Hominin Cognitive Development: Brains, Bodies and Behaviour - A Comprehensive Approach

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Hominin Cognitive Development: Brains, Bodies and Behaviour: A Comprehensive Approach

Janet Sue (Suzi) Wilson

Abstract

The cognitive developments of early hominins, which may have begun as early as the transition to bipedalism following our ancestors' split with the great apes, ultimately enabled these early humans to consider concepts and undertake strategies that were previously unimaginable. Although this evolutionary trajectory has long been an inquiry of interest, cognitive research has often relied on hypotheses drawn from psychological theory or neural evidence provided by brain moulds (endocasts) made from early hominin crania, which can preserve sulci and gyri patterns of the hominin brain. These neuroanatomical landmarks are often difficult to discern with the naked eye; however, technological advancements in medical imaging can now produce digital brain endocasts of early hominins at high resolution. Furthermore, medical imaging can now observe the activated cerebral regions of conscious living humans engaged in various tasks or mere thoughts, thus demonstrating the correlation between these regions and specific actions or mental activity. Thus, the cognitive regions activated during the manufacture of stone tools in modern humans implies that these neural structures were either in development or already formed during Lower Palaeolithic tool-making.

This thesis takes the first comprehensive approach to the study of hominin cognitive development, through the contextualised reassessment of hominin crania/endocasts, in concert with hominin manufactured stone tools. The synthesised evidence herein establishes how changes in hominin behaviour, driven by climate and environmental change, generated post-cranial adaptations which, in turn, resulted in neural adaptations, thereby contributing to the evolution of the brain. The evidence suggests that this likely occurred in a mosaic fashion, perhaps as early as the latter australopithecines. It is also likely that the cognitive advancement of these neural structures and the acquisition of new behaviours had a concomitant effect on one another.

Continued work would benefit from a collaboration between the stone tool specialists and palaeo-neurologists, as well as public access to the digital endocast files.

Hominin Cognitive Development: Brains, Bodies and Behaviour
A Comprehensive Approach

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A thesis presented for the degree of
Doctor of Philosophy
Department of Archaeology
University of Durham
UK
2022

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Statement of Declaration

I, the author of this thesis, declare that this thesis and the work presented herein are my own. No part of the work has been submitted in support of an application for any other degree in this university or any other. Where other sources of information have been used, they have been acknowledged.

Signature: J. Suzi Wilson

Name: Janet Sue (Suzi) Wilson

Statement of Copyright

The copyright of this thesis rests with the author. No quotation from it should be published without the author's prior written consent and information derived from it should be acknowledged.

Acknowledgements

Although I had always wished to study Archaeology, I was not able to pursue it until much later in life. I started taking the undergraduate prerequisites for the Master program at Columbia University whilst I was still working, then formally enrolled in the graduate program full time in 2012. I had planned to study the Etruscans in Italy and even worked on a few Italian excavations in Tuscany, but then I read a book by Paul Pettitt called “Palaeolithic Origins of Human Burial” which changed my life, for which I am extremely grateful.

I am also grateful for the support from my friends, family and colleagues during this journey, especially my academic friends from both Columbia and Durham for their perspectives, advice and commiseration throughout the process, particularly Jill Shapiro, Alison Damick, Houston Wilson, and David Clinnick for their words of wisdom. I am especially indebted to the professors who opened my mind in such a way that I will never see the world the same again. Mark White has provided extraordinary supervision, and I would not be here if not for Paul Pettitt. I am also very appreciative for the opportunity to work with Zoe Crossland, who was my advisor at Columbia, and Ralph Holloway who shared his collection of brain endocasts whilst guiding me in the process. It has truly been a privilege to learn from such exceptional mentors.

Hominin Cognitive Development: Brains, Bodies and Behaviour
A Comprehensive Approach

Introduction

Brains do not fossilize, and following death brain cells are typically the first to die, usually between three and seven minutes, after which the brain begins to liquefy. Finding any Palaeolithic soft tissue is extremely rare, but the hope of ever finding Palaeolithic neural tissue is unrealistic unless and until a Palaeolithic 'ice-man' is discovered. That said, when Professor Raymond Dart first examined the cranium of the hominin found in 1920, which he would later name *Australopithecus africanus*, he noticed that it was filled with a hardened sediment forming a natural mould of the brain. The back of the skull which belonged to this young boy (aka the "Taung Child") was no longer intact, allowing Dart to examine the impressions left behind by the internal table of bone on this naturally made 'endocast', from which he identified several neurological landmarks (Dart 1925). These interior cranial impressions are created by the various peaks (referred to as 'gyri' or 'crests') and valleys (called 'sulci' or 'fissures') of the folding and furrows of the brain ('convolutions'). When these gyri and sulci are visible and specific neuroanatomical landmarks of the cerebral cortex can be identified, they can sometimes provide insight as to how specific components of the brain may have derived in size and/or shape as well as provide evidence with respect to brain lateralisation, asymmetries and reorganisation.

The expansion and reorganisation of the brain over the course of evolution enhanced hominin cognitive capabilities in numerous ways, including but not limited to social, sensory and motor skills. According to neurologists Rizzolatti and Strick, a large portion of this expansion occurred in the prefrontal cortex and inferotemporal cortex, as well as the posterior section of the parietal lobe (2013:419). The posterior parietal cortex is primarily concerned with spatial perception while the inferotemporal cortex plays an important role with the recognition of objects –

abilities that are germane for tool making. These association cortices also integrate information received from various regions and subregions of the brain. As the posterior parietal cortex expanded further into the posterior regions of the brain, occipital areas (such as the primary visual cortex) either contracted in size or compressed into additional convolutions. There has long been a 'chicken and egg' debate among bio-anthropologists and bio-archaeologists regarding the development and reorganisation of the brain: (i) did the brain first increase in size prior to reorganisation; or (ii) did reorganisation occur first, in order to allow for and support the expansion of the brain? Could they have occurred concomitantly?

Indeed, although both medical neurologists and academic palaeoneurologists agree that the reorganisation of the brain occurred at some point over the course of our evolution (Schoenemann 2006; Kolb and Whishaw 2009; Rizzolatti and Strick 2013; Holloway 2015), exactly how and when these various elements of reorganisation transpired during our evolutionary history are debated. Also contested is whether these developments occurred in a mosaic fashion or via a punctuated event that prompted an evolutionary transformation. How can we establish these changes through the evidence in the anthropological/archaeological record?

Brain endocasts are either natural or modelled casts/moulds made from the braincase of crania. In general, they can typically provide useful information regarding size (endocranial volume), shape, lateralisation and cortical asymmetries ('petalias'), but the information in the form of gyri and sulci is often limited, as there are three layers of tissue ('meninges') consisting of dura matter, pia matter and the cerebrospinal fluid, which lie in between the brain and the inner surface of cranial bone. Prior to the advent of digital technology, endocasts were typically made by pouring or injecting a liquid latex (or other by-product) into the cranium, allowing it to harden into a soft pliable form, then extracting it through the foramen magnum.

Today, crania are more often scanned via computed tomography (CT), which can capture the interior of fossil crania at very high resolutions and create three-dimensional digital images ('virtual endocasts') allowing elements of the endocast to be enhanced, rotated, and viewed on a computer screen from all angles. Currently, there are an ever increasing number of software packages such as Almira (aka Avizo), MeshLab, SketchFab, Osirix, and ITK-SNAP, for which these digitized endocasts can be examined, usually as polygon files (.ply files), captured in formats with varying levels of resolution.

Although hospitals associated with universities have been generous in allowing researchers to scan crania at their facilities, their scanners can only produce imagery to a certain level of resolution, beyond which would be unsafe for living human beings. However, non-medical institutions, such as the Max Planck Institute for Evolutionary Anthropology in Leipzig, have CT scanners that can capture imagery at a very high resolution, thus creating digital endocasts that can reveal more detail than what is typically seen with the naked eye or the digital endocasts scanned at lower resolutions at medical facilities.

In addition to the technological advances in digital scanning and software, substantial advances have also been made in modern neuroscience, facilitated by the innovations for imaging the brain. Not only do we now understand most of the functions of the various regions of the cerebral cortex, we also know the hemisphere in which they are typically dominant. Additionally, we are able to observe the neural areas which work in 'association' with each other ('cortices') and how they correlate with a specific behaviour or task (or emotion). Neurologist and Nobel prize winner (Physiology/Medicine) Eric Kandel[1] has stressed the importance of these brain

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[1] *Kandel served as a Senior Investigator with the Howard Hughes Medical Institute, a director of the Kavli Institute for Brain Science, and as a co-director of the Mortimer B. Zuckerman Mind Brain Behaviour Institute at the Columbia University College of Physicians and Surgeons, where he also founded the Centre for Neurobiology and Behaviour (the Department of Neuroscience).*

imaging innovations and how they ". . . permit us to visualize the human brain in action – to identify specific regions of the brain associated with particular modes of thinking and feeling and their patterns of interconnections" (Kandel 2013:3).

Aims and Objectives

This thesis takes a comprehensive approach which investigates the scientific evidence, however limited, from endocasts made from hominin crania in tandem with the behavioural evidence offered by the artefacts (stone tools) in the archaeological record to develop a synthesis of information for better addressing the questions, issues, and debates regarding the evolution of the brain. Also important in this analysis are the effects of climate and environmental change requiring physical and behavioural adaptations for survival. The synthesis produced herein will additionally serve as a 'primer' for future scholars who also wish to engage in the joint task of examining these two disciplines in concert with one another. Although the stone tool specialists are open and welcoming to new researchers, the endocast professionals typically are not –even secretive, at times, by refusing to share their evidence and/or work. Palaeolithic answers are hard enough to come by even with full collaboration of scholars and researchers. Thus, a secondary aim of this thesis is to make the endocast information more readily available to anyone interested in the field (or combined fields).

Chapter One discusses the technical innovations in imaging the brain, which in turn led to the advancements in neuroscience, thus providing the epistemology for how we 'know what we know' today. Building upon that epistemology, Chapter Two is a (hopefully) not-too-tedious overview of the brain itself, with additional focus on the areas of interest for palaeoneurology. Chapter Three provides additional detail of modern brain organisation, specifically with respect to brain asymmetries and lateralisation and how this development might be seen in the fossil record. Both symmetry and asymmetry play important roles in this thesis from the stone tools to the brains that made them. These first three chapters present the foundation for the neuroscience, which will be sought and examined in both the brain endocasts and behavioural evidence of the early hominins.

Chapter Four is dedicated to bipedalism, primarily with respect to (i) how every postcranial change in the body results in a corresponding change in the brain; and (ii) how bipedalism impacted our social relations. The elements of the social brain hypothesis were first published by Maruyama in 1963, presented to the AAA conference and published in 1967 by Ralph Holloway, given the name "The Social Brain Theory" by Leslie Brothers in her 1990 publication, and further developed and elaborated by Clive Gamble, John Gowlett and Robin Dunbar in their respective works as well as their collaborative effort in *Thinking Big* (2014). It is a well-respected theory, needing no further support from this thesis, and any 'holdouts' who may have continued to doubt the connection between brains and socialisation were surely convinced during the Covid pandemic.

Chapter Five describes and analyses the australopithecines, their behaviour and particularly their crania beginning at roughly 4.2 mya as a means to identify evidence of neural change and/or brain reorganisation. It also provides an overview of their postcranial morphology in terms of how it continued to adapt to bipedalism. Also relevant in this chapter is a brief mention of the first stone tools from Lomekwi, discussed further in Chapter Six.

Chapter Six discusses the impacts of the global climate change on the environment, when a cyclical glaciation period began at roughly 3.0 mya, which intensified as it ushered in the Pleistocene. In addition to colder weather, Antón *et al.* suggest that the additional aridity in Africa around 2.5 mya added further stress on the environment which resulted in changes in food sources (2014). Furthermore, there were sympatric hominin species living within close proximity to one another in

Africa and thus competing for sustenance at this time. As a result of these cumulative challenges, hominin brains, bodies and behaviour needed to change and adapt in order to survive. Accordingly, this is also about the time we see one of the earliest assemblages of Oldowan tools at Gona, and Chapter Six also analyses and describes the early Oldowan, its possible makers, and the neural correlates associated with making Oldowan tools based on brain imaging studies by Stout *et al.* (2007, 2008) involving modern human subjects. Although modern human brains are not proxies for hominin brains any more so than extant apes or human children, they do provide insight in terms of the neural structures involved in toolmaking.

Finally, the genus *Homo* fully emerges and evolves in Chapter Seven - their crania, endocasts, postcranial morphology and their toolkits. The variation and speciation issues with early *Homo* are discussed as well as later Oldowan tools and what they might suggest in terms of cognitive advancement. When *Homo erectus* strides onto the set, we almost think we see a modern human – or do we? Recent evidence suggests that erectines may not have been as tall and lean as previously believed. If so, perhaps their increased brain size was more allometric in scope versus exponential. With the exception of the DAN 5 specimen from Gona, the erectine endocasts provide little information, but their Acheulean technology speaks loudly regarding what they could achieve, cognitively. The chapter concludes with African *H. erectus* and the Acheulean around 1.2 mya.

Data and Methods

Initially, the available crania in the fossil record in Africa (only) between 4.2 and 1.2 mya were identified and catalogued for examination, along with their respective endocasts (see Appendix I), which totalled 62 crania. During the initial examination process, most cranial fragments were eliminated unless they provided some evidence of gyri and/or sulci detail, whilst other crania/endocasts were removed due to unsuitability for various reasons (inadequacy, damage, etc.) or lack of access, leaving a net total of 47 specimens examined. Unless indicated otherwise, all crania photographed are replicas and all endocast moulds were made by Holloway.

The scope of the endocast analyses is first, to note overall general observations, including endocranial volume and shape, then to focus on features such as brain asymmetries that might indicate handedness or specific regions, such as Broca's area, to determine if sulci had developed toward what would more closely resemble a derived condition (further explained in the following chapters). Additionally, the position of the lunate sulcus in early hominin endocasts has previously been considered an indicator for brain reorganisation based on its position in the occipital lobes (described further in Chapter 2); however, the identification and location of this sulcus has also been quite contentious, as far back as Dart's initial assessment of it on the first natural endocast discovered. Although the examination of endocasts is one of the only forms of *direct* scientific evidence regarding the neural anatomy of Palaeolithic brains, this study is somewhat limited by what can actually be observed, which is often quite sparse. Thus, stone tools have been examined: (i) to determine what postcranial adaptations may have occurred as a means to assess hominin morphology for making tools; and (ii) as a means to consider the cognitive structures which would have likely needed to be in place in order to produce the stone tools observed.

Finally, although there are few *structural* differences between the neuroanatomy of apes versus the human brain (Holloway 1996), extant primates cannot categorically serve as proxies for early Palaeolithic hominins, nor can modern humans - especially modern human children. Although such studies may be able to provide some insight regarding primate and hominin cognitive evolution, their information should be taken with a grain of salt.

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Chapter 1: The Epistemology of Modern Neural Science

Single-neuron recording and non-invasive imaging and recording techniques have allowed researchers to describe how neural activity in different sensory and motor pathways encodes sensory stimuli and planned actions. Moreover, imaging methods permit direct visualization of the brain in human subjects engaged in mental activity, allowing insight into attention and aspects of consciousness under controlled conditions.

Eric Kandel 2013c:372

The study and understanding of palaeoneurology is dependent upon current and collective knowledge of today's modern neuroscience – particularly concerning the regions of the cerebral cortex that correlate with thoughts, actions and skill sets, as well as the 'association cortices' involving two or more neural regions that work in tandem with one another. The technical innovations, which emerged during the 1970s, provided a means to examine the brain in living conscious human subjects. As a result, we are now able to capture activity in specific regions of the brain whilst the subject is engaged in a task or thought process. Prior to these innovations, the study of neural science in living humans was largely limited to the study of subjects with brain abnormalities (i.e., tumours, disease), impairments from injury, or from performing neuro-autopsies on cadavers. Thus, the history and epistemology of how neural science moved from hypotheses to provable evidence is important for understanding how our brains work, which in turn provides insight into how hominin brains *may* have worked or at least, how they *may* have developed during evolution.

Indeed, during the late 1960s when Morton Fried, Chair of Anthropology at Columbia University, approached biologists Cyrus Levinthal[1] and Eric Kandel about sharing lab space and working with Professor Ralph Holloway on the quantitative histology of the cerebral cortex of various primates, including humans, they replied

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[1] *Levinthal was a molecular biologist who made significant discoveries in molecular genetics*

in the negative. According to Holloway, Levinthal and Kandel responded as follows: "If we do not know what is happening in the brain of *Aplysis* [a sea-slug], how could we possibly learn anything from the primate brain? No.'" (Holloway 2008:4). However, Kandel, also a physician, would later do a complete volte face as indicated by his quote on the preceding page, and in 2000, he received the Nobel Prize in Physiology/Medicine for his research on the physiological basis of memory storage in neurons.

Neuroscience – A Brief History

Neural science emerged during the mid-1900s following the invention and development of the transmission electron microscope, which provided the ability to study the central nervous system at the cellular level. It embraced an interdisciplinary approach that combined molecular biology, neuroanatomy, electrophysiology, and cell and developmental biology, from which it greatly benefitted (Kandel 2013b:3). However, interest in the brain can be traced back to the Egyptians, continued with the Greeks and expanded into other Western cultures, although the ideas and theories of these early 'neurologists' could be neither validated nor refuted prior to the invention of the first microscope in 1590. Furthermore, the study of the brain seemed to lie with philosophers until the 18th century. Although, there was *some* level of crude experimentation on severed heads at the guillotine during the French Revolution, the noteworthy achievements in neural science did not occur until the 19th century when the study of the brain was wrestled away from philosophers to be studied via a more scientific approach.

In 1800, the German neuroanatomist Franz Joseph Gall proposed the notion that the brain did not function as a single organ but was rather the composite of many organs that worked together. He argued that there were at least 27 distinct regions (or organs) of the cerebral cortex,[1] each controlling specific functions (Kandel and Hudspeth 2013:7). Although he was largely correct in that there are indeed different regions which correlate with various functions of mind and body, he did not consider how these various neural areas might work together (as 'association cortices') and/or influence one another, nor did he envision the possibility of brain plasticity.[2] Nevertheless, Gall's theory of cerebral localization, which sets forth how these regions are specialized for different mental and physical processes is now one of the 'cornerstones' of modern neural science (Kandel and Hudspeth 2013:10).

Neural Research from Brain Impairments

Given that invasive experiments cannot be performed (ethically) on humans, biologically based research on cognitive function during the 19th century was largely limited to human brain impairments caused by lesions, other brain afflictions, and/or cranial accidents affecting the brain. One of the most infamous cranial accidents occurred in 1848, in Cavendish, Vermont USA, involving a 25-year-old railway worker named Phineas Gage. Prior to his accident, Gage was reputed to be intelligent, responsible, and socially well-adapted with a good work ethic (Damasio *et al.* 1994; Pinker 2002; Carter 2009; Swaab 2014). He was excavating the terrain for future railroad tracks by drilling holes into the rocks to be removed, then inserting explosive powder into the hole, followed by a long fuse then sand as a buffer to allow the tamping iron to compact the explosive powder for maximum effect. The fuse would then be lit to trigger the explosion. Gage was momentarily distracted and failed to realize that his assistant had not properly covered the explosive powder with sand when Gage began to tamp the iron rod directly onto the explosive powder. As a result, he inadvertently ignited the powder and the ensuing explosion sent the

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[1] The cerebral cortex is the outer grey matter, covering the two cerebral hemispheres.

[2] Plasticity is the brain's ability to change and reorganize its functions

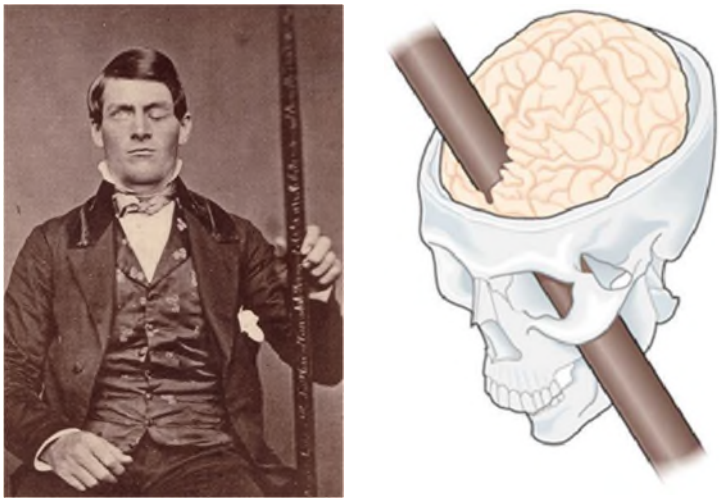


Fig. 1.1 Phineas Gage, with the tamping iron
Olson and Colby 2013:404

109-cm long and 3-cm thick iron rod directly through Gage's left check and the left frontal lobe of his brain, then exited through the top of his skull, landing several metres away (Damasio *et al.* 1994). Although stunned, he remained fully conscious. The impalement left him blind in his left eye, but his intelligence, perception, memory, language skills and motor functions appeared to be intact. However, Gage became rude, unreliable and shiftless (Pinker 2002; Carter 2009; Swaab 2014). He no longer cared for social conventions, often using profanity and offending others, and he had no sense of responsibility (Damasio *et al.* 1994). According to Damasio *et al.*, "Gage exemplified a particular type of cognitive and behavioural defect caused by damage to ventral and medial sectors of prefrontal cortex" (1994:1103). Research also suggests that the damage from the accident likely severed numerous neural pathways, possibly disconnecting sub-cortical structures such as the thalamus, the striatum and the amygdala from the frontal lobes (Thiebaut de Schotten *et al.* 2015:4817). Although it was a most unfortunate accident for Gage, it provided great insight into the various functions, structures, and connectivity of the brain, at the time.

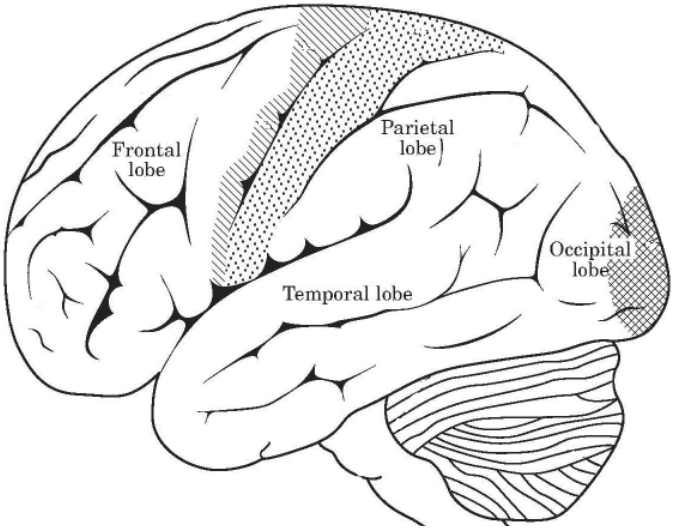


Fig. 1.2 Left View: Lobes of the Brain
Stout et al. 2000:1219

The various and diverse mental processes which predominantly direct and control behaviour lie in the frontal lobe, specifically within the prefrontal cortex (Olson and Colby 2013, Swaab 2014). These processes – both emotional and cognitive – control behaviour in various ways by working through a pathway that begins in the orbitofrontal-ventromedial prefrontal cortex (OF-vMPFC) and extends to the dorsolateral prefrontal cortex (DLPFC), followed by the premotor cortex (PM) and ultimately to the primary motor cortex (M1). Patients with damage to the prefrontal cortex are typically unable to function effectively in daily life, primarily due to the abnormality of their emotional state and disorganized behaviour (Olson and Colby 2013). Injuries, such as those incurred by Gage, to the orbitofrontal-ventromedial area of the frontal lobe produce emotional abnormalities which are especially pronounced and sometimes, the emotional control of behaviour is severely affected (Ibid:407). These conditions make it very difficult for impaired patients to fit in with society, and Swaab has stressed how one of the most important functions of the prefrontal cortex is to ensure that we conform to social norms (Swaab 2014).

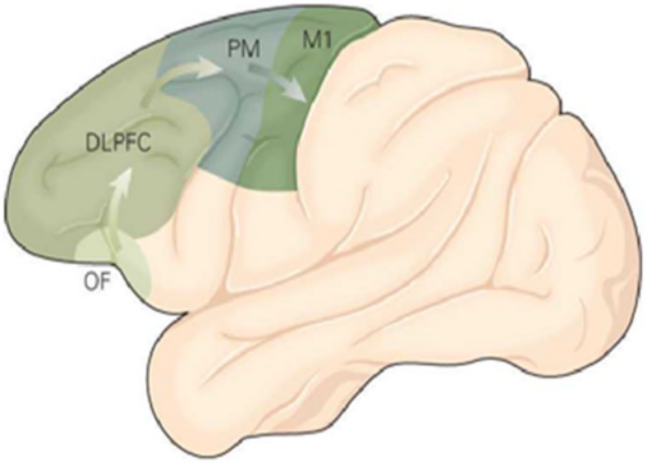


Fig. 1.3 Regions of the frontal lobe
Olson and Colby 2013:403

Broca, Wernicke, Jackson, Fritsch & Hitzig, and Brodmann

In 1861, thirteen years following Gage's accident, French physician Paul Broca performed an autopsy on the brain of recently deceased Louis Victor Leborgne, who had suffered a debilitating stroke in 1839 when he was only 30 years old, leaving him unable to speak anything other than the single word 'tan' (Kandel and Hudspeth

2013:11, Swaab 2014:243). A language disorder that occurs as the result of the destruction of brain tissue is commonly referred to as 'aphasia'. At the time, Leborgne suffered no physical nor other mental impairments. His mouth, tongue and vocal cords were fine, and he could still understand language but had lost his cognitive ability to speak. However, over time his overall health deteriorated, and he soon lost the use of his right arm. Then, his right leg became paralyzed, which was followed by vision impairment. After he died, a biopsy of his brain revealed a large lesion in the posterior region of the inferior frontal gyrus in the left hemisphere, roughly in Brodmann areas 44 and 45, which became known as Broca's area (see Figure 1.4). In total, Broca examined the brains of eight patients who had suffered from aphasia, and brain lesions were found in the same region of all eight patients, which led Broca to conclude that we spoke with the left side of our brains (Kandel and Hudspeth 2013).

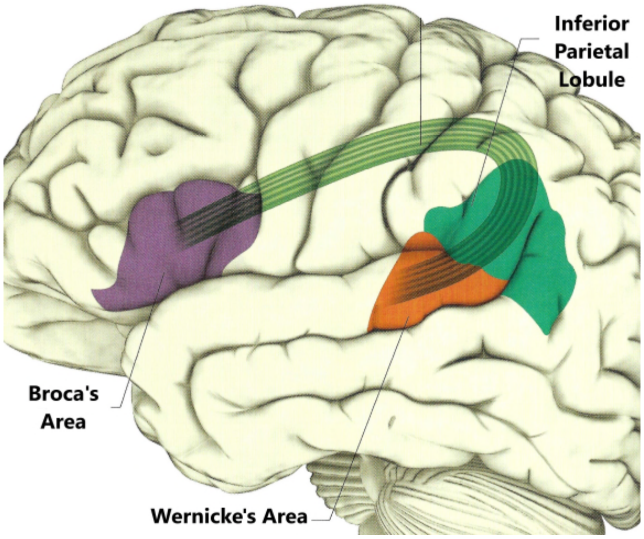


Fig. 1.4 Broca and Wernicke areas
Left lateral (outer) view of Brain
Carter et al. 2009:148

Additional research of the brain's connection to language disorders was pursued by Karl Wernicke. Whereas Leborgne and Broca's other patients were unable to speak, Wernicke's patients suffered from a different type of aphasia: they could speak words but did not understand language in terms of syntax and semantics. The brain lesions that correspond with this type of cognitive disability were discovered in the posterior portion of the temporal cortex where the temporal lobe meets the parietal and occipital lobes, now known as Wernicke's area. Broca's area and Wernicke's area communicate with one another primarily via the arcuate fasciculus ('curved bundle'), which is the primary section of a bidirectional pathway connecting the posterior temporal cortex and inferior parietal cortex to regions in the frontal lobe. Wernicke believed that the regions of the brain were not only specialised as per Gall's theory of cerebral localization, but also that the components of a particular behaviour were generated and processed in several of these different areas of the brain and their referent interconnections, which he referred to as "distributed processing," another founding principle of today's modern neural science (Kandel and Hudspeth 2013:12).

In response to the research on language disorders and their connection to various neural regions, there were also investigations during this time regarding the associations between specific areas of the brain and corresponding actions or behaviours. During the mid to late 1800s, the English neurologist John Hughlings Jackson studied the seizures of his epileptic patients and observed that the spastic involuntary movements caused by an epileptic seizure always spread through the patient's body parts sequentially, although the sequence varied from patient to patient. He named this sequential pattern the "Jacksonian March" and he suggested that the spasms were directly related to neural activity that originated in the region along the central sulcus (later known as the motor cortex). He further proposed that as the epileptic seizure moved through specific sub-regions of the brain, it caused spasms in the body parts which correlated with these sub-regions, neurologically (Kalaska and Rizzolatti 2013:836). He was correct, of course, and his argument for the localization of functions that correspond with the different regions of the cerebral cortex further supported the work of Broca, as well as Wernicke's argument for distributed processing.

Also during this time, experiments providing evidence of brain lateralisation came from Fritsch and Hitzig, who successfully demonstrated in 1870 how movement in a dog's limbs could be produced by stimulating a region in the left hemisphere of the brain with a small electric shock, which would send a neuronal transmission to execute the movement in the right side of the dog's body (Kandel and Hudspeth 2013:11). From these experiments and Broca's work, the hypothesis was made that the left hemisphere of the brain controls the right side of the body and vice versa.

Shortly after Broca and Wernicke convinced the scientific community that specific regions of the brain correspond with both the speech and comprehension of language, the various areas of the brain that correlated with the control of voluntary movements were then identified and mapped, such as the primary sensory cortices for vision, audition, somatic sensation, and taste. However, in spite of the compelling evidence provided by Broca, Fritsch, Hitzig and Wernicke for Wernicke's theory of distributed processing, it remained the consensus during the 19th century that emotion could only be the result of the entire brain – a perspective that did not change until the latter 20th century (Kandel and Hudspeth 2013:16).

During the early 1900s, a new movement was founded in Germany, which sought to establish the regions of the brain based on the structures of nerve cells and variations in their layered arrangements, as well as their associated functions (often referred to as 'cytoarchitecture'). This movement was led by Korbinian Brodmann who was influenced by the neural advancements demonstrated in Karl Wernicke's work. Accordingly, Brodmann divided the cerebral cortex into 52 separate regions based on function and cytoarchitecture (Kandel and Hudspeth 2013:12-13). Figures 1.5 and 1.6 illustrate some of these Brodmann areas from both a lateral (outside) view as well as a medial (inner) perspective of the left hemisphere. Although Brodmann's brain mapping is still used today, it is continually updated as many more functional regions and subregions have been discovered since Brodmann's time. By 2005, approximately 150 distinct cortical areas had been determined in the human brain (Schoenemann 2006:383), and shortly thereafter, a total of 478 functional areas were identified via fMRI studies (Strotzer 2009:182).

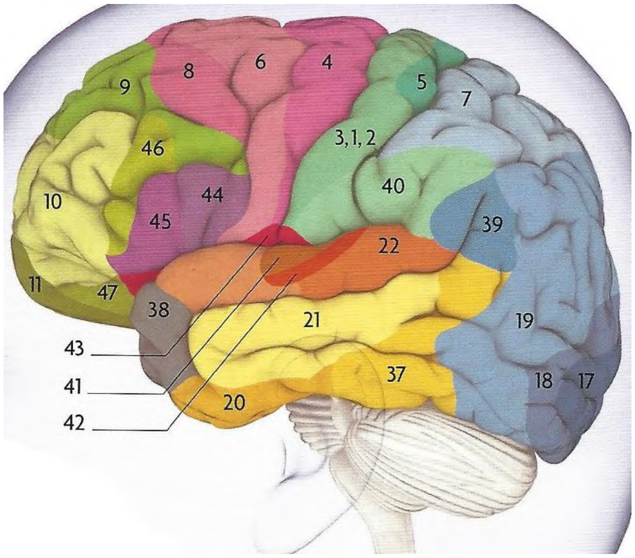


Fig. 1.5 Brodmann areas, lateral (outer) view
Carter et al. 2009:67

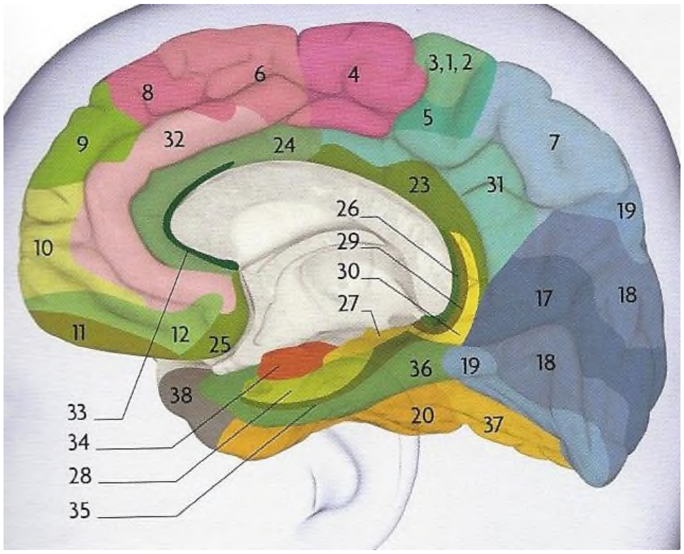


Fig. 1.6 Brodmann areas, medial (inner) view
Carter et al. 2009:67

Although Kandel and Hudspeth concede that the neural regions that originate and process emotion (which lie deep within the temporal lobe) have not been mapped as *precisely* as the systems for sensory, motor and cognitive abilities, they stress how distinct emotions have been successfully elicited by stimulating specific regions of the brain on both experimental animals and humans (2013:13). They additionally note that the localization of these various areas governing the seat of emotion have been very effectively demonstrated in patients with either (i) certain language disorders; or (ii) a particular type of epilepsy that affects the regulations of affective states. During the 20th century, an abundance of compelling evidence for distributed processing came largely from experimentation on various animals, and by the latter half of the century - the importance of the cellular connectivity of these various regions was also realized, as well as the plasticity of the brain. According to Kandel and Hudspeth:

> ". . . all cognitive abilities result from the interaction of many processing mechanisms distributed in several regions of the brain. Specific brain regions are not responsible for specific mental faculties but instead are elementary processing units. Perception, movement, language, thought, and memory are all

> made possible by the interlinkage of serial and parallel processing in discrete brain regions, each with specific functions (2013:17)."

However, brain mapping is not hard-wired, and cortical mapping can change based on an individual's experience and environment (Kandel 2013c:378). For example, owl monkeys were trained to touch a rotating disk with the tip of their middle fingers for food. Following several months, it was observed that the area of the cortex that corresponds to the tip of the middle finger had greatly expanded whilst the cortical areas that correlate to the other phalanges had been proportionately reduced (Ibid). Thus, cortical areas that correspond to limbs or fingers that cease to be used will shrink. In another study involving several monkeys, the nerves to one of the arms were severed, rendering the arm completely useless (Ibid). The monkeys were studied for 10 years or more. In all of the monkeys, the cortical area that represented the face had expanded into the adjacent area of the cortex that had previously correlated with the arm before the nerves were severed.

Kandel asserts that it was through the combination of molecular biology, neurophysiology, anatomy, developmental biology, and cell biology in concert with the study of cognition, emotion, and behaviour in animals and people, that produced what Kandel refers to as a "new science of the mind" (2013b:4). The advances in molecular biology correspond primarily to both the capabilities and connectivity of neurons and neural circuits, whilst advanced imaging technology has made it possible to not only view and image neuronal activity within the brain, but also the means to conduct experimentation by manipulating the electrical activity of neurons and neural circuits to alter behaviour in living human beings (Kandel 2013a:xli).

There are numerous neural imaging devices available today for observing the human brain engaged in various activities, some of which are particularly relevant to the aims of this thesis and will be described below. The following technologies have been employed with modern human subjects to research brain lateralisation, handedness, and/or the regions of the brain engaged during both Oldowan and Acheulean tool-making.

Cerebral Functional Imaging

The neural correlates of the somatic sensory system were initially established early on using very simple tools, such as a rubber reflex hammer, a needle or pin, a tuning fork and some cotton (Kandel 2013c:376). Today's brain imaging technologies can not only identify neural circuits with respect to behaviour, but also examine the *interconnected* brain regions that specifically correspond to various mental processes such as seeing, hearing, feeling, moving, talking, and thinking (Small and Heeger 2013).

To be clear, most functional imaging technologies do not measure neural activity but rather reflect the areas of high energy metabolism in the brain. Although energy metabolism is best defined as the rate at which mitochondria produce adenosine triphosphate ('ATP'), the direct imaging of ATP production is difficult. However, functional imaging can assess the various *correlates* of energy metabolism based on the relationship between haemoglobin (blood flow with oxygen), deoxyhaemoglobin (blood without oxygen), and brain metabolism, which requires oxygen for energy (Clarke and Sokoloff 1999; Small and Heeger 2013). About half of a neuron's energy metabolism is consumed in the basal (resting) state to maintain the resting membrane potential (Small and Heeger 2013). As a result, any change in this membrane potential will signal a change in the rate of energy metabolism.

