; Scythian) (Anderson et al 2023).

Anderson et al (2023) hypothesised that hunting by females was an expected behaviour of hunter-gatherer human communities. The researchers reviewed ethnographic reports of foraging societies (taken from the "D-PLACE" database [15]).

"Of the 63 foraging societies with clear descriptions of hunting strategies, 79% of them demonstrated female hunting" (Anderson et al 2023 p6).

Differences were noted in the tools and skills of female hunters. For example, women used knives while men preferred bows and arrows in the same communities, and evidence of greater flexibility of choice of weapon. "In addition to weapon choices, women further employ a greater flexibility of hunting strategies compared to men. For example, women hunt with a variety of partners, including their husbands, other women, children, dogs, as well as hunting alone. In contrast, men primarily hunt alone, with a single partner (their wife), or with a dog" (Anderson et al 2023 pp6-7).

The focus of the hunt also varied. "The type of game women hunted was variable based on the society. Of the 50 foraging societies that have documentation on women hunting, 45 (90%) societies had data on the size of game that women hunted. Of these, 21 (46%) hunt small game, 7 (15%) hunt medium game, 15 (33%) hunt large game and 2 (4%) of these societies hunt game of all sizes. In societies where women only hunted opportunistically, small game was hunted 100% of the time. In societies where women were hunting intentionally, all sizes of game were hunted, with large game pursued the most" (Anderson et al 2023 p6).

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[15] Anderson et al (2023) issued a correction in relation to their methodology here (Anderson et al 2024) (see https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0309543).

Critics suggested that children accompanying women on hunts would be at risk, and reduce the effectiveness of the hunter. "The importance of infants remaining with adults (versus being parked) is an important part of our lineage, with children accompanying the wide range of expeditions consistently evidenced in the archaeological, as well as the ethnographic record. Data explicitly mentioning that infants are carried while hunting exist for the Aka and the Awa , as well as for foraging bouts that might result in opportunistic hunting (eg: among the Batek and Nukak). Among both the Hadza and the Aka, children (potentially as young as age three) accompany adults on over 15% of hunting trips. The idea that women are hindered by childcare and thus cannot hunt is an area where increasing data collection and thoughtful interpretation is lending a much richer lens to our understanding of human mobility strategies" (Anderson et al 2023 p7).

Increasing evidence is challenging the traditional sexual division of labour among early humans (Anderson et al 2023).

2.3. EARLY TOOLS

Finding the first "tools" of hominins (humans and their ancestors) is an important motivation of researchers. Tools here refer to "systematically produced, sharp-edged flakes for cutting and cobbles or cores for percussion" (Plummer et al 2023 p561) (figure 2.1). The use of such tools named "Oldowan" (after the original site of finds in Tanzania) are viewed as a technological breakthrough (eg: at 2.6 million years ago (MYA)) (Plummer et al 2023) [16].

Around this time (3 - 2.5 MYA) there were overlapping hominins (both in geography and time) including of the genus Homo, and Paranthropus (now extinct genus of hominin) (figure 2.2). O'Brien et al (2023) suggested that this occurred multiple times.

Tools found in Ethiopia's "Afar Triangle", and Nyayanga, Kenya, are attributed to the Oldowan, and "demonstrate that hominins used tools to butcher a variety of animals, including megafauna, and process

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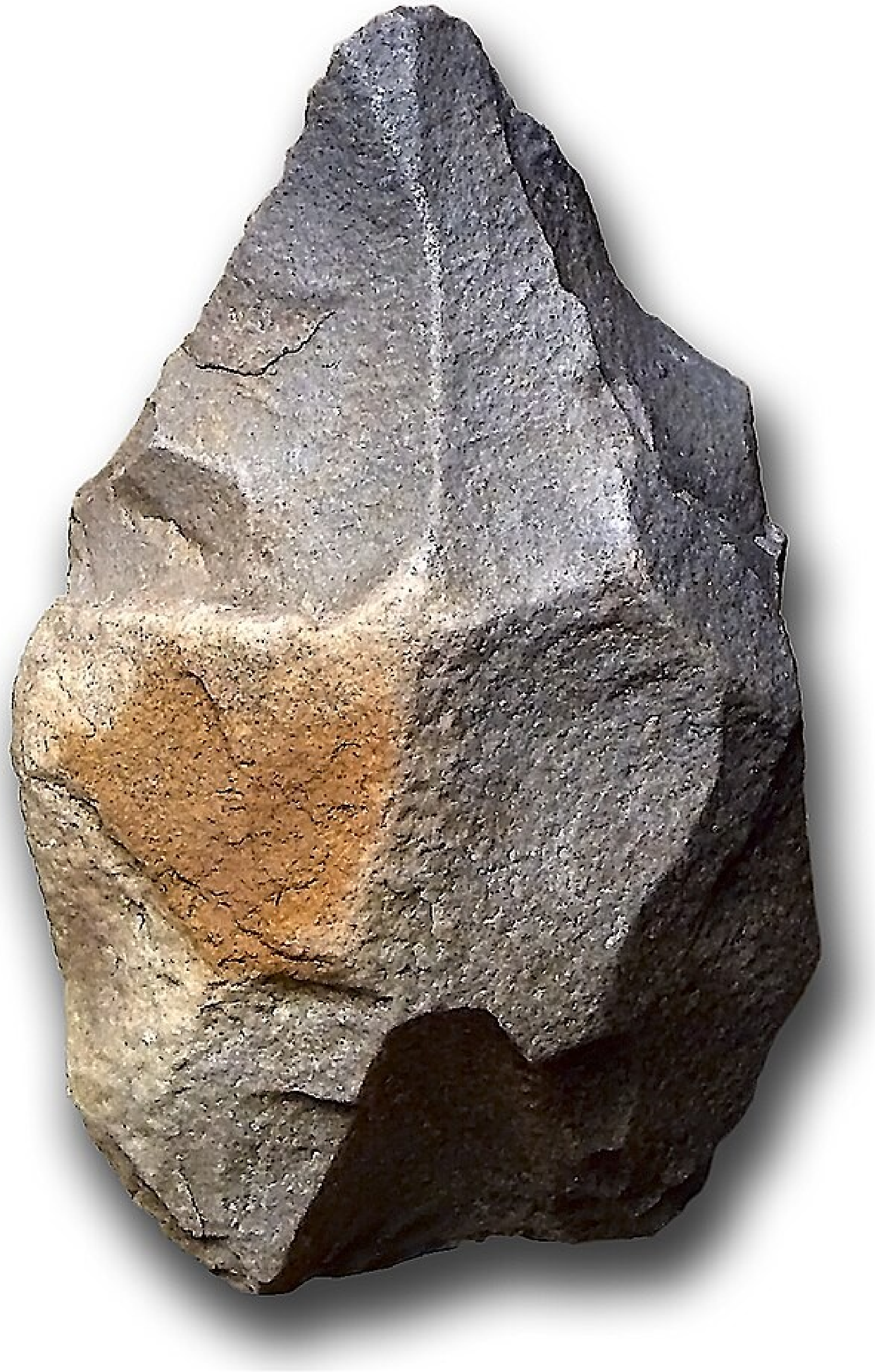
[16] The Olduvai Gorge in Tanzania has been covered at various times by volcanic ash, and this allows archaeologists to use the natural layers for dating. At the bottom of the 90 metre sequence of layers is "Bed I" (1.8 - 1.6 million years ago), while "Bed IV", the upper layer, is dated at 200 000 to 100 000 years ago. Oldowan tools have been found in Bed I (Fletcher 2004) (appendix 2A).

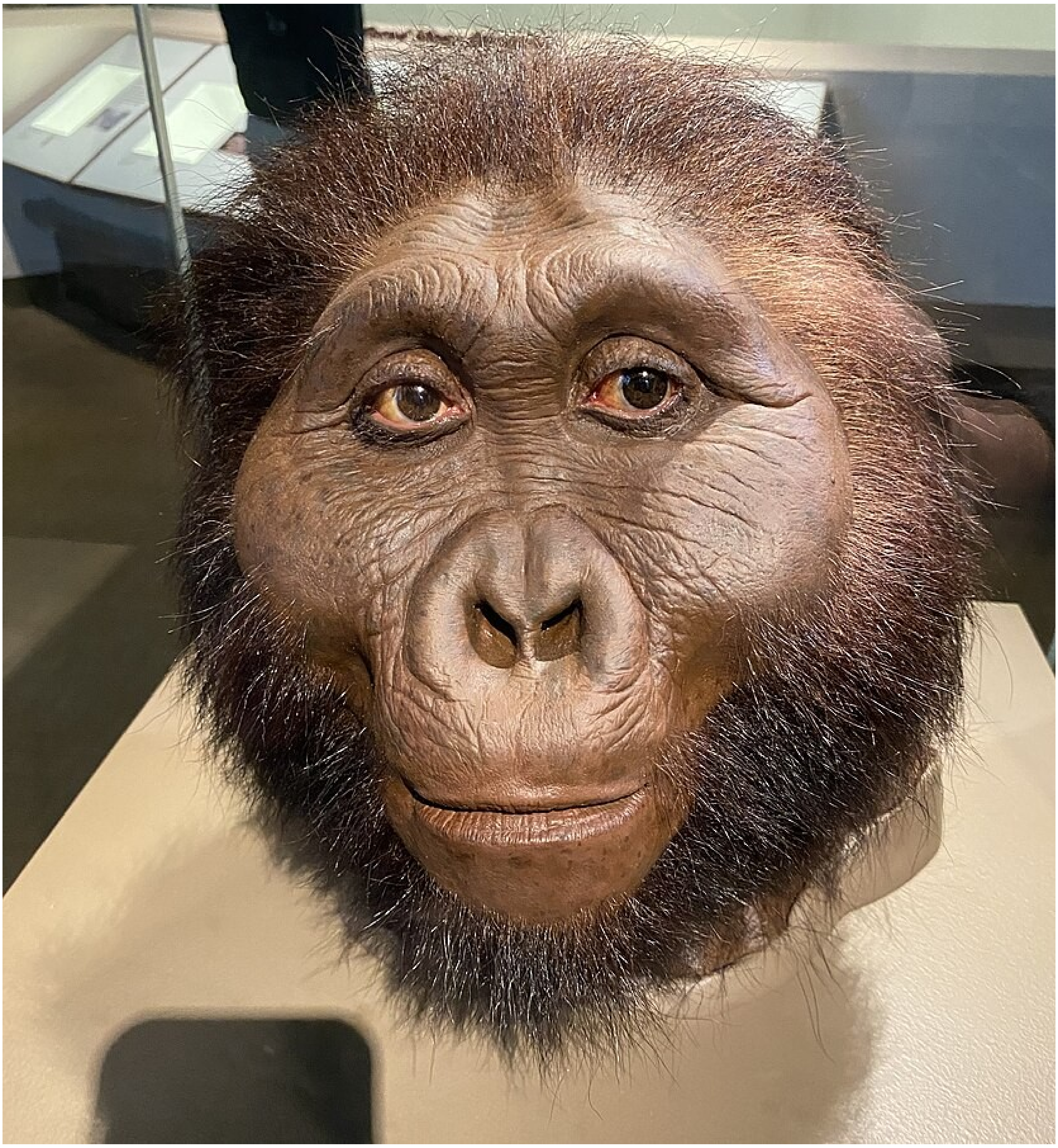


(Source: Locutus Borg; public domain)

Figure 2.1 - Example of an early tool.

diverse plants at Oldowan's inception" (Plummer et al 2023 p561).

Plummer et al (2023) dated the tools at Nyayanya to 3 - 2.5 MYA, and also found teeth of Paranthropus species. The Oldowan is "often attributed" as a product of Homo, but there is evidence of association with Paranthropus (Plummer et al 2023).



(Source: Ryan Schwark; public domain)

Figure 2.2 - Facial reconstruction of Paranthropus boisei at Smithsonian National Museum of Natural History.

With reference to geographical dispersion of hominins, Parenti et al (2024) stated: "Shortly before the Plio-Pleistocene boundary [around 5 million years ago], a yet unknown hominin(s) [possibly an early Homo] enlarged its home range north of equatorial Africa, exploiting a period of humid climate in the Saharan belt... and the moister conditions of the Negev... During this time, hominins left stone tools close to southern Mediterranean shores... and well beyond the Red Sea, first in the Zarqa Valley [modern-day Jordan]... and somewhat later in China [eg: two million years ago]" (p2).

2.3.1. Tool Use

Oldowan stone flakes are considered evidence of hominin tool use, but Proffitt et al (2023) have questioned whether it was intentional tool production. It has been observed that macaques use one stone to hammer down on a nut to crack it, and this "can repeatedly and unintentionally produce conchoidal flakes, comparable to that of Oldowan and Lomekwian [17] stone flake tools" (Eteson et al 2024 p2). However, there is other evidence of "early stone tool industries" in terms of the wide use of stone flakes (eg: shown by cut marks on animal bones), and the numbers produced (Eteson et al 2024) [18].

Tool use is only beneficial if it enables the performing of a task without wasting materials, energy and time. This is assessed with the time taken to perform a task or the number of tries to be successful by modern humans using ancient tools, as well the measurement of muscle activation.