Oxygen and Brain Metabolism

The brain's consumption of oxygen provides the energy required for its physicochemical activity. The brain utilizes oxygen at a very rapid rate and is also dependent upon uninterrupted oxidative metabolism for maintenance of its functional and structural integrity. Although the average sized modern human brain only weighs 1,400 ml, or approximately 2% of total body weight, it accounts for 20% of the body's total consumption of oxygen during a basal state and even more during active states (Clarke and Sokoloff 1999.). Since the oxygen stored in the brain is extremely small compared with its rate of utilization, the brain requires continuous replenishment of oxygen via circulation.

If cerebral blood flow is interrupted completely, consciousness is lost within less than 10 seconds. A 50% drop in cerebral blood flow from its normal rate is sufficient to cause loss of consciousness, which triggers numerous reflexes and other physiological mechanisms to sustain adequate levels of arterial blood pressure at the head level (Ibid). There are also mechanisms that adjust and regulate cerebral blood flow in accordance with changes in cerebral metabolic demand to maintain homeostasis of these chemical factors in the local tissue.

PET Scans

Positron emission tomography ('PET') uses short-lived radioactive isotopes to produce three-dimensional, colour images of the biological functional processes within the body (Stout *et al.* 2000; Small and Heeger 2013; Nordqvist 2015). Although the first human positron imaging device was developed in the 1950s to detect brain tumours using sodium iodide, it was not until the late 1980s that the technology of these early devices had been improved to a level whereby PET scans could be used to observe the specific activated areas of the brain at a high resolution whilst human subjects were engaged in certain cognitive tasks involving thought and language (Small and Heeger 2013). The activated areas illuminated under a PET scan are actually clusters of annihilated positrons.

When a human subject undergoes a PET scan, s/he is first injected with a radioactive isotope such as carbon 11 (^{11}C), fluorine 18 (^{18}F), oxygen 15 (^{15}O) or nitrogen 13 (^{13}N), all of which contain unstable radionuclides and emit positrons that serve as a radiotracer in the body. For brain imagery, the ^{15}O radiotracer is used, which is 'tagged' with a *natural* substance such as glucose, water or ammonia which are also found in and used by the body. Following injection, the radiotracer will go to the specific area of the body that uses the tagged natural chemical for energy (Nordqvist 2015). Each decaying nucleus in an ^{15}O radionuclide emits a positron, which travels a short distance before it collides with an electron, after which they are both annihilated (Stout *et al.* 2000; Small and Heeger 2013). Upon annihilation, two gamma rays are emitted that travel in opposite directions. Thus, the site of positron annihilation imaged may be a few millimetres from the site of origin (Oldendorf 1980; Stout *et al.* 2000; Small and Heeger 2013).

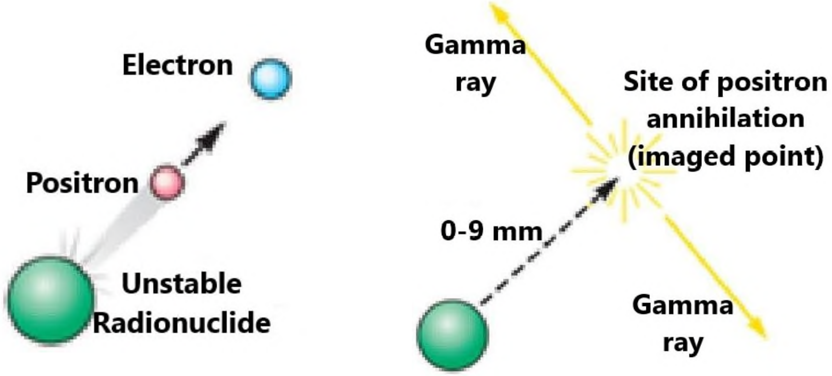


Fig. 1.7 Positron finds/collides with electron resulting in annihilation
Small and Heeger 2013:428
Modified by Suzi Wilson

The patient lays horizontal on the table of the PET scanning machine, with his/her head inside a large circular device containing the gamma ray detectors. As the two gamma rays are *simultaneously* emitted in opposite directions upon the annihilation of the positron, the annihilation is detected by the ‘coincidence detectors’ which only record these simultaneous events. These gamma ray pairing events are then pinpointed by cumulating the collective coincident gamma rays in multiple slices. The clusters of annihilations thereby indicate the enhanced neural activity which is then mapped onto the final PET image. The red and yellow areas indicate high levels of activity but not as high as white, which indicates the highest points of activation. The blue and grey areas indicate minimal activity. PET scans are frequently used in combination with magnetic resonance imaging (MRI) scans and/or X-rays.

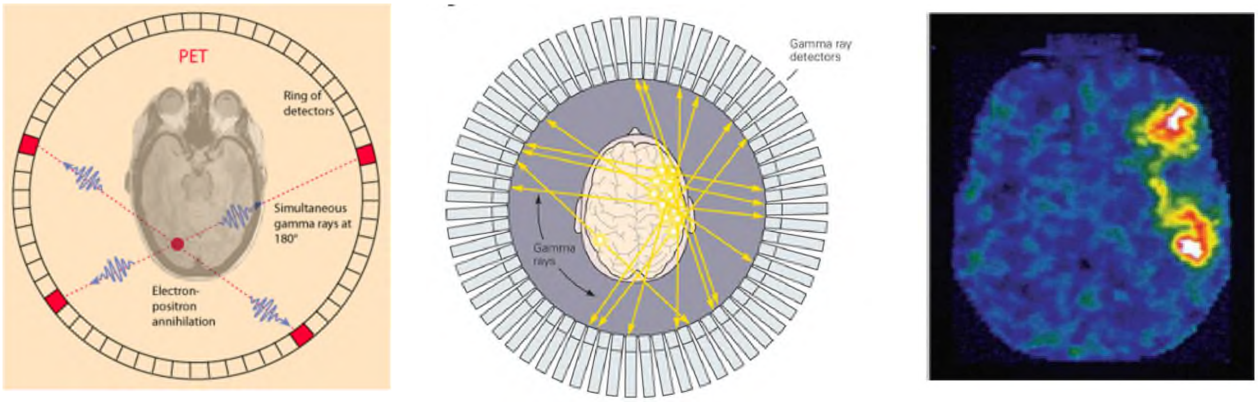


Fig. 1.8 Gamma ray detection and clusters on PET scan imagery Small and Heeger 2013:429

Pet Scans and Archaeology

In 1997, archaeologists Dietrich Stout, Nicholas Toth and Kathy Schick initiated an experimental program, in cooperation with the Indiana University School of Medicine, which used PET scans to determine which areas of the brain displayed heightened activity during Oldowan stone tool production (Stout *et al.* 2000). Toth, an expert flint knapper with over 20 years of experience in making stone tools, was injected with ^{15}O as the appropriate radioactive isotope tracer for tracking the increased blood flow carrying oxygen to the brain (Ibid:1216). The activated areas of the brain are listed in Figure 1.9. These results and others involving Acheulean

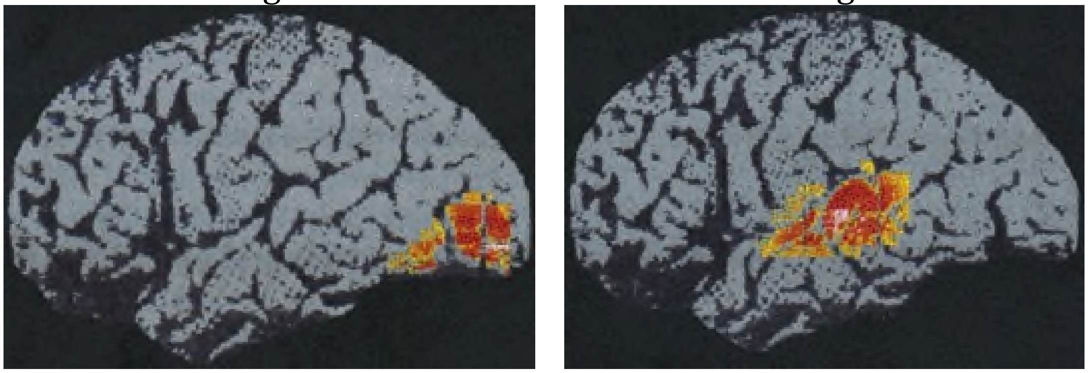
Location	**Brodmann Area**	**General Function**	**Hemisphere**
Superior parietal	7	Spatial cognition	Left
Superior parietal	7	Spatial cognition	Right
Inferior parietal	40	Visualization, motor imagery	Left
Inferior parietal	40	Visualization, motor imagery	Right
Precentral gyrus	4	Primary motor processing	Left
Occipital lobe	19	Secondary visual processing	Left
Occipital lobe	19	Secondary visual processing	Right
Fusiform gyrus	37	Visual association	Right

Fig. 1.9 Areas activated during toolmaking Stout et al. 2000:1217

toolmaking will be discussed further in chapters 2, 6, and 7.

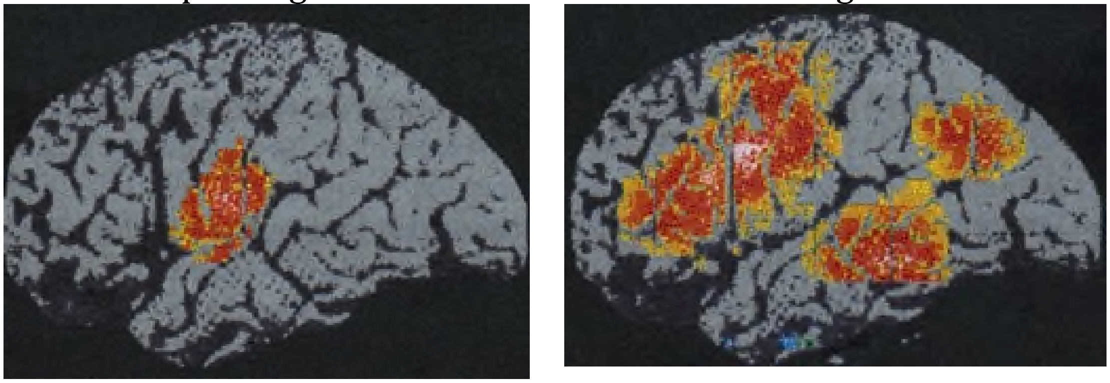
In the late 1990s, Cathy Price also performed several experiments using PET scans to observe the Broca and Wernicke regions, as well as other activated regions of the brain, when the participants were asked to engage in specific activities and mental processing (2000). The four activities/mental processes with the accompanying scans that correspond with each action observed by Price were:

> A. Subjects silently read a word, which produced a response in the primary visual cortex and the visual association cortex.
>
> B. The same word was read aloud to the subjects, which activated Broca's area, the temporal cortex, and the temporal-parietal cortex, where Wernicke's area is found.



A. Looking at Words

B. Listening to Words



C. Speaking Words

D. Thinking of Words

Fig. 1.10 Pet scans of viewing, listening, thinking and speaking operations
Cathy Price 2000:348
Kandel and Hudspeth 2013:13

C. Subjects were asked to speak the word, which engaged Broca's area and the supplementary motor area of the medial frontal cortex.

D. Subjects were asked to consider the word 'brain' with an appropriate verb (such as 'think' or 'remember'), which activated the frontal cortex as well as Broca and Wernicke's areas. These areas also play a role in all cognition and abstract representation (Price 2000; Kandel and Hudspeth 2013).

PET Scan Limitations

The spatial resolution of a PET scan is limited to approximately between six and eight millimetres (Small and Heeger 2013), and PET scans are somewhat invasive in that they require the subject (or patient) to be injected with a radioactive substance. Additionally, the temporal resolution of PET imaging is dependent upon the rate at which positrons are emitted, which can range from minutes to hours depending on the radionuclide and its associated compound (within which it is contained).

Functional Magnetic Resonance Imaging (fMRI)

Magnetic resonance imaging ('MRI') scanners generate magnetic fields and radio waves via electrical current and magnetic components to create detailed images of the organs and tissues within the body (Small and Heeger 2013; Lam 2016; Shohamy and Turk-Browne 2021). This is accomplished via the magnetic properties of hydrogen atoms in the water within the body.

The most important component of the scanning device is a powerful superconducting magnet, quantified in Tesla (T) units with newer machines typically employing 3T, although there are some machines with magnets as powerful as 7T (Shohamy and Turk-Browne 2021). This super-magnet produces a very robust and uniform magnetic field which affects the water protons in the body when the subject is placed in vertical alignment with the magnetic field (Small and Heeger 2013;

Shohamy and Turk-Browne 2021). The body is largely composed of water molecules, and each molecule contains two hydrogen protons. These water protons act like tiny magnets as they revolve around their respective axes in their own tiny magnetic fields. Although they typically move in random directions (different for each proton), once the subject lies down on the table inside the 'bore' of the MRI machine, the super-magnet will force the body's water protons into vertical alignment within its powerful magnetic field.

The second most important component is an electric radiofrequency coil which is a specially designed coil placed near the subject being scanned. A radiofrequency signal then transmits 'pulses' through the subject in a horizontal direction, to create another magnetic field perpendicular to the vertical magnetic field of the super-magnet and water protons (of the subject). This weaker horizontal magnetic field generated by the radiofrequency coil creates a ‘pull’ on the water molecules, but in a different direction. As this 'pull' alters the alignment of the water protons, they begin to ‘wobble’ (or 'precess') around their axes in sync with one another in a rotating motion referred to as ‘precession' or 'resonance.' This resonance, in turn, sends back a current to the coil (same principle, but in reverse)[1], which is what is measured in MRI (Small and Heeger 2013; Shohamy and Turk-Browne 2021). The horizontal magnetic field is then turned off, and the water protons, rotating in precession/resonance, quickly fall out of sync with one another (‘de-

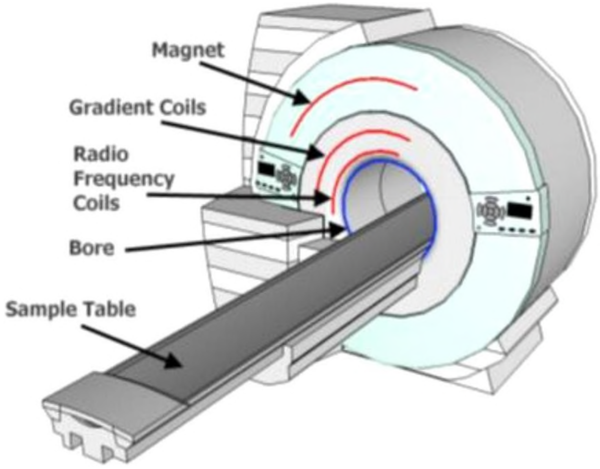


Fig. 1.11 Schematic drawing of an MRI machine
Haynes 2014:258

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[1] *This is somewhat akin to how geomagnetic polarity leaves its mark in the geologic record, when there is a reversal of polarity.*

phasing'), which causes a decrease ('decay') in the measured current. They then re-align themselves ('recovery') with the vertical magnetic field, which occurs at a slower rate than decay. The entire process is repeated several times as the radiofrequency coil is turned on and off to create a series of measurements that reflect the changes in the rate of decay and recovery.

Diseased tissue, such as tumours, can be detected because the water protons in different tissues de-phase at different rates. Three-dimensional images are produced by the various magnetic gradient coils within an MRI scanner that enable the measurement of the MRI signal at multiple locations. Each of these correspond to a small volume of tissue which is produced as a voxel (a three-dimensional pixel) in the MRI imagery.

When scanning neural activity, fMRI blood oxygen level dependent ('BOLD') is used. This technique measures the changes in water protons as they react to changes in deoxyhaemoglobin (i.e., haemoglobin without oxygen) within the magnetic field. When neural activity increases, there is a corresponding increase in the amount of blood flow to the activated regions of the brain. As metabolism is increased in these activated regions, the flow of oxygenated blood (i.e., the delivery of oxygenated haemoglobin) is greater than the consumption of oxygen in these regions leading to a decrease in deoxyhaemoglobin, which therefore results in a greater proportion of oxygenated to deoxygenated haemoglobin.

Fig. 1.12 MRI scanner in the New York Hospital for Special Surgery
www.hss.edu/condition-list_mri-magnetic-resonance-imaging.asp

Haemoglobin contains iron which is exposed when the oxygen is removed from the haemoglobin molecule, and the presence of deoxyhaemoglobin causes an inhomogeneity in the nearby magnetic field. As a result, oxygenated and deoxygenated haemoglobin have different magnetic properties, and water protons which are near a deoxyhaemoglobin molecule experience a magnetic field with a slightly different strength than the other water protons (Small and Heeger 2013; Shohamy and Turk-Browne 2021), thus creating the imagery of activated brain regions with deoxygenated haemoglobin, which are captured on an fMRI scan.

fMRI Limitations

Deoxyhaemoglobin cannot be measured in absolute terms and is dependent upon the interaction between and among cerebral blood flow, cerebral blood volume and the basal state of the brain region being imaged, and additionally - basal states vary from one cerebral region to another. Thus, in any two regions of the brain, different basal states might produce different BOLD responses, even if there are identical changes in oxygen metabolism in both regions. As a result, assuming that the differences in the BOLD responses directly reflect the corresponding changes in oxygen metabolism and neural activity could lead to false conclusions.

fMRI and Archaeology

Subsequent to the PET scan studies previously mentioned, additional studies were performed using fMRI as a means to better gauge between the neural structures involved in Oldowan versus Acheulean industries, as well as those employed by novice versus expert toolmakers (Stout et al. 2010; Stout et al. 2015). The results of these studies will be discussed further in Chapters 6 and 7.

Functional Trans-Cranial Doppler (fTCD)

Although fTCD is not well known and considerably less popular than PET scans or MRIs, it is often employed for studies regarding the lateralisation of the brain (i.e., determining which hemisphere is dominant for a particular task or mental process). For this reason, it is pertinent to the aims of this thesis, specifically Chapter 3. Functional TCD is similar to other imaging technologies that measure oxygen-depleted blood as a means to detect which brain regions are consuming the oxygen and are thus actively engaged. Through the use of ultrasound, high-frequency sound waves are sent through the brain and bounce off moving red blood cells, for fTCD to measure cerebral blood flow velocity (Knecht 2000; Willie *et al.* 2011; Hage *et al.* 2018).

Transducers, which produce the ultrasound waves, are typically placed (externally) on the left and right temporal regions above the zygomatic arches (cheekbones), although fTCD can also be performed through the eyes, below the jaw and the back of the head (Willie *et al.* 2011). These cranial areas offer the least distortion to the sound waves, whilst other regions where the skull is thick can block the transmission. For example, in the brain lateralisation study by Knecht *et al.* (discussed in Chapter 3), approximately 3% of the subjects had to be excluded due to inadequate sonographic penetration of the cranium (2000:2513). The regions of the cranium which are less difficult to penetrate are often referred to as 'windows' (Willie *et al.* 2011; Hage *et al.* 2018.)

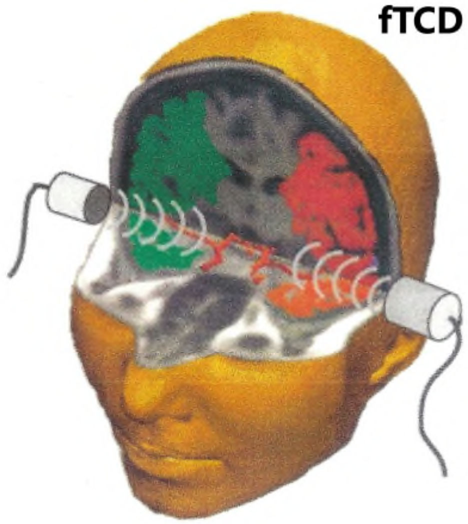

Fig. 1.13 Illustration of fTCD procedure Knecht et al. 2000:2514

The change in cerebral blood flow velocity is correlated with changes in cerebral oxygen intake which enable fTCD to measure brain activity and lateralisation with high accuracy (Hage *et al.* 2018:1). The procedure is non-invasive as well as painless, and subjects are alert and usually participate during an fTCD session. For example, in the lateralisation study by Knecht *et al.*, a letter would appear on a computer screen and the subjects were told to think about all the words that began with that letter, but not speak. Then, the procedure would be repeated with the subjects speaking the words rather than only thinking of them. As a result, Knecht *et al.* used fTCD to determine what percentage of their study population were left-hemisphere dominant for language versus right-hemisphere dominant (Knecht *et al.* 2000:2514).

fTCD Limitations

Sometimes, the crania of the patients/subjects are too thick in all of the potential 'windows,' and thus prevent the penetration of ultrasound transmission.

fTCD and Archaeology

Uomini and Meyer have used fTCD for brain lateralisation studies to investigate the possible correlation between language and the making of Acheulean stone tools.

Functional Near-Infrared Spectrometry (fNIRS) (aka Functional Optical Brain Imaging)

Although fNIRS is a relatively new means for imaging the brain, the underlying principle for taking fNIRS measurements was initially developed in 1977 (Naseer and Hong 2015; Ferrari and Quaresima 2021), which was ultimately developed into a new scanning technology in 1992 (Ferrari and Quaresima 2021). Functional imaging of activated brain regions is achieved via monitoring blood volume and oxygenation levels, based on changes in near-infrared light. fNIRS imaging operates in a somewhat similar fashion to PET scans with respect to how PET detects and images near positron annihilation. With fNIRS, however, an infrared light is emitted into the scalp, which diffuses through brain tissue and results in the scatter of photons. Some of these photons exit the head after passing through activated regions of the brain where changes in blood oxygenation levels are transpiring, and these photons are then measured using strategically placed near-infrared light emitter-detector pairs (Naseer and Hong 2015). It can thus capture the brain regions activated during motor activity by the participants. fNIRS is relatively non-invasive, safe, portable and offers a low-cost alternative to the other imaging technologies previously mentioned. Although initial fNIRS studies began as early as 2004, the technology continues to develop and seems to be increasingly used in tandem with electroencephalography (EEG) as a hybrid approach.

fNIRS Limitations

There is an inherent delay between the changes in blood oxygen levels and the information transfer rate, similar to the limitations discussed for fMRI. Additionally, fNIRS signals are sensitive to noise, even the sound of the participant's heartbeat, which is variable subject to blood pressure. Thus, any environmental noise should be removed or mitigated prior to imaging.

fNIRS and Archaeology

Putt *et al.* employed fNIRS to investigate the neural structures involved in Oldowan versus Acheulean toolmaking, as well as the possible overlap between toolmaking and language (2017).

Summary/Conclusion

Although the mapping of the cerebral cortex was not validated via scientific evidence until the 20th century (Kandel and Hudspeth 2013), today it is possible to record brain activity in conscious living humans from various regions of the brain, which can demonstrate how cognition is processed from these different areas as part of a large-scale network (Olson and Colby 2013). New discoveries in modern neuroscience continue to progress at an exponential rate, and it is very difficult to stay abreast of the latest developments and break-throughs. Hence, the advancements described herein likely represent only a small percentage of the knowledge that has been acquired over the past several years. The neuroimaging described herein will be referred to in later chapters.

The following chapter provides an overview of the components of the cerebral cortex (outer layer of the brain), with elaboration on the neural regions whose evolution can be seen on brain endocasts, and additionally - the specific cerebral areas evidenced to be involved in the making of stone tools. It will also serve as a basic primer for how certain structures, sub-structures, and association areas of the brain function and work in tandem with one another.

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Chapter 2: Neuroanatomy of The Human brain

During the second half of the 20th century, the central focus of biology was on the gene. Now in the first half of the 21st century, the focus has shifted to neural science, and specifically to the biology of the mind. We wish to understand the processes by which we perceive, act, learn and remember.

Kandel and Shadlen 2021:4

This chapter provides an overview of the human brain with focus on the cerebral cortex, the outer covering of the brain whose sulci and gyri can leave fossil imprints on the cranial bone, from which endocast moulds can be made. These sulci and gyri, if present, can provide insight into the structure of early hominin brains and how they may have evolved and reorganised over the course of human evolution. In the absence of such cranial fossil evidence, we can also consider the behavioural evidence, such as tool-making, which would have required the presence or development of certain neural structures as prerequisites for toolmaking. Both methods require a basic understanding of the functions and neuroanatomical structures of the various regions of the cerebral cortex, as well as the effect of postcranial adaptations on the brain. Although the deeper structures within the brain are incapable of leaving fossil evidence, there will be a cursory overview of their functions because they often work in tandem with the regions of the cerebral cortex.

The crania in the hominin fossil record leave very few imprints, at best, and the identification of the few gyri and/or sulci which can be detected are often heavily debated. Nevertheless, they provide the only available source of *direct* scientific evidence for Palaeolithic cognitive study, however sparse. Additionally, these crania can also provide an estimate of endocranial volume as well as information regarding brain asymmetries and lateralisation (discussed in Chapter 3).

The Modern Human Brain

Modern human brain size can vary between approximately 900 ml and 2,000 ml (although 2,000 ml is a very large brain), with variation among population as well as the sexes (Holloway 2015:828). For example, people who live in the Artic tend to have larger brains than people who live in the tropical climates, although the reason for this is unknown (Ibid). The average brain size in modern humans tends to fall between 1,200 ml and 1,400 ml (Rilling 2006, Holloway 2015, Verendeev and Sherwood 2017).

Brain size is often inappropriately associated with intelligence. For example, elephants and whales possess brains considerably larger than humans (7,500 ml or more for whales), but they likewise have considerably larger bodies. Bigger bodies typically have bigger brains, as the brain acts as a central processing unit for all of the body's various parts, thought processes, and motor operations, thereby coordinating and facilitating these conscious functions, as well as controlling unconscious functions such as digestion and heartbeat. Brains have to be large enough to accommodate the demands of larger bodies, otherwise energy efficiencies and response times would be sluggish and health systems could be endangered, but the bodies of different species have different demands for their respective brains. There have been attempts to compare brain encephalization across different species by creating an algorithm or equation, such as the Encephalization Quotient (EQ), which is a ratio of a species' actual brain volume to the volume expected for its body size (Jerison 1973, Schaik *et al.* 2021). However, species' brains differ from one another in terms of both organisation and content. Specific cognitive structures can be more pronounced in some species than others and likewise, the proportions of white matter (neurons, dendritic branching, fibre tracts, etc.) differs from species to species. Thus, attempting to compare cross-species brains using a methodology based only on allometric differences would be flawed, considering how brains across different species are not merely "allometrically scaled versions of the same generalized design" (Rilling 2006:65).

Yet, when making comparisons *within* a particular 'order' (primates, for example), biologists often study allometric relationships by taking the logs (base 10) of the endocranial volume of the specimens then plotting the results on a graph against the logs of body weight for the taxa studied, which results in a sloping linear progression on the graph. The slope of the line that runs through the data points, as well as the correlation coefficient, are then calculated to measure and observe these relationships. Although these slopes and correlation coefficients will vary depending on the group studied, Holloway notes that as the taxa become similar – the slope typically decreases (Holloway 2015:828).

As early hominins began the transition to bipedalism, their upright posture lifted the cranio-facial morphology, which allowed for both a superior and posterior expansion of the brain (Edelman 2004:102). Quadrupeds, have strong nuchal (neck) muscles that hold and support the head against the force of gravity. Although brain expansion in hominin ancestors was not prevented by this posture, the weight of additional brain tissue would rely on additional support and growth from the nuchal muscles, which would emerge as an adaptive response to heavier heads due to larger brains. Thus, these adaptations would have needed to develop in a concomitant fashion. However, once upright posture was adopted on a regular basis via bipedalism, brain expansion was more easily facilitated without dependence upon other anatomical adaptations.

Additionally, brains achieved growth efficiencies via the folding and compressing of the brain into 'convolutions' which produce the sulci and gyri we seek in hominin endocasts. Brain growth, as with other organs/tissue in the body, is achieved through both hypertropy and/or hyperplasia (Cabello *et al.* 2002). Hypertrophy is the increase in cell size whilst hyperplasia refers to an increase in the number of cells (via mitotic division). For example, fat cells in the body typically grow via hypertrophy; however, the mitotic division of fat cells (hyperplasia) can occur in people who are obese (Garaulet *et al.* 2006).

An average human brain contains as many as 100 billion neurons (nerve cells) and one trillion glial cells (Swaab 2014:3). Initially considered to be the 'glue' that held the neurons together, recent studies have demonstrated that these glial cells also provide support and nutrition for the brain, form myelin[1], and are a crucial part of signal transmission within the brain. It is the interaction of all these billions of brain cells that produce what we know as the 'mind' (Swaab 2014:4), although Kandel stresses that in order to better understand the mind, one must first learn how the signalling pathways of neurons are organized as well as how they communicate via synaptic transmission (2013a:4). Indeed, the 'cell' is the basic building block of all organisms, and understanding the capabilities and functions of these neurons and glial cells is crucial for a *comprehensive* understanding of how the brain/mind works, but futile for the aims of this thesis, as Palaeolithic brain tissue is unavailable for study.

Anatomical Directions

The following are the 'navigational' terms of anatomy for referencing directions and locations in the body and brain:

Anterior: Toward the front of the body
Rostral: Toward the front of the face, or nose (from rostrum meaning beak-like)
Superior: Above (directionally)
Posterior: Toward the back/rear

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[1] Myelin is a protective sheath around nerves, which facilitates the quick and efficient transmission of electrical impulses. If damaged, these impulses slow down.

Caudal: Toward the tail/rear

Inferior: Below (directionally)

Dorsal: Back/top side from the Latin 'dorsum' (e.g., dorsal fin)

Ventral: Front side (or underside for quadrupeds) of the body from 'venter' meaning 'belly'. In the crania, ventral usually means toward the jaw.

Medial: Toward midline of the body/brain

Lateral: Opposite of medial; away from the midline, toward or on the side.

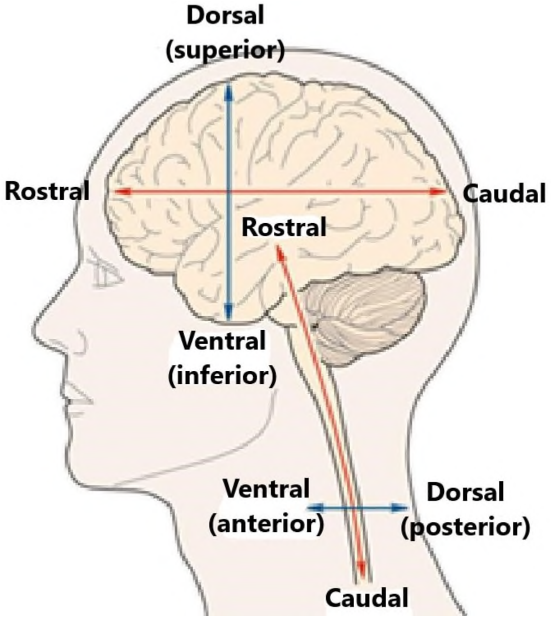
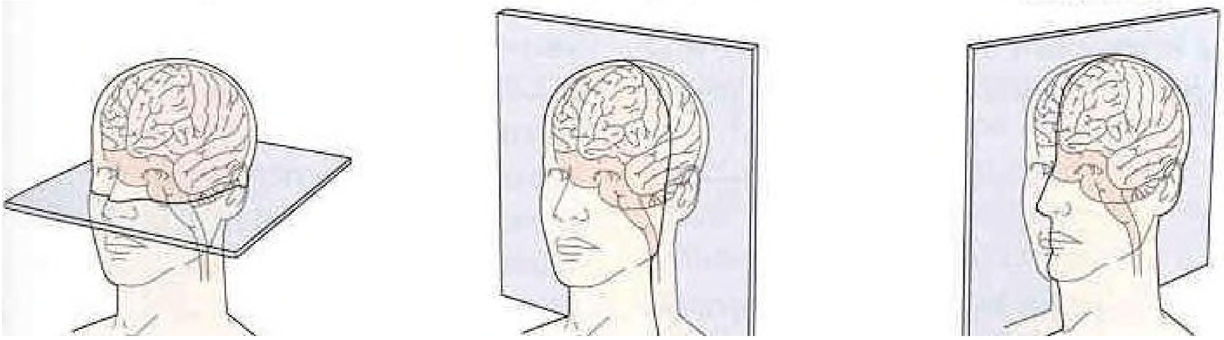


Fig. 2.1 Neuroanatomy navigation terms
Kandel and Shadlen 2021:11
Modified by Suzi Wilson

Planes of the Brain:



Horizontal Plane Coronal Plane Sagittal Plane

Fig. 2.2 Planes of the brain
Kandel and Shadlen 2021:11

The Structures of the Central Nervous System

The central nervous system consists of the spinal cord and the brain. From a broad perspective, the brain can be divided into four sections: the brain stem, the diencephalon, the cerebellum, and the cerebrum. The brain stem is composed of the medulla oblongata, pons, and midbrain, whilst the diencephalon consists of the thalamus and hypothalamus. The cerebrum includes the cerebral cortex, divided into four lobes, and three structures which are located deeper within the brain: the basal ganglia, the hippocampus, and the amygdala. Sometimes, the brain is more broadly divided into three regions: the forebrain, the midbrain, and the hindbrain. The forebrain contains the diencephalon and cerebrum, whilst hindbrain refers to the medulla oblongata, pons, and cerebellum.

Brain Stem

(1) **Medulla Oblongata** – located at the most inferior part of the brain stem and connects with the spinal cord. Helps regulate heart rate, blood pressure, digestion, respiration, and other vital autonomic functions (Kandel and Hudspeth 2013). Also assists with balance, control of neck and facial muscles and neural pathways that correspond with taste and hearing (Amaral and Strick 2013).

(2) **Pons** – just above the medulla and relays information regarding movement and sensation from the cerebral cortex to the cerebellum. The dorsal portion is involved in respiration, taste, and sleep (Amaral and Strick 2013).

(3) **Midbrain** – lies just above the pons and provides informational links between and among the motor system, the cerebellum, basal ganglia, and cerebral hemispheres. The midbrain also corresponds to auditory and visual systems as well as the muscles that control eye movements (Amaral and Strick 2013).

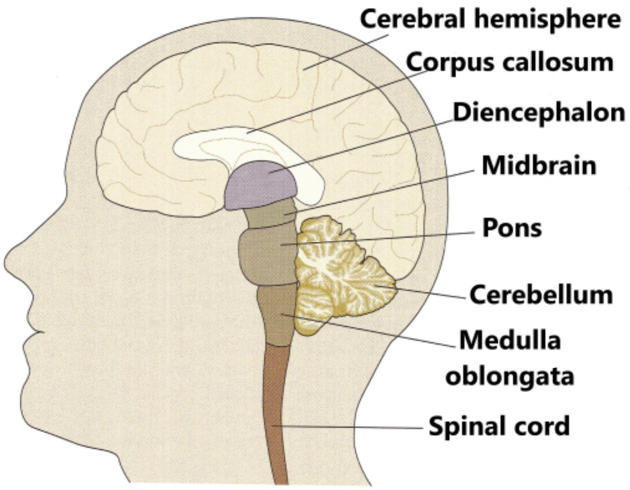


Fig. 2.3 Brain stem and other brain regions
Kandel and Shadlen 2021:15
Modified by Suzi Wilson

Cerebellum

The cerebellum lies caudal to the posterior portion of the cerebral cortex. Until somewhat recently, the main functions of the cerebellum were considered motor coordination and posture, but it has now been revealed how the cerebellum works in tandem with the cerebral cortex and is involved with language and other cognitive functions (Amaral and Strick 2013). It contains approximately 80% of the brain's neurons, which is more than any other single subdivision of the brain (Swaab 2014:270). Additional studies indicate that the *cerebellum* may also be involved in higher cognitive functions (Barton 2012; Swaab 2014).

Diencephalon

The diencephalon is located directly above the midbrain and contains:

(1) Thalamus – serves as a very important information relay system between sensory receptors (other than smell) and regions in the neocortex which process and/or respond to such sensory information (Amaral 2013). The thalamus also connects the cerebellum and basal ganglia to certain regions of the cerebral cortex which are associated with movement and cognition (Amaral and Strick 2013). It is a very important structure for consciousness given that all sensory information (except olfactory) is processed in the thalamus before being relayed to the cerebral cortex (Swaab 2014).

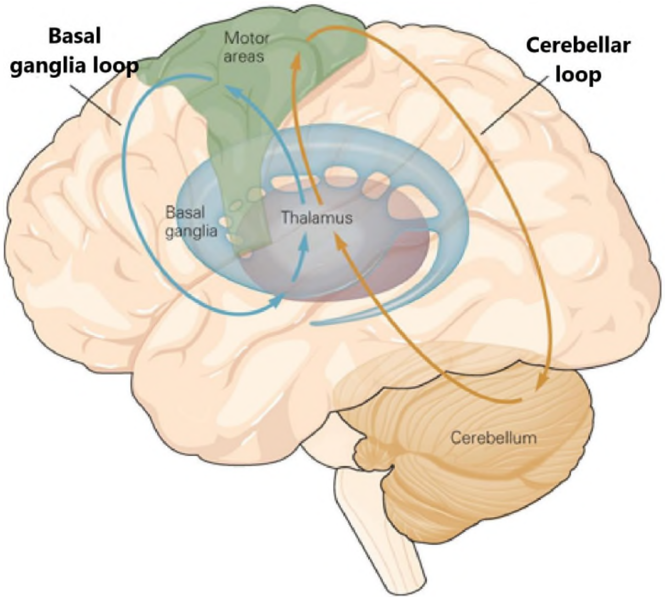


Fig. 2.4 Thalamus, cerebellum, and basal ganglia
Rizzolatti and Strick 2013:416

(2) Hypothalamus – influences several various responses and behaviours via its extensive connections with almost every region of the central nervous system. It lies ventral to the *thalamus* and regulates many processes, such as reproduction, the body's circadian rhythm, body temperature and the secretion of hormones in the pituitary gland (Amaral and Strick 2013; Swaab 2014), and it also plays a role in memory (Swaab 2014). It is responsible for regulating both stress and 'fight-or-flight' response to perceived threats in the environment, and its involvement is crucial in three major systems: (i) the autonomic motor system; (ii) the neuroendocrine system; and the neural pathways that mediate motivated behaviour (Lowell *et al.* 2021).

Cerebrum

The cerebrum consists of the two large cerebral hemispheres (left and right) that lie on either side of the mid-sagittal plane and are connected by a large bundle of nerve fibres called the corpus callosum. The hemispheres are partially separated by a deep groove, known as the median longitudinal fissure. Each hemisphere correlates with sensory and motor processes on the opposite site of the body (i.e. contralateral).

Although the two hemispheres are often depicted as being equal in shape and size, they are not necessarily 'mirrors' of one another as they are neither symmetrical nor structurally/functionally equivalent (Kandel and Hudspeth 2013). Each hemisphere has frontal, temporal, and occipital poles and lateral, medial, or interior surfaces. The medial surface is the middle interior view of the brain, as if sliced down the middle, whilst the inferior surface is the most ventral portion of the brain. The lateral surface, which is the exterior surface area of the cerebral cortex (i.e., the wrinkled outer layer of the cerebrum), can be viewed from either side. In addition to the cerebral cortex, there are three important deep-lying structures within the cerebrum:

(1) Basal Ganglia – plays an important role in motor/movement control and aspects of motor learning (see Figure 2.4) (Amaral and Strick 2013).

(2) Hippocampus – crucial for learning and memory and transfers short-term memory to long-term memory during sleep (Swaab 2014; Amaral and Strick 2013).

(3) Amygdala – involves the expression and reading of emotion and plays a role in our 'fight or flight' response (like the hypothalamus) with respect to our emotional perception of fear whilst also moderating the unconscious physical responses to danger, such as changes in heart rate, breathing, etc. (Kandel and Hudspeth; Swaab 2014; Amaral and Strick 2013). Some psychopaths have been known to have a malfunction in their amygdala, such as Charles Whitman who, in 1966, killed both his wife and mother then climbed the tower at the University of Texas in Austin and fatally shot 14 people whilst wounding 31 others. It was later discovered that Whitman had a tumour in his temporal lobe that was pressing on his amygdala (Swaab 2014:178).

(4) Cerebral Cortex is the furrowed 'grey matter' (as opposed to 'white matter') and outer covering of the cerebrum. It is considered the part of the brain that is most highly developed in humans (Kandel and Hudspeth 2013:5), and thus contains most of the regions of the brain that are responsible for cognitive abilities. The cerebral cortex is deeply folded within its many convolutions of gyri and sulci, and is divided into four lobes which are named for the respective overlying bones of the crania: frontal bone, parietal bone, occipital bone, and temporal bone. These lobes are illustrated in Figure 2.5 as follows: frontal lobe (yellow area); parietal lobe (green area); occipital lobe (blue area); and temporal lobes (red area).

These four lobes will be described in greater detail but from a very broad perspective, the frontal lobe is primarily concerned with short-term memory, the planning of/decision for certain actions, movement (Kandel and Hudspeth 2013), and to ensure that we conform to social norms (Swaab 2014). The parietal lobe corresponds to the various senses, visuospatial integration, body movement (including hand/eye coordination), and our perception of self with respect to body image and relating it to extra-personal space (Kandel and Hudspeth 2013; Bruner *et al.* 2018b). The occipital lobe relates primarily to vision whilst the temporal lobe to auditory abilities. In addition to these four outer lobes, there are also two lobes located deep within the brain referred to as the insular lobe and the limbic lobe.

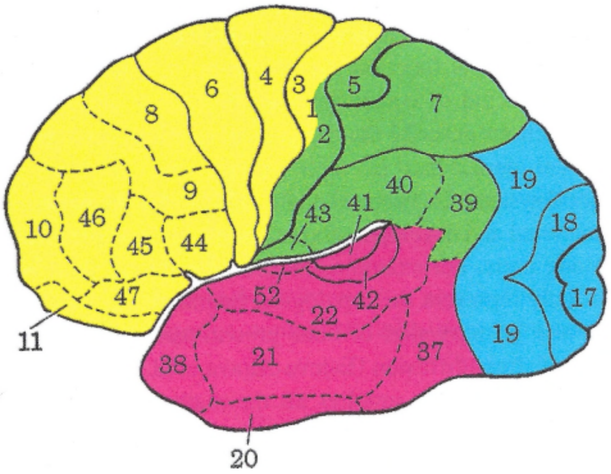


Fig. 2.5 Left lateral view with Brodmann areas
Bruner et al. 2018a:193

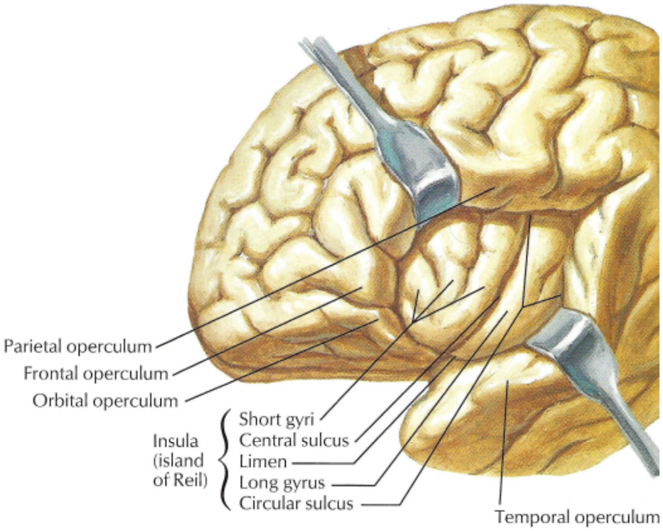


Fig. 2.6 Human insula
Illustration by F.H. Netter
Netter 2011:204

In modern humans, the insular lobe (or insular cortex) is found deeply folded within the lateral sulcus (aka Sylvian fissure); however, prior to hominin brain development, the insula was exposed on the outer layer of the brain (Falk 2014; Hurst 2017; Holloway *et al.* 2018). As the brain reorganised and expanded during evolution, the insula was ultimately operculated (covered) by portions of the frontal, parietal, and temporal lobes (the fronto-parietal-temporal operculum). The insula plays a role in a wide range of numerous functions such as pain perception, self-awareness, speech production, interpersonal experience, and emotional processing.

The limbic *lobe* (from 'limbus' meaning 'edge') was named by Paul Broca in the late 1800s for an arc-shaped region that borders the cerebral cortex and is located deep within the frontal, parietal, and temporal lobes. It is no longer deemed one of the main regions of the cerebral cortex (Amaral and Strick 2013), and today it is more commonly referred to as the limbic association cortex (Olson and Colby 2013). The limbic association cortex is an important region of cognitive function, and the deep-lying structures of the cerebrum (previously discussed) are typically considered part of this cortex.

The Association Cortices

In 1906, the Nobel Prize in Physiology or Medicine was awarded jointly to Santiago Ramón y Cajal and Camillo Golgi for their work on the structure of the central nervous system, specifically functional localisation, and the neuron doctrine (Glickstein 2006). Functional localisation refers to the specific functions of the different areas of the cerebral cortex, and the association areas or cortices, which are several of these localised areas working together.

These association cortices perform complicated tasks, such as organising and integrating information from the different modules[1] of the brain (e.g. auditory, visual, and somatic sensations) which enable the cognitive programming for strategic thinking and appropriate responses to stimuli (Olson and Colby 2013). Accordingly, these regions are crucial for conceiving and developing mental concepts such as

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[1] *By 'modules,' I am referencing regions of the brain, not Mithen's work on 'cognitive fluidity' (1996) or Fodor's Modularity of the Mind (1983).*

those involved in spatial perception and consideration given to objects (Rizzolatti and Strick 2013).

Each of the lobes of the cerebral cortex contain these association cortices which contribute to cognition. The names for these cortical regions are based on the dominant cognitive processing that occurs within that region such as the visual cortex, auditory cortex, and motor cortex (i.e., according to function) (Olson and Colby 2013). These cortex modules are further divided into sub-regions, according to function and/or location. For example, the motor cortex consists of the primary cortex, the premotor cortex, and the supplementary motor area and to some extent, the cingulate motor areas (see Figure 2.7). All association areas have extensive networks or pathways for receiving and sending information – both within and among other the other neural structures of the brain (Olson and Colby 2013).

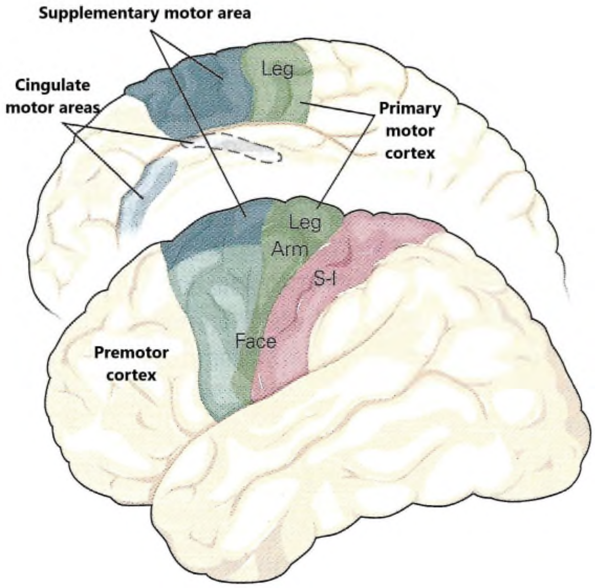

Fig. 2.7 The Motor Cortex in Modern Humans
Scott and Kalaska 2021:820

Neuroanatomical Landmarks

The deeply folded convolutions of the cerebral cortex served as an evolutionary strategy for compacting tissue into limited space as the brain increased in size (Amaral and Strick 2013), and some of the more pronounced sulci can act as landmarks for referencing other regions of the brain. For example, the lateral sulcus is a deep, well-pronounced sulcus which delineates the anterior portion of the temporal lobes from the fronto-parietal regions, whilst another prominent sulcus is the central sulcus, which separates the precentral gyrus (motor functions) in the

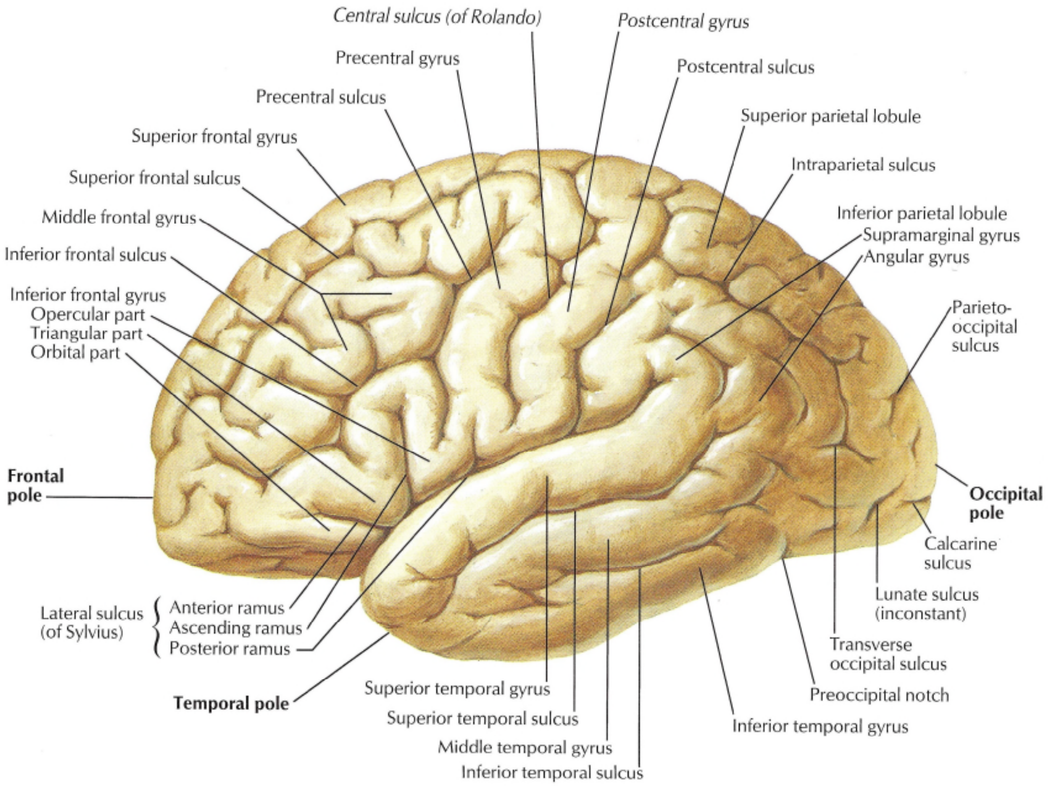

Fig. 2.8 Sulci, gyri, and poles of the human brain
Illustration by F.H. Netter
Netter 2011:104

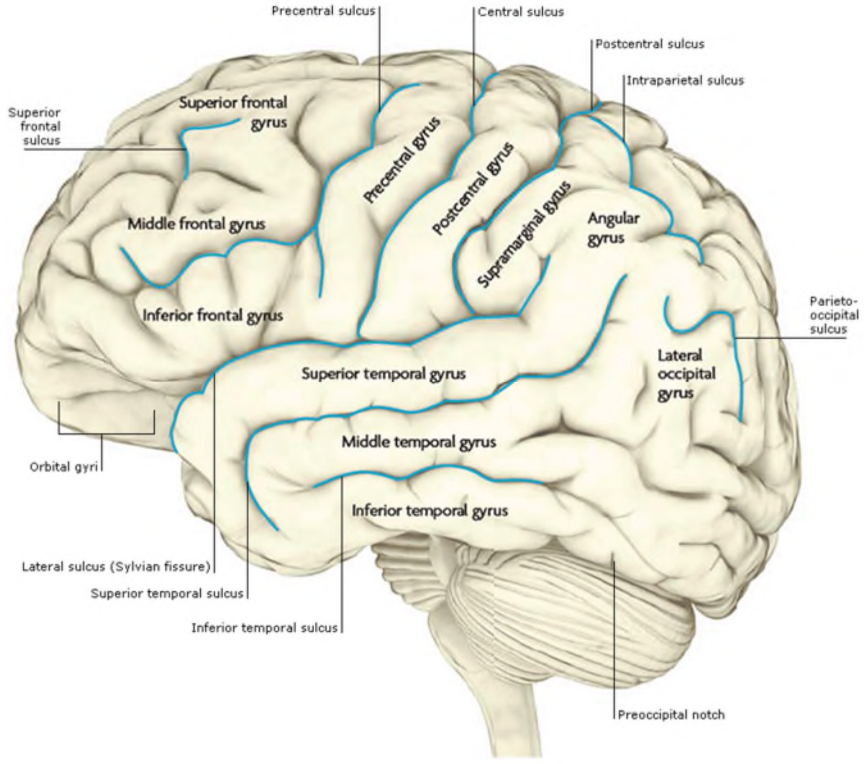

Fig. 2.9 Major sulci and gyri
Carter et al. 2009:66

frontal lobes from the postcentral gyrus (sensory function) in the parietal lobes. These various sulci and gyri are often further divided, as each tiny segment can correlate with a specific function. Figures 2.8 and 2.9 illustrate some of these landmarks.

The Frontal Lobe

Goal-directed motor behaviour is controlled in the frontal lobe, and all regions of the frontal lobe participate in the control of motor behaviour in some form or another (Olson and Colby 2013). The various cortices of the frontal lobe are linked to cognitive skills such as problem solving, memory, language, judgement, sexual behaviour, and emotional expression. Comparative studies between the human frontal cortex and the frontal cortices of apes indicate that the human frontal cortex is not proportionately larger, as once believed, suggesting that the human frontal cortex is, instead, organised differently (Holloway 2002; Semendeferi *et al.* 2002; Teffer and Semendeferi 2012).

The premotor cortex, which correlates with part of Brodmann Area (BA) 6, can be found in the posterior sections of the superior frontal gyrus and the middle frontal gyrus. The anterior region of the frontal lobe contains several modules such as the dorsomedial prefrontal cortex (dmPFC), which is thought to contribute to identity or sense of self as well as empathy and moral judgements; and the dorsolateral prefrontal cortex (dlPFC), which is responsible for executive functions such as the control of behaviour, planning, and working memory. Additionally, the dlPFC receives input from numerous neural pathways (coming from the thalamus, etc.), and it is also part of the information stream that originates in the orbitofrontal cortex (OFC), then to the dlPFC, to the premotor cortex (PM), and finally to the primary motor cortex (M1) (Olson and Colby.

The middle frontal gyrus contains the middle frontal sulcus,[1] a tertiary sulcus whose caudal end, when present, was once believed to indicate a derived condition (Connolly 1950; Falk 2014), particularly in four australopithecine hominin endocasts (Falk 2014). Tertiary sulci are the smallest and shallowest of the sulci in the prefrontal cortex, and they do not begin to emerge until 30 weeks of gestation, deepening at roughly 38 weeks (Miller *et al.* 2021:1701), and thus named for their order in gestational development (Ibid). The middle frontal sulcus consists of three distinct components: anterior, intermediate, and posterior (Petrides 2019; Miller *et al.* 2021), and it was the most caudal portion that was believed to have derived during the reorganisation of the frontal lobes during evolution (Connolly 1950; Falk 2014). However, it was later determined during a study on eight chimpanzee endocasts, that this so-called caudal extension of the middle frontal sulcus can also be observed on extant chimpanzees and likely represents a portion of a different sulcus altogether (Falk *et al.* 2018:56).

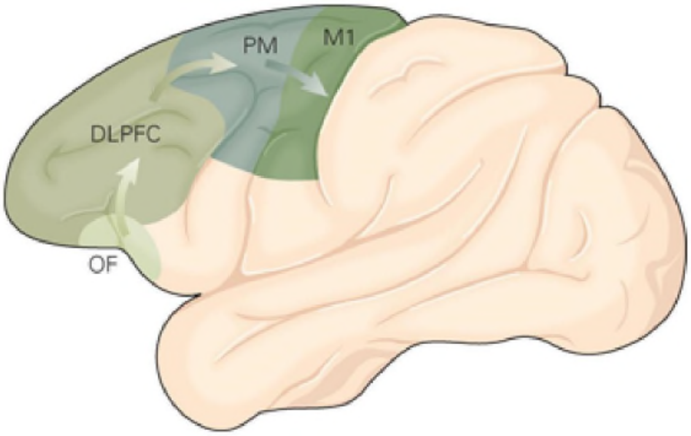

Fig. 2.10 Information pathway from OFC to M1
Olson and Colby 2013:402

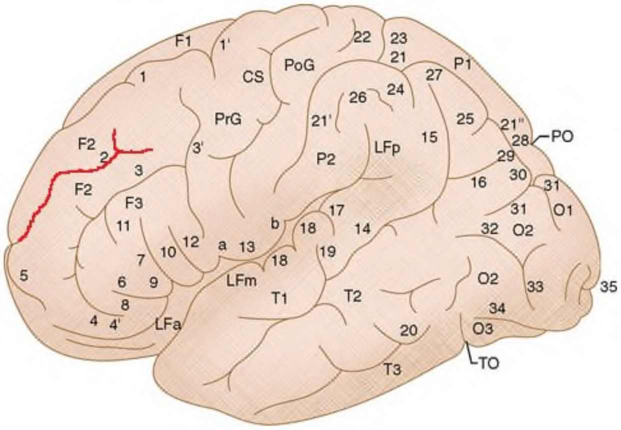

Fig. 2.11 Middle frontal sulcus (in red)
Left lateral view from Duvernoy 1991
Modified by Suzi Wilson

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[1] *The middle frontal sulcus is also known as the medifrontal sulcus, the fronto-marginal sulcus, the intermediate frontal sulcus, and the posterior middle frontal sulcus (Miller et al. 2021:1700), thus adding to the confusion.*

The inferior frontal gyrus is separated from the middle frontal gyrus by the inferior frontal sulcus, which is bordered ventrally by the lateral sulcus (aka Sylvian Fissure). The inferior frontal gyrus contains Broca's area as well as the orbito-frontal cortex, which is a part of the orbito-ventromedial prefrontal cortex (vmPFC). The orbito-ventromedial prefrontal cortex (vmPFC) is associated with emotional control and goal-directed behaviour: (i) it is linked to both the amygdala and hypothalamus; (ii) it receives sensory information from all body sensors (including gustatory); and (iii) its pathway leads to the dorsolateral prefrontal cortex, which then triggers an appropriate motor or behavioural response (Olson and Colby 2013). The orbito-frontal cortex (OFC) portion of the vmPFC is located directly above the eyes on the ventral 'belly' of the frontal lobes (See 'OF' in Figure 2.10 or 'OFC' in Figure 2.12). Its boundaries are unclear as it has numerous functions and relies upon several subregions, including portions of BAs 11, 12, 13, 14, and 47 (Rudebeck and Rich 2018:R1083). BA 47 (pars orbitalis) is associated with memory, emotion, and olfaction (Strotzer 2009) and recently, Sprung-Much and Petrides have advised that a small portion of BA 47, designated as area 47/12, should likely be included in Broca's area (2020:1587). The OFC is of particular interest to the aims of this thesis in terms of how evidence of its evolution can sometimes be seen on hominin endocasts, as well as its crucial involvement in toolmaking with respect to predicting outcomes and learning from mistakes.

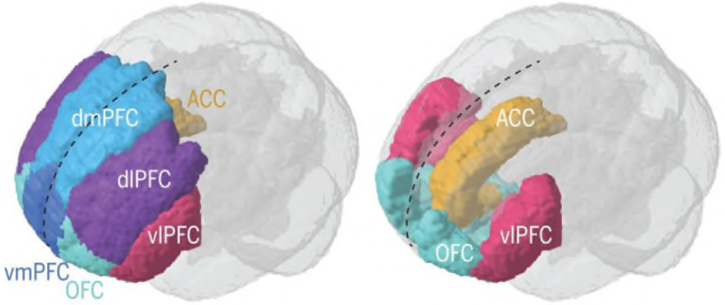

Fig. 2.12 Division of the prefrontal cortex (left side)
Deeper structures on right
Carlen 2017:480

In general, the OFC receives highly processed sensory information as well as input from areas which process high-level emotional and social information. It was previously believed to focus on 'inhibitory control' over behaviour as well as monitoring and interpreting bodily responses during emotional experiences (Rudebeck 2018), such as perhaps a ‘fight or flight’ situation. Although people who have damaged OF cortices typically make bad decisions, exhibit inappropriate and impulsive behaviour, and are unable to socially navigate the world (much like Gage, after losing his left OFC), recent neuron activity studies now suggests that the OFC does not necessarily focus on inhibiting bad behaviour. Instead, the OFC records and stores behavioural stimuli and response instances, either on the part of the individual or as observed in the behaviour of others, as a means for the individual to properly evaluate the likely outcomes produced by an appropriate (or inappropriate) action/behaviour. Thus, rather than inhibiting inappropriate behaviour, the OFC focuses on goal-directed appropriate behaviour based on previous behavioural experiences (Rudebeck and Rich 2018) in order to successfully assess and predict a

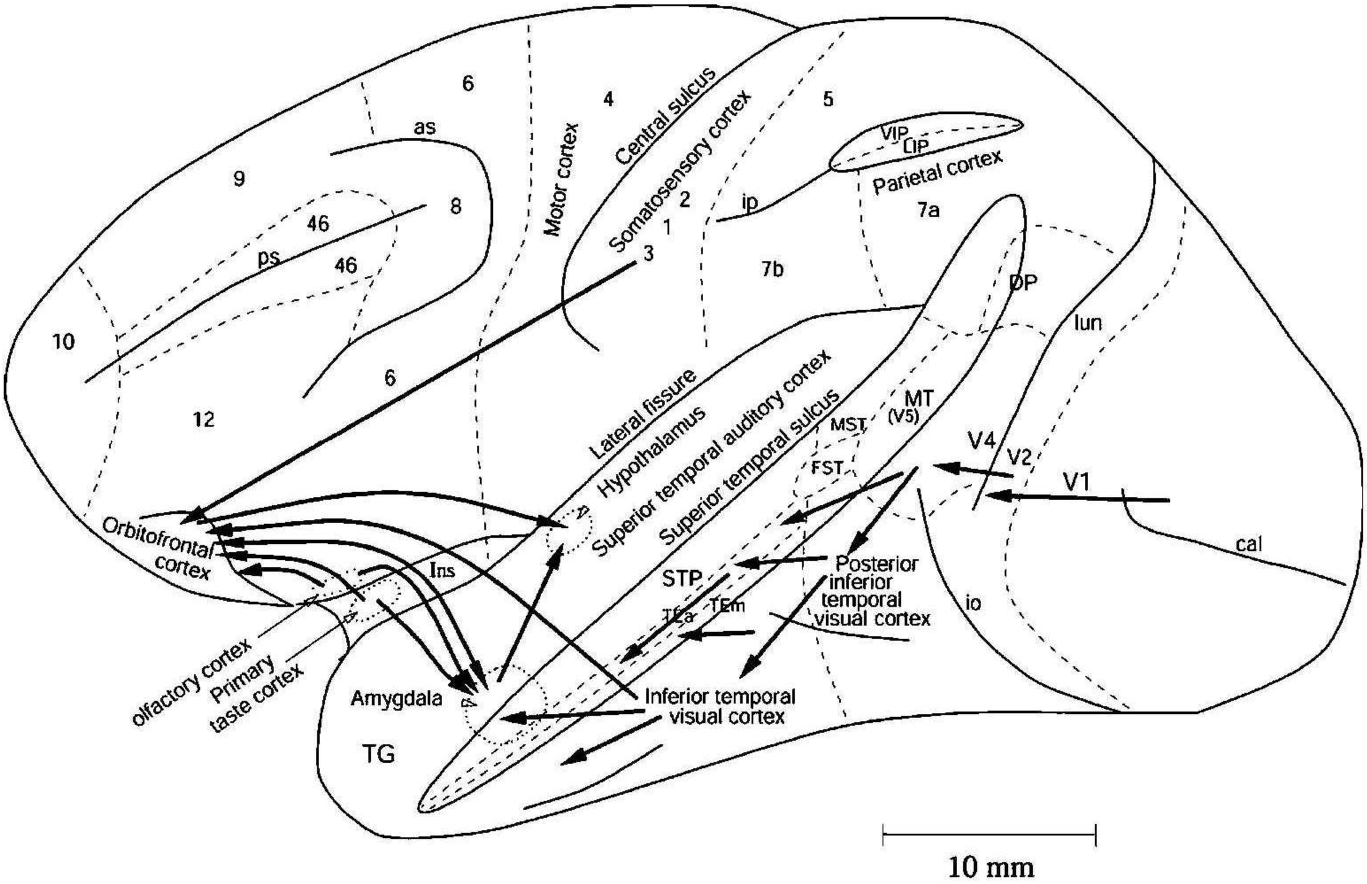

Fig. 2.13 Left lateral view: some of the neural pathways in the brain to and from the OFC
Rolls 2004:13

behavioural response to a behavioural action (or stimulus). It essentially acts as a 'risk assessor' regarding the likely rewards/repercussions of actions/behaviours. Additionally, the OFC plays a major role in emotion, cognition and socialisation (Rudebeck and Rich 2018).

The Evolution of the OFC

As the OFC increased in size over the course of evolution, it convoluted and added associated gyri and sulci as it expanded posteriorly (Connolly 1950: 159, 330; Falk 2014; Hurst 2017). As a result of this and other brain expansion, the laterally exposed surface of the insula in the hominin lineage was ultimately operculated (covered) by the frontal, parietal, and temporal lobes (see Figure 2.6), whilst the insula in the ape lineage continued to have lateral surface exposure. This operculisation process in the hominin lineage can also be observed in the stages of modern human embryonic development.

Figure 2.14 shows the various stages of human foetal brain growth (among different foetuses) from 31.1 weeks of gestational age to 42.6 weeks, during which the triangular-shaped and laterally exposed portion of the insula is gradually buried as the operculum forms over it. 'Sylvian Fissure Operculisation' is a process that can begin as early as 14 weeks in the womb and continues throughout gestation (Quarello *et al.* 2008:44). At roughly 20 weeks, the (proto) parietal lobes and temporal lobes begin to grow more rapidly around the insula, outpacing the frontal lobe (Ibid:47). Thus, the process of operculisation occurs from the posterior to the anterior, resulting in the triangle shape of the portion of the insula which remains exposed. The full operculisation process does not complete until after delivery (Ibid).

As the frontal lobe develops during gestation, the posterior portion of the OFC is pushed back to the anterior edge of the insula, where a portion of the posterior OFC is assimilated into the operculum, whilst the fronto-orbital sulcus, which forms its most posterior boundary, becomes the anterior limiting sulcus (of the insula). Hence, the fronto-orbital sulcus ceases to exist and is now the anterior limiting sulcus (ALS) of the insula, which ultimately becomes part of the circular sulcus (or peri-insula sulcus) surrounding the insula. This process, which occurs in the womb (see gestational covering of the insula in Figure 2.14), is believed to have also occurred over the course of evolution (Connolly 1950:330; Falk 1983:1073; Falk 2014:5; Falk *et al.* 2018:47; Hurst 2017:63). Thus, modern humans do not have a fronto-orbital sulcus, but early hominins and extant apes do, and the ALS of the insula is considered a homologue[1] of the fronto-orbital sulcus found in extant apes.

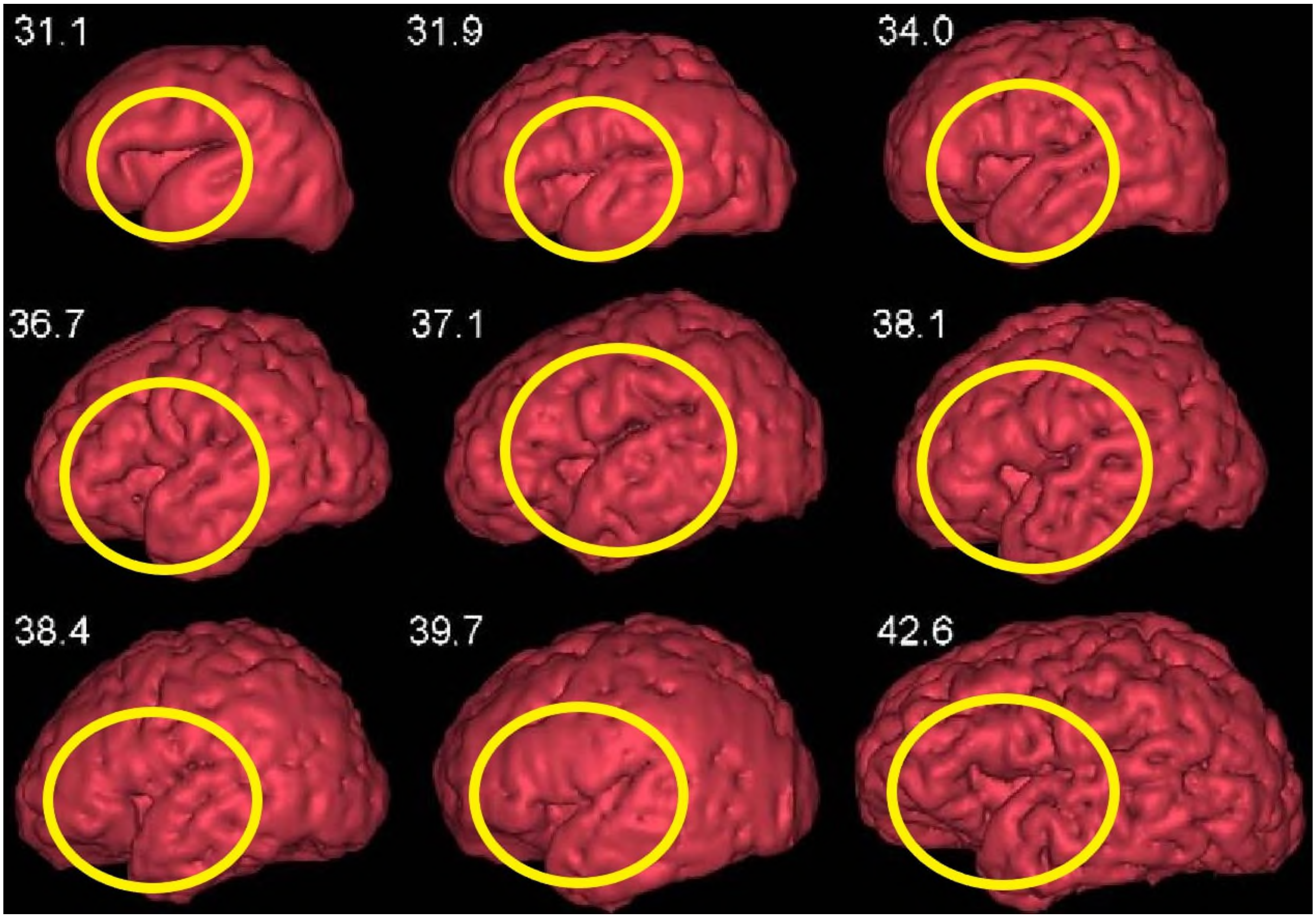

Fig. 2.14 Gestational stages closing the Sylvian Notch and covering the insula
Nishida et al. 2006:1047

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[1] *A homologous feature is similar in structure, whilst an analogue feature is similar in function.*

Although the ALS of the insula continues to delineate the posterior boundary of the OFC when in a derived condition, it is buried under the operculum and cannot be seen. Thus, if an exposed fronto-orbital sulcus is detected on an endocast, then the reorganisation of the frontal lobes has not advanced enough to fully operculate the anterior portion of the insula, which thus signals a more primitive structure (Falk 1983:1073; Hurst 2017:115). However, the absence of this sulcus does not necessarily indicate a derived structure, as absence of evidence is not evidence of absence. Fortunately, there are other means for detecting a derived state of the OFC. Figure 2.15 illustrates the insula (in light blue) of a seven-month-old human foetus, with a dark blue line at the anterior boundary of the insula, representing the most posterior boundary of the OFC. The ALS of the insula is posterior to this dark blue edge of the OFC, abutting the insula, and a portion of the insula is still exposed in the shape of a small triangle, which becomes even smaller as the operculisation process progresses. Thus, a very small triangle (referred to by Hurst as a 'Sylvian notch') detected on an endocast would also indicate a more derived state (Hurst 2017:117), or at the very least, a transitional phase where the operculum covering the insula is in the process of closing versus a fully exposed insula, as seen in extant apes. Figure 2.16 shows the anterior position of the fronto-orbital sulcus

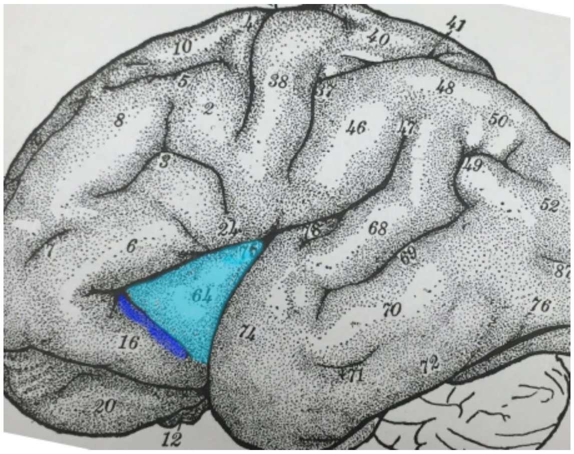

Fig. 2.15 Human foetus at 7 months during the operculisation process. Insula in light blue with OFC posterior border in dark blue Papez 1929, modified by Hurst 2017:74

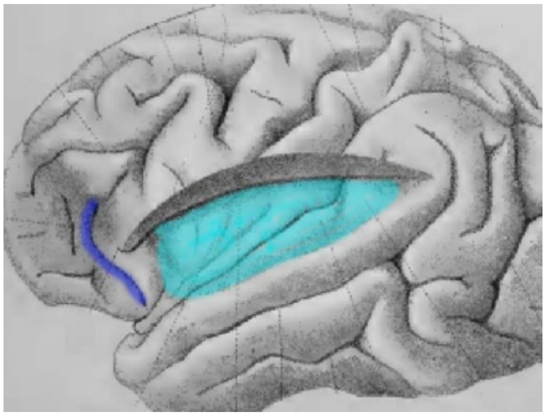

Fig. 2.16 Chimpanzee insula Cunningham 1892 modified by Hurst 2017:73

(in dark blue) to the insula of an adult chimpanzee. Although the great apes are not proxies for early hominins, it is likely that an even more primitive version of this condition was present in our last common ancestor. Hurst additionally suggests that if this dark blue edge is thicker in one hemisphere versus the other, it might indicate some level of brain lateralisation (2017).

Finally, Hurst also believes that when the OFC exhibits a derived structure, its exposed superior boundary is formed by a sulcus which is a branch of one of the rami of the lateral (Sylvian) sulcus (Hurst 2017:115). Likely, he is referring to the horizontal ascending ramus of the lateral fissure which separates the pars orbitalis from the pars triangularis, and thus also delineates the upper boundary of BA 47, part of the OFC in modern humans. Hurst argues that this horizontal sulcus indicates a derived structure of the OFC, and thus implies the absence of the fronto-orbital sulcus, now been buried beneath the operculum and serving as the ALS of the insula (Hurst 2017:115). These features, when visible, will be further discussed in the examinations of the individual endocasts in Chapters 5, 6, and 7.