The biomechanical requirements of early stone tool production and use has been studied in experiments of modern humans and with surface electromyography (sEMG). This measures muscle activity during certain tasks - "hammerstone pounding" (banging a stone down on an object) or knapping (cutting meat from a bone with a stone flake).

Eteson et al (2024) compared 25 adults with varying experience of such tools (none, theoretical only, or practical knapping experience) with 45 stone tools (26 replica Oldowan flakes and 19 hammerstones). A number of

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[17] Relating to a Kenyan archaeological site.

[18] Tools from the Middle Palaeolithic period have been described as the "Mousterian tradition" (40-35 000 years ago), while the "Aurignacian tradition" is 38-22 000 years ago (Upper Palaeolithic period) (Burenhelt 2004).

tries with each type of tool was allowed. The tasks were cracking a macadamia nut, and cutting through faux leather fabric. Measurements of sEMG were taken for three steps - picking up the tool, aiming at the target, and striking the target.

Less muscle effort was involved in successful flake cutting (ie: through the fabric) by those with practical experience than the other two groups. "This relationship between success rates and muscle effort was not observed for the nut-cracking task. Moreover, even though practical experience did not significantly benefit nut-cracking success [extracting nut from cracked shell], experts exhibited increased rates of self-improvement in that task" (Eteson et al 2024 p1). Grip strength did not correlate with stone tool use success.

This study showed the importance of "practical 'know-how'", and raised "the possibility that an increased hominin ability to accumulate practical skill via 'trial and error' likely played a fundamental role in the energy-efficient use of early stone tools. Furthermore,... that stone tool 'know-how' allowed experienced participants to self-learn less familiar tool-using tasks faster" (Eteson et al 2024 p14).

Experimental studies like this are constrained, Eteson et al (2024) admitted, "relying on living participants, it has to be underlined that, while many fossil hominins display fundamental similarities in their limb anatomy with modern humans, the various important differences in ergonomic requirements and morphology are still expected to affect manipulation patterns... Regardless of this bias, it is still reasonable to expect that the use of flake tools likely required similar precision grasping patterns, at least in hominin species... that display several key human-like adaptations (eg: a proportionally longer thumb...). Therefore, modern humans remain the best substitute for experimental studies such as this" (p15).

2.3.2. Non-Humans

Five wild non-human primate (NHP) species have been observed performing stone-tool use behaviours during foraging (table 2.1). "Some similarities between NHP stone-tool use and hominin tool evidence suggest similar evolutionary mechanisms behind the development of stone-tool use behaviours. Understanding the circumstances for the emergence of tool use within a population can help us better understand the cognitive and behavioural driving factors underlying technological and innovation development in our lineage" (Muhammad et al 2024 p2).

SPECIES	LATIN NAME	STUDY
West African chimpanzees	Pan troglodytes verus	Sugiyama & Koman (1979)
Bearded capuchins	Sapajus libidinosus	Fragaszy et al (2004)
Burmese long-tailed macaques	Macaca fascicularis aurea	Malaivijitnond et al (2007)
Yellow-breasted macaques	Sapajus xanthosternos	Canale et al (2009)
White-faced capuchins	Cebus capucinus imitator	Barrett et al (2018)

Table 2.1 - Five NHP species observed in the wild performing stone-tool use behaviour (Muhammad et al 2024).

Muhammad et al (2024) added a sixth species (or technically, a sub-species of the long-tailed macaque) - common long-tailed macaques (Macaca fascicularis fascicularis) - observed on a small island off Thailand. The population here has been observed over ten years, but it was not until the period of the covid-19 pandemic that the stone tools were used to open rock oysters (ie: hitting the oyster with a large stone). Normally, the island is visited by tourists who give the monkeys various foods.

The researchers made observations after the pandemic (in March 2023), and seventeen individuals were seen to perform the behaviour. "The observed stone manipulation pattern was named 'pound-hammering-like' because the monkeys did not handle the stone throughout the usual cracking processes. They dealt with the stone with two hands, raised their hands to their chests, and threw the stone into the oyster beds" (Muhammad et al 2024 p7). The behaviour appears to have developed as a response to lack of tourists during the pandemic.

2.4. APPENDIX 2A - OLDUVAI GORGE

Louis Leakey first found ancient tools at Olduvai Gorge in Tanzania (figure 2.3) [19]. "Even before setting

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[19] The scientific discovery of the site is put at 1911 (Proffitt 2018).

foot at Olduvai Gorge, Louis Leakey was certain that he would find handaxes there (Leakey 1951). Apparently, he did so on the very first day of the 1931 expedition, the first that Louis Leakey ever conducted at Olduvai. More unexpectedly, Louis Leakey also found an archaic, handaxe-free industry in the lower beds of Olduvai (Leakey et al 1931), which then he formally termed Oldowan (Leakey 1936). In one way or another, all studies on the transition from the Oldowan to the Acheulean in East Africa and elsewhere, stem from Louis Leakey's... initial reports at Olduvai, the first site where a stratigraphic sequence showed that handaxes emerged after a core-and-flake technology" (de La Torre et al 2018a p1) [20].

Any interpretations of finds must take account of site formation. These are the processes that lead to the bones, for instance, being found in the spatial pattern they are (eg: water disturbances) (de la Torre and Wehr 2018).

The raw materials used in stone tools depend upon "both raw material availability and hominin preferences for specific materials. Potential raw material sources can be primary (eg: in situ outcrops), secondary (eg: cobbles from drainages derived from primary sources), or tertiary (eg: hominin-made stone caches)" (McHenry and de la Torre 2018 p378). Raw material groups include lavas, quartzite, chert, basalt, and phonolite (McHenry and de la Torre 2018). The distance from the likely source of the materials is important. "The use of rounded blanks for most lava-derived artefacts demonstrates that hominins were accessing lava in local stream channels. Most quartzite artefacts appear to derive from angular blocks, likely acquired at the source (predominantly Naibor Soit hill [north of Olduvai]), though some do appear to be manufactured from stream-transported quartzite blanks" (McHenry and de la Torre 2018 p378).

It is accepted that there was "a certain level of technological complexity during the Oldowan, which is thought now to have included awareness of the differential quality of raw materials, rock type selectivity, (some degree of) procurement planning, adaptability (to landscape variations, raw material distance and particularities of each raw material), technical know-how and relatively efficient flaking skills" (de la Torre and Mora 2018a p236).

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[20] The continuous stratigraphic sequence of tools from core and flake to handaxe at Olduvai Gorge is key to the importance of the site (de la Torre et al 2018b).

The "Henrietta Wilfrida Korongo East East" (HWK EE) site [21] in the Olduvai Gorge is where "a remarkable assemblage of stone tools and faunal remains" have been found (Rivals et al 2018 p203). Tooth wear analysis of the animals found there help "to contextualise variations in hominin and carnivore feeding behaviour" during the two main occupations of the site (Rivals et al 2018 p203). "It is likely that HWK EE represents the behaviour of Homo habilis near the end of its existence, and is an invaluable reference point for understanding the cultural and behavioural mechanisms that may have led to the appearance of Homo erectus and its more advanced Acheulean technology at Olduvai Gorge" (Pante and de la Torre 2018 p114).

Geologist Hans Reck in 1914 named the geological layers "Beds" I to V, and this classification, though subsequently adapted by others (eg: Hay 1976), has remained (Stanistreet et al 2018). "Bed II" covers an interesting period showing the technology transition, and the disappearance of Homo habilis, but appearance of Homo erectus (Stanistreet et al 2018).

The key issue is the transition from Oldowan (core and flake tools) to Acheulean (handaxe) technology at around 1.4 MYA. Finds at other sites suggest around 1.76 MYA (de la Torre et al 2018a) [22]. Leakey (1971) proposed a typology of tool forms including "various forms of choppers (side choppers, end choppers, pointed choppers, two-edge choppers), protobifaces, polyhedrons, discoids, heavy duty scrapers, light duty scrapers, sub-spheroids, burins, hammerstones, utilised cobbles, and light duty flakes" (Proffitt 2018 p92). The differences between the tool technology and what these say about the hominins using them has been debated (eg: "Classic Oldowan" vs "Developed Oldowan/Acheulean transition") (Proffitt 2018) [23].

Pounding tools were important in the absence of fire use with food, and to increase the nutrients obtained from nuts, fruits, and tubers (Arroyo and de la Torre 2018).

One question is whether the technological transition

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[21] The other main site is called "Evelyn Fuchs-Hans Reck" (EF-HR) after the discoverers.

[22] Earlier handaxe sites in Kenya and Ethiopia, for instance (de la Torre and Mora 2018b).

[23] One distinction is "side scrapers" (Neanderthals) and "end scrapers" (humans) (Burenhelt 2004). Leakey (1971) tend towards Oldowan as Homo habilus and Acheulean as Homo erectus (de la Torre et al 2018b). However, "the appearance of Homo erectus/ergaster, sometime between 1.65 and 1.7 MYA... coincides with the emergence of the Acheulean, but this technology also temporally overlaps in part with Homo habilis... and Paranthropus boisei (Prassack et al 2018 p32).

was associated with environmental (palaeo-ecological; table 2.2) changes. Uno et al's (2018) analysis of tooth wear of animals suggested no major vegetation or hydrological changes. "Local climatic and vegetation change does not seem to have played a significant role in the advent of Acheulean technology at Olduvai" (Uno et al 2018 p89). The fossil bird data also helps in establishing the environment (eg: wetlands and crane and ibis) (Prassack et al 2018).

Generalised meat-eating hominins increased competition among carnivores, and the vulnerability among herbivores. The large mammal bones in Middle Bed II (1.7 - 1.4 MYA) suggested a world "much richer in species and includes a much larger number of large-bodied species (>300 kg) than the modern Serengeti. This reflects the severity of Pleistocene extinctions on African large mammals, with the loss of large species fitting a pattern typical of defaunation or 'downsizing' by human disturbance. However, trophic network (food web) analyses show that the Middle Bed II community was robust, and comparisons with the Serengeti community indicate that the fundamental structure of food webs remained intact despite Pleistocene extinctions" (Bibi et al 2018 48).

- Palaeo-ecology studies "offer captivating glimpses into long-lost worlds and uncover drivers underlying long-term biodiversity patterns..." (Pittman and Wang 2023 p1). The methods include dental micro-wear analysis to show the food eaten and available at the time, jaw "mechanics", and body mass data extrapolated from fossils to show the quantity of food available.

- "Closer to the present, ancient DNA preserved in all kinds of sediments, namely the ancient environmental DNA (eDNA) or sedimentary ancient DNA (sedaDNA), offer the chance to sample and sequence degraded nucleic acids of some extinct species" (Pittman and Wang 2023 p1). But avoiding contamination with modern DNA is a challenge (Pittman and Wang 2023)

Table 2.2 - Palaeo-ecology.

The "Olduvai Geochronology Archaeology Project" (OGAP) was set up in 2008. de la Torre et al (2018a) introduced a special issue of the "Journal of Human Evolution" that reported the work of this project between 2008 and 2016. For example, de la Torre and Mora (2018a) reported on the excavation of over 18 000 pieces of stone tools.

The OGAP has pushed back the age of the site. For example, Leakey (1971) estimated 0.7 to 1.0 MYA (de la Torre et al 2018c) [24].

(Source: emmyanne29; public domain)

Figure 2.3 - Site of Olduvai Gorge.

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3. DEBATING HOMO NALEDI

At the "Rising Star Cave" system in South Africa, a new species of hominin was discovered in recent years - Homo naledi (eg: Berger et al 2015). This species was small-brained compared to Homo sapiens (approximately 450-600 vs 1400 cm^3 skull capacity [25]) (Martinon-Torres et al 2024) [26] [27]. What "human" behaviours did this now-extinct hominin perform?

Two behaviours in particular have become the focus of debate among researchers - deliberate disposal of the dead, and the production of rock art. Evidence is ambiguous and/or indirect, which leads to different interpretations. The burying of the dead revolves around the position of bones found, for example, and the marks on the cave walls as "engravings". Table 3.1 summarises some of the key publications in the debate.

FOR	AGAINST
Dirks et al (2015) Berger et al (2023a; 2023b)	Val (2016) Martinon-Torres et al(2024)

Table 3.1 - Examples of publications for and against Homo naledi burying the dead, and producing rock art.

Martinon-Torres et al's (2024) position is that "the evidence presented so far is not compelling enough to support the deliberate burial of the dead by H.naledi nor that they made the purported engravings. Substantial additional documentation and scientific analyses are needed before we can rule out that natural agents and post-depositional processes are responsible for the accumulation of bodies/body parts and to prove the intentional excavation and filling of pits by H.naledi. Moreover, detailed analyses are needed to demonstrate that the so-called 'engravings' are indeed human-made marks and that, like the purported evidence of fire use, they can be securely linked to H.naledi" (pp1-2).

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[25] Homo naledi 560 cm^3 (Marshall 2022).

[26] Homo naledi was about 144 cm high on average and weighed around 40 kg. "It had a strange mix of primitive and modern features, with ape-like shoulders and a brain little bigger than a chimpanzee's" (George 2022 p8).

[27] "Big brains aren't necessarily linked to intelligence. Human populations in colder environments have larger brains, but that is because of 'thermal packaging' that keeps the neurons warmer and thus able to function" (Lynne Schepartz of University of Witwatersrand in Marshall 2022).

"Burying the dead" would mean digging a pit, putting the corpse inside the pit, and covering it with sediments. The debate revolves around the anatomical evidence (eg: the scatter pattern of the bones), and the landscape (ie: a pit shape). Related to this is the need for "tools" to undertake the work, and a light source (ie: fire). Both the presence of stone artefacts ("tools"), and the evidence of fire are disputed [28].

The "rock art" debate revolves around incised markings on the walls which could be geometric shapes. "The claim is made that the surfaces with the engravings appear to have been prepared and smoothed, using percussive blows by a hard object, the application of sediment before and after the etchings and engravings were made to create visual contrast, and residues that created a sheen, possibly representing repeated handling or rubbing of the rock", explained Martinon-Torres et al (2024); "though no evidence (grooves, tool marks, incisions etc) is provided to support this hypothesis" (p4), they pointed out. An alternative explanation is clawing by animals (Martinon-Torres et al 2024).

Martinon-Torres et al (2024) criticised the "pro" side for the use of social media to create the impression of facts, beyond the scientific evidence, particularly as many of the articles were pre-prints (eg: Berger et al 2023a; b). These are publications before full peer review and acceptance in an academic journal. Martinon-Torres et al (2024) ended: "We should not mistake open science with open opinion, where social media, outreach events and blogs are considered scientifically valuable and more appropriate vehicles for knowledge growth. Would it be acceptable to prematurely publish and spread untested results if these could have an effect on health and well-being? We advocate that the standard for scientific rigour should be the same in all fields..." (p7).

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[28] The evidence for includes lumps of charcoal, burned bones, hearths, and baked clay, as well as blackened areas and soot particles on the cave roof, argued Lee Berger (George 2022).

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4. BIPEDALISM

4.1. OVERVIEW

The date when hominids first walked on two legs is generally thought to be six million years ago (MYA) (based on fossils of Orrorin tugenensis) (Wilson 2022). DeSilva (2022) described how between seven and 5 MYA human ancestors "started doing something no mammal had done before: walking on two legs" (p66). But the movement from four to two legs was not the popular "March of Progress" (a linear progression over time), rather "various hominin species living in different environments throughout Africa, sometimes contemporaneously, evolved different ways to walk on two legs" (DeSilva 2022 p66).

DeSilva et al (2019) analysed foot fossils from various sites and identified "five different foot morphs, possibly indicating five distinct ways of walking upright" (DeSilva 2022 p71) (table 4.1).

"Although all five of these hominin feet exhibit both ape-like and human-like features, these traits occur in a completely different combination in each foot and do not follow the predicted pattern of becoming less ape-like and more human-like over time" (DeSilva 2022 p72).

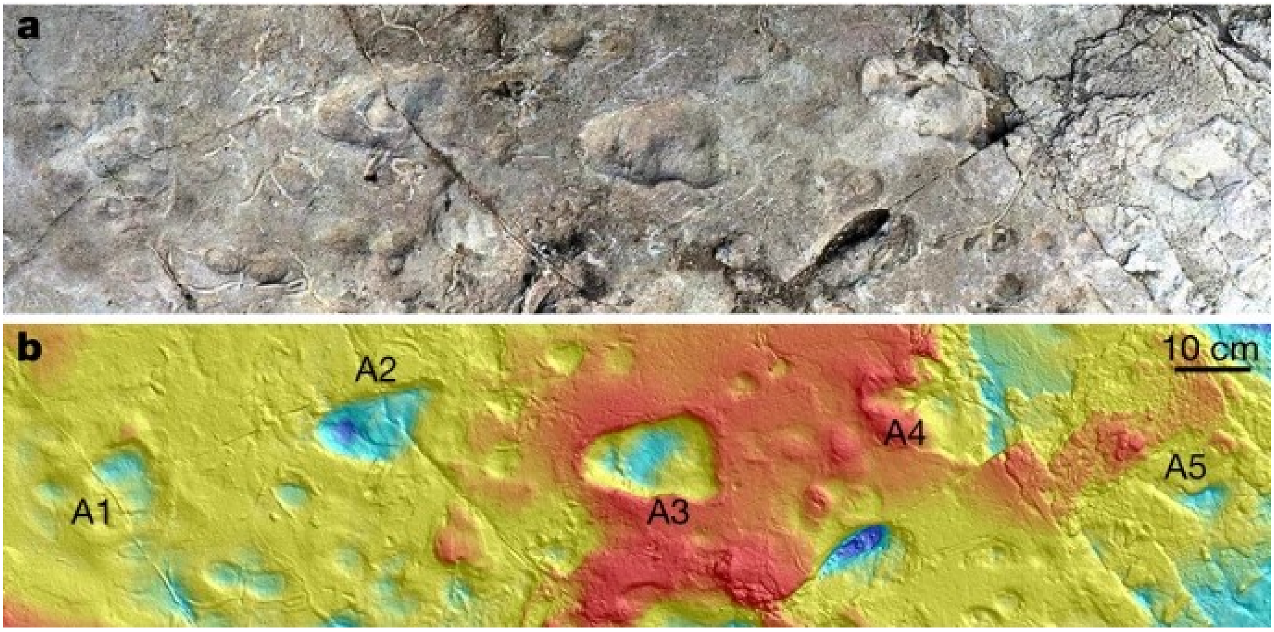
DATE	LOCATION OF FIND	SPECIES	COMMENT
4.4 MYA	Aramis, Ethiopia	Ardipithecus ramidus	"Transition foot" from chimpanzee, can grasp and walk
4.4 MYA	Gona, Ethiopia	Ardipithecus?	
3.67 MYA	Sterkfontein, South Africa	??	"Little Foot"
3.4 MYA	Burtele in Woranso-Mille, Ethiopia	??	"strikingly primitive foot" (DeSilva 2022 p72)
3.2 MYA	Hader, Ethiopia	Australopithecus afarensis	big heel, stiff mid-foot

Table 4.1 - Five different foot morphs and fossils (DeSilva 2022).

Footprint evidence is another source of information (appendix 4A). At Laetoli, Tanzania, for instance, two sets of footprints were found in the 1970s, named as "Site A" and "Site G" tracks [29]. The latter were believed to have been made by Australopithecus afarensis (19 hominin footprints made by 2, 3 or 4 individuals) (DeSilva 2022).

Site A tracks (figure 4.1) were attributed to a bipedally walking bear by Russ Tuttle (eg: 1984). However, this idea has been rejected by an experiment with American black bears walking through mud on their hind legs (McNutt et al 2021). A re-examination of the tracks, reported by McNutt et al (2021), suggested an undetermined hominin made the footprints.

Tuttle (2008) proposed criteria for the identification of tracks as hominin, including digit lengths, shape of the hallux (big toe), and the presence of a prominent medial longitudinal arch (Helm et al 2023).



(a = generated using photogrammetry; b = contour map generated from a 3D surface scan)

(Source: McNutt et al 2021; Creative Commons Attribution 4.0 Internal Licence)

Figure 4.1 - Five hominin footprints in Site A tracks at Laetoli, Tanzania.

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[29] "Site S" tracks were discovered in 2015 (DeSilva 2022).

Daver et al (2022) proposed the origins of bipedalism as 7 million years ago based on thigh and forearm bones found in the Djurab desert in Chad, and identified as a hominin species Sahelanthropus tchadensis. These researchers pointed out that the "morphology of the femur is most parsimonious with habitual bipedality, and the ulnae preserve evidence of substantial arboreal behaviour. Taken together, these findings suggest that hominins were already bipeds at around 7 MYA but also suggest that arboreal clambering was probably a significant part of their locomotor repertoire" (Daver et al 2022 p94). Key features of the femur included a rough surface at the top where the buttock muscles attached (Wilson 2022).

But it is unknown if the bones in this study came from the same or several individuals (Wilson 2022). While Roberto Macchiarelli pointed out that many primates stand occasionally on two legs, but this is not the same as bipedalism (Wilson 2022).

4.2. TAILS

Hominoids lost their tails around 25 million years ago, probably when hominins and apes diverged from ancient Old World Monkeys (Xia et al 2024). Xia et al (2024) isolated the genes involved, and suggested that a sudden loss of tails rather than gradual shrinking occurred (Le Page 2021). These researchers concentrated on 31 human genes initially. The TBXT gene was the eventual focus. Genetically engineered mice with different versions of the gene were created, and they showed different tail development. A certain version of the gene led to neural tube defects, which affects 1 in 1000 human babies today. "Thus, tail-loss evolution may have been associated with an adaptive cost of the potential for neural tube defects, which continue to affect human health today" (Xia et al 2024 p1042).

The sudden loss of tails fits with the fossil record which shows no evidence of a slow reduction in tails, but "for now we have too few fossils to rule it out" (Carol Ward in Le Page 2021).

Why did evolution select for no tails in ape ancestors? One explanation relates to its disadvantage when walking upright, but fossils show that tailless apes walked on all fours (Le Page 2021).

4.3. FOOTWEAR

"The development of clothing was of great importance in human evolution, and footwear can be regarded as a form of complex clothing... When and where humans began to fashion footwear, for occasional or regular use, is an unresolved palaeoanthropological question. Unfortunately, it can be assumed that sparse or minimal evidence is likely to remain of the perishable organic substances that would have been used" (Helm et al 2023 p79). The oldest reported surviving footwear, which was made from woven sagebrush bark, was dated at 10 500 - 9200 years ago (Helm et al 2023). Earlier dating may be possible using footprints or tracks.

Ancient footprints (ie: naked feet) have been found as well as footprints that show ancient footwear. It is possible that shod feet occurred over 100 000 years ago, and not only early humans wore footwear. Preserved footprints of shod feet have no details of toes, and show extremely clean edges, for instance (Marshall 2023).

Lockley et al (2008) listed 63 sites of hominin tracks, and Bennett and Morse (2014) forty-four sites. Others have subsequently been added (Helm et al 2023). Helm et al (2023) reported possible shod-hominin tracks at sites in South Africa.

Other sources of evidence include analysis of ancient foot bones to show changes due to wearing footwear, or examination of tools to see if it was possible to make footwear (and clothing) (Marshall 2023).

4.4. APPENDIX 4A - LEARNING MORE FROM FOOTPRINTS

"Archaeologists had barely bothered to look for fossil footprints for decades, assuming them to be vanishingly rare... [but] analysing details like the size and spacing of the footprints allows us to recreate snippets of people's lives" [eg: a hunt] (The leader 2022 p5). Footprints can provide "a new window" on the existence of ancient humans - from nervous shuffles to determined sprints" (Barras 2022 p41). Hatala et al (2020) agreed: "Footprints are often ephemeral but when preserved in the geological record, these ichnofossils can provide unique snapshots of the lives of ancient organisms" (p1).

For example, sloth and human tracks from White Sands National Monument in New Mexico, USA, showed human hunting interactions. "Behavioural inferences from these trackways indicate prey selection and suggest that humans were harassing, stalking, and/or hunting the now-extinct giant ground sloth in the terminal Pleistocene" (Bustos et al 2018 p1). An estimated date of the tracks was 15 500 - 10 000 years ago.

"The site consists of more than a hundred sloth and human tracks. Sloth tracks are readily distinguished from human tracks based on their elongated kidney-shaped tracks and claw marks. Sloth tracks vary from 30 to 50 mm deep, 300 to 560 mm long, and 100 to 350 mm wide. The sloth tracks show evidence of eversion, consistent with biomechanics of the ground sloth" (Bustos et al 2018 p1).

However, The leader (2022) was cautious: "We can reconstruct the cut and thrust of an animal hunt, but we must be careful not to assume we know how the hunters actually felt" (p5).

Also the size and shape of the foot can give information about the height and sex of the individual (Barras 2022). For example, Hatala et al (2020) analysed over 400 human footprints from Engare Sero, Tanzania [30], that were made in the Late Pleistocene period. The following information was ascertained from the tracks: "Speed estimates show that the trackways reflect both walking and running behaviours. Estimates of group composition suggest that these footprints were made by a mixed-sex and mixed-age group, but one that consisted of mostly adult females. One group of similarly-oriented trackways was attributed to 14 adult females who walked together at the same pace, with only two adult males and one juvenile accompanying them" (Hatala et al 2020 p1).

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5. BEHAVIOURS

5.1. PROTO-WRITING

"Around 37,000 years ago humans transitioned from marking abstract images such as handprints, dots and rectangles on cave walls to drawing, painting and engraving figurative art" (Bacon et al 2023 p371). For example, in caves at Lascaux, around 21 500 years ago, "body shapes and pelage details were used to convey information about the sequence of rutting of several prey species on the cave's walls, in what was essentially an ethological calendar..." (Bacon et al 2023 p371). At least 400 European caves have non-figurative signs, discovered first in the late 19th century (Bacon et al 2023).