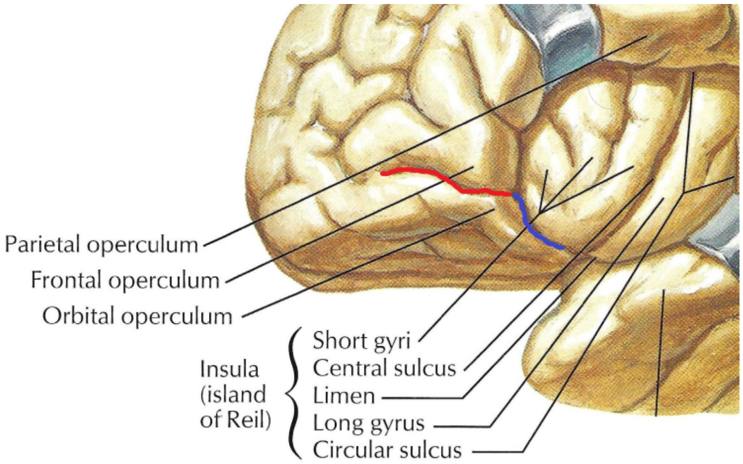

Fig. 2.17 Anterior ramus of the lateral sulcus (in red); anterior limiting sulcus of the insula (in blue)
Illustration by F.H. Netter
Netter 2011:204, modified by Suzi Wilson

Broca's Area

Broca's area, involved in language production and comprehension, consists of BA 45 and BA 44. Figure 2.18 illustrates the configuration of the inferior frontal gyrus containing BA 47 (pars orbitalis) in yellow (portions of which are included in the OFC, discussed above), which is ventral to BA 45 (pars triangularis) in light blue, positioned just anterior to BA 44 (pars opercularis) in dark blue. These regions (and others) helped form the fronto-parietal-temporal operculum covering the insula. During this process over the course of evolution in the hominin brain, it is believed that these regions derived as the operculum was forming, with BA 45 and BA 44 migrating posteriorly and becoming separated by the new horizontal and ascending rami of the lateral (Sylvian) sulcus (Connolly 1950:159, 330; Falk 2014; Falk *et al.* 2018). In the ape lineage (which did not undergo the operculisation process covering the insula), BA 45 is located more anterior and superior to BA 44.

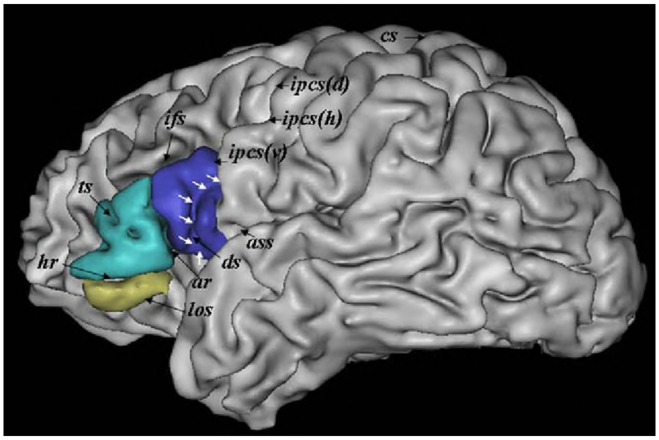

Fig. 2.18 BA 44 (dark blue), 45 (light blue) and 47 (yellow); Keller et al. 2009:32

BA 45 is more involved in the semantic aspects of language processing, and thus plays a role in verbal memory, whilst BA 44 is more concerned with the phonological processing and production of language, and thus, is located closer to the motor centres for the mouth and tongue (Amunts *et al.* 2004). The pars orbitalis (BA 47) lies just inferior to BA 45, and although some had included it as part of Broca's area (Sherwood *et al.* 2003; Wisco *et al.* 2007) prior to the new findings previously mentioned, most excluded BA 47 and considered only BA 44 and BA 45 to constitute Broca's area (Foundas *et al.* 1998; Amunts *et al.* 1999; Amunts *et al.* 2003; Poza-Rey *et al.* 2017). However, it now appears that a small portion of BA 47 (designated as BA 47/12) should likely be considered part of Broca's area (Sprung-Much and Petrides 2020:1587).

Broca's area is also of interest to this thesis due to its involvement with motor sequencing and motor skills. Whilst Broca's area is primarily concerned with the development of speech during the first two years of life, it is also involved with the ability to combine objects manually as well as the use of tools (Greenfield 1991). During a PET scan study, subjects were asked to imagine a hand movement, and Broca's area was activated - even though the area of the motor cortex associated with the hand was not (Ibid). Roland's research in the 1980s, which assessed cerebral blood flow in various regions whilst conducting tasks, established Broca's involvement in both grammatical descriptive speech and motor sequencing (1985).

Broca's Cap

Academic palaeoneurologists have designated a neural region which consists primarily of BA 47 and a portion of BA 45 as Broca's cap, which sometimes protrudes anteriorly and can be seen on hominin endocasts. Falk identifies it as the protrusion of an 'orbital bulge' near the temporal pole, which she notes is referred to as the cap, orbital cap, or Broca's cap (Falk 2014:5). In a primitive state, it is bounded anteriorly by the fronto-orbital sulcus (Falk *et al.* 2018:53). Ponce de Leon *et al.* further describe Broca's cap as a "bulge on the lateral fronto-orbital surface of endocasts, mostly comprised of BA 45 and BA 47 with its inferior delimitation coinciding with the lateral orbital sulcus" (Ponce de Leon et al.2021:1). Falk has questioned the value of Broca's cap in the examination of hominin endocasts (2014). However, Ponce de Leon *et al.* note how this endocranial region might provide insight regarding frontal lobe reorganization during hominin evolution, especially with respect to the OFC and/or Broca's area (2021:1).

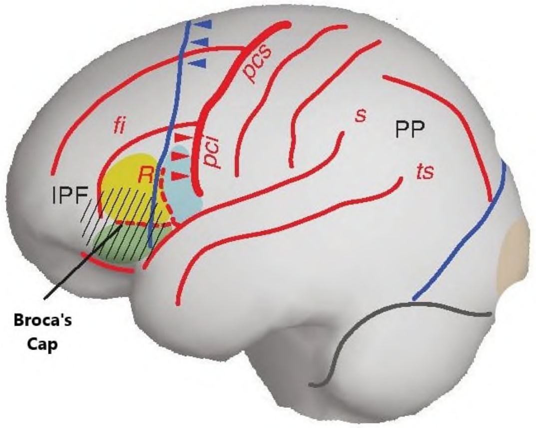

Fig. 2.19 Broca's cap Ponce de Leon et al. 2021:1

The Motor Cortices

The precentral gyrus represents the most posterior section of the frontal lobe and runs directionally along the coronal plane, next to the central sulcus which also borders it caudally. This gyrus contains the primary motor cortex and largely correlates with BA 4. The premotor cortex is directly anterior to it, whilst the supplementary motor area (SMA) is located within the most superior portion of the premotor cortex and anterior to the primary motor cortex, and both regions correspond largely with BA 6. The motor cortices, as well as the relevance of BA 4 and BA 6, will be discussed further in Chapter 6.

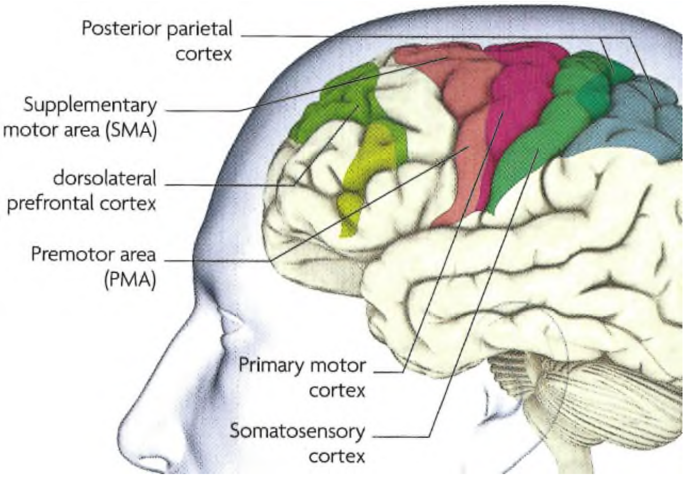

Fig. 2.20 Parietal Motor Cortices
Carter et al. 2009:117

The Parietal Lobes

The parietal lobes are delineated anteriorly by the *central sulcus* whilst their posterior limit borders the parieto-occipital sulcus, between the parietal lobe and the occipital lobe. The lateral sulcus separates the parietal lobe from the anterior portion of the temporal lobes, but the boundary is somewhat ambiguous posteriorly. The parietal lobe consists of four major regions: (i) the postcentral gyrus (PCG), which contains the primary somatosensory cortex and Brodmann areas (BA) 1, 2, and 3, is located in the most anterior region of the parietal lobes, abutting the central sulcus

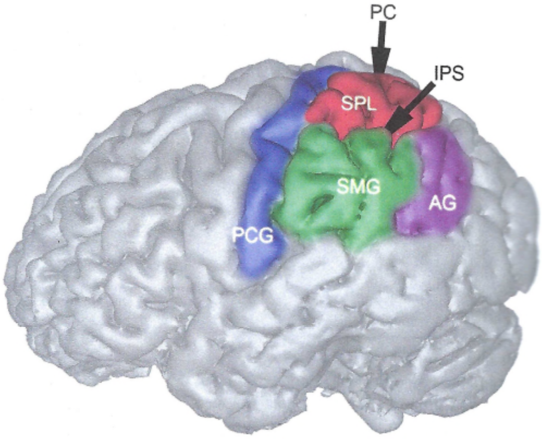

Fig. 2.21 Parietal lobe regions
Bruner 2018b:220

across from the precentral gyrus in the frontal lobes; (ii) the superior parietal lobule (SPL) with BA 5 and BA 7; (iii) the inferior parietal lobule (IPL),containing the supramarginal gyrus (SMG, BA 40) and the angular gyrus (AG, BA 39); and (iv) the parietal operculum (BA 43), which houses the secondary somatosensory cortex (where we feel pain and other senses), a small region located near the lateral sulcus (see Figure 2.22). Sometimes the inferior parietal lobule is dropped in favour of giving the supramarginal gyrus and the angular gyrus their own subregions (Wild 2017; Bruner 2018b), whilst the parietal operculum is often referred to what Bruner calls "the deep medial cortex" (2018b:220). The inferior and superior parietal lobules are separated by the intraparietal sulcus (IPS), an important landmark sulcus which originates from, and is perpendicular to, the postcentral sulcus. It then extends posteriorly through the parietals to ultimately join the transverse occipital sulcus in the occipital lobes. It serves not only as a neurological landmark for identifying other sulci, gyri, and regions of the brain but its regions are also very involved during tool-making, discussed further in Chapter 6.

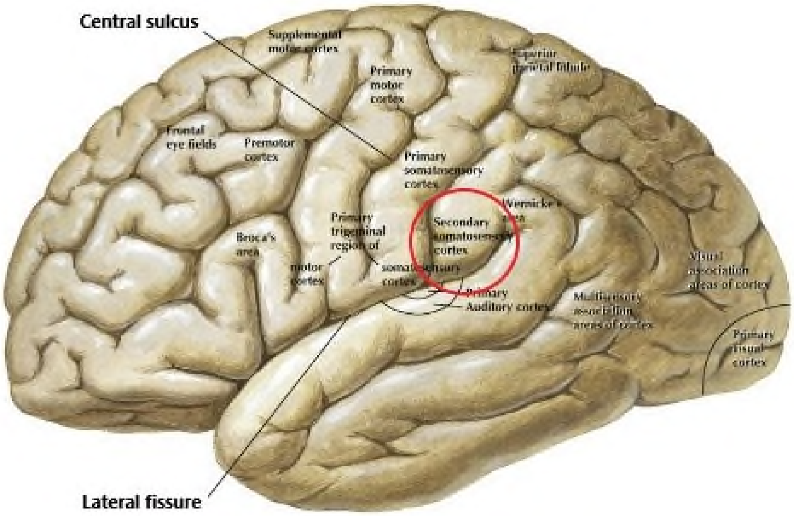

Fig. 2.22 Left Parietal lobe regions
Illustration by F.H. Netter, Modified by Suzi Wilson
Felton et al. 2016:54

The parietal lobes are of particular interest to the aims of this thesis, in part because of their expansion over the course of evolution (especially in the inferior parietal lobule), but also due to the neural substrates within the parietals, which play important roles for capabilities in tool-making (Stout and Chaminade 2007; Kolb and Whishaw 2009; Rizzolatti and Strick 2013; Bruner 2018b). Clinical observations on humans, as well as electrophysiological studies on monkeys, have demonstrated how the parietal cortex is specialized for using sensory information for spatial perception, cognition, and the guiding of motor acts (Kandel 2013b:388; Olson and Colby 2013: 399). The parietals are responsible for visuospatial integration as well as how the body perceives and processes information received from the environment, especially in terms of depth perception, and the ability to correctly process an object in 3D (Orban *et al.* 2006). Once an object has been perceived and assessed, the parietal cortices also help coordinate body movement, including hand-eye coordination involving decisions such as grasp choices (Stout 2010).

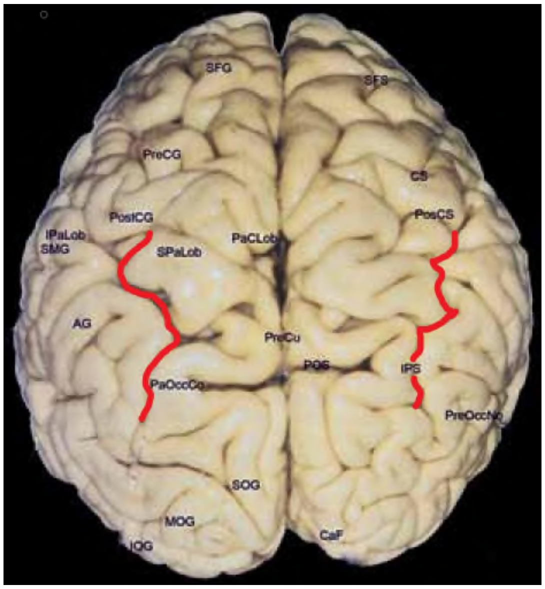

Fig. 2.23 Intraparietal sulci in red
Ribas 2010:11
Modified by Suzi Wilson

The parietal lobes are also key for how we perceive and internally represent personal space (as in space on the body), peri-personal space (space within one's grasp) and extra-personal space (space beyond one's grasp) (Kandel 2013b). Finally, the parietals are involved in the way we perceive and remember things, such as self-awareness, egocentric memory, and mental imagery. Accordingly, they also play a role in how we believe we are perceived by others (Olson and Colby 2013; Bruner 2018b).

The Postcentral Gyrus and the Parietal Operculum (aka the Primary and Secondary Somatosensory Cortices)

The parietal cortex receives somatosensory and visual information, which it integrates with spatial perceptions in order to program and guide motor actions. The postcentral gyrus and the parietal operculum serve as the somatosensory region of the brain. The somatic sensory cortex consists of three main parts as follows: (i) the postcentral gyrus contains the primary somatosensory cortex (also known as S- I, which includes BA 1,2,3a, and 3b) and is located just posterior to the central sulcus and across from the primary motor cortex in the frontal lobe; (ii) the secondary somatosensory cortex (aka S-II) lies within the parietal operculum (BA 43) and abuts the primary somatosensory cortex ventrally; and (iii) the posterior parietal cortex (superior parietal lobule, Figure 2.21) with BA 5 and BA 7.

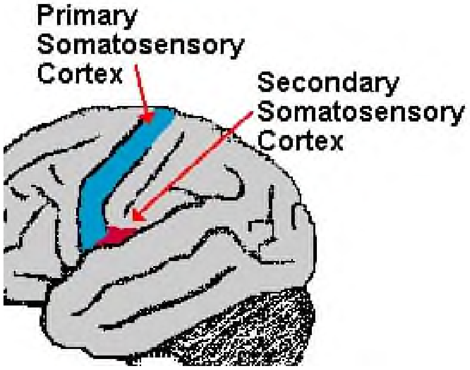

Fig. 2.24 S-I and S-II
Guy-Owens 2021
simplypsychology.org/somatosensory-cortex.html

The primary somatosensory cortex contributes to motor acts, whilst the ventral and posterior regions (near the vision centre of the occipital lobes)are more concerned with spatial perception and cognition (Olson and Colby 2013). The primary somatosensory cortex contains numerous sensory receptor regions, each receiving

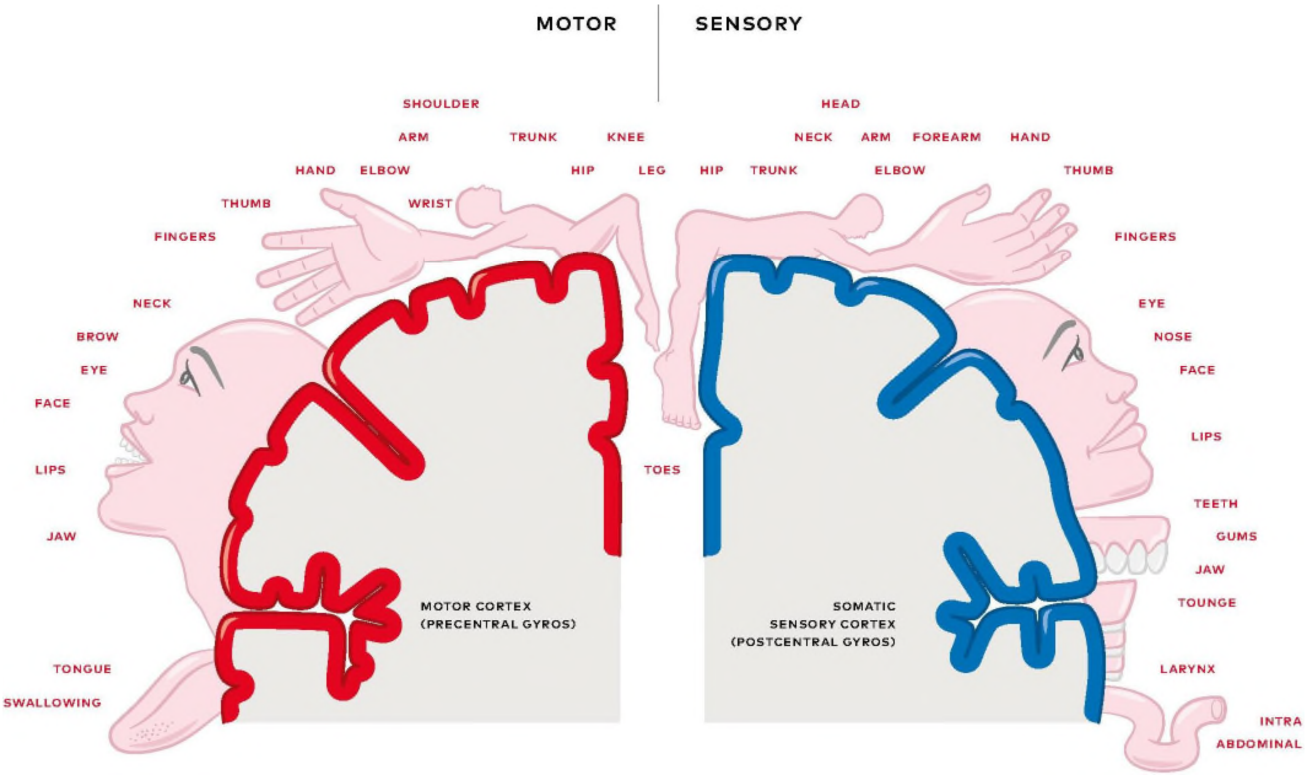

Fig. 2.25 Motor and Sensory maps
Nicholas et al. 2019:36

sensory information from a specific part of the body, and each of these receptor areas lie directly across the central sulcus from their counterparts in the primary motor cortex of the frontal lobe, which connect with the same specific body part, capable of voluntary movement. These corresponding subregions of the sensory and motor cortices are often depicted as 'homunculi' which illustrate how the tiny subregions for motor control and movement correlate with those for sensory reception.

Superior Parietal Lobule

The superior parietal lobule consists of BA 5 and BA 7 and is situated posterior to the primary somatosensory cortex. Within this region, sensory information is received and processed to program and guide arm movements to objects within peri-personal space (within arm's reach) for the hand to touch or grasp (Rizzolatti and Kalaska 2013). When we focus on an object in space (as a stimulus), the response of neuronal activity is independent of whether we are just thinking about the object or reaching for it - the firing rate of the neurons increases by the same amount (Kandel 2013b:388). According to Kandel, the posterior parietal cortex connects with the prefrontal cortex for both the planning and execution of movements for the eyes and hands (Ibid).

From the visual cortex, information travels through one of two major pathways: the dorsal visual pathway or the ventral visual pathway. The dorsal visual pathway sends spatial information to the parietal association cortex, where it is processed then sent to the frontal association cortex (Olson and Colby 2013). Olson and Colby emphasize how the "parietal cortex may have initially

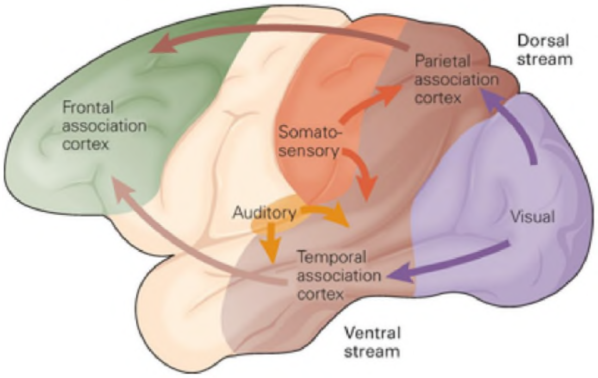

Fig. 2.26 Dorsal and Ventral Streams Olson and Colby 2013:397

developed the capacity to represent where things are relative to the body in order to guide actions, such as grasping, and then developed the ability to represent where things are relative to each other without reference to the body" (2013:397).

The Praecuneus

Another subregion of the superior parietal lobule is the praecuneus, which is located within the medial surface of the brain, facing the midsagittal plane, and thus cannot be seen. However, it is another organizational hub that serves an important role in visuospatial integration, and it is believed to be a neurological specialization of *Homo sapiens* which evolved only within the last 150,000 years, based on the comparative studies of late erectus/early sapiens cranial (and endocast) shape, which focused on the parietal lobes (Bruner *et al.* 2017; Bruner *et al.* 2018b). Bruner and Pearson argue that parietal expansion in the human lineage was a two-step process, with the second stage occurring much later based on the notable absence of second stage parietal 'bulging' in cranial fossils between 150k and 200k (2013:38; Bruner et al. 2017:1058).

Inferior Parietal Lobule (Angular Gyrus and Supramarginal Gyrus)

Whilst the superior parietal lobule is primarily concerned with somatosensory information, the interior parietal lobule focuses on functions related to spatial cognition (Colby and Olson 2003). Just as the superior parietal lobule processes sensory information to guide limb movement toward objects in peri-personal space, the inferior parietal lobule processes visual information regarding the physical properties of objects and associates those properties with specific motor acts (Rizzolatti and Kalaska 2013).

The inferior parietal lobule is separated from the superior parietal lobule by the intraparietal sulcus and consists of the angular gyrus (BA 39) and the supramarginal gyrus (BA 40). It lies posterior to the postcentral sulcus and spreads ventrally into the terminal portions of the superior temporal gyrus and middle temporal gyrus of the temporal lobe. This region processes and interprets a wide range of information. The angular gyrus and supramarginal gyrus are highly lateralised, and thus their dominant functions will vary between the left and right hemispheres. These various functions include, but are not limited to, semantic processing, number processing, reading, and comprehending words, memory retrieval, spatial perspective, body image, empathy, and social cognition (Swaab 2014; Seghier 2013).

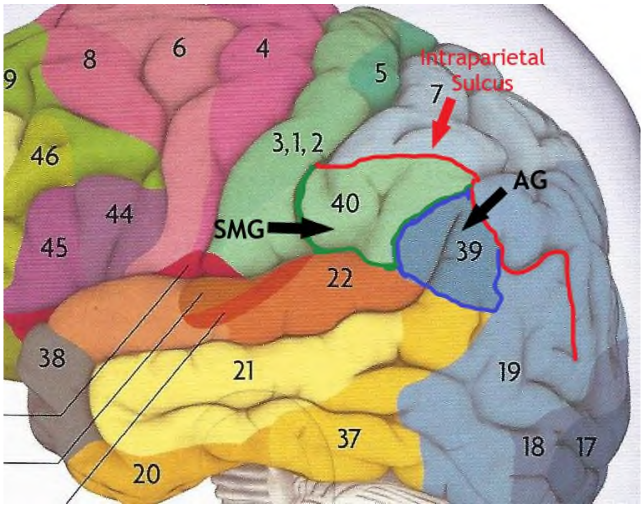

Fig. 2.27 Inferior parietal lobule
Supramarginal and angular gyri
Carter et al. 2009:67
Modified by Suzi Wilson

The angular gyrus lies at the juncture where the parietal, temporal and occipital lobes meet. It participates in relaying information regarding word recognition, and semantic processing to Wernicke's area, but it is also involved in other operations related to language as well as number mechanics, memory, social cognition, and spatial cognition (Seghier 2013; Price *et al.* 2015; Ingelström and Graziano 2017). Additionally, it receives and integrates sensory information from both the body and the environment, which is crucial for self-consciousness and self-awareness (Swaab 2014). Finally, it also appears to play a causal role in agency (Ingelström and Graziano 2017). Additionally, it processes multisensory information then transmits it to other regions of the brain, essentially serving as a major interface hub to comprehend observed actions/events, solve problems and "manipulate mental representations" (Seghier 2013:43). When the angular gyrus is deprived of oxygen, the sensory information coming from the body is prevented from being integrated and processed, which can disrupt one's consciousness of one's body and produce out-of-body and/or near-death experiences (Swaab 2014:165, 315).

The supramarginal gyrus also contributes largely to visual word recognition, especially with respect to semantic processing. The right supramarginal gyrus plays an important role in empathy, as well as overcoming emotional egocentricity when making social judgments (Stoeckel *et al.* 2009; Silani *et al*. 2013; Preckel *et al.* 2018).

The Temporal Lobes

The temporal lobes are located just below the lateral sulcus, which separates them from the frontal lobes and the anterior portion of the parietal lobes. The superior temporal gyrus of the temporal lobes extends into the ventral portions of the parietal lobes, making it difficult to discern where Wernicke's area (BA 22) ends and the inferior parietal lobule begins (see Figures 2.27 and 2.28).

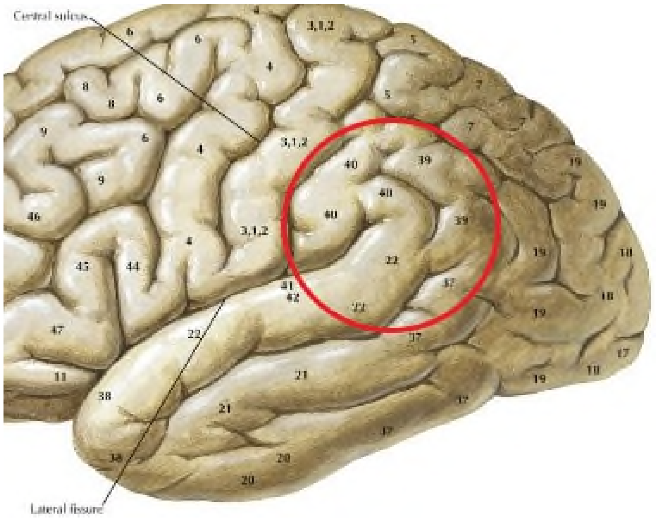

Fig. 2.28 Inferior parietal lobule and Wernicke
Illustration by F.H. Netter
Modification by Suzi Wilson
Felton et al. 2016:54

Although Wernicke's area (associated with the comprehension of spoken and written language), lies mostly within the superior temporal gyrus, a small portion of it merges with regions associated with the angular gyrus and supramarginal gyrus. It is therefore not surprising that there is functional overlap among Wernicke's area, the angular gyrus, and the supramarginal gyrus regarding recognition and semantic processing, and thus, this region could be considered a language comprehension cortex. Accordingly, the ventral inferior parietal lobule areas which immediately surround Wernicke's area are often referred to as Geschwind's territory (Carter *et al.* 2009:148).

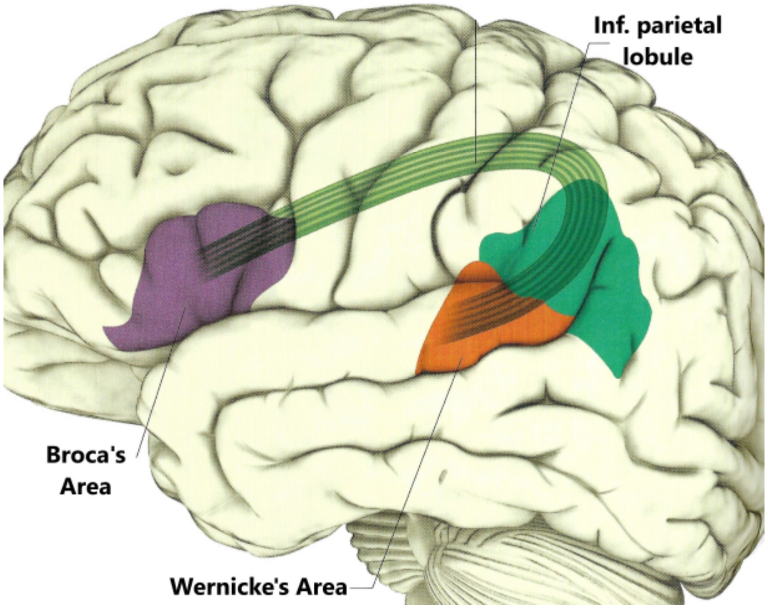

Fig. 2.29 Language Centres
Carter et al. 2009:148

The auditory cortex is embedded within BA 22 where sensory input is received from the ears, then processed in order to identify these sounds as words, music, or other sounds. The frequency of sound is perceived as pitch whilst the intensity of sound is perceived as loudness. The sounds which are identified as words are transformed into full comprehension for semantic and syntactic language.

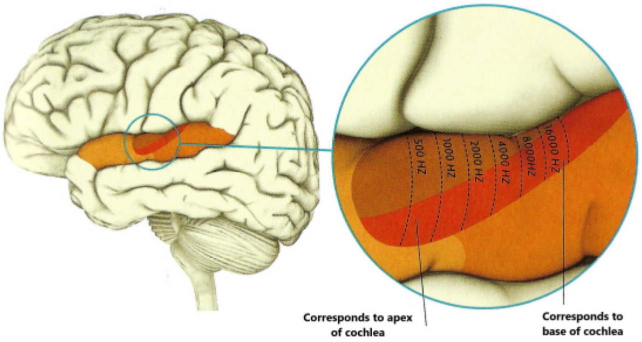

Fig. 2.30 Auditory Association Cortex
Carter et al. 2009:91

The superior temporal gyrus is also involved in the recognition of facial *expressions*, whilst the middle temporal gyrus is important for recognising faces and gauging distances, as well as an assisting role in word recognition. Ventral to the middle temporal sulcus is the inferior temporal gyrus which is also involved in facial feature recognition and the recognition of numbers. Also of interest is that it is the primary centre for the perception and recognition of objects (Albright 2013). Thus, the temporal cortex serves as an important 'recognition centre' for the brain. The ventral visual pathway (see Figure 2.26) receives visual information from the visual cortex concerning shape, colour and texture then relays that information to the temporal association cortex where it is integrated with sensory information related to sound and touch before sending it on to the ventral frontal cortices (Olson and Colby 2013). After the frontal cortex receives this information, an emotional response to these objects or other stimuli is triggered. However, an object must first be recognized before it can attain any emotional significance, and such recognition occurs in the temporal lobes (Olson and Colby 2013). Finally, the deeper structures within the temporal lobes correspond to memory and emotion.

The Occipital Lobes

The occipital lobes, located in the most posterior region of the brain, extend anteriorly from the occipital pole (the most caudal point) to the parieto-occipital sulcus, dorsally, and then laterally (and ventrally) to the pre-occipital notch. However, some occipital tissue merges with the regions of the parietal and temporal lobes, making it difficult to delineate between the full extent of the occipital cortex and the regions where it converges with the other lobes – especially the medial and ventral temporal cortices (Kolb and Whishaw 2009; Iaria and Petrides 2007). The pre-occipital notch (aka the pre-occipital tentorium plica, aka the POTP) is a tent-shaped fold of meningeal dura at the bottom-most lateral view of the point directly in between the occipital lobes and the most ventral portion of the temporal lobes, and thus serves as a neuroanatomical landmark for gauging the full temporo-occipital boundary (Reis *et al.* 2016). This fold of tissue can sometimes be detected on an endocast, but its identification is often debated.

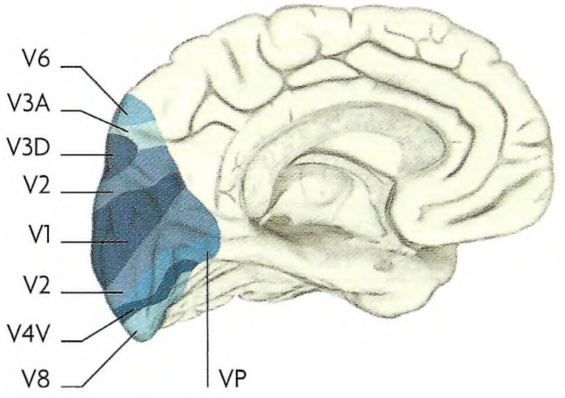

Fig. 2.31 Visual cortex, medial view
Carter et al. 2009:82

The occipital lobes are the visual information processing centre (i.e., visual cortex) of the brain, typically divided into ten[1] visual regions, several of which are located medially within the brain (see Figure 2.31). The primary visual cortex (aka PVC or the striate cortex or V1) is found in and around the banks of the calcarine sulcus in BA 17 at the most posterior region of the occipitals. The PVC receives sensory information from the eyes via the thalamus (de Sousa *et al*. 2010), which it processes then sends to other regions of the brain. It is surrounded by the V2 visual area (BA 18) which, in turn is surrounded by BA19, which includes V3, V4, and V5 (Kolb and Whishaw 2009).

Together, BA areas 18 and 19 are often referred to as the extrastriate cortex. Note how the ventral medial portion of BA 19 bleeds into the posterior areas of the temporal lobes. Although V4 was originally believed to be a 'colour perception' area, subsequent studies now suggest a prominent role for V4 in object recognition and the processing of shape information (Roe *et al.* 2012). Most relevant to this thesis is the lunate sulcus, which once occupied a more anterior position in early hominin brains, but was displaced posteriorly during brain expansion and reorganisation over the course of evolution.

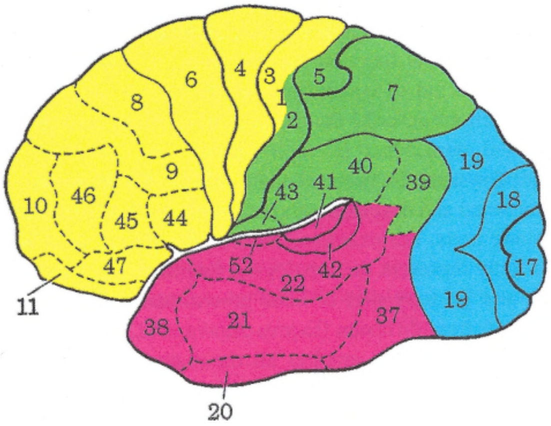

Fig. 2.32 Visual Cortex (blue) Lateral View
Bruner et al. 2018a:193

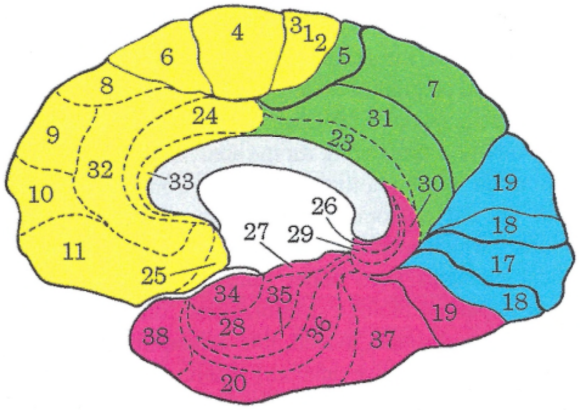

Fig. 2.33 Visual Cortex (blue) Medial View
Bruner et al. 2018a:193

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[1] *V5 is located ventro-laterally and thus, cannot be seen in Figure 2.31, which is a medial view.*

The Lunate Sulcus

In extant apes and some monkeys, the lunate sulcus (LuS) forms the anterior boundary of the primary visual cortex (Bonin and Bailey 1947; Allen *et al*. 2006); however, its position (when present) in modern human brains is located much more posteriorly, near the occipital pole. As mentioned, employing the brains of extant apes as proxies for early hominin brains is problematic as it would imply that the brains of apes have not evolved following our split with their lineage. It is, thus, important for palaeoneurologists to present these comparisons with the understanding that it is useful only as a means to possibly gauge how hominin brains may have derived from our last common ancestor (LCA) versus presenting the brains of extant apes as the same as the LCA, from which our brains derived.