The meaning of these non-figurative signs from the Upper Palaeolithic period has "eluded researchers" (Bacon et al 2023 p371). Using a database of such images, Bacon et al (2023) argued that the three most frequently occurring signs - line, dot, and Y - "functioned as units of communication... [Specifically] "when found in close association with images of animals the line <|> and dot <•> constitute numbers denoting months, and form constituent parts of a local phenological/meteorological calendar beginning in spring and recording time from this point in lunar months" (Bacon et al 2023 p371). While the Y sign means "to give birth" as in a tally of months until that point (Bacon et al 2023).

Is this evidence of writing? Certainly not, if writing is assumed to be "written language, ie: not only acts as a notational system but one which has a connection to the phonetic form of the language spoken by the writer" (Bacon et al 2023 p385). The origins of writing is traditionally part at 330 BCE with pictograms (Bacon et al 2023). But Bacon et al (2023) viewed the signs as "proto-cuneiform". Cuneiform (script) account keeping began with numerical signs (Bacon et al 2023). Put simply, the signs are small steps on the road to a full writing system. Though Bacon et al (2023) were aware that not everyone would be convinced by their interpretation of the three signs and the idea of a phenological/meteorological calender.

Garcia-Bustos et al (2023) are an example of the critics. These researchers focused on Bacon et al's (2023) interpretation of the signs as (i) misinterpretations, (ii) not existing, and (iii) signs not related to animal figures.

Gargas cave in Southern France contains 231 hand stencils, 124 with missing digits, suggesting a sign language. Ideas include a way of counting or some kind of hunting code (George 2023). "While these stencils might look like mere doodles to the untrained eye, they are often found deep in caves in hard-to-reach places, suggesting that they had some special significance" (George 2023 p39).

But are the hand stencils with missing digits due to hand mutilation or just hidden fingers? This is a debated question. Another issue is who created the stencils - Homo sapiens or Neanderthals (George 2023)?

5.2. ANCIENT SURGERY

Bones of a child found in Borneo from 31 000 years ago show the amputation of a foot, and survival afterwards. What is important is evidence of skills to stop someone bleeding to death or dying from infection, which were the major hazards of surgery before modern medicine (Wilson 2022).

The skeleton was discovered in 2020 in a cave called "Liang Tebo" in East Kalimantan (Indonesian Borneo). The skeleton ("Tebo 1" - sex undetermined) had died at around 20 years old, and the amputation had been up to ten years earlier. The relatively clean cut suggested a blade rather than a crushing injury or predator bite (Maloney et al 2022).

Survival after such an amputation would have been difficult without social support, so this is an insight into Stone Age/Late Pleistocene life. Maloney et al (2022) commented: "we infer that the Late Pleistocene 'surgeon(s)' who amputated this individual's lower left leg must have possessed detailed knowledge of limb anatomy and muscular and vascular systems to prevent fatal blood loss and infection. They must also have understood the necessity to remove the limb for survival. Finally, during surgery, the surrounding tissue including veins, vessels and nerves, were exposed and negotiated in such a way that allowed this individual to not only survive but also continue living with altered mobility. Intensive post-operative nursing and care would have been vital, such as temperature regulation, regular feeding, bathing, and movement to prevent bed sores while the individual was immobile. The wound would have been regularly cleaned, dressed, and disinfected, perhaps using locally available botanical resources with medicinal properties to prevent infection and provide anaesthetics for pain relief. Although it is not possible to determine whether infection occurred after the surgery, this individual evidently did not suffer from an infection severe enough to leave permanent skeletal markers and/or cause death" (p551).

Maloney et al (2022) outlined the situation prior to their findings: "The prevailing view regarding the evolution of medicine is that the emergence of settled agricultural societies around 10,000 years ago (the Neolithic Revolution) gave rise to a host of health problems that had previously been unknown among non-sedentary foraging populations, stimulating the first major innovations in pre-historic medical practices1. Such changes included the development of more advanced surgical procedures, with the oldest known indication of an 'operation' formerly thought to have consisted of the skeletal remains of a European Neolithic farmer (found in Buthiers-Boulancourt, France) whose left forearm had been surgically removed and then partially healed. Dating to around 7,000 years ago, this accepted case of amputation would have required comprehensive knowledge of human anatomy and considerable technical skill, and has thus been viewed as the earliest evidence of a complex medical act" (p547).

5.3. ATTENTION DEFICIT HYPERACTIVITY DISORDER

What is now classified as "Attention Deficit Hyperactivity Disorder" (ADHD) may have evolved in early humans because the characteristics were advantageous. For example, impulsivity may encourage individuals to move which is useful as resources become depleted (Ly 2024).

Barack et al (2024) studied this idea with an online foraging game. Over five hundred US players had to collect berries from bushes, as many as possible in eight minutes with the choice of staying at one bush or moving to another. There was a time penalty (ie: "travel time") of choosing to move to a new bush. When the travel time was varied, participants stayed longer at one bush when the travel time was longer.

Participants who scored high on ADHD symptoms (as measured by the ADHD Self-Report Scale; ASRS; Ustun et al 2017) collected more berries, mainly because they spent less time at one bush. "Humans and other apes are quite sophisticated foragers, but like almost every other animal, we tend to stay too long in a patch. So moving early is beneficial because it cuts down on that overharvesting, which might be where the impulsivity characteristics of ADHD come in useful" (David Barack quoted in Ly 2024). But Annie Swanepoel questioned how realistic the game was (Ly 2024).

5.4. SKULL INJURIES

Skull finds are often damaged in some way. The question is whether the damage was before death or after. Ante-mortem injuries give clues to the life of individuals of the time.

In some cases, the same skull will be interpreted differently - ie: both as ante- and post-mortem by different researchers. One such case is known as "Cro-Magnon 2" from a rock shelter on the banks of the Vezere river in southwest France. Human remains were first found here in 1868, and subsequent dating suggested around 33 000 years ago (mid-Upper Paleolithic) (Knusel et al 2023).

The damage to the skull of "Cro-Magnon 2" was described in the late 19th century as an ante-mortem violent blow that may have been fatal, while roughly a century later, a post-mortem pickaxe blow during excavation was blamed (Knusel et al 2023).

Modern scanning technology has been used in the last thirty years. Knusel et al (2023) considered this evidence and favoured a before-death explanation. They stated in technical language: "The right frontal cranial defect of Cro-Magnon 2 indicates a low velocity but forceful impact producing a blunt-force penetrating neuro-cranial injury when the bone retained its elastic (ie: in vivo) properties. Because there is evidence of intra-cranial reactive bone, the appearance of this lesion is also indicative of an ante-mortem injury. Intra-cranial porous bone formation indicates intra-cranial haemorrhaging and the location of a haematoma, which is consistent with initial survival of the injury and a likely indication of the manner of death after a period of time from secondary effects, such as shock, blood loss, and infection, in the pre-antibiotic era" (Knusel et al 2023 p11).

The conclusion is that the injury was "more likely the result of interpersonal aggression rather than an accident" (Knusel et al 2023 p10). But there were not other skulls with similar injuries at the discovery site which suggested that "this does not appear to have been received during a mass killing, but as an isolated event" (Knusel et al 2023 p11).

Research Topics

1. Modern scanning techniques used.

2. The history of the finds at Vezere Valley site.

3. Similar injuries found at other sites around the world from the same period.

4. The state of humans in mid-Upper Paleolithic era (ie: in terms of evolution of anatomically modern humans).

5.5. BURIALS

"Mortuary (or funerary) practices is a general term describing deliberate activities with the body after death. For example, intentional burial has been dated to 100 000 years ago for AMHs (Marsh and Bello 2023).

Differences in behaviour in different periods have been inferred from finds in Europe (Marsh and Bello 2023):

Aurignacian (46 - 26 000 years ago) - "The Aurignacian technocomplex includes fine blades and bladelets..., and an organic tool industry characterised by worked wood, bone, and antler... Complex artistic behaviour are attested to with the production of pendants, bracelets, ivory beads, cave wall paintings..., the engraving of three-dimensional figurines..., and the first example of musical instruments... The funerary behaviour during the Aurignacian in Europe is largely undetermined" (Marsh and Bello 2023 p2).

Gravettian (33 - 21 000 years ago) - This period/culture is "largely distinguished from the Aurignacian with the innovative developments of new tool technologies that include blunted-back knives, tanged arrowheads, and boomerangs... Other innovations include the use of woven materials and oil lamps made of stone.., and artistic manifestations are expressed in cave paintings and the carving of small, portable Venus figurines made from clay or ivory, and jewellery... The complex behaviour of the Gravettian found a major expression in elaborated funerary practices, with single and multiple burials often accompanied by ornamental beads and the abundant use of ochre" (Marsh and Bello 2023 p2).

Epigravettian (24 - 12 000 years ago) - "Continuing the Gravettian tradition, funerary behaviour is a major facet of the Epigravettian, with primary burials identified as its main expression... Gravettian burials were often associated with grave goods of bivalve shells and engraved faunal remains, alongside the presence of ochre and, in some cases, the deliberate modification of the burial environment that include engraving of cave walls and the positioning of rocks over or around the bodies" (Marsh and Bello 2023 p2).

Magdalenian (23.5 - 13.5 000 years ago) - Marsh and Bello's (2023) analysis of 59 sites found that thirteen had cannibalised human remains. "Given the similarities of the anthropic modifications observed on the cutmarked and cannibalised human remains across sites, the high frequency and geographic distribution of this practice, and the association, in some of the sites, of cannibalism with the ritualistic manipulation of human remains, it is proposed that cannibalism during the Magdalenian was practised as a form of funerary behaviour rather than for necessity or as gastronomic cannibalism. Funerary cannibalism appears in greater abundance during the Middle Magdalenian whilst primary burials are more common during the Upper and terminal Magdalenian" (Marsh and Bello 2023 p1).

5.5.1. Human-Animal Co-Burials

Whole animals or animal parts have been found in human graves at various archaeological sites. One interpretation of their presence is as ritual offerings of food, but this explanation is "less satisfying" in the case of horses and dogs (Laffranchi et al 2024).

Dogs have been found in human burials from around 12 000 years ago, for instance, and horses from 2000 BCE (Laffranchi et al 2024).

Laffranchi et al (2024) concentrated on joint human-animal burials at "Seminario Vescovile" (Verona, Italy) 3rd to 1st century BCE (Late Iron Age). The presence of horses can be taken as symbols of the high social status of the human, linked to the "Celtic" goddess Epona, or related to the practice of horse riding by the individual when alive. Similar suggestions may account for the dog co-burials.

The researchers found it difficult to give "simple, straightforward explanations" because of the variability in the co-burials. Three trends were noted. First, "the absence of dietary, genetic, demographic, and funerary similarities among burials containing animals as well as a lack of association between these mortuary practices and the straightforward notion of social status based on age, sex, and/or close biological kinship..." (Laffranchi et al 2024 p21). Second, the importance of varied cultural traditions of the time and surrounding areas, and finally, the role of ritual and economic factors in dog co-burials.

5.6. CULTURAL BURNING

The cultural practice of burning vegetation reduced the risk of wildfire spread in the past. "For thousands of years, humans have harnessed fire for various purposes, including fire management itself. The term 'cultural burning' refers to the practice of systematically applying frequent low-intensity fire to the land, as used by many Indigenous groups globally. Cultural burning relies on an intimate relationship with the land, creating fine-scale spatial heterogeneity that promotes high biodiversity, improves hunting opportunities, interrupts fuel load connectivity, and serves various cultural and spiritual purposes" (Mariani et al 2024 p567).

Mariani et al (2024) used the example of southeast Australia, and reconstructed shrub cover from pollen assemblages in sedimentary deposits. The researchers stated: "Comparing 2833 records for vegetation cover, past climate, biomass burning, and human population size across different phases of human occupation, we demonstrated that Indigenous population expansion and cultural fire use resulted in a 50% reduction in shrub cover, from approximately 30% from the early to mid-Holocene (12 to 6 thousand years ago) to 15% during the late to mid-Holocene (6 to 1 thousand years ago). Since the start of British colonisation to the present, shrub cover has increased to the highest ever recorded (mean of 35% land cover), increasing the risk of high-intensity fires" (Mariani et al 2024 p567).

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6. MOVEMENTS AND POPULATION CHANGES

"Archaeological evidence attests multiple early dispersals of Homo sapiens out of Africa, but genetic evidence points to the primacy of a single dispersal 70-40 [000 years ago]" (Shipton et al 2024 p1) [31].

Arrivals occurred in different parts of the world at different times (table 6.1).

Marine Isotope Stage (MIS) [32]	Date (000 years ago)	Arrival
8	300 - 243	Eurasia
5a	82 - 71	South-East Asia
4	71 - 57	Sumatra
3	57 - 29	Sahul (combined continent of Australia and New Guinea)

Table 6.1 - Some arrival dates of Homo sapiens around the world (Shipton et al 2024).

Dating the spread of Homo sapiens to specific areas of Eurasia is made by the tools found, for example. This includes into southeastern Europe 47 000 years ago (based on finds of "Initial Upper Palaeolithic (IUP) technology"), western Siberia by 45 000 years ago, and northeastern Asia by 40 000 years ago (Yang et al 2024).

Europe

Slimak et al (2022) reported hominin fossils (nine dental specimens from at least seven individuals) at Grotte Mandrin in France which suggested the presence of AMH here between 56 800 and 51 700 years ago. This is earlier than the traditional view of 45 to 43 000 years ago (eg: Benazzi et al 2011). The earlier that humans arrived in Europe, the more likely meetings with Neanderthals and inter-breeding, and ultimately replacement.

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[31] The genus Homo is not the only primate to have moved out of Africa, a number of other catarrhine primates also expanded or shifted their ranges into Eurasia, includes macaque ancestors (Roos et al 2019).

[32] This is a way of dating based on deep sea cores. The current period is MIS1. General information about MIS dating at https://en.wikipedia.org/wiki/Marine_isotope_stages.

The researchers explained: The results from Grotte Mandrin presented here show that instead of recording a single event of population replacement as often argued elsewhere in Europe, a much more complex process of modern human appearance and Neanderthal disappearance appears to have occurred in Western Europe. We document at least four alternating phases of replacement, with Neanderthals occupying the area around Mandrin from MIS [Marine Isotope Stage] 5 up to ~54 [000 years] BP [Before Present]..., a modern human incursion at around 54 [000 years] BP (56.8 to 51.7 [000 years] BP...) followed by Neanderthal reoccupations..., and a second modern human phase from ~44.1 to 41.5 [000 years] BP... onward" (Slimak et al 2024 p10).

China

Generally it was believed that early humans reached China 40 000 years ago (Marshall 2024), but research by Yang et al (2024) pushed that date back 5000 years further. This was based on stone tools at a site (Shiyu) in northern China.

There are claims of humans in China 260 000 years ago, but this view has been criticised (Marshall 2024).

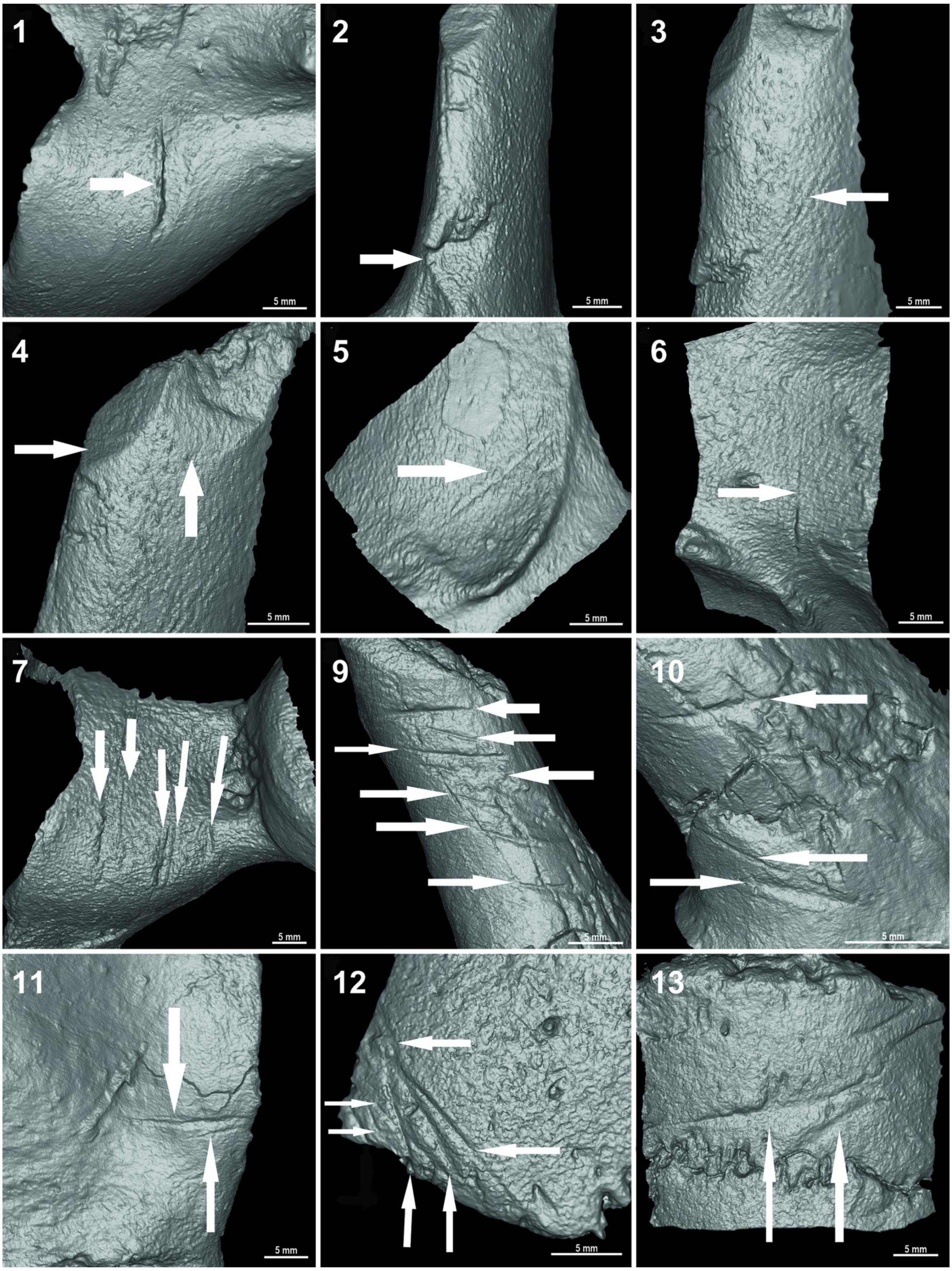
Pacific

Gaffney et al (2024) provided evidence that humans arrived in the Pacific, specifically the Raja Ampat Islands, north-west of New Guinea, 55 - 50 000 years ago. Evidence of plant processing was found.

South America

Del Papa et al (2024) used cut marks suggesting butchering on the bones of extinct mammals to date humans in South America (at the last glacial maximum; 21 090 - 20 811 years ago) (figure 6.1).

Cut marks in bones represent direct interactions between the cutter and the victim, but the "challenge for such evidence is to demonstrate that it was human made, discarding post-mortem and peri-mortem modifications from non-human agents" (Del Papa et al 2024 p2).



(Source: Del Papa et al 2024 figure 10)

Figure 6.1 - Three dimensional reconstruction of cut marks on bones of extinct animal (Neosclerocalyptus).

Extinction Threat

Hominins experienced a population bottleneck between around 930 000 and 813 000 years ago, and may have fallen to 1300 "breeding individuals", according to Hu et al (2023). These researchers attributed the bottleneck to climate change, including severe drought in Africa and Eurasia. The bottleneck coincides with a gap in fossil records, and a time when a new ancestor of Homo sapiens evolved. Hu et al (2023) favoured Homo heidelbergensis.

At this time a number of different species existed - Homo heidelbergensis, Homo rhodesiensis, Homo antecessor, and Homo bodoensis - and "it is unclear which of these is our ancestor. There is also debate about whether they were indeed separate species" (Le Page 2023 p8).

There have been critics of Hu et al (2023), which is based primarily on statistical analysis. These researchers used a method called "FitCoal", which projects "current human genetic variation backward in time, to estimate the size of populations at specific points in the past" (Ashton and Stringer 2023 p947).

Ashton and Stringer (2023) challenged the gap in the fossil records in the period referred to by Hu et al (2023), as well as whether Homo heidelbergensis evolved at this time. The effects of the bottleneck were "limited geographically and chronologically" (p948), they argued.

There has been a population bottleneck identified when humans started to move out of Africa around 60 000 years ago (Le Page 2023).

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7. SINCE 12 000 YEARS AGO

7.1. OVERVIEW

Larsen (2023) noted that "the remarkably dynamic record of biological change, adaptation, stressors, and circumstances that have altered the behaviour and well-being of Homo sapiens over the course of the most recent 12,000 years of human evolution, one of the most dynamic periods of human adaptation and evolution and the remarkable challenges to health and well-being" (p1). The most important change at the beginning of this period was the "agricultural transition", initially in the Levant region of the Eastern Mediterranean, but plant and animal domestication was global (Larsen 2023).

"Many authorities view the transition from foraging to farming as a long process taking upward of several thousand years in some settings. However, in terms of the six or so million years of hominin evolution, the transition from foraging to farming is an eye-blink in time. By every measure, the agricultural transition and the accompanying onset of the Anthropocene have played central roles in shaping health and its challenges, increasing conflict and competition for territory, access to key foods and other resources, rising levels of infectious disease, behavioural adaptations involving reduced physical activity and mobility, migration, permanent or near-permanent settlement, and the threat of or engagement in inter- and intra-community violence and warfare" (Larsen 2023 pp1-2).

7.2. TRANSITION PROCESS

The spread of domestication and farming (and languages) occurred via human movements and meetings. But did farmers migrate with their way of life (ie: demic diffusion) or did hunter-gatherer groups adopt farming from neighbouring farmers (ie: cultural diffusion) (Stoneking et al 2023)?

Genetic investigations can help in answering this question by showing the movements of groups based on ancestry (while the family tree of languages is also used). But "such genetic investigations are not without complications. As discussed in more detail by Diamond and Bellwood [2003], these include clinal admixture between expanding farmers and hunter-gatherers, resulting in decreasing genetic contributions by farmers toward the periphery of expansions; some hunter-gatherer groups adopting farming by cultural diffusion; farmers reverting to hunting and gathering (if, for example, they enter areas that are unsuitable for the domesticates they are bringing); language shift by resident groups with little or no incorporation of genes from the expanding population; replacement of the original language spoken by farmers in their homeland after the expansion (leading to discrepancies between genes and languages); and expansions of hunter-gatherers. An additional complicating factor is colonialism and the associated genetic, demographic, and territorial impact on indigenous groups" (Stoneking et al 2023 p1).

Stoneking et al's (2023) genetic analysis found a highly complex picture depending on the part of the world studied. For example, there was "a plethora of ancient DNA data from Europe, and these firmly support an appearance of Anatolian-related ancestry in Europe that coincides with the spread of farming technology, confirming that farming spread primarily via demic rather than cultural diffusion" (Stoneking et al 2023 p3). While in West Africa, archaeological and genetic evidence suggested "not a single demic expansion but rather characterised by multiple expansion phases, with a population collapse inferred between 1.4–1.6 kya [thousand years ago] in the Congo rainforest" (Stoneling et al 2023 p2). In the Amazon area of South America, the spread of languages could suggest cultural diffusion.

Stoneking et al (2023) ended: "Although strong genetic signals of expansion can be identified that link the spread of farming and some language families (eg: Bantu, Austronesian), even here there is significant heterogeneity in the genetic outcome of the interactions between expanding farmers and indigenous hunter-gatherers (eg: complete or near-complete replacement of the pre-farming groups in Malawi and Mozambique by expanding Bantu groups vs extensive admixture between Bantu and Khoisan-speaking groups in southern Africa). In other areas of the world, the links between expansions and agriculture are more tenuous (eg: the Americas), possibly because of extensive post-expansion admixture or other complications" (p8).

7.3. EARLY VILLAGES

The first villages, and sedentary and semi-sedentary communities were small (defined as tens to hundreds of individuals, but "mega-sites" (with thousands of inhabitants) also appeared in time (Pearson et al 2023).

The genetic relatedness of the early settlers was important. There was the risk of close inbreeding if only kin (endogamous relationships) lived together in small settlements, thus the need for "new blood" (exogamous relationships). Pearson et al (2023) analysed tooth enamel from ninety-nine individuals buried at three sites in Turkiye 7000 years ago to understand kin relationships. Strontium and oxygen isotopes in the enamel gives information about whether individuals were locals.

Ninety-two of the individuals appeared to have spent their childhood locally. The researchers argued that cultural and biological mechanisms thus existed to avoid close inbreeding as most individuals were locals in the early villages (and so possibly genetically related in some way). Mega-sites would have been more mixed (locals and non-locals).

7.4. FARMING AND BODY SIZE

The move from the hunter-gatherer lifestyle to farming has been generally viewed as a positive thing, though some have questioned this (eg: Diamond 2010) (Marshall 2023) [33].

One piece evidence is height. Well nourished individuals grow taller in terms of future generations, but the first farmers were shorter than hunter-gatherers (Marshall 2023). The "anti-farming" explanation is that cultivating crops was a negative for humans.

Stock et al's (2023) analysis of over 35000 skeletons from 366 archaeological sites found a gradual decline in average body size from 34 300 years ago to 6000 years ago, and then an increase. So, humans were

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[33] The transition to farming also included the "secondary products revolution" (Greenfield 2010) - "the use of domestic animals for byproducts such as milk, wool, or as a source of labour for agricultural subsistence" (Stock et al 2023 p2).

getting smaller before they took up farming.

One theory for this was the overhunting of large prey which forced humans to eat small prey and manage plants (eg: Ben-Dor and Barkai 2021).

But simply comparing foragers/hunter-gatherers and farmers is problematic for Stock et al (2023) as "foragers are known to have extensively managed wild plants prior to full agriculture, and the process of plant domestication and the associated shift to crop farming is associated with hundreds or thousands of years of cultural and domesticate co-evolution, during which many farming populations practised mixed subsistence strategies and continued hunting and foraging" (p1).