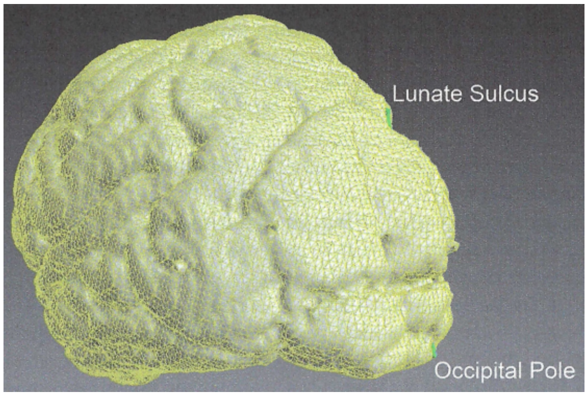

Fig. 2.34 Adult Female Chimpanzee brain
Todorov and de Sousa 2018:268

We do know that the LuS was located more much anteriorly in the last common ancestor than where it is found today in both modern humans and extant apes (demonstrated in Chapter 5). However, it migrated further posteriorly in the hominin lineage than in that of the apes. As a result, its detection on an endocast can provide yet another means for tracing when the expansion and reorganisation of the brain occurred, although its identification on various endocasts has been hotly debated.

Most of the descriptions of the lunate sulcus in modern humans provided by the medical community are only slightly better than the physical description of an elephant as provided by the six blind men following their physical examination. According to Iaria *et al*., the lunate sulcus [when present] is a "dorso-ventrally oriented sulcus that lies at the most caudal part of the lateral occipital lobe, often forming a concavity toward the occipital pole (2008:177). Ribas suggests that it is "typically oriented vertically, immediately facing the occipital pole" (2010:12). Iaria *et al*. add that it is a hard sulcus to identify in MRI images, due to its shape and location on the "lateral to medial curvature of the occipital pole" (2008:177). Allen *et al.* additionally note the curvature of the LuS in terms of how it forms an arc, and further describe it as "beginning superiorly close to the medial margin of the hemisphere" (2006:868). Furthermore, the occipital sulci in modern humans are highly variably.

In modern humans, the LuS more often appears as a segmented sulci versus a continuous arc. Allen *et al.* researched the LuS in 110 human brains (220 hemispheres) in living individuals using high-resolution MRI and found that when present, the vast majority of the LuS appeared as segmented sulci, which they referred to as a 'composite lunate sulcus' (2006:867). Out of the 220 hemispheres examined, only three (1.4%) were identified with a continuous LuS, similar to the continuous crescent-shaped form of the LuS found in apes (Ibid). Of further interest is that the researchers could only identify the LuS (in either composite or continuous form) in only 65 (29.5%) of the 220 hemispheres studies (Ibid). In a similar study, Malikovic *et al*. found the LuS in 33.3% of the cases examined (2012:69). From this information, we can surmise that the LuS in modern humans: (i) can generally be found in roughly one-third of the population; (ii) is located either on or near the occipital pole in the most posterior region of the occipital lobe; and (iii) likely consists of several small segmented sulci (versus a continuous sulcus) in a curvature shape.

In hominin endocasts, the LuS is often difficult to find and frequently debated. A positive identification of a LuS usually relies on its proximity to other neuroanatomical landmarks, which is also an arduous task due to the wide variability of the occipital sulci. Other than the occipital pole and occipital extension of the intraparietal sulcus, there are few occipital sulci that can reliably serve as neuroanatomical landmarks due to this range of variability. Although the occipital sulci are important for the study of endocasts, it is challenging to definitively identify them if there are no other landmarks available for reference. Furthermore, it was not until the 1990s that the nomenclature for the occipital sulci was standardised as well as adequate descriptions agreed upon for each sulcus (Iaria and Petrides 2007; Watson *et al.* 1993; Zeki *et al.* 1991). In 2007, neurologists Iaria and Petrides performed fMRIs on the occipital regions of 40 normal adults (i.e., 80 hemispheres) and additionally examined the brains of 20 cadavers as part of their research regarding the variation of the occipital sulci. According to their study, the calcarine sulcus is one of the more constant sulci in the occipital lobes (2007:243), but it is located almost entirely within the medial area of the brain, which cannot be seen on endocasts. It extends from the splenium of the corpus callosum (i.e., posterior end of the centre of the brain) to the occipital pole (Iaria and Petrides 2007; Iaria *et al.* 2008; Ribas 2010). As a result of its length, it is often divided into three sections: (i) the anterior calcarine sulcus, (ii) the calcarine sulcus proper (aka the "truncus"); and (iii) the retro-calcarine sulcus (Malikovic *et al.* 2010; El Mohamad *et al.* 2019). The retro-calcarine sulcus, which is the only portion visible on the cerebral cortex of human brains, often fans out into an upper and lower part (often resembling a 'fishtail') near the occipital pole, which can be seen in approximately 69% to 70% of cases studied (Iaria *et al*. 2008:179; Ribas 2010:12; Mohamad *et al.* 2019:183).

However, in extant apes, the lateral calcarine sulcus is regularly seen on the lateral surface of the occipitals and is much more pronounced, appearing in a shape closer to that of a large 'y' versus a 'fishtail.' When seen in modern humans, only the portion called the retro-calcarine sulcus is visible and always located within very close proximity to the occipital pole and caudal to the LuS. Thus, it is only this most caudal section, resembling a 'fish-tail' near the occipital pole, which can sometimes be observed on a brain endocast. Other relevant occipital sulci include the lateral occipital sulcus, the inferior occipital sulcus, and the transverse occipital sulcus, which are described as follows:

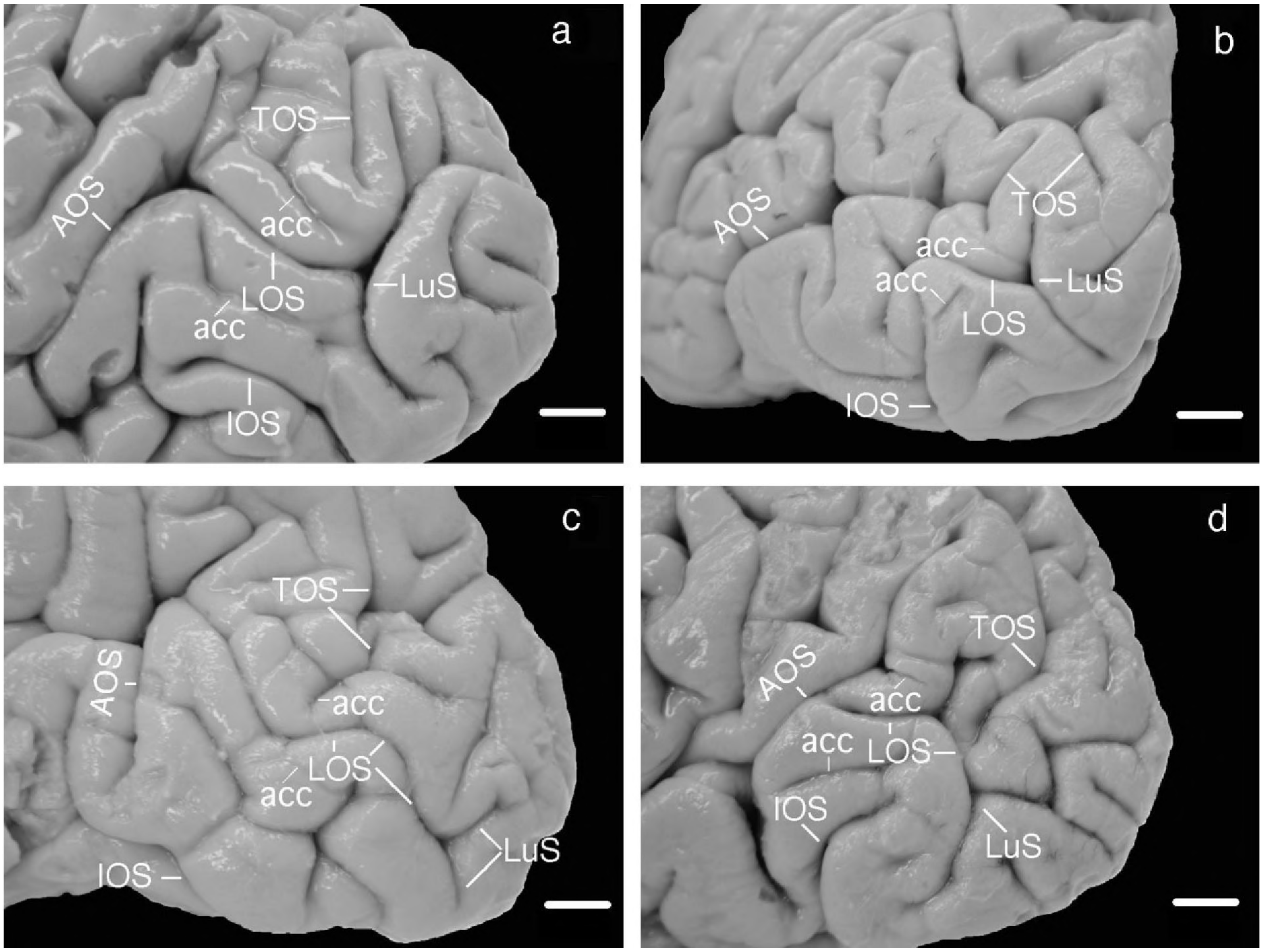

Fig. 2.35 Four of the post-mortem brains examined. Note the variation from brain to brain, with some sulci more pronounced, and the variation of the directions and curves of the various sulci. Iaria and Petrides 2007:247

- The transverse occipital sulcus (TOS) is found in the superior part of the occipital lobe, just caudal to the parieto-occipital fissure, and joins with the occipital extension of the intraparietal sulcus. The TOS runs somewhat dorsoventrally, although like all sulci, it is not a straight line and varies considerably. The TOS is relevant to this study because of its proximity to the intraparietal sulcus, from which other sulci can be referenced.

- The lateral occipital sulcus (LOS) lies ventral to the TOS and is located immediately anterior to the LuS, as discussed below. In fact, one of the older names for this sulcus was the prelunate sulcus (Iaria and Petrides 2007:247). The LOS is relevant because of its proximity to the lunate sulcus.
- The lunate sulcus (LuS), previously described, appears in the shape of a small crescent moon, when visible, near the most posterior section of the occipital lobe (Allen et al. 2006:868).
- The inferior occipital sulcus (IOS) is located almost on the base of the occipital lobe, and its caudal end runs within close proximity of the most ventral part of the LuS.

Therefore, if examining the parieto-occipital region of a modern human brain, one should be able to locate the intraparietal sulcus and follow it posteriorly to the occipital region where it joins with the TOS. Ventral to the TOS lies the LOS, which precedes the lunate sulcus, typically found on the curvature of the occipital pole, when it is visible (Iaria and Petrides 2007). Although there is consensus that the LuS migrated posteriorly over the course of evolution, the argument is over when this 'pushback' occurred, particularly with respect to whether it preceded the substantial increase in endocranial volume or before, which will be discussed in Chapter 5.

Behaviour and Environment Can Change the Brain

As mentioned, brain plasticity refers to the brain's capability to change in terms of both structure and function. Although the mapping of the brain, which commences in infancy, was previously considered to be permanent by the time we reached adolescence, it is now known that changes in cortical mapping are ongoing, although the facility of change varies from one individual to another (Kandel 2013b:378).

The evidence presented in Chapter 1 regarding the cortical changes in owl monkeys (Chapter 1), as well as the diminution of cortical region in the brains of monkeys after the nerves in an upper limb were severed, demonstrate how the areas of the brain that correspond with lesser used (or unused) body parts tend to atrophy whilst those correlated with areas of increased usage expand. Hence, every postcranial change in the body will produce a corresponding change in the brain. An additional experiment on monkeys was conducted whereby the skin of two adjacent fingers was surgically altered to connect the two fingers as one unit. As these fingers were forced to work together, the cerebral information received from the skin on these fingers increased, which ultimately impacted the usual pattern of connectivity from what is genetically programmed to that imposed by the surgical alteration, as one unit versus two. Although these patterns of connectivity (i.e., the way we typically use our fingers) are genetically programmed (Kandel 2013b:379), these experiments demonstrate that cerebral patterns are modified through experience, surgery, and postcranial adaptation in hominins. This has also been established in modern humans.

Syndactyly is a congenital condition where the fingers of the human hand are fused into a single unit, and the area of the human brain which correlates with a syndactyl hand is significantly less than what is typically seen in the brain area representing a normally developed hand. Following surgery to separate the fingers, the areas in the cortical region corresponding to the individual digits gradually begin to distance themselves from one another. In one patient, the length between the representational areas for the thumb and little finger increased to 1.06 centimetres after 26 days, whilst the fingers of another patient came to be individually separated neurologically within a few weeks (Ibid).

Conclusion

This chapter has presented an overview of the cerebral cortex, as well as some of the deeper structures within the brain. Although these deeper structures cannot be seen on endocast, they 'talk' to the modules on the cerebral cortex, and thus their involvement in some functions may be implied. More detailed information has been provided for specific features of the brain which can be detected on hominin endocasts, in terms of what their presence or migration might suggests regarding when certain aspects of cognitive advancement may have occurred or begun in the hominin lineage.

Additionally, the experiments and case studies presented herein demonstrate how the 'plasticity' of the brain can produce neural adaptations prompted by postcranial adaptations via the behaviour of individuals, even within a very short period. Changes in behaviour and concomitant (or related) modifications of postcranial morphology, possibly as adjustments to the environment, will necessarily have a corresponding effect in the brain. Moreover, these neurological alterations from generation to generation may have had long-term impacts which ultimately led to species-wide permanent neural adaptations. These neurological and postcranial adaptations will be further explored in the chapters to follow.

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Chapter 3: Brain Organisation: Asymmetries and Lateralisation

Over the course of hominin evolution some regions of the brain, such as the parietal lobes, expanded whilst other areas, such as the primary visual cortex in the occipital lobe, contracted (laterally). Although neurologists agree that a reorganisation of the brain certainly occurred, exactly how and when the various elements of reorganisation came into being are highly debated. The most contentious argument is with respect to whether the reorganizational changes transpired prior to brain enlargement or afterward, but also debated is the manner of *how* brain reorganisation and development materialised. In particular, the debate focuses on whether the various aspects of reorganisation occurred concomitantly as a single punctuated event or gradually over time, with some regions changing sooner than others in a 'patchwork' fashion or what is commonly referred to as a 'mosaic' form of evolution. It is also possible that some regions evolved in a mosaic pattern, whilst others came into being rather suddenly (or at least 'suddenly' for evolutionary change).

Many neurological alterations were the result of early hominins adopting new behaviours, which prompted adjustments in postcranial morphology which then generated a corresponding adaptation in the brain. For example, the transition to bipedalism (discussed in Chapter 4) would have resulted in many changes to the motor cortex, to correspond with the adapting postcranial morphology, and neurological areas associated with balance, perspective, and visuo-spatial integration would have also been affected. Considering how the physical changes required for habitual bipedalism appear in the fossil record in a mosaic fashion, it seems likely that their analogous areas in the brain would have evolved in a similar manner.

Holloway has long argued how the increase in brain size alone is insufficient to explain the evolution of human behaviour and the brain (Holloway 1967, 1968, 1979, 1983), and he suggests that the first major reorganization of the brain occurred in early hominins between approximately three to four million years ago, which affected the posterior parietal lobes, the anterior occipital lobe, and the superior temporal portions of the cerebral cortex (Holloway 1996:42). The scientific evidence for some of these changes can be observed in the fossil record via the sulci marks found on brain endocasts, when present. However, the interpretation regarding these sulci landmarks, as well as other aspects of Holloway's theses have been contested. According to Holloway, another reorganisation occurred in the frontal lobes, primarily in the third convolution of the inferior frontal gyrus, which includes Broca's area, and yet another reorganisation transpired with the emergence of brain asymmetries, which indicate specific hemisphere specialization (Ibid). This chapter focuses on the emergence of brain asymmetries and brain lateralisation.

Brain Lateralisation

As initially discussed in Chapter 1, brain lateralisation refers to the specific neurological areas of the brain which are typically dominant in either the left or right hemisphere for performing certain actions, behaviours or thought processes, versus their counterparts in the opposite hemisphere. For example, most people are more emotionally expressive (subconsciously) on the left side of the face versus the right side (Nicholls *et al*. 2004), and similarly we tend to prefer hearing sound in the right ear versus the left (Davidson and Hugdahl 1995). The dominant region also tends to be more developed (i.e., larger) than its homologue in the opposite hemisphere, which results in brain asymmetries which can observed on hominin endocasts, when present.

Brain lateralisation is believed by many scholars to have likely developed at least by the emergence of the genus *Homo*, and possibly as early as the australopithecines, based largely on the study of hominin brain asymmetries (Holloway and De La Coste-Lareymondie 1982:101; Cashmore *et al.* 2008:7; Uomini

2015:131, 135). It provides yet another means for the brain to acquire efficiencies via a 'division of labour' aspect similar to other efficiency adaptations such as the manner in which the brain 'convoluted' in order to accommodate the growth of additional tissue. Although brain asymmetries can also be found in non-human primates (and other animals), they are not as pronounced as those found in humans, particularly in the language regions (Holloway and De La Coste-Lareymondie 1982:107; Toga and Thompson 2003:39; *Li et al.* 2018:290; Li *et al.* 2019:1148). Neubauer *et al.* stress how humans and nonhuman apes (gorillas and orangutans more so than chimpanzees) share an overall pattern and shape regarding asymmetries, based on their 2020 study comparing the brains of 228 modern humans, chimpanzees, gorillas, and orangutans (2020:8), yet they agree that the *degree* of certain asymmetries was less in the great apes versus modern humans and additionally emphasize the greater extent of variation in human asymmetry patterns versus the great apes (2020:2). Li *et al.* believe that brain lateralisation appeared in the hominin lineage as the result of a punctuated genetic change (Li *et al.* 2019:1141), but Neubauer *et al.* argue that Li *et al.* do not consider other possibilities concerning how brain asymmetries may have derived in the both the hominin and nonhominin lineages following the split with the great apes from the LCA (2020:6). However, Neubauer *et al.* also recognize that lateralisation with respect to function is most likely triggered, at least in part, by anatomical brain asymmetry (2020:7).

Examples of brain lateralisation include the language centres of the brain (Broca and Wernicke regions) and analytical processing, which tend to be dominant in the left hemisphere of the brain, whilst the regions responsible for visuospatial-constructional skills and the centre for emotions tend to be dominant in the right hemisphere (Holloway and De La Coste-Lareymondie 1982:101; Grimaud-Herve and Lordkipanidze 2010:71; Papadatou-Pastou 2011:251,257; Kriegstein and Brust 2013:1536). However, language studies employing digital imaging technologies such fMRI, PET, and fTCD have revealed that although the language centres in the left hemisphere are more highly activated during speech and language use, almost all individuals likewise activate their right hemisphere to some extent whilst having a conversation (Papadatou-Pastou 2011:252; Buckner *et al.* 1995; Knecht *et al.* 2000; and Springer *et al.* 1999). Indeed, although there are many regions of the brain that tend to be dominant on one side or the other, both hemispheres nevertheless work together and demonstrate 'complementary specialisation' (Bradshaw and Nettleton 1983; Papadatou-Pastou 2011:251). Furthermore, both hominins and modern humans have occasionally been found to be dominant in the opposite (atypical) hemisphere of the brain from most individuals, which many believe to be somehow related to hand preference.

The first awareness of brain asymmetries and lateralization may extend as far back as the 5th century when Hippocrates noted that head wounds on one side of the body sometimes causes seizures in the opposite side (LeMay 1992:493; Adams 1849:386). In 1877, Broca observed that "Man is, of all the animals, the one whose brain in the normal state is the most asymmetrical" (Broca 1877, Harrington translation 1987:65). Indeed, in 92% to 99% (95% on average) of modern humans, Broca's area is more developed in the left hemisphere than the right, based on functional imaging and cortical stimulation studies (Branch *et al.* 1964:402; Loring *et al.* 1990:831; Sherwood *et al.* 2003:1; Poza-Rey *et al.* 2017:34). All of Broca's 25 patients who had tumours on Broca's area in the left hemisphere of their brains were also right-handed. As a result, it was initially believed that because there must be a correlation between right-handedness and a left dominant Broca's area, then left-handed individuals must likewise have a right dominant Broca's area (Knecht *et al.* 2000:3523; Papadatou-Pastou 2011:251), which did not turn out to be the case.

Approximately 85% to 90% of the population is right-handed whilst the remaining 10% to 15% is either left-handed or ambidextrous (Chui and Damasio

1980; Amunts 2000; Cashmore *et al.* 2008, Papadatou-Pastou 2011). Considering how 85% to 90% of the population is right-handed, whilst 95% of the population is left dominant for Broca's area - one can understand how a correlation between Broca's area and handedness might be assumed. Many scholars still support this hypothesis yet others believe that whilst some left-handers *may* be right dominant for speech, the majority are left-dominant for speech, just like the right-handers. Between 70% and 80% of left-handers are estimated to be language dominant in their left hemispheres (Amunts *et al.* 2000; Papadatou-Pastou 2011; Poza-Rey *et al*. 2017). However, the possible correlation between handedness and the lateralisation of Broca's area is more complex than solely the choice of hand preference.

Knecht[1] *et al.* further investigated the relationship between right Broca dominance and left-handedness via the study of 326 brains of healthy individuals using functional trans-cranial doppler imaging (fTCD). They found that right Broca language dominance increased linearly with the *degree* of left-handedness, as considered on a spectrum between strongly left-handed and strongly right-handed (Knecht *et al*. 2000:2516). The more right-handed a subject was on the spectrum (or the less left-handed), the less likely the incident of right hemisphere language dominance occurred. However, in strong left-handers the right Broca language dominance was nearly seven times more likely to observed (Ibid:2513). Hence, the degree of left-handedness seemed to affect the likelihood of right Broca language dominance. Overall, right-hemispheric language dominance increased linearly with the degree of left-handedness from 4% likely to occur in strong right-handers to 15% in ambidextrous individuals and 27% in strong left-handers (Knecht *et al.* 2000:2512).

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Other Brain Asymmetries and Handedness

Other asymmetries based on the shape of the brain have also been considered to be correlated with handedness. When the crania of the 'London Skull' (an early *Homo sapiens*) and 'Gibraltar Man' (*Homo neanderthalensis*) were discovered in the early 20th century, several archaeologists and paleoanthropologists were convinced that the asymmetries of the right and left occipital regions - one side being larger and protruding further than the other - were related to handedness (LeMay 1977:252). In 1910, Sir Arthur Keith determined that Gibraltar Man was right-handed because the left occipital pole of the cranium was longer than the right (LeMay 1992:496; Keith 1910), whilst in 1925, the London Skull was suggested by anatomist G. Elliot Smith to be left-handed because the right occipital bone protruded further than the left (LeMay 1992; Smith 1925). Since the early 1900s, many studies have been performed to measure and analyse not only the right and left occipital protrusions of modern and ancient humans but also the corresponding protrusions *diagonally* across the brain from the protruding occipital lobe to a possible protrusion in the frontal lobe. Meanwhile, the research continued for examining the relationship between the lateralisation of Broca's Area and handedness.

Population-level right-handedness is often considered a defining characteristic of humans (Cashmore 2008). Accordingly, hand preference is of particular interest to paleoneurologists regarding the evolution of the brain and the production of stone tools. However, the correlation between brain asymmetries and handedness has yet to be fully unpacked, and Amunts *et al.* (2000) insist that although there have been several studies demonstrating that both the asymmetry in the occipital/frontal lobe pattern and the lateralisation of Broca's Area must somehow correlate with handedness –a definitive neural substrate for handedness has not been found (Ibid). Furthermore, a genetic basis for explaining this relationship has likewise not yet been identified (Schmitz *et al.* 2017).

The typical cerebral asymmetry pattern for right-handedness in early humans, found at least as far back as the genus *Homo* and perhaps earlier (Holloway and De La Coste-Lareymondie 1982; Cashmore *et al.* 2008; Uomini 2015), is an extended (and usually wider) left occipital lobe that is accompanied diagonally by an extended (and again wider) right frontal lobe (Bear et al. 1986; Witelson and Kigar 1992). This diagonal extension pattern is often referred to as a 'brain torque' or 'petalia,' although the definition for petalia varies somewhat from author to author. It is speculated that this brain asymmetry results from the counter-clockwise torque pattern in which the brain develops in the womb (Li 2019; Toga and Thompson 2003). Based on a 2019 study by Li *et al.* in which the brains of 91 humans and 78 chimpanzees were scanned during embryological development using MRI, it was believed that brain torque was specific to humans and that it is the product of inter-related features (Li *et al.* 2019). However, the 2020 study by Neubauer *et al.* demonstrated the presence of brain asymmetries in non-human primates, and further revealed that the brains of gorillas and orangutans were more asymmetrical than chimpanzees, thus evincing that brain asymmetry is not so 'specific' to humans, but rather a matter of degree (Neubauer *et al.* 2020).

In most cases, the asymmetry in humans is more pronounced in the left occipital extension versus the right frontal extension, and the overall pattern does seem to be associated with right-handedness (LeMay 1977; Holloway and De La Coste-Lareymondie 1982; Grimaud-Herve and Lordkipanidze 2010; Bruner and Pearson 2013; Neubauer *et al.* 2020). However, the link between the reverse asymmetry (wider and/or extended right occipital/left frontal) and left-handedness is not so simple. Whilst a pronounced left occipital/right frontal petalia does seem to correlate with right-handedness, the brains of left handers tend to be less asymmetrical (i.e., more symmetrical) with little or no obvious extensions on the reverse right occipital/left frontal diagonal pattern.

Prior to the late 20th century, the technology was not yet available for acquiring highly accurate detailed measurements of brain asymmetries with respect to both size and protrusion in the brains of *living* human beings. Thus, Geschwind and Levitsky[1] (in 1968) measured the planum temporale of 100 post-mortem (but pathologically free) modern human brains, and found statistically significant asymmetries. The planum temporale is an auditory processing structure located caudally to the primary and secondary auditory cortices (Meyer *et al.* 2012); part of Wernicke's area (BA 22); and is involved with phonological encoding and speech perception, as well as serving as the epicentre of the language cortices (Toga and Thompson 2003). Of the 100 brains examined, the planum temporale was, on average, about one-third larger in the left temporal lobe in 65 of the brains studied (or 65%) and larger on the right side in only 11 (Geschwind and Levitsky 1968:186). The remaining 24 specimens had equal-sized plana temporale. The researchers expressed interest as to whether brain asymmetries might be related to handedness, but the handedness of the individuals of the brains studied was unknown and the subjects were deceased. As a result, this information was unavailable to Geschwind and Levitsky for correlation studies (Ibid), which is unfortunate given how more recent studies of brain asymmetries tend to focus on the planum temporale because of its relationship to handedness and language laterality (Toga and Thompson 2003). In humans, the planum temporale can be up to ten times larger on the left side than its homologue in the right hemisphere (Ibid:39).

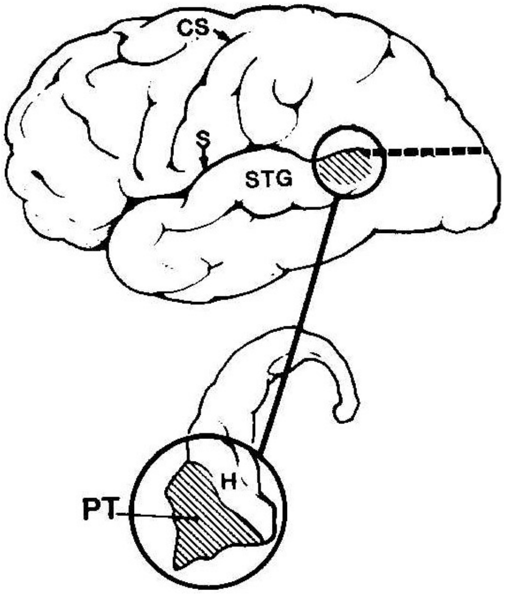

Fig. 3.1 Planum Temporale (PT)
Galaburda et al. 1987:855

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Following Geschwind and Levitsky's study, new technologies became available that allowed for the examination of cerebral asymmetries in the brains of *living* people, which could be detected at both the macroscopic and microscopic level (Chance and Crow 2007). Although today's technology provides for the detection of an asymmetry at only half a millimetre, many scientists initially believed that such a small incongruity would probably be too small for a statistically significant correlation (LeMay 1992). However, only a few millimetres can be meaningful when studying the petalias of the human brain. According to Chance and Crow[1], a petalia can be most simply defined as ". . . the appearance of more tissue at the poles of the hemisphere on one side than the other" (2007:98), but for others, a petalia only refers to an extended and wider occipital lobe on either the left or right side (LeMay 1992:496). In Figure 3.2, Chance and Crow demonstrate what they consider to be three different types of brain petalias as follows: (i) Brain A illustrates a petalia with a left occipital extension and an accompanying right frontal extension; (ii) in Brain B, the entire right hemisphere has shifted anteriorly beyond the left hemisphere; and (iii) Brain C depicts an asymmetrical distribution of brain tissue, also referred to as

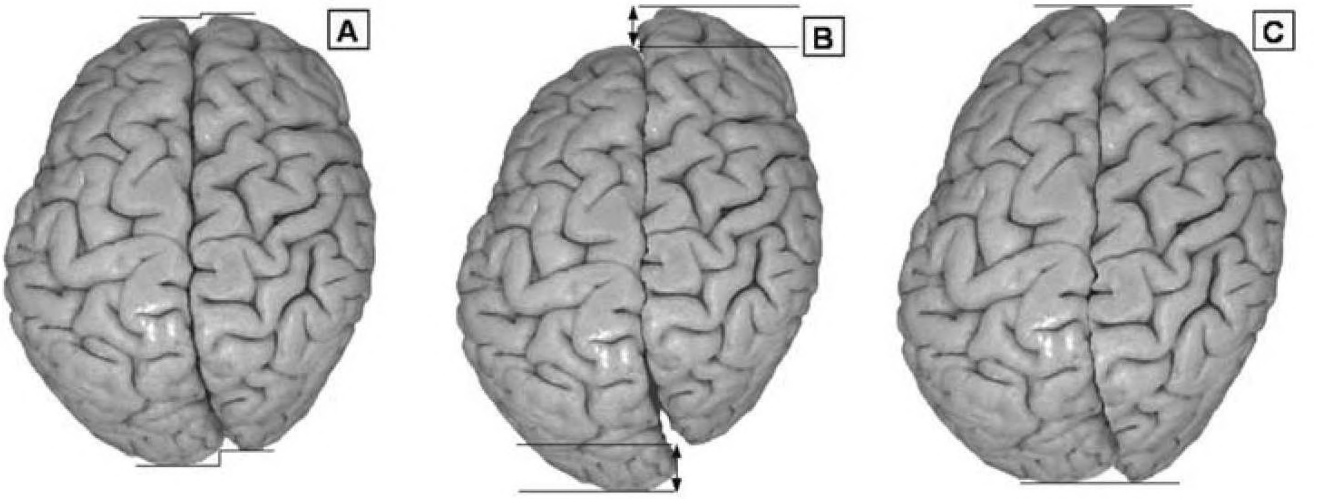

Fig. 3.2 Brain petalia examples
Chance and Crow 2007:87

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‘bending’ (Chance and Crow 2007:87, Li et al. 2019:1142). (Chance and Crow note that the petalias on Brain B and C have been augmented for illustrative purposes.) The view of each brain was taken from above; with the upper portion of the photo indicating the most anterior region (frontal lobe) while the bottom represents the posterior section of the brain (occipital lobe). During the late 1970s, LeMay[1] conducted a study examining brain petalias in conscious living humans representing a sample set of near equal right-handers and left-handers. Of the 244 subjects scanned using cerebral CTT technology, 120 were determined to be right handers whilst 124 were left handers.

To better qualify handedness, she asked the subjects if they had always preferred their current dominant hand or if they preferred a different hand during childhood, considering how parents will sometimes force their children to write with their right hand, regardless of the child’s natural preference. Additionally, some of the subjects might be ambidextrous or use their right hands for writing but left hands for sports, tools, etc. Therefore, LeMay’s study initially classified handedness into four categories as follows: (i) strongly right-handed; (ii) strongly left-handed; (iii) mildly right-handed; and (iv) mildly left-handed. However, LeMay ultimately reduced the categories to only strongly right-handed or strongly left-handed and included many of the mildly left-handed subjects in the strongly left-handed category in order to conduct a binary statistical study (LeMay 1977:244).

LeMay also measured how much a petalia extended anteriorly or posteriorly (and in what direction) and the width of the petalia in the occipital and frontal lobes. Widths were measured approximately 5 millimetres from the ends of the hemispheres. In general, the direction of the brain torque tended to be the same (left occipital to right frontal) for both the right and left-handers, but the width differences were much more pronounced in the right handers as were the brain extension

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measurements (Ibid:247). The results suggest that there is a correlation between both the protruding left occipital/right frontal configuration, coupled with wider hemisphere widths, and right handedness. The data is particularly telling with respect to the extension of the left occipital pole, which occurred in 92 of LeMay's 120 right-handed subjects (77%), whilst the data from left-handers did not indicate *significant* asymmetries. The left-handers demonstrated a higher percentage of protruding right occipital/left frontal configurations (also with greater widths) than the right hander group, which would be expected, but overall – only a small percentage (approximately 35%) of the left-handers followed this pattern.

	Frontal Lobes – Width			**Occipital Lobes - Width**		
	Left Lobe Bigger	**Same Size**	**Right Lobe Bigger**	**Left Lobe Bigger**	**Same Size**	**Right Lobe Bigger**
Right Handers	23	34	73	79	30	11
Left Handers	33	39	49	45	41	32

	Frontal Lobes - Torque			**Occipital Lobes – Torque**		
	Left Lobe Extends	**No Ext.**	**Right Lobe Extends**	**Left Lobe Extends**	**No Ext.**	**Right Lobe Extends**
Right Handers	17	24	79	92	13	15
Left Handers	43	22	44	44	35	43

Fig. 3.3 Lateralisation results
LeMay 1977:245-246

By the 1990s, LeMay's research had shown that although left-handedness might be natural or genetic (Annett 1978), it could also be the result of environmental issues such as trauma or toxins as an infant or toddler (Satz 1972; Habib *et al.* 1990). Furthermore, other reports indicate a connection between left-handedness and autoimmune diseases, Hashimoto thyroiditis and in those with learning disabilities (LeMay 1992:499). As a result, it is difficult, if not impossible, to definitively identify whether a person is *organically* left-handed (i.e., genetically), or if he/she adapted left-handedness *environmentally* from the influence of one or more contributing factors. Furthermore, there are also those who are ambidextrous or semi-ambidextrous, preferring to do some tasks with the right hand whilst using the left hand for others. As a result, LeMay suggests that the term 'left-handed' is "somewhat ambiguous" and believes it would be more useful to consider a population as either "right-handed" or "not right-handed" (LeMay 1992:493).

Although any postcranial change in the body produces a corresponding change in the motor cortex, neural adjustments could occur in other regions of the brain as well (depending upon the postcranial change). Accordingly, it seems possible that a left-hander attempting to perform tasks with the right hand could affect brain lateralisation/asymmetries in addition to the impacts in the motor cortex. Imitation is the common basis for learning tasks for both non-human primates and modern humans (and presumably early humans). According to Rizzolatti and Craighero:

> "A category of stimuli of great importance for primates, humans in particular, is that [which is] formed by the actions done by other individuals. If we want to survive, we must understand the actions of others. Furthermore, without action understanding, social organization is impossible" (2004:169).

Mirror neurons are a type (or subset) of visuomotor neurons that fire when an individual undertakes a particular action *as well as* when an individual observes another individual undertaking the same (or similar) action (Di Pellegrino *et al.* 1992; Jeannerod 1994; Gallese *et al*. 1996; Rizzolatti *et al*. 1996; Rizzolatti and Craighero 2004). Mirror neurons were first discovered in area F5 of the monkey premotor cortex (Rizzolatti and Craighero 2004:169). Prior to the benefit of a fully syntactic and semantic language, imitation and gesturing were likely the only means to share behavioural culture.

Therefore, if a left-handed early human was attempting to learn a task from a right-hander, s/he would have likely attempted to mimic the actions of the right-hander in terms of using the same hands as the right-hander for motions or holding objects. Using the less dominant hand for an action that required the dominant hand would have produced a negative impact on the learner's skill set. It would be interesting to know how long the learner attempted to employ the same hands as the instructor for the task, and at what point did s/he switch hands (if at all). Fortunately, there are other clues in the fossil record that can provide an indication of handedness.

In the 1960s, researchers found that handedness of early humans could be determined through the examination of the anterior teeth of fossil dentition based on the direction of tool marks left on the enamel when hominins would employ their mouths as a 'third hand' (Brace 1967; Bermúdez de Castro et al. 1988; Bruner and Lozano 2014). For example, hominins would hold a material between their teeth and their non-dominant hand in order to use their dominant hand to cut the material with a lithic tool. Sometimes, the tool would inadvertently scratch or scrape the labial enamel of the anterior teeth resulting in an oblique striation (frequently referred to as a 'non-feeding mark' or 'non-masticatory'), which was typically oriented to either the left or right depending on the hand used to cut the material. From this information, the individual's hand preference can be inferred (Lozano *et al*. 2009; Hillson *et al*. 2010; Frayer *et al*. 2012, Poza-Rey *et al.* 2017). However, once an individual reached the age of 35 (middle age by Palaeolithic standards), the dental crown is worn down, and the striations are often lost (Poza-Rey *et al*. 2017).