There was also great variety in the transition to farming around the world linked to climate. Southwest Asia saw the earliest transition, which spread through migration into Europe. But there were differences depending on the part of Europe (Stock et al 2023).

Stock et al (2023) compared stature and body size of peoples in the Levant, Europe, the Nile Valley, South Asia, and China (using publicly available data [34]). They stated three questions to answer:

i) Does body size reduce with the transition to agriculture? As mentioned above, declines had preceded the transition period.

ii) Does body size vary between regions depending on the degree of domestication? Body mass was stable over time in the Levant and China, where there was domestication, but also "an extended period of mixed foraging and agricultural subsistence" (Stock et al 2023 p1).

iii) Does adult body stature increase with milk consumption (lactation persistence)? The "Lactose Growth Hypothesis" (eg: Wiley 2018) proposed that "the ability to digest primary dairy products and lactose increased available dietary energy, shifted the energetic biology of human growth, and fuelled regional differences in human body size" (Stock et al 2023 p2). In central and northern Europe there was support found by Stock et al (2023) for this idea.

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[34] See https://borealisdata.ca/dataset.xhtml?persistentId=doi:10.5683/SP3/RTPPWX.

7.5. VIOLENCE

Concentrating on early farmers in Northwestern Europe, and using bioarchaeological evidence, Fibiger et al (2023) found that "violence was endemic in Neolithic Europe, sometimes reaching levels of intergroup hostilities that ended in the utter destruction of entire communities [35]. While the precise comparative quantification of healed and unhealed trauma remains a fundamental problem, patterns emerge that see conflict likely fostered by increasing competition between settled and growing communities, eg: for access to arable land for food production" (p1).

The use of sharp cutting edge weapons, for instance, leave distinctive fracture patterns on human skeletons, which is the type of evidence used by researchers.

The position of physical violence as widespread at this time challenges the previous view of Neolithic Europe as generally peaceful (eg: Tilley 1996).

Going back further in time, Gilbert et al (2023) attempted to reconstruct the evolution of lethal violence across the ape lineage using phylogenetic methods. Data on 301 primate species were analysed. Key traits underpinning lethal violence were identified. The researchers argued that three in particular were present in the Pan-Homo last common ancestor - male coalitions, male dominance over females, and male-based territorial defence - though they felt it was "not particularly prone to violence" (Gilbert et al 2023 p19). Violence, however, was "likely based on competition between males and not on any coalitionary violence between groups" (Gilbert et al 2023 p19). Indirectly, this supports the idea that group violence emerged when humans settled.

Violence among our ancestors tends to be studied in three ways (Gilbert et al 2023) - extrapolations from hunter-gatherer societies living today, fossil records, and living primate species.

7.6. CLIMATE CHANGE

Archaeological evidence helps in understanding the human response to past rapid climate change events and environmental change. Flexibility of a society was key (Robbins Schug et al 2023).

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[35] There is a debate as to whether the term "war" should be used for violent conflict at this time (Fibiger et al 2023).

"Case studies confirm that human communities responded to environmental changes in diverse ways depending on historical, sociocultural, and biological contingencies. Certain factors, such as social inequality and disproportionate access to resources in large, complex societies may influence the probability of major socio-political disruptions and reorganisations — commonly known as 'collapse'" (Robbins Schug et al 2023 p1).

For example, migration was a successful strategy for coping with dwindling local resources in sub-Saharan Africa 10 000 to 5000 years ago. The Gobero archaeological site in central Niger provides evidence here. There are burials that can be grouped into two periods - 9700 to 8300, and 7200 to 4900 years ago - and inbetween that was the "arid event" (otherwise the climate was relatively humid). The later-period skeletons belonged to a society that "ranged more widely to meet their subsistence needs. These skeletons showed fewer signs of childhood growth disruption, indicating that expanding their foraging and hunting territory in the later period allowed for successful adaptation to increasing aridity. The flexibility of this small-scale society enabled them to persist and thrive in a context of environmental change" (Robbins Schug et al 2023 p5).

In some situations, "both migration and intergroup conflict have indeed occurred in association with past climate change, but there are also many cases where this does not occur in a predictable fashion. Throughout most of human prehistory, conflicts seem to have been resolved without escalating to violence" (Robbins Schug et al 2023 p6).

Endemic malnutrition was another issue with climate change, but "hunger and food insecurity in the past resulted from a combination of socio-cultural and environmental forces. Particularly for complex societies built on structural inequality, famine and skeletal emaciation resulted from a lack of access to food, not from a lack of food. However, there are also risks of endemic malnutrition resulting from environmental degradation in small-scale societies without the hierarchical social organisation of structural inequality" (Robbins Schug et al 2023 p7). Societies already occupying marginal areas for survival were at greater risk of malnutrition when the climate changed. For example, monocropping for agricultural production was a risk factor (eg: Inamgaon archaeological site in west-central India 3400 years ago) (Robbins Schug et al 2023).

7.7. ANCIENT PATHOGENS

Settlement and domestication of the "agricultural transition" gave opportunities for pathogens. "This agricultural transition is also linked to a demographic transition, where fertility rates increased, and an epidemiological transition (often called the first epidemiological transition), where the parasitic and infectious disease burden increased as a result of poor sanitary conditions associated with sedentism and increased close contact with domesticated animals" (Lewis et al 2023 p1). The environment (eg: temperature, rainfall, deforestation), and the dietary shift of humans (eg: dairy products) also gave pathogens new possibilities.

Hunter-gatherers were affected by "heirloom pathogens afflicting us since (and prior to) our divergence from other hominids" (Lewis et al 2023 p6), and pathogens found in the environment. Early farming settlements added the risk of "spillover" (zoonotic) pathogens from animals, and high population density aided their transmission.

The study of pathogen genomics can help in understanding the evolution of pathogens in early settlements [36]. Lewis et al (2023) explained: "Ancient DNA analyses provide a window into past patterns of pathogen distributions and evolutionary changes as well as timing. An excellent example is that of Yersinia pestis [plague], a bacterial pathogen for which we currently have the most genome data from ancient individuals. These data show that in addition to being the cause of the historically known plague pandemics, Y.pestis also affected people as early as the Late Neolithic and Early Bronze Age. Significantly, analyses of the earliest cases point to the presence of strains that may not have been flea transmitted (inferred from genetic analyses), leaving the mode(s) of transmission and potential reservoirs unclear, as well as cases that point to an extended period of overlap with strains that do show the genomic changes (both chromosomal and plasmid) that signal flea transmission or at least better flea transmission" (p5).

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[36] Using dental samples from twelve Neanderthals and 34 AMHs, Klapper et al (2023) were able to to extract genomic information about microbes of the time (100 000 years ago onwards). The researchers found a class of previously unknown metabolites which they called "paleofurans". The first draft genome of an ancient bacteria was reported by Bos et al (2011).

7.8. CONSEQUENCES

The consequences of the transition to farming include population growth, and changes in the age distribution of populations/societies. The production of readily stored food meant less risk of starvation as an everyday event, except where harvests and crops failed and whole societies suffered together.

"Age-independent mortality" can be seen as a consequence of farming. The age of skeletons prior to the transition to farming show a simple pattern (ignoring infant mortality) where old individuals were more likely to die. This is "age-dependent mortality". Age-independent mortality describes death at different ages, and is a sign of new risks, for instance. For example, crop failure leading to death of the whole society (any age group), or inter-group conflict/warfare and death of fighting-age individuals. Living in larger communities also saw higher disease risk.

Milner and Boldsen (2023) summed up: "In archaeological contexts, an increase in age-independent mortality might be attributable to recurrent, highly transmittable, and severe infectious diseases where their spread was facilitated by regional trade networks or tightly integrated political systems. Cultural behaviour can also play a part in it through excess mortality in age groups where deaths are typically infrequent, notably among adolescents and young adults. In early agricultural societies, for example, it might have been an outcome of warfare or heavy labour demands that fell disproportionately on those who were physically the most capable. An indicator of age-independent mortality does not tell us what caused the deaths. But it does provide a means of assessing the degree to which various human groups were prone to such mortality" (p3).

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8. LEARNING ABOUT HOMININ EVOLUTION FROM BABOONS

8.1. INTRODUCTION

Fischer and Zinner (2020) outlined the three main areas of research that help in understanding in hominin evolution general and humans specifically:

i) Drawing conclusions about behaviours from fossils and artefacts.

ii) Population genetics and analysis of ancient DNA.

iii) Study of the behaviours of close living relatives of humans (eg: chimpanzees). This is sometimes called the cladistic approach.

A variation is to study a living species based on "not their close phylogenetic relationship with humans but whether these species live and evolved under similar ecological conditions as early hominins, most likely the savannah and woodland biome of Africa" (Fischer and Zinner 2020 p1). Baboons (genus Papio) are a good example here. "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 pp1-2) [37].

The genus Papio [38] comprises six species distributed throughout sub-Saharan Africa and southwest Arabia, and showing "a range of social systems and ecological adaptations that make them one of the most diverse of primate genera in these respects" (Fischer and Zinner 2020 p2) (table 8.1) [39].

Fischer and Zinner (2020) introduced a special issue of the "Journal of Human Evolution" on baboon research as related to understanding human evolution. They focused on

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[37] Baboons have often been used as "analogues and avatars" (Jolly 2009) of human evolution (Bonnell et al 2019).

[38] "Modern baboons" (Gilbert et al 2018).

[39] Five adult coat colour are seen in the six species (Elton and Dunn 2020).

two areas of interest - baboon evolution, and the behaviours and social systems.

- Most authors recognize six baboon species: hamadryas (Papio hamadryas), Guinea (Papio papio), olive (Papio anubis), yellow (Papio cynocephalus), chacma (Papio ursinus), and Kinda (Papio kindae). However, there is still debate regarding the taxonomic status, phylogenetic relationships, and the amount of gene flow occurring between species" (Martinez et al 2019 p1).

- Martinez et al (2019) used data from Gorongosa National Park (GNP) in Mozambique, where there are over 200 baboon troops, to understand gene flow between species. The baboons here have been classified as chacma, but some showed characteristics of yellow baboons (eg: yellow fur colour). Analysis of 43 crano-facial features from eleven specimens from GNP (compared with 352 baboons elsewhere in Africa) showed that Gorongosa baboons have a mosaic of features common to southern yellow baboons and a sub-species of chacma baboons (Papio ursinus griseipes).

Table 8.1 - Gorongosa baboons.

8.2. BABOON EVOLUTION

The origins of the genus Papio in the fossil record are "not clear" (Gilbert et al 2018 p38). Living species appear to be closely related to Theropithecus, Lophocebus and Rungwecebus (Gilbert et al 2018).

In terms of the modern baboon (Papio hamadryas), cranial and dental features are used to link this species to early fossil taxa in South Africa (eg: Papio izodi; Papio robinsoni; Papio angusticeps) (Gilbert et al 2018). "No definitive Papio fossils are currently documented in eastern Africa until the Middle Pleistocene, pointing to southern Africa as the geographic place of origin for the genus" (Gilbert et al 2018 p38).

Skull form and body mass are key differences between modern and ancestral baboons, according to Elton and Dunn (2020). In particular, larger body mass of living species based on reconstructions of ancestral species, which appears as the animal exploits terrestrial habitats in the Pliocene period. With the difference between male and female body mass, sexual selection is "most likely" involved more than environmental factors (Elton and Dunn 2020).

Past climate change is a driver of the evolutionary history of hominins, and baboons. Not only was the habitat changed, which impacted the living species at the time, but also gene flow between populations, particularly in relation to hybridisation, and new species. Chala et al (2019) attempted to plot this process for baboons since the Last Glacial Maximum (23 -19 000 years ago) as a model for hominins.

8.3. BEHAVIOURS AND SOCIAL SYSTEMS

Hammerschmidt and Fischer (2019) observed: "Baboons are an intriguing model for addressing questions regarding signal repertoire evolution, because their social systems vary greatly in terms of social organisation and competition among males and females. In brief, four of the six 'species' of baboons, namely chacma (Papio ursinus), Kinda (P.kinda), yellow (P.cynocephalus), and olive (P.anubis) baboons (collectively known as 'savannah baboons') live in more or less stable female-bonded societies with male dispersal, while hamadryas (P.hamadryas) and Guinea baboons (P.papio) live in multi-level nested societies. There is a remarkable gradient in male competition from south to northwest..., with extremely high competition among males and pronounced female nepotism in chacma baboons, in contrast to the high degree of tolerance and cooperation among Guinea baboon males..., female-biased dispersal... and consequently, rather weak bonds among females" (p2).

Non-human primate vocalisations can be studied to help in understanding the evolution of language. The acoustic structure of these vocalisations is "largely genetically fixed. Yet, appreciable differences between different genera and species may exist. Environmental conditions, sexual selection, and characteristics of the social system have been invoked to explain these differences" (Hammerschmidt and Fischer 2019 p1). Concentrating on chacma, olive and Guinea baboons, Hammerschmidt and Fischer (2019) found the same general call types, but subtle acoustic differences within call types (grunts and loud calls) between the species. Generally the vocalisations were found to be "highly conserved", and not to vary with social system.

Hammerschmidt and Fischer (2019) analysed recordings of vocalisations by baboons from other studies (table 8.2). Only recordings from a distance of less than ten metres were used.

The theories of the evolution of language can be divided into two groupings. Firstly, "that language has appeared in our species following the emergence of a

SPECIES	DATE	LOCATION
Guinea baboon	January 2010 - July 2011; supplemented February 2018	Niokolo-Koba National Park, Senegal
Olive baboon	(a) November 2005 - April 2007; (b) April - July 2007	(a) Gashaka-Gumti National Park, Nigeria; (b) Bundongo Forest Reserve, Uganda
Chacma baboon	January 1998 - June 1999	Okavango Delta, Botswana; Table Mountain National Park, South Africa; Tsaobis Leopard Park, Namibia

Table 8.2 - Location of collection of data used by Hammerschmidt and Fischer (2019).

distinctive morphological or other feature associated with it... Following this approach, researchers tend to focus their attention on features that are supposed to be unique to humans. For example, Lieberman et al (1969) claimed that humans are unique among primates in having a low larynx in their vocal tract and assumed that this can explain why humans are the only species to have speech" (Fagot et al 2019 p39). Alternatively, language "emerged from a unique assemblage of complementary anatomical (body and brain) and cognitive processes" (Fagot et al 2019 p39).

Fagot et al (2019) favoured the latter approach, and focused on the baboon as a model for the study of language evolution. These researchers outlined four relevant processes:

i) Cognitive functions that are core to language - eg: memory capacity; categorisation of objects (eg: four-letter words vs non-words in an experimental situation).

ii) Vocal production - ie: precursors of speech.

iii) Gestural production and cerebral lateralisation (eg: handedness).

iv) Cumulative culture - ie: sharing of information across generations.

Humans are commonly monogamous (ie: form stable breeding bonds), and can the study of baboons help in understanding the evolution of this behaviour? Crouse et al (2019) responded that the stability of breeding bonds "likely depends on many aspects of primate socio-ecology, including how life history, group size, demography and population density vary in response to seasonality, distribution of food resources, and the availability of refugia" (p3).

These researchers developed a simulation model of possible breeding scenarios called "BEGET" (Behaviour, Ecology, Genetics, Evolution and Trade-offs). The following hypotheses were tested: "Stable breeding bonds have been proposed to evolve either (1) because males can monopolise females when food distribution forces females to forage in small groups or (2) because females exchange exclusive mating for male services, such as protection from infanticide" (Crouse et al 2019 p1).

BEGET was an example of "experimental evolution", focused on male behaviour - either "Rover" males who search for and mate with any sexually receptive females, or "Loyalist" males who form stable associations with particular groups of females.

It was found that "Loyalists achieved greater reproductive success than Rovers only when females were in groups smaller than four. Both Rovers and Loyalists sometimes evolved infanticidal behaviour, but the presence of infanticide benefited Rovers rather than Loyalists, suggesting that the evolution of stable breeding bonds depends on the spatial distribution of females, rather than the risk of infanticide" (Crouse et al 2019 p1).

Bonnell et al (2019) also performed a simulation study, but to understand group structures, and foraging behaviour. Models varied from more to less centralised structures, and the group size. A centralised structure is a group with a small core. A core is defined as "a set of interdependent individuals, and peripheral individuals are those that are influenced by the core but not by each other" (Bonnell et al 2019 p16). Three types of foraging environment were modelled - uniform distribution of resources, single high-density patch, and several high-density patches.

In a uniform situation, groups with larger cores outperformed those with smaller cores, but in high density situations the groups varied in success - ie: "groups with smaller cores could sometimes outperform groups with larger cores across the range of group sizes, although they could also do much worse" (Bonnell et al 2019 p17).

Ritualised greetings (ie: "exchanges of non-aggressive signals"; Kutsukake et al 2006) are seen among males living in multi-male groups, as in Guinea baboons.

"This species lives in multi-level societies where several 'units' comprising a primary male, females with young, and occasionally a secondary male form a 'party', and two to three parties form a gang. Adult males maintain affiliative relationships with preferred male partners whom they support in coalitions, regardless of kinship" (Dal Pesco and Fischer 2018 p87).

Dal Pesco and Fischer (2018) observed in particular 24 adolescent and adult males in 2014 and 2015 in Niokolo-Koba National Park, Senegal. The overall community was around 400 individuals in five parties and two gangs. Frequency and intensity of greeting events were scored.

"Greetings were defined as ritualised interactions between two individuals characterised by an approach, an exchange of behavioural elements such as hip-grasp, embrace, or penis diddle and, in most cases, a retreat... Approach and retreat are characterised by a distinct gait that is frequently associated with ear-flattering, lip-smack, and grunt vocalisations... The approaching individual was considered the initiator of the greeting (ie: greeter, while receiver is greetee). Greetings often involve brief exchange of behavioural elements, but physical contact does not always occur. A greeting interaction was scored when at least one of the following behavioural elements was observed: mount, penis diddle, polonaise (ie: two individuals face the same direction; one hip-grasps and walks forward on two legs while maintaining a hold of the hips of the other; the pair move forward for a short distance), embrace, hip-grasp, hind-quarter touch, tail over body/head, touch, present, head bob, and prancing" (Dal Pesco and Fischer 2018 p90).

Greetings occurred "almost exclusively" between males of the same party. "Although affiliation did not predict overall greeting rate, intense and potentially costly greetings were more likely between males with stronger affiliative relationships. Greetings in Guinea baboons appear to signal commitment among party members, test relationships among spatially tolerant partners, and accentuate relationship strength among highly affiliated males. Although ritualised baboon greetings lack the symbolic component of human rituals, they appear to serve similar functions, specifically to strengthen in-group affiliation and promote co-operation" (Dal Pesco and Fischer 2018 p87).

It is interesting to compare these findings to other baboon species. For example, "in chacma baboons, where affiliation and coalition are non-existent and males usually keep their distance, greetings are virtually absent” (Dal Pesco and Fischer 2018 p96). While, Dal Pesco and Fischer (2018) continued, “olive baboon greetings have been described as tentative, with males frequently attempting to greet but struggle to establish greeting roles and complete these attempts... In hamadryas baboons, males frequently did not engage in physical contact during greetings..., while in yellow baboons... hind-quarter presentations were associated with the most intense forms of aggressive and submissive behaviours. Thus species characterised by more competitive and hierarchical male-male dynamics... exhibit less elaborate greeting repertoires” (p96).

Among olive baboons, for example, males form strong ties with certain lactating females. These relationships have been called “friendships” (Smuts 1985), and involve “high levels of proximity, grooming, and support, and low rates of aggression” (Stadele et al 2019 p82). One explanation is the “parenting effort hypothesis” (ie: the male is the father of the female’s offspring), which has been found in yellow and chacma baboons (eg: Buchan et al 2003). Alternatively, there is the “male mating effort hypothesis” (or “care-than-mate”; Menard et al 2001), which proposes that “males form a relationship with the lactating female that persists into the fertile phase and increases the males' chance of siring the female's next offspring” (Stadele et al 2019 p82).

Stadele et al (2019) investigated these two hypotheses with data from wild olive baboons in Kenya. Two groups of approximately fifty individuals each were observed between 2013 and 2016, and genotyping from faecal samples was undertaken. Fifteen-minute focal sampling of adult females was performed. “During focal sampling, observers continuously recorded all of the focal female's social interactions. Observers recorded the type of social behaviour, the identity of the partner, and whether the interaction was initiated by the focal female, the partner, or jointly. On average, every female was the focal of an observation once every four days. All data were collected on hand-held computers in the field and transferred onto computers for error-checking and storage. Aggressive interactions and supplants were also recorded ad libitum by observers” (Stadele et al 2019 p83).

The data supported both hypotheses. The males were more likely to be related to the female’s offspring, and were more likely to sire the next offspring. “Thus, in olive baboons, the development of stable breeding bonds and paternal investment seem to be grounded in the formation of close ties between males and anestrous [not in heat] females" (Stadele et al 2019 p81).

Hamadryas and Guinea baboons are different to the other four species (chacma, olive, Kinda, and yellow baboons; COKY) in having one-male units (OMUs), multi-level societies, and male social philopatry ("growing up and remaining with kin and other familiar individuals"; Jolly 2020 p5). COKY live in multi-male multi-female groups with female philopatry and males dispersing at sexual maturity (Jolly 2020) (table 8.3).

Hamadryas and Guinea baboons	Chacma, olive, Kinda, and yellow baboons
• Often split into OMUs, and clans/parties for foraging based on long-term male-male relationships. Clan or party is a combination of OMUs. • Females jealously guarded by leader or dominant male in OMUs. OMUs include one or more adult females, immature animals (offspring), "leader", and sometimes peripheral male "follower".	• Female-female relationships are basis of troop structure. • Immigrant males face competition and agonistic interactions with other males. • "Friendships" between male and oestrous female.

Table 8.3 - Key differences in social structure between two sets of baboon species.

Jolly (2020) argued that male philopatry evolved in the common ancestor of hamadryas and Guinea baboons as a response to the expansion of range in East and West Africa during the Pleistocene period. This is the "philopatry at the frontier hypothesis" (Jolly 2001) [40]. Ancestral olive baboons "reinvented" male dispersal which eventually spread into modern day COKY (Jolly 2020).

Swedell and Plummer (2019) proposed that the society of Homo erectus was similar structurally to that of hamadryas baboons using behavioural and genetic data from the latter, and archaeological data from the Oldowan site in Kenya dated at two million years ago. It is the multi-level society of the baboons that interested the

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[40] "The frontier hypothesis suggests that male philopatry became the norm because rapid, invasive expansion changed the cost-benefit ratio, putting male dispersers at a relative disadvantage" (Jolly 2020 p10).

researchers in terms of its application to understanding hominins two million years ago.

The researchers explained that hunting and active scavenging by coalitions of males was supplemented by female acquisition of resources (ie: gathering), which promoted co-operation, as did the increased costs of reproduction for females. But this "would have been alleviated by co-operation and food sharing within and between the sexes, thereby reducing the risk of any one family having a food shortfall... Together, these factors would have favoured a multi-level society in which the various levels of society served different functions and social bonds were maintained within and between social units" (Swedell and Plummer 2019 p10).

The idea is of "a complex society linked by male-male, male-female, and female-female bonds at multiple levels of social organisation in Plio-Pleistocene hominins" (Swedell and Plummer 2019 p1), as seen in hamadryas baboons.

Petersdorf et al (2019) focused on the Kinda baboon with long-term data from the Kasanka Baboon Project in Zambia [41]. The researchers explained their interest: "Based on observations of large group sizes, combined with low degrees of sexual dimorphism and large relative testis size relative to other baboon species, we test the hypothesis that Kinda baboons have evolved under reduced direct, and increased indirect, male-male competition" (p1). The upshot is a queueing-based rather than a contest-based male dominance system. The alpha male is replaced by the "next in line" rather than there being contests between males to gain dominance. The researchers saw this as having "potential to offer new insights into the selective environments that may have been experienced during hominisation" (Petersdorf et al 2019 p1).

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9. LEARNING FROM OTHER NON-HUMAN PRIMATES

9.1. APES SHARE FOOD

Exchanging and sharing food "has perhaps been of particular importance in human evolution" (Benozio et al 2023 p1), and is the basis of many social relationships. Reciprocal food exchange can be generalised (ie: "help anyone if helped by someone") and direct (ie: "help someone who helped you before") (Benozio et al 2023).

Great apes engage in reciprocal activities like grooming and play, but what about food exchanges? But the evidence is rare, and one reason is that "great apes have evolved to view food as a target of competition, determined by dominance, not as a commodity for social exchange and friend-making" (Benozio et al 2023 pp1-2).

Benozio et al (2023) performed an experiment involving thirteen chimpanzees, five bonobos, and 48 human children aged four years old on this topic. The participants could share food with an unseen partner or not as they wanted after believing the partner had or had not shared food with them. "Positive reciprocity" was sharing food after believing partner had shared, while "negative reciprocity" was "no-food for no-food".

The apes showed positive reciprocity to the same level as the human children (75-80% of trials), but negative reciprocity to "a lower extent than children" (Benozio et al 2023 p1).

The apes in the experiment were captive, and food was provided regularly. In the wild, "obtaining food is never guaranteed in competitive social environments, thus food likely is to be viewed as a commodity to compete for, rather than to trade with. Conversely, food is provided on a regular basis for captive chimpanzees. Food is thus more likely to be viewed as an abundant resource, and this should increase the possibility of being tradable" (Benozio et al 2023 p6).

The researchers concluded that "while a potential mechanism of fostering co-operation (via positive reciprocal exchanges) may be shared across species, a stabilising mechanism (vis negative reciprocity) is not" (Benozio et al 2023 p1). Negative reciprocity "could be an essential piece in the evolutionary story regarding the function of punitive sanctions to stabilise group-level co-operation" (Benozio et al 2023 p7).

9.2. VOCAL LABELLING

The use of a vocal label ("personal name") for an individual and that individual to know that label are "high cognitive functions in social animals" (Oren et al 2024 p996). These abilities have been reported in two species other than the humans, according to Oren et al (2024) - dolphins (Janik et al 2006) and elephants (Pardo et al 2024).