In the late 1980s, Bermúdez de Castro *et al.* applied this technique to detect handedness in the previously-known-as-Heidelberg individuals recovered from the Sima de los Huesos site in the Atapuerca Mountains, recently re-dated to 430 kya (Bermúdez de Castro *et al.* 2004; Arsuaga *et al.* 2014). Of the 28 individuals recovered, 20 were found with associated anterior teeth. These individuals included both males and females, and all ages were represented, except for infants. The studies determined that there were labial striations on the anterior teeth of all the individuals, caused by using the anterior teeth as a tool (Bermúdez de Castro 1988; Lozano *et al.* 2008; Lozano *et al*. 2012; Bruner and Lozano 2014). Furthermore, the direction of the labial striations indicated that most of the Sima individuals appeared to favour their right hands based on the direction of the striations. In 15 of the individuals, a right oblique striation was the most common whilst in four of the individuals, more vertical marks were present (in addition to the right obliques). Only one individual seemed to indicate no preference (Lozano *et al.* 2008, 2009).

Handedness in early hominins can also be detected through tool production and use (Cashmore *et al.* 2008; Uomini 2015). Stone knapping creates flake scatters that form patterns indicating where and how the knapper sat (and which hand s/he used to knap), and sometimes these patterns have been found in the fossil record (Wenban-Smith 1989, 1997; Uomini 2015; Garciá-Medrano *et al.* 2019). In the early 1980s, Nicholas Toth conducted a handedness study focused on the orientation of flake pattern after being released from the core. Toth assumed that a right-handed knapper would rotate a core clockwise whilst a left-handed knapper would rotate the core counter-clockwise, which would be reflected in the pattern left by the detached flakes (1985). Toth examined hominin tool production sites in Koobi Fora and found that the right-handed patterns consistently outnumbered the left, presenting a case for the lateralization of the brain between roughly 1.9 to 1.4 mya (1985:611). Although some of Toth's underlying assumptions for his core rotation hypothesis were met with criticism (Cashmore *et al.* 2008), it is nevertheless an interesting approach for identifying handedness in the fossil record.

Uomini also believes that the wear on the tools themselves can reveal how they were held and in which hand, as well as the direction the tool moved during use (Uomini 2008). She further observes how bone 'retouchers' (used to sharpen tools) recovered by Rigaud in southwestern France often left diagonal marks, which likely indicated the hand holding the retoucher, and she also notes how hand stencils in cave art can suggests handedness implied by the opposite hand of the stencil negative, based on the work of Faurie and Raymond (Uomini 2015). Both examples indicated that handedness among the samples observed was proportionately the same as modern populations (Faurie and Raymond 2004; Rigaud 2007; Rigaud *et al.* 2013). It does seem that the lithic evidence implies a predominately right-handed population among toolmakers (Uomini 2015; M. White 1998; M. White *et al.* 2019).

In the early 1980s, Holloway and De La Coste-Lareymondie performed a study in which the brain endocasts of 190 specimens were examined for asymmetry patterns. The specimens consisted 40 gorilla, 41 bonobo, 34 chimpanzee, 20 orangutan, 41 hominins and 14 modern humans. Of the hominins, 11 were australopithecines, 20 were *Homo erectus* and ten were Neanderthals. Although there are few fully complete crania in the fossil hominin record without any distortion, the sample set was carefully appraised and considered a respectable representation based on the data sample available at the time. When the hominin endocasts were compared with the modern human sample set, the *combination* of petalia patterns did not appear significantly different, according to the researchers (Holloway and De La Coste-Lareymondie 1982:107). However, whilst their results suggested that human brains are more asymmetrically organised than pongids (i.e., stronger and more pronounced), the portion of the sample set consisting of the 11 australopithecines did not support the same conclusion (Ibid).

A more recent study on the correlation between handedness and brain lateralization was performed by Poza-Rey, also on the fossil crania recovered from the Sima de los Huesos site in Spain. Of the 17 crania (or partial crania) recovered from the 28 individuals, 16 were digitally scanned at a high resolution by Poza-Rey and colleagues with slice thickness of 0.50 mm, producing digital brain endocasts for the study (Poza-Rey *et al*. 2017:35). Of the 16 crania scanned, petalias could be identified and measured in nine individuals, whilst Broca's area could be observed in thirteen individuals, all with some level of lateralisation on one side or the other. In total, there were 14 endocasts which demonstrated asymmetry through either petalias or where a dominant Broca's area could be established or both.

In the nine complete endocasts with petalias, the results suggested that five were right-handers whilst four were not right-handers, which is an unexpected result. Poza-Rey *et al.* noted how some specimens showed a ". . . remarkable lack of asymmetry" (Poza-Rey *et al.* 2017:41) and acknowledged that the proportion of right-handers and not right-handers differed greatly from the typical proportion found in modern human populations of right-handers, which typically represents between 85% to 90%. The results for the lateralisation of Broca's area yielded five left hemispheres dominant for language and eight with Broca's area dominant in the right hemisphere, which is highly unusual compared to the modern human general population. Even more puzzling is that the dental striations on the anterior teeth of the applicable crania were re-examined for handedness and according to Poza-Rey *et al.,* the striations confirmed that 16 of the 20 individuals with anterior teeth were, indeed, determined to be right-handed based on a right oblique dominant pattern (2017:41).

Poza-Rey *et al.* offer possible explanations for these divergencies from the norm, but at the same time they acknowledge that these results may suggest a lower degree of lateralization of the brains in the Sima group of individuals or at least – a *different* degree of lateralization than in modern human groups (Poza-Rey *et al.* 2017). One of their explanations notes how daily activities during this period were most likely learned by imitation. Whether it was making stone tools or peeling fruit, the action was likely learned by mirroring the actions of an adult, which would include using the same hands in the same manner, as previously discussed. If so, it would seem that this imitation would have most likely affected left-handers (assuming the teachers were right-handed) thereby forcing themselves to use their non-dominant right hands. This 'forced' right-handedness would have prompted changes to the brain, given its plasticity to adapt and adjust. At the same time, forced handedness would have likewise occurred if right-handers were learning from left-handers. However, the asymmetry study by Poza-Rey *et al.* indicates an almost equal number of right-handers to not right-handers. Considering that the labial striations indicated that the Sima population was predominantly right-handed, these mixed results could possibly be explained by the following: (i) the not right-handers were ambidextrous, using their right hands for cutting material between the teeth and left hand, whist using the left hand dominantly for other activities; (ii) the full lateralisation of the brain resulting in demonstrative cranial asymmetries had either not yet fully evolved in the Sima population or the degree of lateralisation compared to modern humans was different (as Poza-Rey *et al.* suggested); (iii) interpretation error; (iv) there is no correlation between either Broca's area and/or petalias and handedness; or (v) this sample size is too small to draw meaningful conclusions.

Unfortunately, neither the actual Sima crania nor the high resolution virtual endocasts have been made available for other paleoneurologists to examine, but it seems unlikely that the team led by Poza-Rey misinterpreted the results. However, this explanation remains a possibility unless and until this information is released for others to examine. Regardless of whether or not hand preference in some way corresponds to either petalias or the dominant Broca's area, both the high incident of right occipital/left frontal petalia orientations as well as the high percentage of right dominant Broca areas seems highly unusual. This is especially perplexing considering how the labial striation studies on the anterior teeth (of the same individuals) by Bermúdez de Castro *et al.* yielded predominantly right-handers. As a result, this case study will remain an anomaly unless and until additional information can be provided or the endocasts are made available to the public.

Handedness

In modern humans, it does appear that a left occipital/right frontal petalia correlates with right-handedness, based on the other studies presented herein. However, the studies do not support a right occipital/left frontal combination as indicative of left handedness (or non-right-handedness), and suggests only that this petalia orientation tends to occur more in left-handers than right-handers. In other words, *non*-right handers cannot definitively be determined from a petalia, and LeMay cautions that the relationship between asymmetries and handedness is "far from absolute" (LeMay 1992:497), whilst Chui and Damasio argue that brain asymmetries and hand preference might be independent variables (Chui and Damasio 1980). Regardless, the majority of the evidence for a correlation between a pronounced left occipital/right frontal petalia and right handedness is compelling. The conclusions of the early study by Holloway and De La Coste-Lareymondie in 1982 and the recent studies by Li *et al.* and Neubauer *et al.* presented findings which demonstrate how brain asymmetries are more pronounced in humans than non-human primates and are independent of brain size (Holloway and De La Coste-Lareymondie 1982; Li *et al.* 2019; Neubauer *et al.* 2020). Although these asymmetries can only suggest hominin *right* handedness (and not left handedness) when a left occipital/right frontal petalia is present, they also imply the presence of some level of brain lateralisation and to some extent, possible brain reorganisation.

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Chapter 4: Bipedalism, Hominins and the Brain

There is no consensus regarding the definition of the family Hominidae.
Tim D. White (2002:407)

Bipedalism is a highly specialized form of locomotion that began to develop during the late Miocene, following the human ancestral lineage split with that of the non-human apes, which occurred roughly between 7 and 5 million years ago (Cartmill and Smith 2009:168; Harcourt-Smith 2013:1; Gamble *et al* 2014:88). Shortly thereafter, possible indications of early bipedalism began to appear in the fossil record in species such as *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and the *Ardipithecus*[1] species.

There have been numerous hypotheses over the years as to *why* our ancestors became bipedal (Harcourt-Smith 2013) which are not particularly relevant to the aims of this thesis, yet a few aspects from some of the more prevailing theories are important to note. The 'energy efficiencies' of bipedalism do not imply that bipedal walking conserves more energy than quadrupeds, but rather that bipedal walking is a more efficient means of locomotion when compared to inefficient quadruped 'knuckle-walking' in terms of knuckle-walking pre-hominin ancestors or extant knuckle-walking apes (Steudel 1996; Leonard and Robertson 1997). For example, chimpanzees were deemed the "least energetically efficient mammals" of the various mammals observed (with respect to locomotion) in a study conducted during the 1980s (Steudel 1996:347). Also, one of the more popular myths regarding the origins of bipedalism is that our ancestors adopted bipedal locomotion in order to '*run* across the savannahs' after climate change occurred, which had allegedly reduced a large portion of the wooded landscape to open grasslands. However, the pelvis and other related lower body morphology did not fully develop the more efficient means

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[1] *Although some argue that both Sahelanthropus tchadensis and Orrorin tugenensis should be included in Ardipithecus.*

of walking until the emergence of *Homo*, and the smooth 'striding gait' was not mastered until *H. erectus* (Berger *et al.* 2010:196; Berger 2012:120). Thus, it is unlikely that hominins were able to 'run' until at least *H. erectus* (Bramble and Liebermann 2004) and more likely resorted to arboreal locomotion through the trees if they needed to move quickly to escape predators. Furthermore, based on ecological and environmental studies, the full expansion of the open C_4 (secondary) grasslands did not occur until the late Pliocene or early Pleistocene (if not later), well beyond the timeline for habitual[1] bipedalism (Reed: 1997; Bobe and Behrensmeyer 2003).

Certainly climate change played a role in the full adaptation to bipedalism, as the Pliocene not only ushered in cooler temperatures around 5.3 mya, but also climate variability and fluctuation (Potts 1996:922); however, there has been increasingly less emphasis placed on climate alone as a single catalyst in favour of a wider lens that examines a combination of environmental factors that likely affected major adaptations, speciations, and extinctions during this period (Anton *et al.* 2014), discussed further in Chapter 6. Regardless of what prompted our ancestors to adopt a bipedal form of locomotion, it is considered one of the two primary criteria in order for a species to be designated a 'hominin,' namely that the species had acquired some element of adaptive anatomical change that demonstrates bipedalism as a regular means of locomotion.

The term hominin refers to the tribe Hominini, which is part of the subfamily Homininae from the family Hominidae. This is a relatively recent change in nomenclature, which began a departure from use of the term 'hominid' during the early to mid-2000s. According to Erin Wayman with the Smithsonian National Museum of Natural History (U.S.), the family Hominidae was broadened to include

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[1] *The reference to "habitual bipedalism" is often debated due to the amount of time hominins spent in the trees. This thesis deems 'arboreal' and 'terrestrial' as describing 'lifestyle' whilst "habitual bipedalism" indicates the form of locomotion favoured terrestrially.*

the great apes (orangutans, gorillas, chimpanzees and bonobos), who are closely related to humans (2011). From the family Hominidae, the subfamily Homininae then excludes the orangutans, which are Asian great apes and more distantly related to modern humans than the African great apes, based on biomolecular studies (T. White 2002:407). The tribe Hominini narrows further by eliminating the gorillas, thus leaving the human lineage, its close extinct relatives (referred to as 'hominins'), and Pan (chimpanzees and bonobos), although there is debate as to whether or not Pan should be included in the Hominini tribe. It should also be noted that some scholars still use the term 'hominid' either as a means to distinguish a human lineage member from the great apes or to mean a 'hominin' or even a 'proto-hominin' (to be discussed).

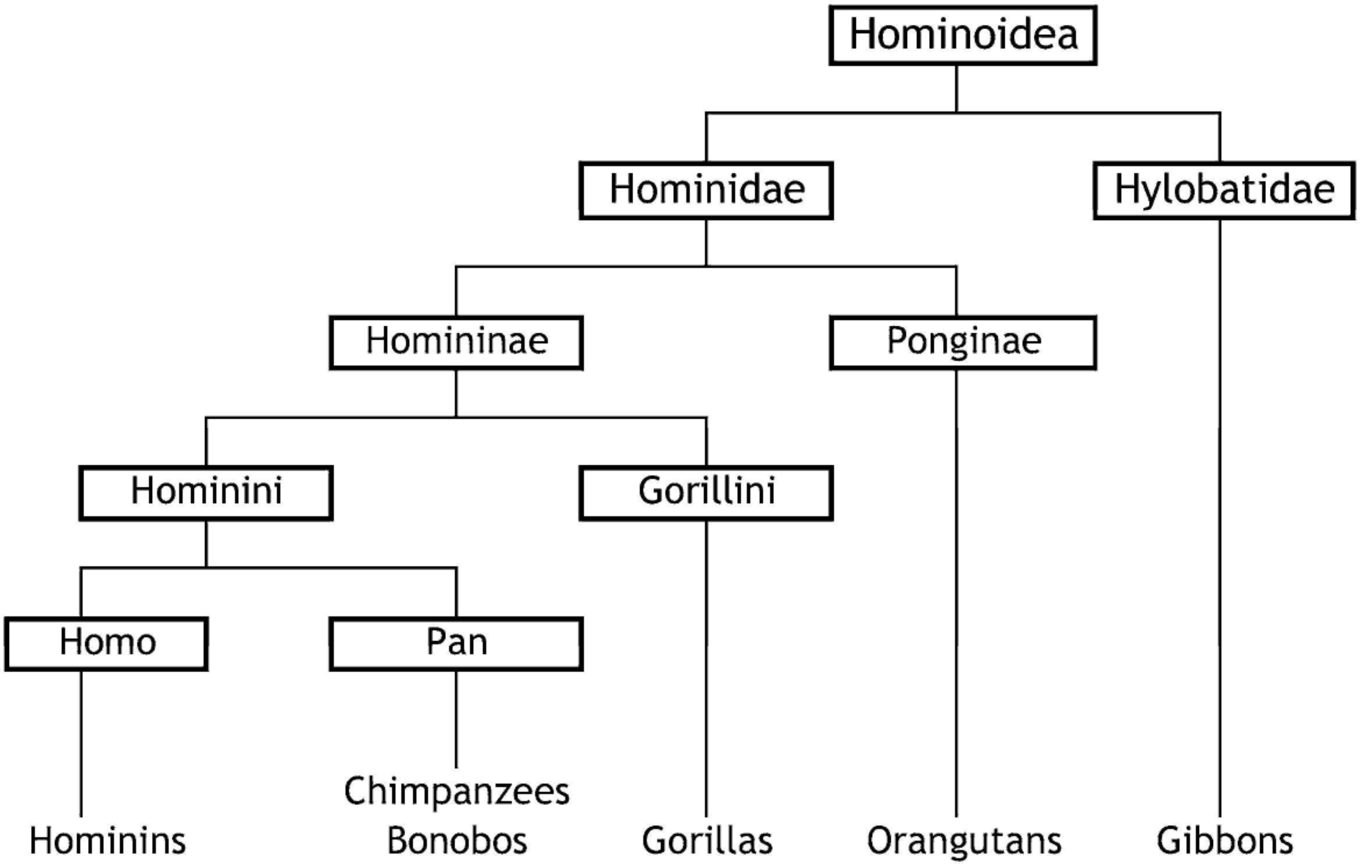

Fig. 4.1 Homo Phylogeny
Suzi Wilson

The other criterium for hominin designation is to possess at least some of the supporting dentition features, such as smaller canines and a reduction in the CP_3 honing complex[1] (Stanford *et al.* 2017:297,302). The CP_3 honing complex is commonly found in fossil apes[2] where the large upper canines slide neatly into a space (or diastema) of the lower jaw, where the canine is then sharpened (or 'honed') against the third premolar. Although what constitutes a hominin is frequently under discussion, debate, and review as the result of new discoveries, this very general rule of thumb tends to be the largely accepted practice, although arguments pertaining to the proto-hominin species continue to be debated.

Although various species may have practiced or experimented with bipedality on at least a part time basis, habitually walking upright would ultimately require substantial morphological adaptations for quadrupeds, including major structural changes to the cranium, spine, pelvis, legs, ankles, feet, joints and soft tissue (Harcourt-Smith 2013; Stanford *et al.* 2017). The spine needed to transition from a 'C-shape' (which would otherwise apply pressure to the upper torso, pushing it to fall forward whilst attempting to stand upright) to an 'S-shape' which centres and balances the body over the legs and feet. Accordingly, the cervical part of the spine and cranium would need to reposition anteriorly, which would additionally provide better balance. The fossil evidence for this particular adaptation can be seen in the position of the foramen magnum, where the cervical spine articulates with the cranium. The foramen magnum of quadrupeds lies at the base (underside) of the skull at the back of the head, which would need to transition forward as part of the adaptative process. Posterior to the foramen magnum on the occipital bone (back of

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[1] *The third premolar (aka the 'honing' tooth) of the CP_3 honing complex is actually now the first premolar in primates, but it is referred to as the third premolar in fossil primates because the first and second premolars were lost in evolution (Stanford et al. 2017:299).*

[2] *and some monkeys (von Bonin and Bailey 1947)*

the skull), strong neck muscles attach to a large cranial surface called the nuchal (neck) plane, which support the quadruped head against the force of gravity. As a result, the size and location of the nuchal plane on the skull can often indicate whether or not the nuchal muscles were supporting a head held in an upright position on the basal portion of the skull for bipedal hominins, versus a posterior portion for quadrupeds.

For energy efficiencies and additional balance, the pelvis acquired a wider, curved 'bowl-shape' with a short broad ilium[1], and the femur became angled from the hip joint to the knee, as means to more easily maintain one foot on the ground and underneath the centre of gravity while walking bipedally, to avoid falling to the unsupported side. For example, chimpanzees rock from side to side when walking bipedally in order to maintain balance, which wastes a lot of energy. The medial condyles (where the femur meets the tibial plateau of knee) increased in size in order to bear the weight of the body, which was previously spread across four limbs (and

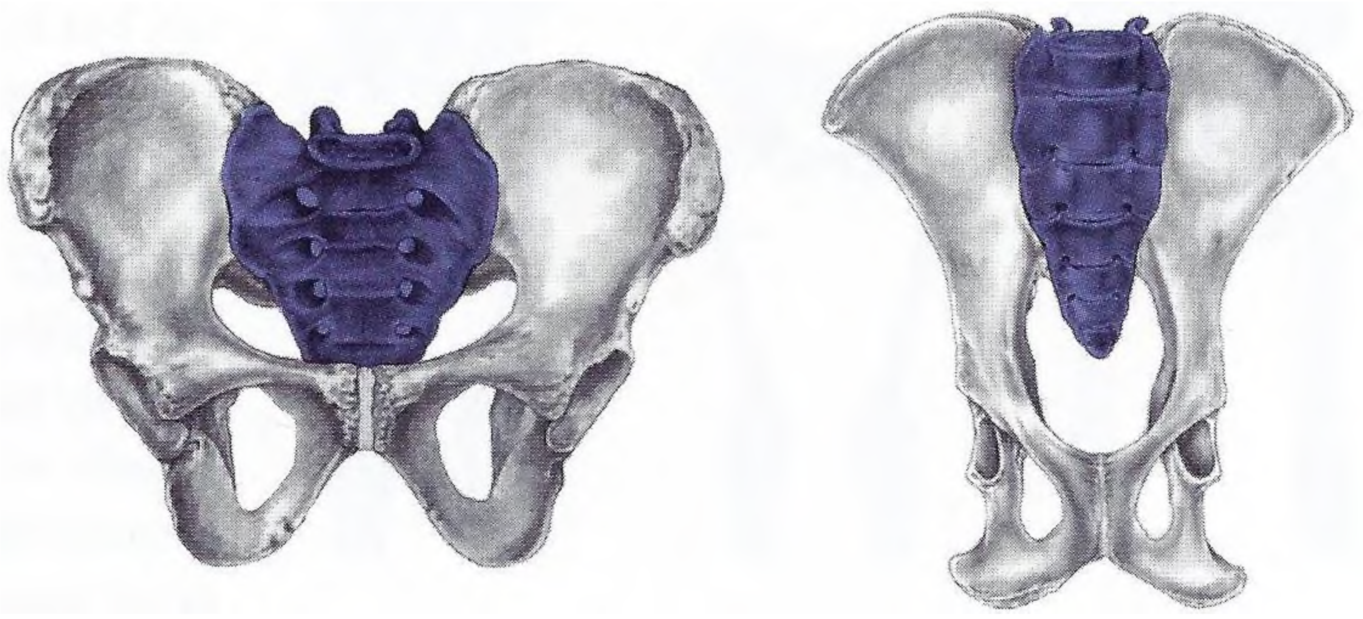

Fig. 4.2 Human pelvis on left and Great Ape pelvis on right. Note how the human ilium is broader and shorter, and the pelvis is also shorter, wider and bowl-shaped for balance.
Stanford et al. 2017:295

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[1] *The ilium is where the gluteal muscles attach (Stanford et al. 2017:295).*

four sets of joints) in quadrupeds, and the groove for the patella deepened in order to prevent dislocation. The feet and toes shortened, and the feet also developed arches for shock absorption. Although the big toe was now shorter, it also became more robust in order to provide forward propulsion by bending backwards and pushing off from the ground, which is referred to as 'dorsiflexion'.

In order for a quadruped to make this complex transition to habitual bipedal locomotion, the numerous skeletal and soft tissue adaptations would have occurred over a long extensive period. During this transition, any anatomical change in the body would have a corresponding change in the brain - especially in the motor cortices, as demonstrated in Chapter 2. Other areas of the brain, such as those associated with visuo-spatial skills and balance (particularly in the parietal lobes and cerebellum), would have been affected as well.

Gerald Edelman[1] has argued that prior to bipedalism, pre-hominin cranial morphology was somewhat restricted without room for growth (2004:102). Once a more erect posture was achieved and the foramen magnum had re-positioned forward, there was less pressure on these muscles as well as the spinal cord, thereby lifting the cranio-facial morphology and thus allowing the cerebral cortex to expand both superiorly (upward) and posteriorly (back). This by-product of bipedalism is of particular interest because, regardless of how much time early hominins may or may not have spent in the trees, the crux of the matter is that once they were committed to terrestrial bipedalism versus quadrupedal knuckle-walking locomotion, they inadvertently created a means for their brains to expand. As bipedalism became increasingly habitual, the hands and wrists also adapted due to a change in use.

Knuckle-walking requires 'stiff' wrists to avoid bending or overextension when pressure is exerted on the knuckles, but this 'locking' mechanism that protects the

[1] *Edelman founded and directed the Neurosciences Institute in San Diego and served as president of the Neurosciences Research Foundation.*

wrists also limits rotation (Tuttle 1967:192). Once knuckle-walking was abandoned, the hands and wrists could adapt/develop greater mobility, if not also dexterity, as an additional means for connecting with the environment, and John Barrett emphasizes how the evolution of manual dexterity played a major role with respect to the exploration of objects and materials (2013:11). Furthermore, once the arms and hands were no longer required for locomotion, they were now also free for uses such as carrying items (e.g., food and children), throwing objects, and other abilities that would continue to develop, albeit over a long period of time.

Although Darwin felt the value of standing upright was primarily the freedom it afforded the hands to hold and wield weapons, he also noted how it facilitated the development of the prehensile hand for gathering food and making tools (Darwin 1871:35). Habitual bipedalism or bipedal standing would have also enhanced the early hominins' ability to view their surroundings and watch for predators. Furthermore, upright posture provides a more direct and intense contact between the eyes – one that would have likely affected social relations. In this regard, certainly the loss of pigment in the sclera ('whites') of the eyes would have played a role in terms of pre-language communication, and perhaps this loss of pigment was a necessary adaptation following bipedalism as a means to better gauge and express intentions in these more direct social settings presented by upright posture. Edelman likewise stresses how our social and communicative abilities were enhanced by bipedal posture, and he suggests that the arms and hands may have been used to develop a rudimentary sign language (2004:102), whilst Barrett additionally notes how the observations and explorations of the environment could now be shared through the recognized direction of the gaze between two individuals (2013:11). Most relevant was the ability to use the index finger to point. Pointing, which enhances our communication as a means to gesture and index, was an important milestone in our social development. Svante Pääbo discusses how there are very few detectable cognitive differences between young humans and young apes until they are approximately ten months old (2014:205). After that, observable differences start to occur and at approximately one year old, baby humans start pointing. They point at others, at themselves, at cats, walls, flowers – anything, but not necessarily because they want to draw attention to the object itself, but rather because they are fascinated with their ability to draw someone else's attention to whatever it is they are pointing to (Ibid).

Although the ancestors of the first hominins underwent extensive physiological changes in order to morphologically transform into habitually bipedal hominins, the timing of these developments cannot (yet) be anatomically determined with any degree of certainty. However, it seems likely that additional psychological adaptations that perhaps enhanced our socialization would closely follow bipedalism given the importance of reading and relaying intentions in these new amplified social situations as a result of upright bipedal posture. In turn, the deepened social relations that developed among these early hominins would ultimately serve to further stimulate brain development. Just as the postcranial morphological adaptations in the body had corresponding changes (and in some cases – expansions) in the brain, a new and enhanced socialization would have also required changes, if not advancements, in the brain in order to mediate these new social situations (Holloway1967; Brothers 1990; Gamble *et al.* 2014). Holloway (based on the work of Maruyama) has argued that it was these increasingly complex social situations that provided the 'initial kick' for enhanced cognitive abilities[1] (Holloway 1967; Maruyama 1963). However, it was bipedalism that first prompted the heightened socialization among the first hominins as a result of their upright posture, which also facilitated the means to accommodate a larger cerebral cortex. These aspects of

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[1] *Later named the "Social Brain Theory" by Leslie Brothers (1990).*

greater socialisation and body language and/or gestural communication will be discussed further in the following chapters.

The Bipedal Transition and Proto-hominin Discoveries

In 2001, an expedition team led by Michel Brunet discovered a fossilized, mostly complete cranium (specimen TM 266) in the Djurab Desert in northern Chad, which was initially estimated to date between 5.2 and 7 million years old[1], although Brunet believes that it is more likely between 6 and 7 million years old (Brunet *et al.* 2002:145). The team nicknamed the cranium "Toumaï", which means "hope of life" in the Goran language, but it is better known by its scientific name of *Sahelanthropus tchadensis* (Ibid). The position of the foramen magnum had begun to shift anteriorly, more so than what would typically be found in quadrupeds, indicating that the head was more often held in an upright position and thus evincing that locomotion was likely *predominantly* bipedal (Cartmill and Smith 2009; Gamble *et al* 2014; Stanford *et al.* 2017). Likewise, the nuchal plane on the bottom of the skull was horizontal, indicating that the head was supported by the neck muscles in an upright position. The cranium had a less prognathic face than expected for early hominins, with somewhat smaller canine teeth and a non-functional CP_3 honing complex, but its brain size was small, estimated at only between 360 and 370 ml (Zollikofer *et al.* 2005:758). Although many believe that *Sahelanthropus tchadensis* was habitually bipedal based on these and other features (Brunet *et al.* 2002; Zollikofer *et al.* 2005), others remain sceptical, often based on the same fossil evidence as well as a partial femur more recently recovered, which may or may not be associated with specimen TM 266 (Wolpoff *et al.* 2002, 2006; Macchiarelli *et al.* 2020). Thus, whether or not *Sahelanthropus tchadensis* should be considered a 'hominin' remains debateable.

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[1] *Based on biostratigraphic correlations with East African sites.*

Another important discovery in 2001 was made in the Tugen Hills of Kenya, where Pickford and Senut found several cranial fragments and postcranial remains estimated to be approximately 6 million years old (Pickford and Senut 2001; Cartmill and Smith 2009; Stanford *et al.* 2017). Of particular interest were portions of a femur which, along with a few other unusual traits, persuaded Pickford and Senut to give the specimen a new genus name, arguing that *Orrorin tugenensis* was a hominin based on several postcranial features which indicated bipedal locomotion (Pickford and Senut 2001:22). Whilst the femur *does* support that *Orrorin tugenensis* was likely bipedal at least some of the time, there is unfortunately not enough fossil evidence[1] to definitively conclude that s/he was a hominin, and like *S. tchadensis* – the bipedality and possible status as a hominin for *Orrorin tugenensis* remain debated. Other contenders for the title of 'earliest hominin' are two species from the *Ardipithecus* genus, which lived between roughly 5.8 mya and 4.4 mya (Stanford *et al.* 2017).

In 1994, the Middle Awash team led by Tim White, Berhane Asfaw, and Gen Suwa excavated a late Miocene site at Aramis and found seventeen fossil specimens of a new species they named *Ardipithecus ramidus*, who lived around 4.4 mya (T. White *et al.* 1994; T. White *et al.* 2006; T. White *et al.* 2009). Over the ensuing years as hundreds of more fossils were recovered, it was revealed that a smaller set of these specimens represented a different and older species: *Ardipithecus kadabba*, who lived between approximately 5.8 mya to 5.5 mya (T. White *et al.* 2006:883; T. White *et al.* 2009:63; Stanford *et al.* 2017:302). The arguments in favour of the *Ardipithecus* species as hominins are largely based on dentition whilst the arguments for bipedalism are not as strong. The pelvis and anterior position of the foramen magnum for *Ardipithecus* does indicate bipedalism at least part of the time, but like *Sahelanthropus tchadensis* and *Orrorin tugenensis*, the fossil evidence falls short of the

[1] *For example, the lower end of the femur is missing, so there is no way of knowing if the femoral condyles had become more robust in order to support weight from an upright position, or if the femur had become more angular creating a more valgus knee (Cartmill and Smith 2009:145,166).*

suite of adaptive traits necessary for conclusively identifying habitual bipedalism in any of these *Ardipithecus* species, and as a result - none are unequivocally accepted as human ancestors. However, these taxa are often referred to as "Early Possible Hominins" (EPHs)(Hunt 2015:114).

The first fossil evidence to conclusively confirm bipedalism was found in Laetoli near Olduvai Gorge in Tanzania during the summer of 1976 whilst Mary Leakey's excavation team was unwinding after work by flinging dried elephant dung at one another (Agnew and Demas 1998:46). When Andrew Hill dropped to the ground to avoid getting hit and landed on an exposed volcanic tuff, he inadvertently discovered fossilised animal tracks in the volcanic ash, which in turn, led to other fossilised tracks. Two years later, geochemist Paul Abell found the first bipedal footprint near the Ngarusi River, which dated to between 3.6 and 3.7 mya (Leakey and Hay 1979:318; Agnew and Demas 1998:46; Stanford *et al.* 2017:292). It was presumed that the footprints were made by three australopithecine individuals, and it would later be determined that the first australopithecines appeared no later than 4.2 mya, with a morphology that supports both hominin dentition and habitual bipedal locomotion (Leakey *et al*. 1995; Ward *et al.* 2001; T. White 2002; Cartmill and Smith 2009; Stanford *et al.* 2017).

Although most agree that *Australopithecus* at 4.2 mya is the first indisputable hominin (Hunt 2015), an older potential candidate entered the running in 2017, when late Miocene footprints with some hominin-like characteristics were discovered near Trachilos on the western-most edge of Crete in Greece (Gierliński *et al.* 2017), which have been recently dated to between 6.272 and 6.023 mya via cyclo-stratigraphic data based on magnetic susceptibility (Kirscher *et al.* 2021). Although controversial, two narrow trackways were found *in situ*, impressed into a compact substrate within a natural outcrop above the beach. The impressions are plantigrade (entire sole of the foot) with five-toed feet which also indicate a well-developed ball with a bulbous hallux, yet without a significant gap between the hallux and the second digit (Gierliński *et al.* 2017:704). However, it is not particularly 'hominin-like' with respect to its proportionately shorter and narrow heel, plus it lacks an arch (for shock absorption when walking bipedally). Gierliński *et al.* note that there are no imprints of claws in the footprints, but they also acknowledge that bears with similar 'heart-shaped' soles do not always leave impressions of their claws in tracks (Ibid). The trackmaker for the Trachilos footprints would be older than *Orrorin tugenensis* and either the same age or somewhat younger than *Sahelanthropus tchadensis*; however, nothing is known about the foot morphology of these African species.

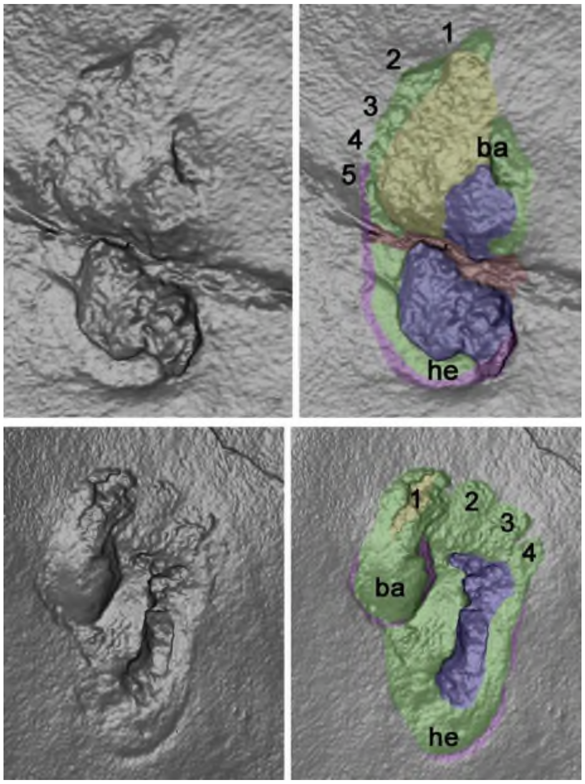

Fig. 4.3 Trachilos Footprints
Gierliński et al.2017:705

In another part of Greece, a mandible was recently found whilst a tooth was recovered in Bulgaria, both of which indicate possible hominin-like dentition and are believed to represent an early Messinian primate named *Graecopithecus* (Böhme *et al.* 2017; Fuss *et al.* 2017; Gierliński *et al.* 2017). However, the mandible was dated to 7.75 mya whist the tooth was dated to 7.24 mya (Böhme *et al.* 2017), suggesting that *Graecopithecus* is too old to be the Trachilos trackmaker,

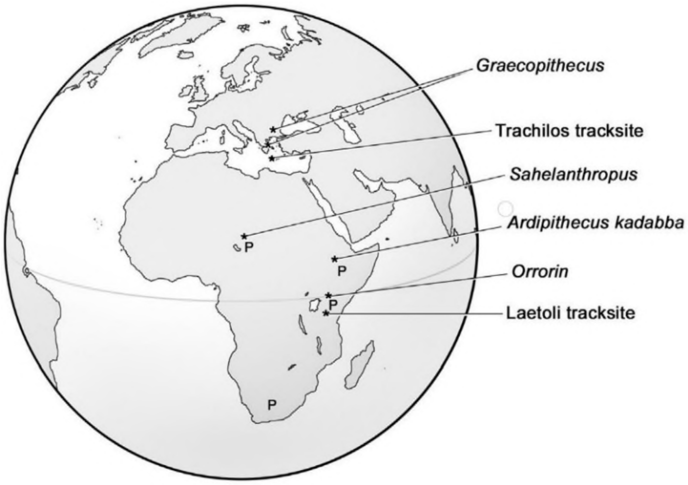

Fig. 4.4 Hominin and Proto-hominin Sites
Gierliński et al.2017:705

unless additional fossils are recovered that suggest otherwise. It is also possible that the tracks were made by an as-of-yet unknown hominin, but unfortunately, there is currently a dearth of hominin (or proto-hominin) fossils recovered from this area that fall within the same time-frame. Then again, perhaps the Trachilos trackmaker was, indeed, an ancestral bear.

Summary/Conclusion

Although there are numerous hypotheses for the possible reasons that hominins became bipedal, we will likely never know why this adaptation occurred. Presently, the first known hominins who definitively employed a basic form of habitual bipedalism were the australopithecines at 4.2 mya. Regardless of the underpinning drivers for bipedalism, it provided long-term collateral benefits for hominins such as lifting the cranio-facial morphology, thereby facilitating the expansion of the brain. Just as each of the numerous postcranial morphological adaptations acquired for bipedalism produced corresponding changes in the brain, there were additional morphological changes in the shoulders, arms and hands, now that these limbs were no longer needed for locomotion, which would likewise produce corresponding changes in the brain. Furthermore, upright posture impacted social relations, and this new complexity would have also prompted additional neurological adaptations in both the frontal and temporal lobes.

As will be seen in the following chapters, the fossil evidence for significant brain expansion in hominins postdates the archaeological evidence for the first knapped stone tools, yet somehow small-brained hominins managed to come up with the idea and strategy (however poor) to create stone tools (however crude), thus supporting the argument for brain reorganisation prior to brain expansion. The australopithecine endocasts, as well as the stone tools recovered during their life span, will be explored in Chapter 5.

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Chapter 5: The Australopithecines – The First (Uncontested) Hominins

One of the main functions of the brain is to direct the body's purposeful interaction with the environment. [. . .] Evolution has endowed mammals with adaptive neural circuitry that allows them to interact in sophisticated ways with the complex environments in which they live.

John F. Kalaska and Giacomo Rizzolatti (2013:835)

Australopithecus is presently considered the first *uncontested* hominin based primarily on its diminished CP_3 honing complex, thicker enamel, and the compelling evidence presented by its postcranial morphology for habitual bipedalism (Lovejoy 1988:125; White 2002:407; Cartmill and Smith 2009:169; Stanford *et al.* 2017:310). For example, their tibiotalar joint surfaces lie at right angles to the axis of the tibial shaft (indicating a valgus knee), and the tibial plateau of their knees had expanded in order to support the enlarged femoral condyles, which together bear the majority of the weight of a now upright head and torso. The adoption of bipedalism as a habitual form of terrestrial locomotion serves as an important benchmark in hominin lineage.

In 1924, the first australopithecine skull was found, encased in a small block of limestone that had been blasted from a vertical depth of approximately 50 feet by miners working the Buxton Limestone Quarry in Taung, South Africa, located approximately 80 miles north of Kimberly (Dart 1925). Professor Raymond Dart examined the cranium of a small child,[1] brought to him by one of his students, and determined that a new species had been discovered, naming it *Australopithecus Africanus*, "southern African ape" (Cartmill and Smith 2009:130; Stanford *et al.* 2017:307). Despite Dart referring to the specimen as an 'ape', he ultimately (and publicly) hypothesised that *Australopithecus* was ancestral to *Homo sapiens*, provoking a controversy that would take 20 years of additional discoveries and scientific analyses to resolve (Rak 1983). Today, there are seven recognized

[1] *Known as the "Taung Child"*

species of *Australopithecus* (White 2002:409) with an arguably additional five species, over which there is much debate regarding whether or not these fossil specimens deserve their own taxon.

The essence of the controversy focuses on whether or not the morphological differences of the specimen(s) in question are significant enough to warrant the recognition of a new species (or in some instances, a new genus) or if these differences can be simply explained as variation *within* the species. Those who advocate for new species are typically known as the 'splitters' whilst those who argue that the morphological changes are merely variation are known as the 'lumpers.' Fuelling this ongoing debate is the inadequate specimen sample size in the fossil record.

There is also an ongoing discussion with respect to the possible splitting of the *Australopithecus africanus* species into two (or even three) separate species, which has been a concern that dates back to the first *A. africanus* discoveries. Technically, a genus must include an ancestor and all of its descendants, (referred to as a monophyletic clade) to conform to present day proper zoological nomenclature (Ward 2015:132). However, this bar is an arduous standard to meet for the australopithecines considering the small sample size, as well as the difficulty in tracing descendants and ancestors. The respective arguments for these issues will be discussed in the individual species sections.

There has also been a shift regarding the proper nomenclature for the robust australopithecine species (*Australopithecus robustus, Australopithecus boisei*, and *Australopithecus aethiopicus*) towards the use of *Paranthropus*[1] as their genus instead of *Australopithecus*, which again focuses on the phylogenetic relationships among species and specifically whether or not the paranthropines truly represent a

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[1] *When the first robust australopithecine was found in South Africa in 1938, Robert Broom gave it the name Paranthropus robustus, indicating both a new species and genus (Broom 1938:379).*

monophyletic clade,[1] although recent phylogenetic analyses seem to support the paranthropines as a monophyletic clade based on their many similarities in dental and craniofacial features, which would place them in their own genus (Wood and Constantino 2007; Ward 2015). Ward, however, argues that "the genus *Australopithecus* itself is certainly not monophyletic and so itself is an invalid taxon," and she additionally notes the confusion created when making an adjustment in nomenclature to an already uncertain phylogeny whilst so much uncertainty exists regarding the relationships between and among these early hominins (Ward 2015:133). She is correct, of course, but the name *Paranthropus* nevertheless seems to be winning out in the recent literature as a means to brand these three species as the more robust forms, and regardless of what name is used as a reference to these robust hominins - they are nevertheless considered australopithecines, which continues to add to the confusion.

Finally, with respect to the terms 'robust' and 'gracile' describing the overall morphology of the various australopithecines, Tim White *et al.* have argued that it is inappropriate to describe any australopithecine species as 'gracile' considering the large size of their teeth and other robust features, and thus 'less robust' would be a more proper description (T. White *et al.* 1981:446). It is a valid point, but the term 'gracile' continues to be used in the literature, although its use has admittedly diminished somewhat in favour of 'less robust.'

Early Australopithecines

Australopithecine specimens have been found in eastern, southern, and central Africa, but the majority of these fossils have been recovered throughout the Great Rift Valley in East Africa, particularly the region known as the Afar Triangle, although

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[1] *A monophyletic clade refers to a group of taxa which consists only of an ancestral population and all of its lineal descendants, characterised by shared derived characteristics which distinguish them from other species.*

many australopithecine fossils were also recovered in the Sterkfontein Caves and other sites in South Africa. The Rift Valley encompasses an area that runs from the Ethiopian coastline on the Red Sea in a south by southwestern direction through Kenya and Tanzania, and additionally includes an area to the west of Lake Victoria that surrounds Lake Tanganyika, Lake Kivu and Lake Edward. Fortunately, the East African Rift Zone is an area also known for both its active and dormant volcanos, which make it somewhat easier to acquire chronometric estimates for these fossils using radioisotope dating methods such as Potassium-Argon (^{40}K/^{40}AR) and/or Argon-Argon (^{40}Ar/^{39}AR). However, volcanic activity did not extend to South Africa where the Sterkfontein caves are located just northwest of Johannesburg, and where the first adult[1] australopithecine (TM 1511) was discovered by Robert Broom 12 years following the discovery of the Taung Child, once again as the result of mining (Broom 1936a:487). Furthermore, the limestone mines could not be archaeologically excavated whilst they were actively in operation, and thus - no fossil specimens could be recovered *in situ*. Instead, archaeologists were only permitted to go through the dump boxes to search and retrieve fossils among the other debris. The South African dating challenges will be discussed further in the chapter.

Fig. 5.1 The Great Rift Valley
Radar topography image by NASA
https://geology.com/articles/east-africa-rift.shtml

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[1] *The first adult Australopithecine specimen (a small tooth) was actually discovered in 1935 by Louis Leakey in Tanzania, but it was misidentified as a cercopithecid (monkey) for many years (T. White 2002:407).*

The life span of the australopithecines is estimated from approximately 4.2 mya with *A. anamensis* (T. White 2002:411; T. White et al. 2006:883; Du *et al.* 2020:3) to as late as approximately 1.4 million years ago with *Paranthropus boisei* (Stanford *et al.* 2017:307; Toth and Schick 2018:9), spanning an overall stretch of about 2.8 million years. The australopiths present a number of interesting traits across a wide radiation[1] of species. In general, they were small-bodied, typically averaging between roughly 30kg and 45kg in weight, with small-sized brains estimated between 340 to 500ml in volume (Cartmill and Smith 2009; Stanford *et al.* 2017), although some exceptions apply. There was considerable sexual dimorphism (see Figure 5.2 for modern example) among the australopiths, which was more pronounced in some species than others. As a result, the size differential has often contributed to debate over whether a particularly smaller or larger specimen is evidence of a new species, sexual dimorphism, or simply within the range of variation. The australopithecines also had prognathic faces, extending forward beyond the zygomatic arches (cheek bones), although their faces were shorter than *Ardipithecus* or modern apes (Ward 2015; Stanford *et al.* 2017), and prognathism varied from species to species.

Fig. 5.2 Modern human Sexual dimorphism
Shaq O'Neal and Simone Biles
Simone_Biles Twitter Feb- 2017

They additionally had large jaws, but again, the size varied quite a bit among species as well as between male and female specimens. For example, some of the

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[1] *Adaptive radiation refers to a process in which the species of genus develop and diversify rapidly from an ancestral species into many new forms as the result of environmental changes.*

more ‘robust’ species (*Paranthropus*) had massive jaws, which is evidenced not only by the mandibles, but also by the sagittal and temporo-nuchal crests on the crania which support the muscles of mastication (i.e., chewing muscles). In other words, the more robust species, and even some of the gracile species (males, in particular), had cranial bone crests that extended from the upper portion of the skull whose sole purpose was to support these well-developed muscles that operated their imposing jaws.

As hominin brains increased in size over the course of evolution, faces tended to decrease and become less prognathic. Cartmill and Smith note that all australopithecine crania seem to adhere to two general (but not absolute) rules regarding the relative aspects of ‘face and skull,’ which tend to be characterized by the following:

> “1. The more the lower face projects in front of the zygomatic arches, the larger the posterior temporalis[1] becomes; and
> 2. The larger the jaws are relative to the brain, the more extensive the air sinuses of the skull become.” (2009:171).

Cranial variation is often pronounced, particularly between the sexes as well as the species.

The following sections describe each of the australopithecine species and corresponding fossil specimens, with additional detail provided for the relevant specimens with behavioural (i.e., stone tools) and/or scientific endocast evidence, as well as a description and discussion, where applicable, of the crania and brain endocast features. These are presented in chronological order with two exceptions from South Africa (specimens StW 573 and StW 578), whose species are unidentified[2] and date to approximately 3.67 mya. Although their morphology suggests a species

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[1] *The temporalis is a broad muscle of mastication located on the side of the head on top of the temporal bone that elevates and retracts the mandible, as well as move it from side to side.*

[2] *Clarke has unofficially named these specimens A. prometheus (2013:121).*

closer to *A. afarensis* than *A. africanus* (which emerged in South Africa approximately 200,000 years later than the first *A. afarensis*), they are likely either a variation of *A. afarensis* ancestral to *A. africanus*, which would evince a much greater geographical reach for *A. afarensis* than initially believed (T. White 2002:414), or a very early version of *A. africanus*. Accordingly, these specimens will be discussed in context with the *A. africanus* crania found in South Africa where StW 573 and StW 568 were recovered *in situ* from the Sterkfontein Caves. The species section begins with the oldest australopithecine discovered to date – *Australopithecus anamensis*.

Australopithecus anamensis (4.2 – 3.8 mya)[1]

Although we are currently unable to definitively determine which of the australopith species the *Homo* lineage descended from, we are relatively certain that *Homo* derived from their lineage, which began with *A. anamensis* (White *et al.* 2006:883; Kimbel et al. 2006:135; Cartmill and Smith 2009:170; Du *et al.* 2020). Furthermore, there is compelling fossil evidence that *A. anamensis* was ancestral to *Australopithecus afarensis* (Ward *et al.* 2001; Kimbel *et al.* 2006), although that phylogeny has recently been challenged by Haile-Selassie *et al.* who believe the two species overlapped for at least 100,000 years (2019:218).

In 1994, Meave Leakey and team discovered dozens of *A. anamensis* bone fragments at various sites (primarily Kanapoi and Allia Bay) near Lake Turkana in northern Kenya, which have been dated to between 4.2 and 3.8 mya (M.G. Leakey *et al*. 1995; Ward *et al*. 2001; Cartmill and Smith 2009; Stanford *et al.* 2017). Although these *anamensis* remains were not the first australopithecines discovered, they were the oldest and hence the earliest species of *Australopithecus*. Fieldwork, conducted in the Kanapoi region between 2003 and 2008, uncovered nine new *anamensis* fossils,

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[1] *The temporal ranges observed for the various hominin species tend to be generally accepted as averages based on statistical confidence intervals, but in reality, are likely underestimated due to the incomplete fossil record as well as sampling (Du et al. 2020). Brown et al. (2013:18) and Haile-Selassie et al. (2019:2018) believe that A. anamensis probably existed until at least 3.8 mya.*

which date to between 4.195 and 4.108 mya and consist predominantly of portions of mandibles, maxilla and teeth (Ward *et al.* 2013), although postcranial fossil specimens have also been recovered. In 1965, a distal humerus from the arm was discovered by a team from Harvard University, which has now been re-classified to *A. anamensis*, and over 100 *anamensis* fossils (mostly craniodental) have now been recovered from Allia Bay and Kanapoi (Ward *et al.* 2020).

Although the postcranial fossil specimens of *A. anamensis* evince habitual terrestrial bipedalism, their dentition was more primitive and ape-like, including a CP_3 honing complex. Their teeth were also still relatively large and formed a U-shape arcade versus the parabola-shaped arcade of later hominins. However, the canine teeth and molars are smaller than those of both *Ardipithecus* and extant African apes. Additionally, their teeth had thicker dental enamel, which (like bipedalism) is generally considered a hominin synapomorphy (Beynon and Wood 1986; Grine and Martin 1988; Schwartz 2000; Cartmill and Smith 2009).

Until recently, no *anamensis* cranium had been discovered, although a small portion of a left temporal bone was found in Kanapoi (Leakey *et al.* 1995). The Kanapoi bone (KNM-KP 29281B) is too small for any indication of brain size/volume, but it contained an external acoustic meatus (ear hole) with an oval cross section, another hominin feature not seen in *Ardipithecus* fossils or extant apes (Cartmill and Smith 2009:169). However, the meatus was small in size similar to the apes versus the later australopith species (M.G. Leakey 1995; Ward 2001). Then in 2016, a nearly complete hominin cranium (MRD-VP-1/1) was recovered at the Worsano-Mille site in the Afar region of Ethiopia and dated to approximately 3.8 mya (Haile-Selassie *et al.* 2019:214). The fossil was assigned to *A. anamensis* based on both the taxonomic and phylogenetic morphology of the canine, maxilla and temporal bone, which are similar to previously found specimens. Prior to this discovery, the craniofacial morphology of *anamensis* was almost entirely unknown. Based on the size and shape of the previously recovered maxilla and mandible fossils, as well as the temporal bone fragment, the *anamensis* face was presumed to have been *moderately* prognathic with large jaws. (Stanford *et al.* 2017; Cartmill and Smith 2009). However, the discovery of MRD revealed a long, robust, and *highly* prognathic face with a large right canine tooth and a well-developed sagittal crest (to support the massive muscles of mastication), although the crest was not particularly surprising given the previously known size of their jaws. The MRD cranium will be discussed further in the endocast section of this chapter, alongside *afarensis* crania for comparison.

Prior to the discovery of the *A. anamensis* cranium, it was also assumed that some of the larger males might have weighed as much as 50 kg based on their proposed relativity to the maxilla, mandibles, teeth, and postcranial fossils recovered (M.G. Leakey et al. 1995; Ward et al. 2001; Cartmill and Smith 2009). However, the size of the MRD cranium suggests that *anamensis* might have been a smaller male than originally believed (Haile-Selassie *et al.* 2019). An important feature of the cranium is the high degree of postorbital constriction (i.e., the narrowing of the skull behind the eye sockets), which is also very noticeable in non-human primates. A small amount of postorbital constriction is usually indicative of a large brain, or having room for a large brain, whilst a large amount of postorbital constriction reduces the braincase and accommodates a large mastication muscle, discussed further in Chapter 6.

In 1981, a frontal bone fragment (specimen BEL-VP-1/1) with *reduced* postorbital constriction was recovered from the Middle Awash, Ethiopia (Asfaw 1987). The fossil was dated to >3.9 mya and at the time, believed to represent a Pliocene hominin morphologically close to the split between the hominins and African apes (Asfaw 1987:623). However, the recently recovered MRD cranium revealed that *A. anamensis* did *not* have reduced postorbital restriction. Given that *A. afarensis* derived with reduced postorbital restriction, Haile-Selassie *et al.* suggests the BEL-VP-1/1 fragment be assigned to *afarensis*, which indicates an overlap of *anamensis* and *afarensis* in the Afar Triangle for approximately 100,000 years (2019). Prior to the discovery of the *A. anamensis* cranium, Brown *et al*. had also proposed an overlap based on fossil specimen teeth discovered in Fejej, Ethiopia, dating to between 4.2 and 4.0 mya (2013:15). The teeth were initially believed to be affiliated with *A. afarensis*, although it now appears that the teeth more likely belong to *A. anamensis* (Ward 2014), and many continue to argue for a linear (anagenetic) progression between the two species, even though the dating of the newly discovered *A. anamensis* cranium would suggests otherwise.

However, the fossil specimens from Worsano-Mille, Allia Bay, Asa Issie and Kanapoi suggests that there were four "time-successive but allopatric *A. anamensis* populations" with morphological variation, and Haile-Selassie *et al.* believe MRD is most similar to the 'family' from Kanapoi and Asa Issie (2019:219). They further note it is unlikely that the *anamensis* population represented by MRD could have been ancestral to *A. afarensis* considering that MRD at 3.8 mya postdates BEL-VP-1/1, now considered to be the oldest *afarensis* at 3.9 mya (Ibid). However, Tim White cautions that "with such limited evidence, it is far too soon to revise our understanding of Lucy's origins" (Barras 2019). Accordingly, Haile-Selassie *et al.* admit that despite the apparent overlapping, it is still likely that *afarensis* derived from *anamensis*, but did so via a 'speciation event' where a small group of *A. anamensis* became genetically isolated and evolved into *A. afarensis* (2019:219).

MRD (*A. Anamensis*)

This nearly complete cranium was recovered in two large pieces from the Woranso-Mille area within the Afar region of Ethiopia. It has retained several primitive features such as the asterionic notch (discussed later) and a low squamosal suture (between the parietal and temporal bones), which is only slightly arched compared to modern humans. The temporal bone has a small external acoustic meatus (ear hole), similar to the only other *anamensis* temporal bone recovered (specimen KNM-KP 29281B, previously mentioned). The sagittal crest begins more anteriorly than other hominins, and it extends posteriorly to the nuchal lines. Similarly, the length of the nuchal plane is longer than expected, even for the earliest hominin.

Fig. 5.3 MRD Cranium
Photo by Dale Omori
Cleveland Museum of Nat History
SciNews August 2019
http://www.sci-news.com/othersciences/anthropology/australopithecus-anamensis-skull-07542.html

Haile-Selassie's team had the cranium scanned via the microcomputed tomography scanner at the Penn State University Center for Quantitative Imaging, and an endocast was digitally created in Avizo v.9.3, using only the right side of the endocranium due to the level of distortion on the left side (2019). A mirror image of the right side was then created to compensate for the missing left side, and endocranial volume was estimated between 365 to 370 ml, smaller than any of the adult *A. afarensis* crania and similar to *S. tchadensis* (Ibid:218). The team did not report the presence of any relevant sulci or other landmarks, and the digital endocast has not been made available to the public.

Australopithecus afarensis (3.9 - 2.9 mya)

Although there is an abundance of *A. afarensis* postcranial specimens in the fossil record, few crania have been recovered, the majority of which are only partial crania. From the meagre evidence available, *A. afarensis* exhibited small braincases typically averaging between 350 to 500 ml for adults, which is slightly larger than modern apes. Their faces were highly prognathic with swept-back cheek bones, and their temporal muscles were set posteriorly on the skull at a bit of an angle (i.e., steep nuchal planes and high nuchal lines) versus modern human crania which have low nuchal lines and horizontal nuchal planes. *A. afarensis* had large jaws and well-pronounced temporo-nuchal crests, as well as instances of sagittal crests, for the attachment of the large muscles for mastication, all of which are found more commonly in males than females (Kimbel and Rak 1985; Kimbel *et al.* 1994, 2004; Cartmill and Smith 2009; Stanford 2017), whilst their cranial bases were flat and unflexed. The cranial bases of modern humans have a higher degree of basicranial flexion which provides for a deeper and wider posterior cranial fossa, which house the brain stem and cerebellum, possibly as an adaptation to accommodate brain growth.

In 1973, the first *Australopithecus afarensis* remains were discovered in Hadar, Ethiopia, located within the Afar Triangle in the Eastern Rift Valley. This region is of particular interest to geologists given its history of volcanic activity and the three tectonic plates that compose its foundation (See Fig. 5.1 and 5.4). However, it has also been known for its remote and inhospitable nature, as described by the British explorer L.M. Nesbitt, in his book entitled *The Hell-Hole of Creation* (1935). It was not until nearly thirty years later that any interest was taken in the Afar Triangle when Maurice Taieb, in the 1960s, conducted a study of the geological evolution in this area during which he discovered a number of fossil deposits, believed to be Pliocene. In 1972, Taieb returned to the region with D.C. Johanson, Y. Coppens, and J.E. Kalb to conduct a six-week investigation of both geological and palaeontological interests, after which the International Afar Research Expedition ("I.A.R.E.") was formed, and the first field exploration began in 1972 (Johanson *et al.* 1982).

During the first field season, over 89 localities were mapped in Hadar, and Johanson discovered the first hominin fossils (Johanson, *et al*. 1982). At the close of the IARE project in 1977, more than 240 hominin specimens, representing a

minimum of 35 individuals, had been recovered (Ibid 1982:373). However, following the 1974 collapse of Emperor Haile-Selassie's regime, a moratorium was placed on fieldwork in 1982, which was not lifted until 1990. At that time, the IARE was reorganized until the leadership of Donald Johanson, William Kimbel, and Robert Walter as the Hadar Research Project (aka the "HRP") (Johanson 2004).
Since the 1960s, thousands of *afarensis* fossil finds have been discovered in the Afar Triangle and other regions in east Africa, including the Laetoli beds in Tanzania. However, the vast majority (approximately 90%) of these specimens were recovered in Hadar (Stanford 2017; Johanson *et al.* 1982, 2004; Kimbel *et al.* 2006).

The Hadar Formation is a minimum of 280 metres thick and has exposure along the Awash River providing fossil-rich lacustrine and fluvial sediments (Johanson *et al*. 1982, 2004; Brown *et al*. 2013). Most of the australopithecine fossils discovered in this formation were found in an area of approximately ten square kilometres north of the Awash River (Brown *et al.* 2013). The formation is divided into four members, divided (from the base up) as: Basal, Sidi Hakoma, Denen Dora,

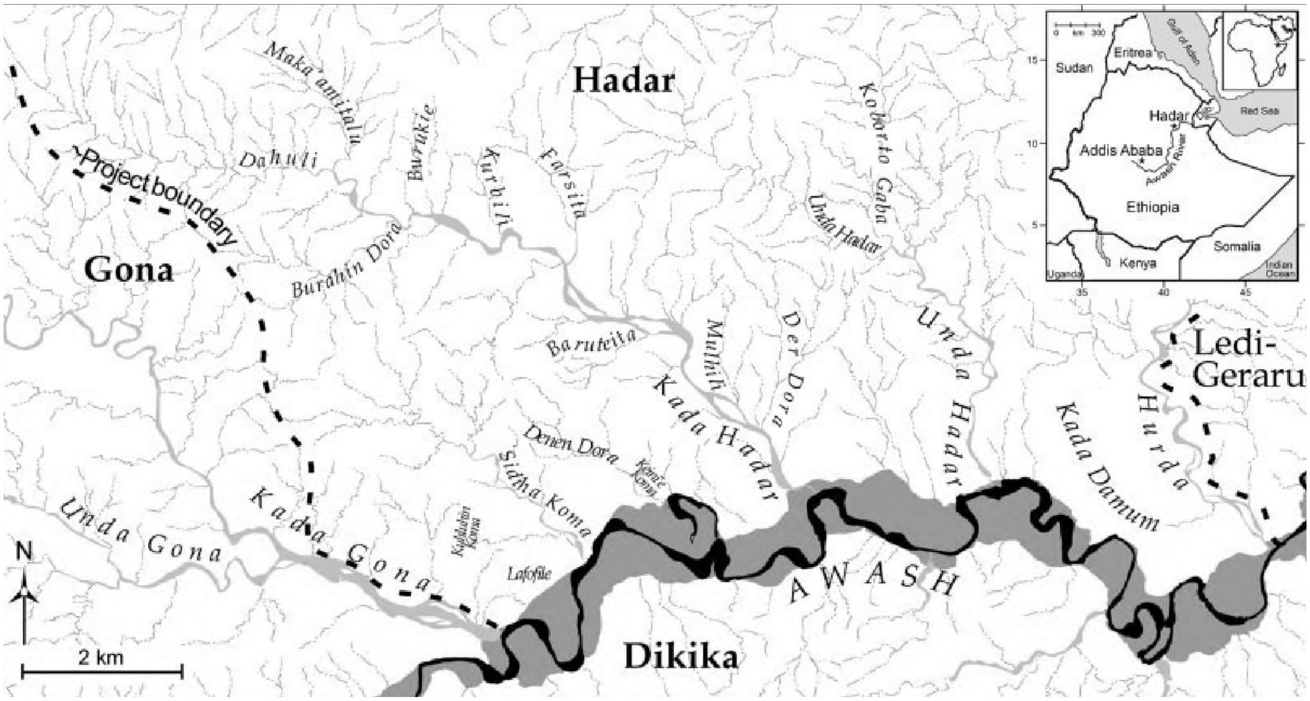

Fig. 5.4 Map of Hadar, its members, and its proximity to Dikika
Kimbel and Delezene 2009:6

and Kada Hadar containing several vitric tuffs[1] providing feldspars, obsidian and other material for K/Ar and/or ^{40}Ar/^{39}Ar dating[2] (Johanson 2004; Brown *et al.* 2013). Chronology was compared to palaeomagnetic polarity transitions representing the Mammoth and Kaena subchrons (Brown *et al.* 2013:14).

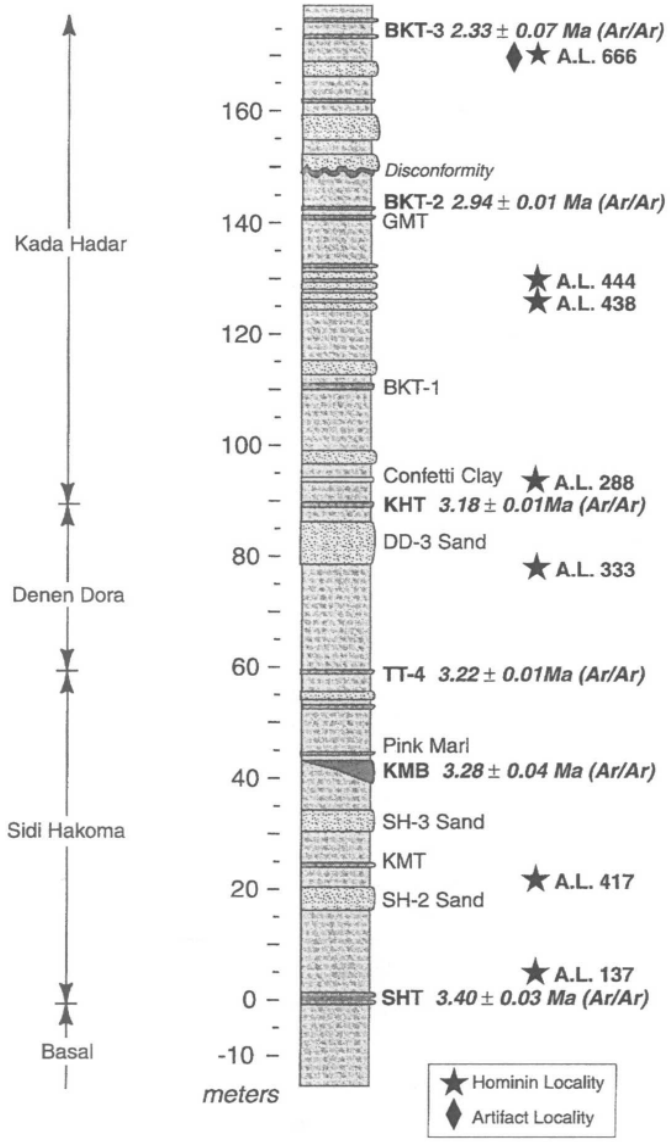

Fig. 5.5 Hadar Formation Stratigraphy
Kimbel, Rak and Johanson 2004:9

Most of the *A. afarensis* specimens collected in this formation were found in the Sidi Hakoma (SH) and Denen Dora (DD) members, although one of the most complete *afarensis* post-cranial skeletons (AL 288-1, aka "Lucy") was recovered from the Kada Hadar Member (Kimbel and Delezene 2009; Brown 2013). These fossil finds have provided valuable insight and anatomical evidence into *A. afarensis*, especially Lucy at the time of her discovery. Her physiology presented an amalgamation of both ape-like and human-like traits, commonly referred to as a 'mosaic' of features.

[1] *A tuff is a type of rock consisting of at least 75% volcanic ash, ejected during a volcano eruption.*

[2] *During the 2000s, several formations in East Africa were re-dated using K/Ar or ^{40}Ar/^{39}Ar technologies on alkali feldspar crystals from the pumice clasts within these tuffs (see McDougall & Brown 2006, 2008). However, in most cases there was very little adjustment from the original dating.*

Post-cranially, there are multiple examples of most parts of the skeleton, making *A. afarensis* the most well-represented hominin in the fossil record (Ward 2015). Sexual dimorphism was well-pronounced in *afarensis* with males approaching approximately twice the size of females (McHenry 1991, 1992; Kimbel 1988; Ward 2015). Males are estimated to have weighed between 45 and possibly as large as 70 kg, whilst females weighed only between 28 and 40 kg (McHenry 1991, 1992). Stature for *afarensis* is estimated between 105 cm and 151 cm (McHenry 1992), with Lucy's height believed to be a bit over a metre tall (Stanford 2017:310). The postcranial fossils indicate that *afarensis* was firmly committed to terrestrial bipedal locomotion. For example, instead of an opposable big toe (such as that of a modern ape), *A. afarensis* had a large hallux in line with the other phalanges of the foot (Ward 2015), which provides the dorso-flexion 'push off' of the hind leg required when walking bipedally. Lucy's pelvis had undergone major modification giving her a shorter and wider ilium, making it easier for the muscles to stabilize the body whilst walking. The spine had adjusted from a 'C' shape to an 'S' shape, and the hips abducted outward (and connected with what became a valgus knee), to prevent the upper torso from tipping forward. According to Lovejoy, Lucy's femoral neck had adjusted exclusively for bipedality, and the postcranial evidence for habitual bipedalism is conclusive (1988:125).

However, *A. afarensis* also had long arms (albeit somewhat shorter than their ancestors) compared to the length of the femora, as well as the retention of other upper body morphologies that suggest *afarensis* still spent time in the trees, likely to escape predators or obtain food. Yet Lovejoy argues that the anatomical features of their upper body, which provide arboreal access, should not detract from their designation as a fully adapted bipedal (Ibid), and Carol Ward insists that given the anatomical evidence of the knees, legs and feet - terrestrial bipedality in *A. afarensis* was clearly favoured over arboreal locomotion (2015:135). Furthermore, it has been more recently determined that all of the australopiths, at least until as late as 2.0 mya, had retained some level of an arboreal lifestyle (Kivell 2011:1416; Dunmore 2020:914).

Although the fossil record has produced an abundance of postcranial finds representing *afarensis*, unfortunately there are no fully complete crania – only partial crania and cranial fragments have been recovered. Two of these partial crania were discovered in many pieces and reconstructed: AL 444-2 from approximately 50 fragments and 822-1 from over 200 fragments (Kimbel and Rak 2010:3366). In general, *afarensis* had a very prognathic face and a skull base that was relatively flat (similar to extant apes) with a domed cranial vault (Cartmill and Smith 2009; Stanford 2017). Endocranial volumes averaged between 380 to 430 cc (T. White 2002:411), and they had large anterior teeth, similar in size and shape to that of *A. anamensis* (Cartmill and Smith 2009). However, the canine teeth are somewhat smaller than *anamensis*, and there is no CP_3 honing complex. Also similar to *anamensis*, the dental arcade is U-shaped, with molars and premolar teeth that are larger than *anamensis*, but not as large as later hominins (Ibid). Additionally, many specimens had premolars with two cusps.

In 1985, Kimbel and Rak performed a detailed analysis on hominin sutural patterns in the cranial area surrounding the asterion, a landmark on the lateral posterior sides of the skull where three sutures meet: the lambdoid suture, the parieto-mastoid suture, and the occipito-mastoid suture. The study revealed how the *A. afarensis* crania were affected by the large muscles of mastication, which lift the mandible for chewing: (i) the temporalis, located on the sides of the braincase; and (ii) the masseter, which sits on the outside of the jaws. According to Kimbel and Rak, these muscles would exert opposing forces that would pull the cranial bones in opposite directions from their respective adjoining sutures (1985). As a result, the sutural pattern in this area, named the ‘asterionic notch’ by Kimbel, is reinforced with an imbrication of the edges versus a clean 'edge-to-edge' articulation, as would be found in modern humans as well as other australopithecine species (Ibid). Kimbel and Rak also note that there are considerable differences between the *A. afarensis* 'asterionic notch' feature and the other species studied (primarily *A. boisei* and *A. robustus*), particularly regarding how the *A. afarensis* 'notch' was nearly identical to that of extant great apes (Ibid:51).

Kimbel and Rak also note that it would be highly unusual to observe this feature in subsequent hominin species, and the morphology of *A. africanus* crania seem to be completely lacking any resemblance to an asterionic notch (Ibid). They additionally observed that the cranium of KNM-ER 1805[1] (*H. habilis*) exhibits what appears to be the asterionic notch (Ibid), but KNM-ER 1805 has an unusual morphology whose proper taxonomic assignment continues to be debated (discussed in Chapter 7).

The following is a list of the *A. anamensis* and *A. afarensis* cranial specimens examined. Although many small cranial fragments have been found, most have not been included in this analysis because of their inability to offer any relevant information. Likewise, some of the partial crania (and accompanying endocasts) only offer minimal information. The endocasts made from the crania of infants and children, in particular, are often lacking in sulci or gyri markings on the interior table of bone, although there are a few relevant exceptions. Dating of the specimens is based on Kimbel *et al.* 1994 and Kimbel *et al.* 2004, whilst sources for the endocranial volumes are discussed within the individual specimen sections.

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[1] *Kimbel and Rak note how the cranial cresting pattern on KNM-ER 1805 is very similar to that of A. afarensis, yet there is little else in its overall morphology suggesting that it should be included with any of the Australopithecine species.*

Crania of *A. anamensis* and *A. afarensis*

Specimen	Location	MYA	Age/Sex	Brain Volume	Description
MRD (*anamensis*)	Worsano Ethiopia	3.8	Adult male	365-370 ml	Nearly complete skull
DIK-1-1 (afarensis)	Dikita Ethiopia	3.3	3-yr old female	273–277 ml	Nearly complete skull
AL 333-45 (afarensis)	Hadar	3.2	Likely male	500 ml	Most of skull sans frontal lobe
AL 333-84 (afarensis)	Hadar	3.2	N/A	N/A	Temporal fragment only
AL 333-105 (afarensis)	Hadar	3.2	juvenile	310 to 317 ml (400 est. as adult)	Face & frontal lobe only
AL 288-1 (aka "Lucy") (afarensis)	Hadar	3.2	Female	375-400 ml	Cranial fragments
AL 162-28 (afarensis)	Hadar	3.18	Likely female	375-400 ml	Occipital and partial parietal
AL 822-1 (afarensis)	Hadar	3.1 Est.	Likely female	385 ml estimate	Nearly complete from fragments
AL 444-2 (afarensis)	Hadar	3.0 Est.	Male	545 – 560 ml	Nearly complete from fragments

DIK 1-1

The cranial specimen and partial skeleton were recovered from Dikika in the Afar Triangle region of Ethiopia during the 2000, 2002, and 2003 field seasons. The excavation team was led by Zeresenay Alemseged in association with the Dikika

Fig. 5.6 DIK-1-1 (Selam)
Stanford et al. 2017:312

Research Project and the Max Planck Institute for Evolutionary Anthropology (Alemseged *et al.* 2006:296). Specimen DIK-1-1, aka "Selam," is believed to be a female toddler and represents the oldest *A. afarensis* cranium in the fossil record, dating to approximately 3.3 million years old via stratigraphic scaling (Hadar formation) and known chronostratigraphy (Ibid). The midface, temporal bone and cranial base were covered in matrix, but the cranium is largely intact except for parts of the frontal squama and the majority of both parietal bones. There is slight distortion at the back of the calvaria which has pushed the nuchal region forward. The mandible is complete, and the hyoid bone[1] in the throat is intact, but with morphology that more closely resembles an extant juvenile ape than that of a modern human child (Alemseged *et al.* 2006:298).

The approximate age at death was recently recalculated to 2.4 years old based on high resolution CT scans of the molars (Gunz *et al.* 2020:4). The recovery of the partial cranium and postcranial skeleton of such a young specimen provides a better understanding for the ontogenetic development that occurred in the species. Based on dentition, Gunz *et al.* believe the specimen is likely female (Ibid). The face morphology is prognathic and more closely resembles *afarensis* than *africanus*. Brain volume based on CT scans was initially estimated by Alemseged *et al.* to be approximately 235 ml, without accounting for the distortion of the occipital region, then revised to an endocranial volume between 275 ml and 330 ml after correction (Alemseged *et al.* 2006:297).

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[1] *The DIK-1-1 hyoid bone, which is the oldest found in hominins, has a slender 'greater horn' whilst the body is expanded anteriorly (Alemseged et al. 2006:298).*

More recently, Philipp Gunz and Simon Neubauer, with the Max Planck Institute, have rescanned several *A. afarensis* crania (including DIK-1-1) using both conventional and synchrotron computed tomography in order to produce high resolution virtual endocasts. The DIK-1-1 skull was reconstructed digitally, with an endocranial volume calculated to between 273 to 277 ml after corrections (Gunz *et al.* 2020:3). The natural endocast of matrix offered little information to the naked eye, and the remaining bit of matrix inside the cranium was removed using segmentation programs Avizo, VGStudioMax, and Geomagic (Ibid). Segmentation can discriminate between bone and stone based on density, and is frequently employed for digitally removing matrix in crania. The DIK-1-1 skull was then scanned with high resolution synchrotron computed tomography to create a digital endocast, which revealed "an unambiguous impression of a lunate sulcus in an anterior [ape-like] position, even after correction for taphonomic distortion" (Gunz *et al.* 2020:1).