Oren et al (2024) added a third species in marmoset monkeys. "Marmosets are highly social primates that live in small family groups (two to eight animals). Marmosets rely heavily on vision but also exhibit a complex array of social calls. One such call is the phee call, a contact call, ranging from 5.5 to 10 kHz, which marmosets use to form dialogues with other group members in a turn-taking manner when out of sight and to encode caller-related social information such as caller identity and sex" (Oren et al 2024 p996).

Analysis of recordings of spontaneous phee calls between pairs of marmosets suggested vocal labelling. Ten monkeys from three different family groups were paired in an experimental room with a visual barrier forcing them to communicate acoustically.

The researchers ended: "The vocal labelling of others... represents a learned, highly flexible call production that requires brain mechanisms for representations of others as discrete concepts, vocal learning, imitation, and modification of the acoustic fine structure of calls. These mechanisms might be similar to those that facilitated the evolutionary transition from non-linguistic communication to language in our pre-linguistic humanoid ancestors" (p1003).

9.3. COMPOSITIONALITY

Many animals communicate with sounds, but the ability to combine sounds (words) in a creative way is seen as a unique human language capacity. This is sometimes called compositionality - "the capacity to combine meaningful elements into larger meaningful structures" (Berthet et al 2025 p104).

Compositionality can be "trivial" (or "intersective") or "non-trivial" (or "non-intersective")

(Berthet et al 2025). The former is defined as "each element of the combination contributes to the meaning of the whole independently of the other element, and the combination is interpreted by the conjunction of its parts", while, with the latter, the "units constituting a combination do not contribute independent meaning, but instead, they combine so that one part of the combination modifies the other" (Berthet et al 2025 p104).

This ability has been now reported in a study with bonobos by Berthet et al (2025). "Previous studies have found that other animal species can combine their calls, but only in 'trivial' combinations that simply add the meanings together. Human language is much more powerful: Speakers can combine words into more than the sum of their parts. For instance, 'tall cook' is a trivial combination — it means someone who is tall and a cook. But 'good cook' is not someone who is good and a cook: They might be good at cooking, but terrible in other areas — perhaps a dangerous driver. This combination of words generates a new meaning [non-trivial compositionality]" (O'Grady 2025 p19).

Berthet et al (2025) followed wild bonobos in the Democratic Republic of the Congo over eight months. Extensive recordings of vocalisations were made along with over 300 contextual features (eg: who made the vocalisation; what the vocaliser was doing at the time; how other bonobos responded to that vocalisation). Seven hundred different vocalisations were distinguished based mostly on two distinct calls combined (eg: "whistle and peep"; "high hoot and low hoot") (O'Grady 2025).

The findings suggested that "bonobos have a 'precursor' to the human capacity to combine units of language to create new meanings... Both bonobos and humans may have inherited the ability from our common ancestor some 7 million years ago..." (O'Grady 2025 p19).

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10. MISCELLANEOUS ANCIENT ANIMALS AND ORGANISMS

10.1. NIMRAVIDS IN NORTH AMERICA

Around 35 million years ago (MYA) the Mid-West of the now USA (eg: Oregon) was dense jungle and inhabited by nimravods (or false sabre-toothed cats; "superficially 'cat-like' carnivores"; Barrett 2016 p1) [42]. Their fossils disappeared around 23 MYA, and there is a "Cat Gap" for 6.5 million years (Whyte 2022).

Nimravids (Nimravidae) [43] were named in the 19th century (first described in 1851; Barrett 2016), and classified as members of the cat family because of shared characteristics with that family (eg: teeth specialised for eating meat; retractable claws; a tail to help with balance). But subsequent differences to cats were noted (eg: flat-footed walk like bears rather than on their toes; five toes vs four of felines). In the mid-20th century major taxonomic revisions, and nimravids were classified as their own family (Whyte 2022). "They aren't felines, but feliforms" (Paul Barrett in Whyte 2022).

More recently, Barrett (2016) used the "phylogenetic species concept" (PSC) where a species is defined as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990 quoted in Barrett 2016). PSC is a means by which to group organisms based on shared and unique evolutionary history. The conclusion was twelve "valid species" of nimravids in North America.

As for the "Cat Gap" in North America, it could be an anomaly (ie: no fossils deposited in the rocks but the animals existed or unknown fossils found and not yet

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[42] From Late Eocene period to end of Oligocene (35.5 - 23 MYA), nimravids in North America, Europe, and Asia (Barrett 2016). The Late Middle Eocene to the Early Oligocene (41 - 30 MYA) was a climatically dynamic period (Poust et al 2022).

[43] See images and more general information at https://en.wikipedia.org/wiki/Nimravidae#.

dated). But the consensus is a real event (Whyte 2022).

If so, why did the nimravids disappear? One explanation is volcanic activity, while another is a period of cooling and drying (which particularly impacted prey). Nimravids were "hyper-carnivorous" - ie: teeth adapted to eat meat only - and "such specialisation often leads to an evolutionary dead end" (Whyte 2022 p45) [44].

The "Cat Gap" in North America was ended by the arrival of Pseudaelurus [45] (believed to be the common ancestor of North American cat species) from Siberia vis the Bering land bridge during the "Ice Age", and cat-like animals called barbourofelids [46] (that died out 5 MYA) (Whyte 2022).

10.2. KANGAROO EXTINCTIONS

Extinctions of animals were common in the Late Pleistocene period, particularly so in Australia that lost 90% of large species by 40 000 years ago, many being kangaroos (Arman et al 2025).

Species can be vulnerable to extinction due to a number of factors, like small geographical range, high specialisation (in diet), rarity, and large body size (Arman et al 2025).

What caused the extinctions of kangaroos in Australia? One possibility is an over-specialised diet in a time of climatic-driven fluctuations in vegetation. Arman et al's (2025) analysis of teeth and skulls (technically, cranio-dental morphology) refuted this idea.

Another theory is the presence of humans who appeared between 65 000 and 40 000 years ago (Arman et al 2025).

10.3. GIGANTOPITHECUS BLACKI

Gigantopithecus blacki was the largest primate ever at 3 metres tall, with a mass of 200-300 kg, and unusually large molars, living in Southern China (Zhang et al 2024) [47].

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[44] Going back in time, Mesonychia (https://en.wikipedia.org/wiki/Mesonychia) and Oxyaenodonta (https://en.wikipedia.org/wiki/Oxyaenidae were the hyper-carnivores before the Late Eocene (40 - 37 MYA), and before carnivoraforms (crown carnivorans and relatives) (Poust et al 2022).

[45] See images and more general information at https://en.wikipedia.org/wiki/Pseudaelurus.

[46] See images and more general information at https://en.wikipedia.org/wiki/Barbourofelidae.

[47] General information about Gigantopithecus at https://en.wikipedia.org/wiki/Gigantopithecus.

Present from 2.2 MYA to 420 - 330 000 years ago. "During this time, G.blacki underwent morphological changes including an increase in tooth size and dental complexity, seemingly indicating a dietary change in response to ecological pressure. Reconstructions of G.blacki diet based on the dental anatomy indicate a specialised herbivore with adaptations for the consumption of abrasive food, heavy mastication of fibrous food and a fruit-rich diet" (Zhang et al 2024 p535).

Its extinction (between 295 - 215 000 years ago) has been linked to "enhanced environmental variability from increased seasonality, which caused changes in plant communities and an increase in open forest environments. Although its close relative Pongo weidenreichi [48] managed to adapt its dietary preferences and behaviour to this variability, G.blacki showed signs of chronic stress and dwindling populations. Ultimately its struggle to adapt led to the extinction of the greatest primate to ever inhabit the Earth" (Zhang et al 2024 p535).

10.4. SURVIVAL OF MAMMALS

An asteroid hit the Earth around 65 MYA, and the "Age of the Dinosaurs" ended. Mammals survived and took over. This simple picture is troubling to Brusatte (2022) because relatively little is known about how mammals survived at this time.

Small-bodied mammals had existed alongside large-bodied dinosaurs from around 225 MYA. Between 201 and 66 MYA, "a bounty of pint-sized mammals - none larger than a badger - lived underfoot of the dinosaurs. Among them were scurriers, climbers, diggers, swimmers and gliders. It was these animals that developed the classic mammalian blueprint: hair, warm-blooded metabolism, a complex line-up of teeth (canines, incisors, pre-molars, molars), and the ability to feed their babies milk" (Busatte 2022 p22). For example, multituberculates [49] consumed a new type of food - fruits and flowers, and three other groups developed from these that exist today - egg-laying monotremes, marsupials, and placentals (Busatte 2022).

Fossils from the northern Great Plains in the USA, for example, have helped in understanding mammals post-asteroid. Survivors were smaller than other mammals, and had teeth indicating generalist, omnivorous diets (eg:

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[48] General information at https://en.wikipedia.org/wiki/Pongo_weidenreichi.

[49] See details at https://en.wikipedia.org/wiki/Multituberculata.

eutherians [50]) (Busatte 2022).

10.5. ADOLESCENT GROWTH SPURT

"Life history theory addresses how organisms balance development and reproduction. Mammals usually invest considerable energy into growth in infancy, and they do so incrementally less until reaching adult body size, when they shift energy to reproduction. Humans are unusual in having a long adolescence when energy is invested in both reproduction and growth, including rapid skeletal growth around puberty. Although many primates, especially in captivity, experience accelerated growth in mass around puberty, it remains unclear whether this represents skeletal growth" (Sandel et al 2023 p1).

Is the skeletal growth of the adolescent growth spurt unique to human then? Sandel et al (2023) sought data to answer this question from wild chimpanzees in Uganda.

Generally there is a problem in collecting data to answer this question, as Sandel et al (2023) explained: "Measuring growth in free-living animals is challenging. In some species, animals are immobilised and captured to obtain weights and other measurements... Occasionally, it is possible to obtain mass by luring animals onto scales... But methods involving capturing or feeding pose a risk to animal health, and ethical considerations may preclude making direct measurements... Alternative technologies can estimate size non-invasively. These include digital photography combined with parallel lasers to estimate limb lengths and body areas... and the use of urinary creatinine as a proxy for muscle mass... None of these methods, however, assess overall bone growth, especially as measurements of body weight reflect both hard and soft tissue, and photographs of body parts often can only measure two-dimensional size and fail to capture the overall accrual of bone" (p2).

Sandel et al (2023) used two biomarkers of bone turnover - osteocalcin and collagen - which can be detected in urine. Urine was collected by the researchers within minutes of release on leaves or the ground, or caught in plastic bags from chimpanzees in trees from 109 individuals in the Kibale National Park between 2016 and 2018. Adolescence was defined by the emergence of secondary sexual characteristics (eg: enlarged testes), aged 9-16 years old.

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[50] More details at https://en.wikipedia.org/wiki/Eutheria.

Evidence was found to support an adolescent growth spurt in the skeleton, especially for males. For males the values of the two biomarkers peaked at age 9.4 to 10.8 years old.

The researchers concluded: "Biologists should avoid claiming that the adolescent growth spurt is uniquely human, and hypotheses for the patterns of human growth should consider variation in our primate relatives" (Sandel et al 2023 p1).

10.6. ANCIENT VIRUSES AND MENTAL ILLNESS

"Psychiatric disorders such as schizophrenia, bipolar disorder, major depressive disorder, attention deficit hyperactivity disorder, and autism spectrum conditions have a substantial genetic component. Genome-wide association studies (GWAS) have highlighted a polygenic architecture underlying susceptibility to these conditions, meaning that many loci across the genome incrementally contribute to risk" (Duarte et al 2024 p1).

Human endogenous retroviruses (HERVs) have been implicated in major psychiatric conditions. "HERVs are 'non-coding' sequences comprising of genetic material that originated from the infection of germ cells with ancient retroviruses during evolution, which now constitute approximately 8% of the human genome. After the initial infections took place, these sequences inserted in the genome and multiplied themselves using a 'copy-and-paste' mechanism known as retro-transposition. At present, there is no evidence that these elements are currently retro-transposing, and studies suggest the majority of HERV insertions occurred over ~1.2 million years ago. Instead, they have been hypothesised to regulate neighbouring genes, as most HERV sequences comprise of solitary viral promoters known as long terminal repeats (LTRs). However, many sequences additionally contain remnants of viral genes (eg: gag, pol, env) that may encode additional biological functions, other than just regulating gene expression locally" (Duarte et al 2024 p2).

Duarte et al (2024) found HERV expression signatures specific to schizophrenia risk, schizophrenia and bipolar disorder, and major depressive disorder, but not autism spectrum conditions or ADHD in the cortex of 792 post-mortem brain samples of Europeans (from the "CommonMind Consortium" dataset).

"It is not clear yet how the expression of the high confidence risk HERVs may play a role in psychiatric disorders. It was previously hypothesised that differential HERV expression in psychiatric cases was likely to be a by-product of immune responses against current or past infections. Indeed, HERV expression is modulated by exposure to several pathogens, and can activate inflammatory cascades. This is an interesting theory that corroborates the fact that individuals with psychiatric disorders typically have higher incidences of infections" (Duarte et al 2024 p7).

10.7. REFERENCES

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