From what I can see on their image of the digital endocast, I agree with their assessment regarding the lunate sulci in an anterior position, as there are no other occipital sulci with semi-circular shapes that would appear in the positions and locations as the lunate sulci. Although Gunz *et al.* argue that their identification of the lunate sulci is supported by their identification of other occipital sulci in relative position to the lunate sulci, it is difficult to see the supporting sulci from the images provided in the article or supplementary materials, and the original 3D polygon images have not been shared with the public by the Max Planck Institute.

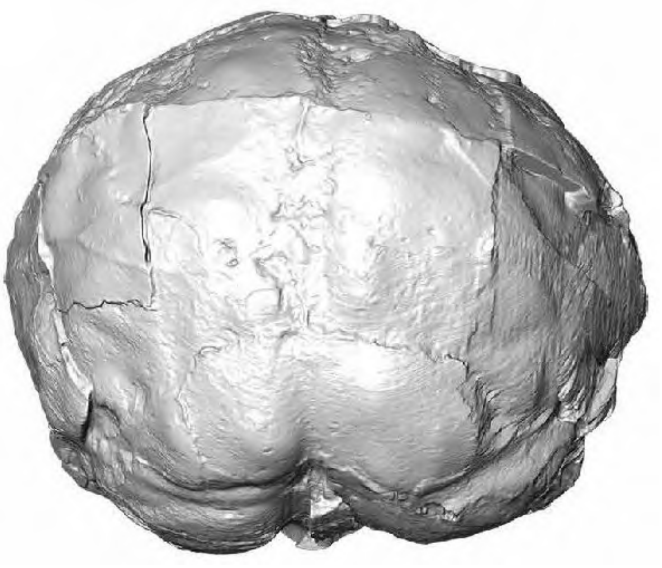

Fig. 5.7 Un-retouched photo of DIK-1-1 digital endocast (See also Figs. 5.8 & 5.9 for labels, etc.) Gunz et al. 2020:4

Although Gunz *et al.* did provide an additional photographic image of the DIK-1-1 endocast, which they have colour-coded and identified the various (Figure 5.8), it does not entirely agree with the original un-retouched photo. For example, the left intraparietal sulcus is relatively easy to see in Figure 5.7, as it transverses from the parietals to the occipital lobe, and I have highlighted its path in red in Figure 5.9.

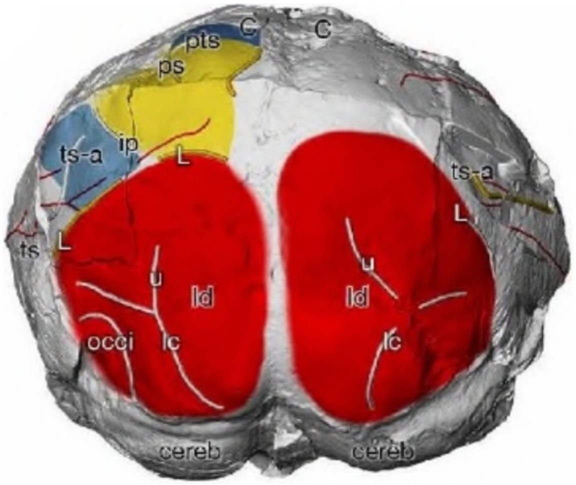

Fig. 5.8 Colour-coded image provided by authors
DIK-1-1 digital endocast
Gunz et al. 2020:4

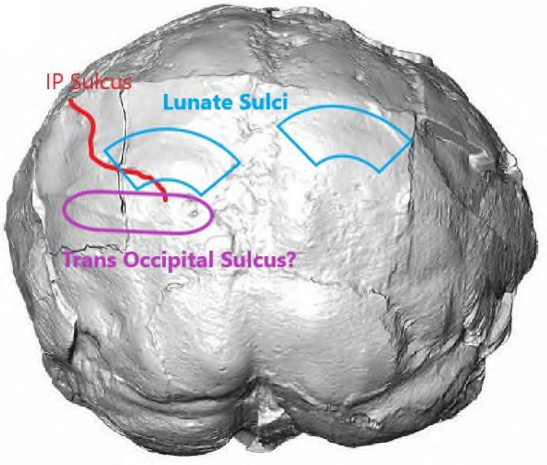

Fig. 5.9 Original photo of DIK-1-1
Gunz et al. 2020:4
Modifications by Suzi Wilson

However, in the colour-coded version provided by Gunz *et al.*, it appears as a nearly straight line, which would be highly unusual, and they end it at the anterior border of the lunate sulci (which is where it terminates in *Pan*[1]). On the original photo, it extends past the lunate sulci and appears to almost join an unnamed sulcus, which seems to transverse horizontally across the occipital (and possibly into the temporal lobes). This sulcus very closely resembles the transverse occipital sulcus, found in the superior part of the occipital lobe in modern humans, just caudal to the parieto-occipital fissure. As previously mentioned, the intraparietal sulcus extends into the occipital lobe and joins with the transverse occipital sulcus, which is what appears to be happening in the original photo. However, if the features identified by Gunz *et al.* are truly the lunate sulci (as they appear to be), the transverse occipital

[1] *The genus Pan includes both chimpanzees and bonobos and is the genus closest to Homo sapiens.*

sulcus would lie superior to them, so perhaps this un-named feature could be a meningeal artery. Likewise, the size, path and location of the calcarine sulci, drawn on the colour-coded image are also somewhat questionable, only because their detail cannot be fully discerned on the un-retouched imagery provided by Gunz *et al.*

As mentioned in Chapter 2, the occipital sulci (in modern humans) exhibit extreme variation (Iaria and Petrides 2007; Iaria *et al.* 2008; Ribas 2010; Malikovic *et al.* 2012), and it is no easy task to properly identify them. On the other hand, it seems unreasonable for scholars, however well-reputed, to ask that we simply 'take their word for it' without providing proof of the full supporting evidence. Hopefully, the Max Planck Institute will ultimately share their digital imagery with the public at some point in order for other scholars to properly examine and draw their own conclusions. Regardless, the work of Gunz *et al.* demonstrates the much higher level of scientific evidence that can be gleaned from a hominin brain endocast using today's modern technology.

DIK-1-1: Correlation with Stone Tools

In 2009, four animal fossils were found by the Dikika Research Project, adjacent to the site where DIK-1-1 was discovered. All four fossils had surface modifications which appeared to be stone-tool cut marks and were subsequently examined via optical and environmental scanning electron microscopy (ESEM). The fauna fossils were discovered in a niche where the area on either side has established $^{40}Ar/^{39}Ar$ dating at 3.42 and 3.24 mya, respectively, and stratigraphic scaling between these areas plus additional geological evidence indicate that the fossils are older than 3.39 mya (McPherron *et al.* 2010).

It was determined that the marks on two of the four fossils were made prior to fossilization, based on secondary electron imaging (SEI) and energy dispersive X-ray (EDS) spectrometry data (McPherron *et al.* 2010:857). Furthermore, these cutmarks and percussive marks lacked the typical morphology of ‘trampling’ or the result of biochemicals (Ibid). DIK-55-2 is a right rib fragment from a large ungulate whilst DIK-55-3 is a femur shaft fragment from a young bovid. The cutmarks were likely made to de-flesh the bones whilst the percussive marks were probably to gain access to the bone marrow.

Although the presence of these cutmarks establish the earliest hominin use of sharp-edged tools, it cannot be determined if these early tools were knapped by hominins or nature-made and merely collected by hominins for tool use. However, the bone specimens do evince the earliest consumption of meat by hominins, which is considerably earlier than previously assumed (de Heinzelin *et al.* 1999:627). Presently, the only known hominin to occupy the Lower Awash Valley during this time period was *Australopithecus afarensis*.

AL 333/333w ‘first family’

During the 1975 field season conducted by the I.A.R.E., an assistant palaeontologist (Mike Bush) discovered teeth on the steep hillside at AL 333/333w (Johanson *et al.* 1982). The remains initially recovered between 1976 and 1977 at this locality represented a minimum of 13 individuals, representing both sexes and of various ages, and dating to approximately 3.2 mya (Kimbel *et al*. 1994; Johanson 2004). By mid-2000, additional specimens have been recovered bringing the minimum number of individuals up to 17 (Johanson 2004). According to Johanson *et al*., excavation revealed the “exact stratigraphic location” where the specimens were found, indicating that the accumulation may represent a catastrophic event, resulting in this unusual death assemblage (1982:375). The following three specimens are from this group of individuals, often referred to as the ‘first family.’

AL 333-45

The specimen represents a partial adult cranium, likely male, which is missing the frontal lobes and a few other smaller sections. It was recovered in 1975 at Hadar (DD-2) and dates to 3.2 mya (Johanson *et al.* 1982; Kimbel *et al.* 1994). Discovered *in situ*, there was considerable post-mortem distortion in the calvaria, which resulted in the displacement of several bone fragments in the parietal and occipital regions (Kimbel *et al.* 1982). During December of 1979, the cranium was disarticulated, cleaned and reconstructed by Kimbel and T. White (Ibid). The cranium is somewhat large for *A. afarensis*, with a brain volume estimated at nearly 500 ml by Holloway *et al*. (2004:47), especially when compared to AL 162-28 and other female specimens, which further demonstrates the sexual dimorphism in *A. afarensis*. Accordingly, the mastoid processes are well developed[1] as are the various cranial crests (Kimbel *et al.* 1982), and an asterion notch can be identified. The nuchal plane on the occipital bone is very steep (Kimbel *et al.* 1982; Ferguson 1992).

Fig. 5.10 AL 333-45 Restored cranium
Left lateral view
Ferguson 1992:29

Kimbel *et al*. note that both the external surface area as well as the interior table of bone have lost detail as the result of abrasion and exfoliation, particularly on the upper anterior portion of the left parietal (1982). There is little to see on the endocast mould made by Holloway *et al.* (2004). The white portion is the endocast whilst the orange section represents the area of the cranium that is missing. From

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[1] *The mastoid processes are one of the key indicators for identifying the sex of a crania. Males tend to have well-developed mastoid processes and orbital ridges.*

Fig. 5.11 AL 333-45 Endocast mould
Right lateral view
Photo by Suzi Wilson

my examination, I could identify the right occipital pole, both transverse sinuses, and the occipito-marginal sinus, which is somewhat difficult to discern but can be traced to the sigmoid sinus. These sinuses are part of the cranial venous system that drains deoxygenated blood from the brain and returns it to the heart.

The occipito-marginal sinus is comprised of two parts: (i) the occipital sinus, which is a smaller continuation of the superior sagittal sinus, just below the 'confluence of sinuses' (see Figure 5.12), which partially drain into it; and (ii) the marginal sinuses, which lie inside the rim of the foramen magnum (between the dural leaves) and drain into a number of plexus venous channels around the spinal cord (Panigrahi *et al.* 2012). How blood is drained from the brain is primarily determined by posture and to some extent, respiration (Panigrahi *et al.* 2012; Ruíz *et al*. 2002). In modern humans, outgoing blood from the brain typically drains from the sagittal sinus to the transverse sinuses (left and right) then onto to sigmoid sinus before choosing a route to return to the heart. In an upright position, it tends to drain from the sigmoid sinuses through the internal and external vertebral venous systems around the spinal column; however, in a prone position, blood tends to favour a drainage route from the sigmoid sinuses through the internal jugular veins (Ruíz *et al*. 2002; Panigrahi *et al.* 2012).

As an adaptation to bipedalism, the occipito-marginal sinus likely became enlarged as a means to accommodate upright posture and gravitational forces on blood flow, prior to the development of the transverse and sigmoid sinuses (Aurboonyawat *et al.* 2007; Panigrahi *et al.* 2012). As the sinus system continued to adapt to bipedalism and additional drainage pathways emerged, the occipital-marginal sinus became less dominant. This speculation is based on the observations of venous system development in young non-bipedal children under two years old (Aurboonyawat *et al.* 2007:341; Panigrahi *et al.* 2012:2118). According to Falk and Conroy, all four specimens from Hadar[1] as well as the robust australopithecine species[2] have this enlarged sinus pathway as evidenced on the occiput (1983:780; Kimbel *et al.* 1982).

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[1] *Two of the Hadar specimens referred to were only cranial fragments and not included.*

[2] *P. robustus, P. aethiopicus, and P. boisei*

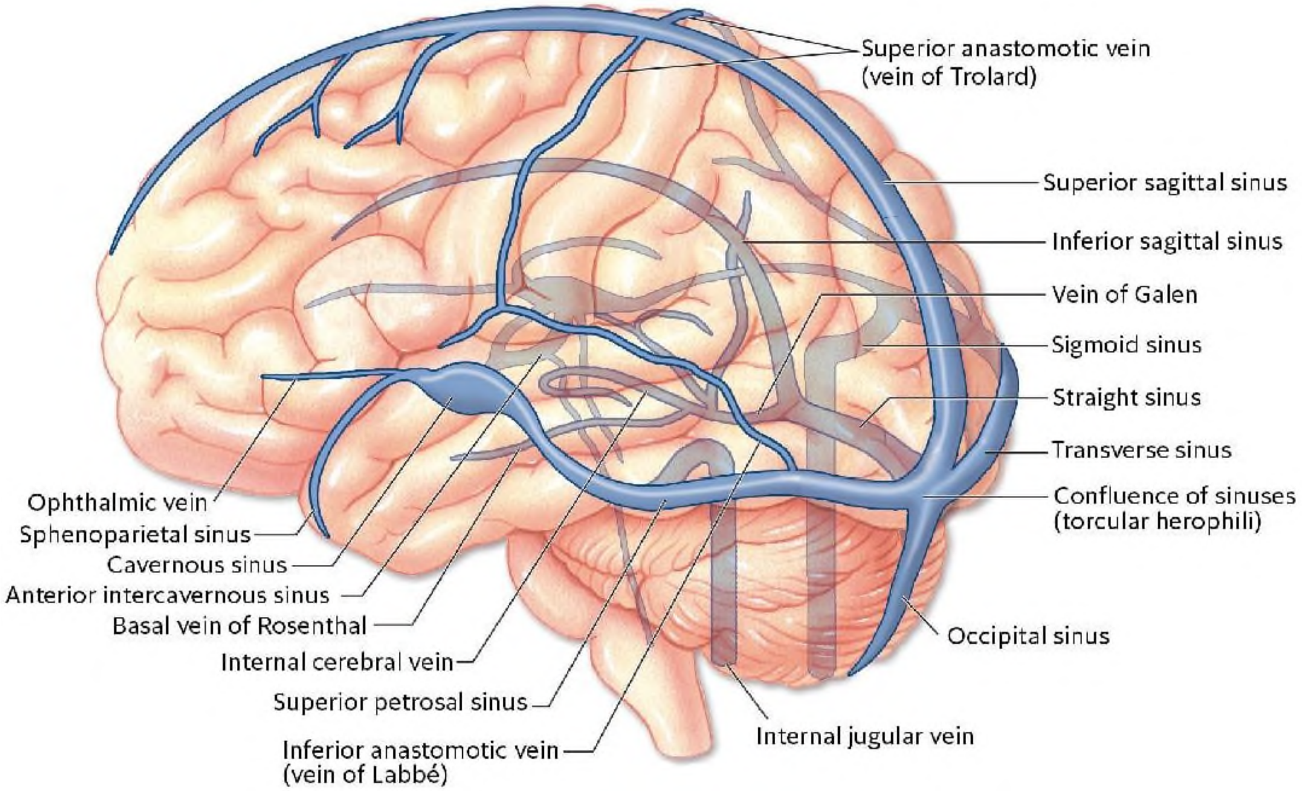


Fig. 5.12 Venous Sinus System
Kristoffersen et al. 2018:2

In further studies, Conroy *et al.* confirm that the enlarged occipital-marginal sinus condition is only common in the robust australopithecine species and *A. afarensis* specimens from Hadar, and it is absent in *A. africanus* (Conroy *et al.* 1990; D. White and Falk 1999). Other than the enlarged occipito-marginal sinus, the few landmarks that could be identified on AL 333-45 are not particularly insightful with respect to brain evolution or re-organisation for this specimen. However, AL 333-45 is one of the largest crania discovered for *A. afarensis*.

AL 333-84

Specimen 333-85 represents the right temporal fragment of an adult. There are no identifiable landmarks on the internal table of bone (and thus, no endocast), but it has been included to note both the large mastoid region and right mastoid process, similar to AL 333-45. Additionally, there is the presence of an asterionic notch (Kimbel and Rak 1985).

AL 333-105

Fig. 5.13 AL 333-105 Cranial face
Kimbel et al. 1982:497

Most of the facial bones are present in this cranial specimen of a small child, albeit cracked in many places that have caused minor shifts (Kimbel *et al.* 1982). The anterior portion of the right temporal bone is intact, but the area posterior to the external auditory meatus is missing, as is the dorsal region. Only the posterior section of the left temporal bone remains. The basal area below the temporals is in good condition but the rest of the base is highly distorted due to breakage (Kimbel *et al.* 1982, Holloway *et al*. 2004). Additionally, a small piece of the right parietal bone remains near the pterion, as well as a portion of the left parietal near the asterion, and Kimbel *et al.* note that there is no asterionic notch (1982). Age has been estimated at two years and five months based on upper dentition (Gunz *et al.* 2020:4).

Holloway *et al.* estimated the brain volume of the juvenile to be approximately 320 ml, which he believed would have produced a brain volume of approximately 400 ml had the child lived to be an adult (Holloway 2004:45). More recent digital reconstructions by Gunz *et al.* similarly produced an estimated endocranial volume between 310 and 317 ml, noting how the specimen is slightly larger than DIK-1-1 (2020:3). Although the specimen represents a toddler, the brain had already imprinted some convolutional detail on the endocast observed in Holloway's lab, and additional detail is provided in the imagery from Gunz *et al.* 2020.

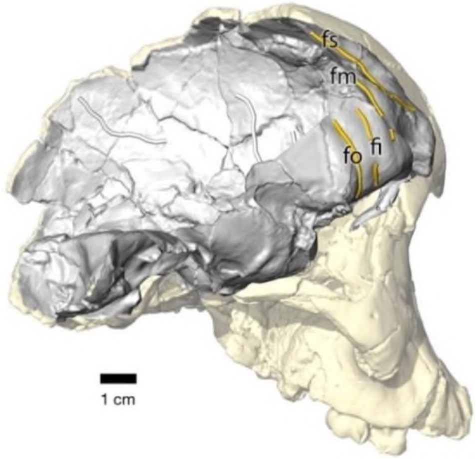


Fig. 5.14 AL 333-105 endocast
Right lateral view
Fronto-orbital (fo); middle frontal (fm) and superior frontal (fs) sulci
Gunz et al. 2020:S6
Supplementary materials

The inferior third frontal convolution (Broca's area) is missing on the left side, but the Broca's cap region on the right side indicates some development. Most notable is the fronto-orbital sulcus (fo) marking the posterior boundary of the orbito-frontal cortex, which indicates a more primitive structure as discussed in Chapter 2. Gunz *et al.* also suggested that 333-105 likely had an "ape-like brain organization," but without the missing parietal and occipital, a definitive conclusion cannot be drawn (2020:2). Finally, the specimen also exhibits what appears to be an enlarged right marginal sinus, which Kimbel *et al.* also made note of in their description as a "very strong sulcus for the right marginal sinus" (1982:483).

AL 288-1 (Lucy)

Specimen AL 288-1 was discovered in the Afar Triangle of Ethiopia in November 1974 by Donald Johanson (Johanson *et al.* 1982; Johanson and Wong 2009). At the time, she was the youngest specimen to be recovered from the lower Kada Hadar Member, KH-1 sub-member of the Hadar formation (Kimbel and Delezene 2009). Lucy dates to approximately 3.2 mya via $^{40}Ar/^{39}Ar$ dating (Kimbel and Delezene 2009; Johanson and Wong 2009), and she was named for the popular Beatles song at the time. However, the Ethiopian Ministry of Culture, Bekele Negussie, suggested they name her "Denkenesh," which means 'you are marvellous' in the Amharic language (Johanson 2004:468, Johanson and Wong 2009:8).

Lucy's skeleton is one of the more complete *A. afarensis* postcranial skeletons in the hominin fossil record (Kimbel and Delezene 2009; Stanford *et al.* 2017), yet only six pieces of her fractured cranium were recovered: (1a) an occipital fragment; (1b) a left parietal fragment; (1c/g) a biparietal fragment; (1d) a left zygomatic fragment; (1e) a parietal fragment; and (1h) and a right frontal fragment (Johanson *et al.* 1982). From the position of these fragments, Lucy's brain volume has been roughly estimated as between 375 and 400 ml (Holloway *et al.* 2004:45). Holloway made

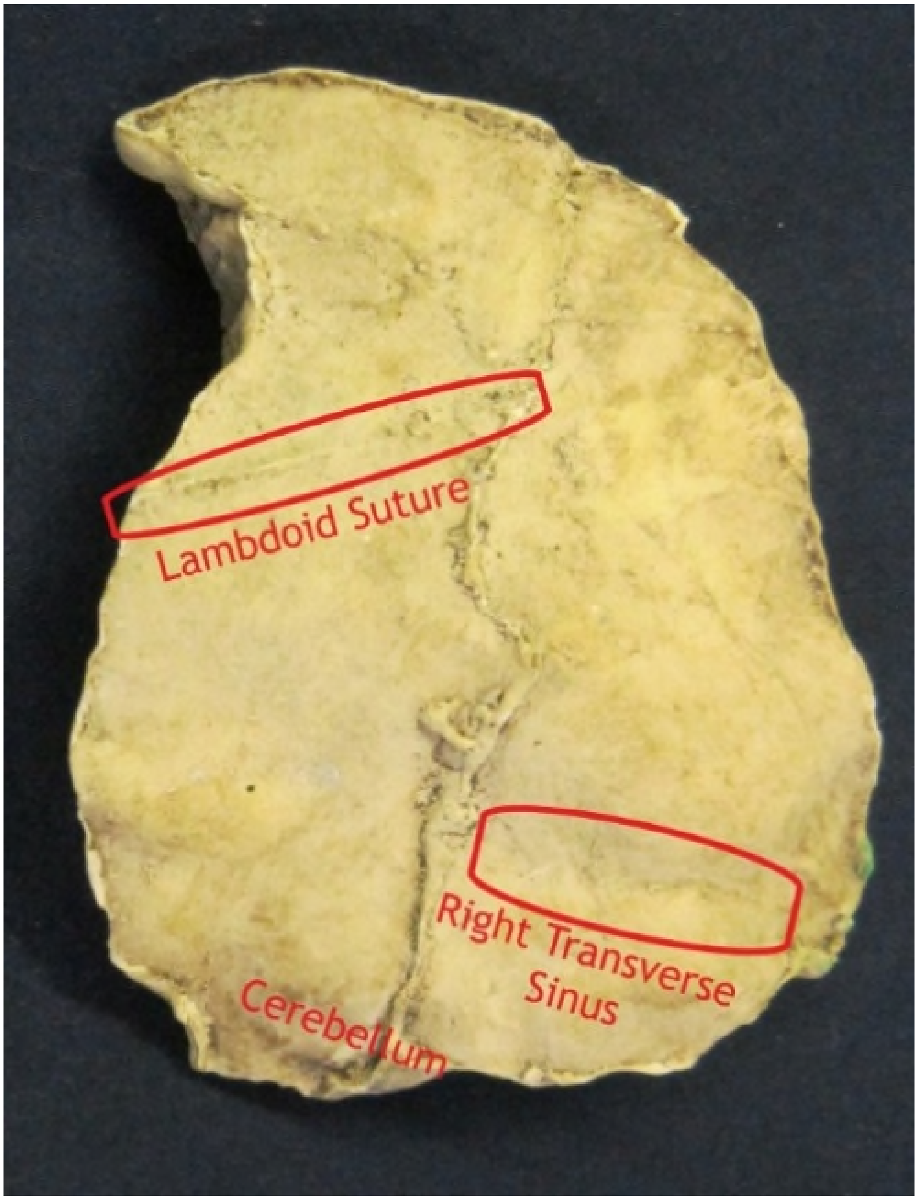


Fig. 5.15 Occipital Fragment (1a)
Photo by Suzi Wilson

endocasts of the fragments that might have sulci or sinus information to offer, but only the occipital fragment yielded any markings of interest that could be interpreted as cranial landmarks. In Figure 5.15, a portion of the lambdoid suture can be identified on the left portion of the endocast, extending medially to intersect with the main sinus that extends posteriorly to the cerebellum and anteriorly across the top of the head forming the superior sagittal sinus. The right transverse sinus of the venous sinus system can also be seen positioned just superior to the upper portion of the cerebellum.

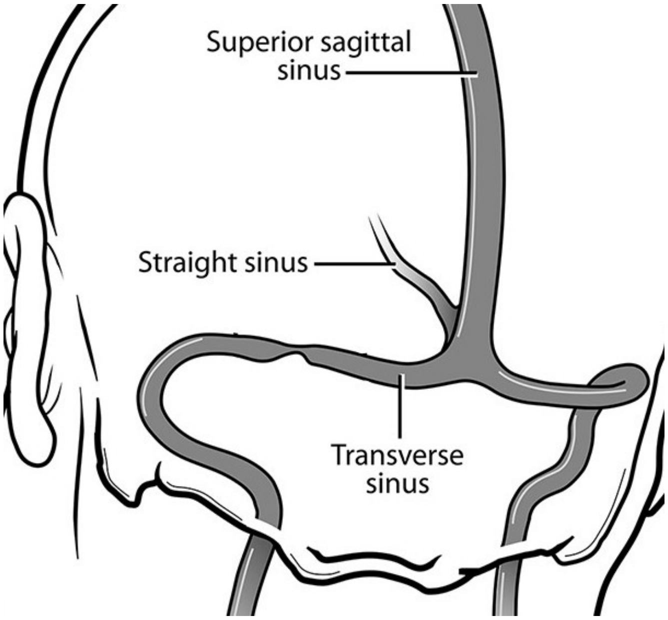


Fig. 5.16 Posterior view of the venous sinus system
Cappuzzo et al. 2018:3, Fig. 2

AL 162-28

The posterior portion of a calvaria, likely female, was recovered in the KH-1 Member of the Hadar Formation in 1974 by the I.A.R.E., led by D.C. Johanson and others (Johanson *et al.* 1982). Specimen AL 162-28 was dated via stratigraphic scaling and known chronostratigraphy as 3.18 million years old. The specimen consists of the majority of the occipital and left parietal bones, as well as some sections of the right occipital and parietal bones. Although the partial calvaria in the Holloway lab is a replica of the original, the endocast observed was moulded from the original calvaria, which currently resides at the Cleveland Museum of Natural History (and made by Ralph Holloway with assistance from D.C. Johanson and B. Lattimer).

There is no distortion in the calvaria, which allows for a better assessment of brain volume, estimated by Holloway to be just under 400 ml (Holloway 1983:420).

Fig. 5.17 AL 162-28 Partial cranium
Photograph by Suzi Wilson

Falk agreed that the brain volume is less than 400 ml, but preferred a volume range of 350ml to 400 ml (1985a:45). There is also a pronounced temporo-nuchal crest between the midline and the asteria for the attachment of some relatively large neck muscles, indicating that the neck was still transitioning to bipedalism (common for *afarensis*). Likewise, there is an asterionic notch caused by the large mastication muscles, as previously mentioned. Finally, the lambdoid suture can be somewhat easily traced, although it has become smooth and somewhat nondescript.

The original endocast examined in Holloway's lab is white, which did not photograph well with respect to the various markings and landmarks. However, a line-stiple drawing made by John Gurche (for Holloway) better illustrates the endocast's landmarks as well as its points of contention (see Figure 5.18). I observed a small indentation on the left parietal which, to the naked eye, is very convincing as a portion of the intraparietal sulcus, which separates the inferior parietal lobule from the superior parietal lobule. Holloway was likewise of the opinion that this indentation, which he identified as "Groove A" in Figure 5.18, is the intraparietal sulcus, as did Falk (Holloway 1983:420; Falk 1985a:46). The parietal surface was covered in small round notches, suggesting convolutions in the parietal lobes. Posterior to Groove A is a faint depression ("Groove B") that lies slightly anterior to the lambdoid suture. Holloway does not interpret this feature as a sulcus but rather an indention that was caused by the inferior lip of the parietal bone where it meets the lambdoid suture (Holloway 1983), similar to an asterionic notch. Falk initially argued that Groove B represented the lunate sulcus in a more anterior position than what is typically seen in modern humans, and more closely resembled the position associated with *Pan* (Falk 1985a:46). In response to Falk, Holloway and Kimbel argued that Falk's orientation of the endocast was

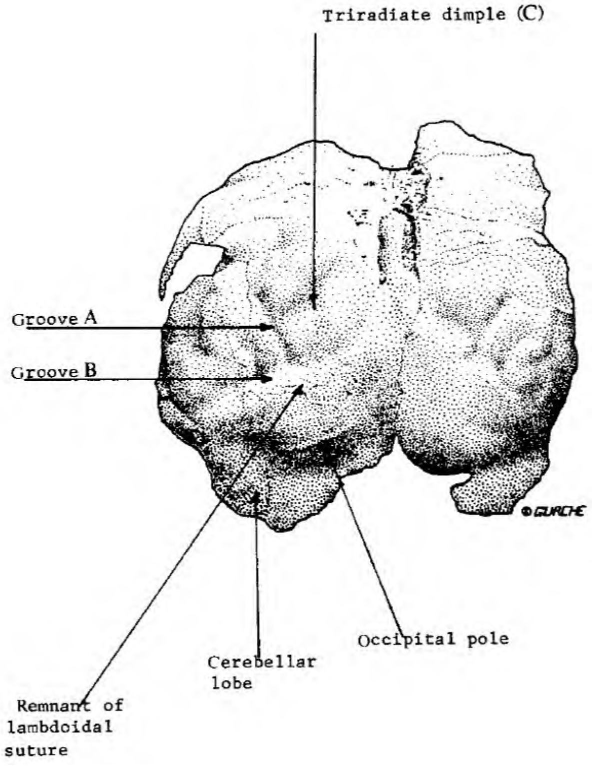


Fig. 5.18 Line-stiple drawing of endocast by Mr. John Gurche provided courtesy of Ralph Holloway

approximately 39 degrees too "flat" (in terms of slope), resulting in a mis-interpretation of features (1986: 536). Furthermore, they additionally note that the lambdoid suture is approximately 2 mm posterior to the feature in question (i.e., Groove B vs. Falk's lunate sulcus).

In response to Holloway and Kimbel, Falk argued that the feature she considers to be the lunate sulcus (in a *Pan*-like position) could not be due to the lipping of the suture because the feature is 5 mm anterior to the lambdoid suture versus the 2mm as argued by Holloway and Kimbel (Falk 1986:537). My measurement between the lambdoid suture and the feature in question is 1.9 mm. Falk further notes that the feature "merges with the intraparietal sulcus, as does the lunate sulcus in *Pan*; it is rostral to the lambdoid suture as is the lunate sulcus in *Pan*; and has a sulcus-like texture and shape similar to the lunate sulcus in *Pan*" (Ibid:537).

From my observation of the endocast mould, the intraparietal sulcus, indeed, appeared to end at Groove B, and if Groove B is a sulcus versus an indention due to bone lipping, it might also be the transverse occipital sulcus, which the intraparietal sulcus joins with in modern humans. I agree with both Holloway and Falk in the identification of Groove A as the intraparietal sulcus, but in my opinion, there is simply not enough information provided by Groove B or elsewhere on the endocast to make a definitive identification of what this feature represents. Furthermore, are these two features enough to make a firm identification of the overall occipital sulci configuration and whether or not some level of brain reorganisation has occurred? In this case, I think not.

Holloway's suggestion that Groove B is a depression due to lipping makes sense, based not only on how these bones typically overlapped but also because of Groove B's location relative to the position of what Falk, Holloway and I believed to be the intraparietal sulcus. Nevertheless, Groove B is a feature which cannot be identified with absolute certainty due to the lack of additional supporting cranial landmarks. In Falk's second response to Holloway and Kimbel, she also came to this conclusion stating "I do not think the calvaria of AL 162-28 is complete enough to allow speculation about where the locations and relative positions of both features would have been on the endocast" (Falk 1986:537). Indeed, it is very difficult to positively identify a single occipital sulcus without context, given the wide range of diversity and variation of the occipital sulci in modern humans, but especially when there are no other definitive landmarks from which one can draw reference.

However, Gunz *et al.* recently created a high resolution virtual endocast of AL 162-28 using conventional and synchrotron computed tomography as a means to detect additional occipital sulci, previously unseen with the naked eye (2020). Indeed, the scans revealed two crescent-shaped sulci anterior to 'Groove A' in both hemispheres (see Figure 5.19 as indicated by the black arrows), which have the appearance of lunate sulci in very anterior positions. The slightly curved line in orange indicates the location of the feature initially suggested by Falk as a possible lunate sulcus (albeit Falk identified it in the left hemisphere).

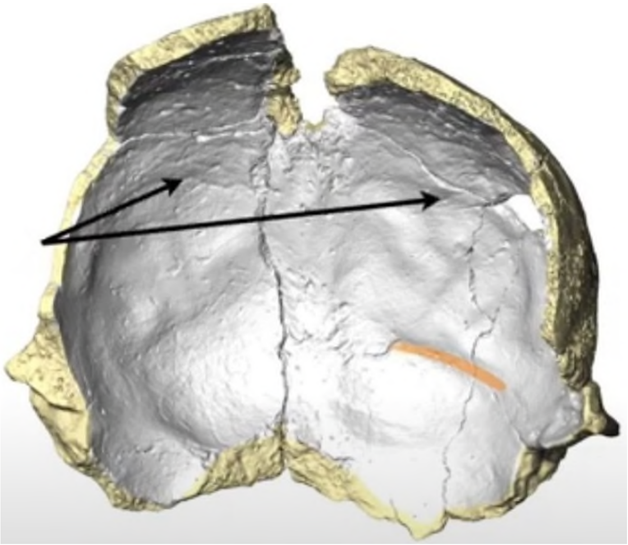


Fig. 5.19 Virtual Endocasts AL 162-28
From Gunz 2020 AAPA Presentation
www.youtube.com/watch?v=FAIoK4mtkzM

If Gunz *et al.* are correct in their identification of these anteriorly placed lunate sulci, then the Groove A sulcus cannot be the intraparietal sulcus, as identified by Holloway, Falk and myself. Based on the location and position of Groove A, relative to the location of what Gunz *et al.* have identified as lunate sulci, as well as Groove A's position in relation to what appears to be the parietal-occipital sulcus, Gunz *et al.* have determined that Groove A must be the lateral calcarine sulcus (2020:2).

Considering how the lateral calcarine is never anterior to the lunate sulci (as the intraparietal sulcus would be), this is the only other viable option for a somewhat vertical feature such as Groove A, based on the features identified by Gunz *et al.* as the lunate sulci.

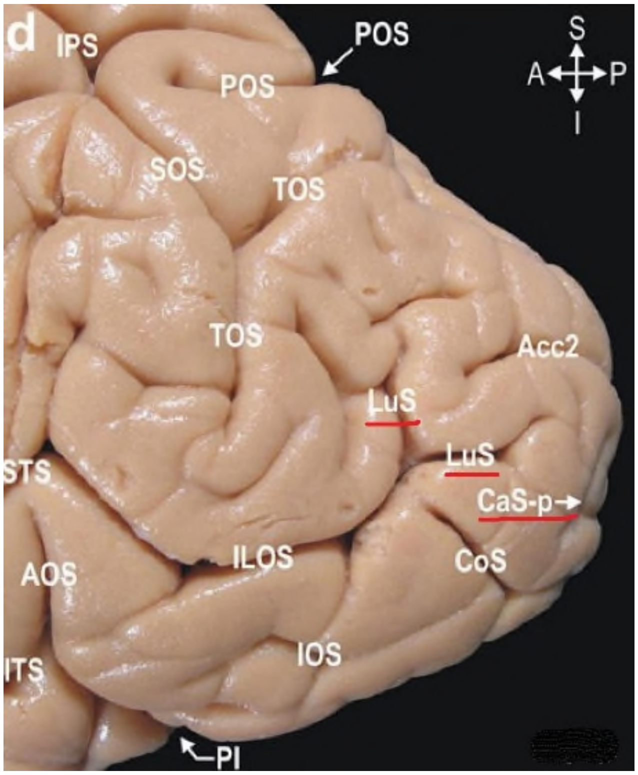


Fig. 5.20 Modern human occipital lobe
Lunate sulcus (LuS) &
Lateral calcarine sulcus (CaS-p)
Malikovic et al. 2012:65

As mentioned, the calcarine sulcus/fissure in modern humans is located almost entirely within the medial area of the brain, with only a small portion sometimes appearing near the occipital pole in roughly 69% to 70% of the population (Iaria *et al*. 2008:179; Ribas 2010:12; El Mohamad *et al.* 2019:183). In extant apes, however, calcarine sulcus can be viewed laterally and appears as a continuous sulcus in a pronounced 'y' shape versus a tiny 'fishtail' shape near the occipital pole as it appears in modern humans.

Figure 5.22 is a comparison of the digital endocast of AL 162-28 with the digital endocasts of a chimpanzee MRI and a chimpanzee CT, from Gunz *et al.* 2020 with the identified features labelled and in colour. The lunate sulci can be seen in red, in an anterior position whilst the blue features

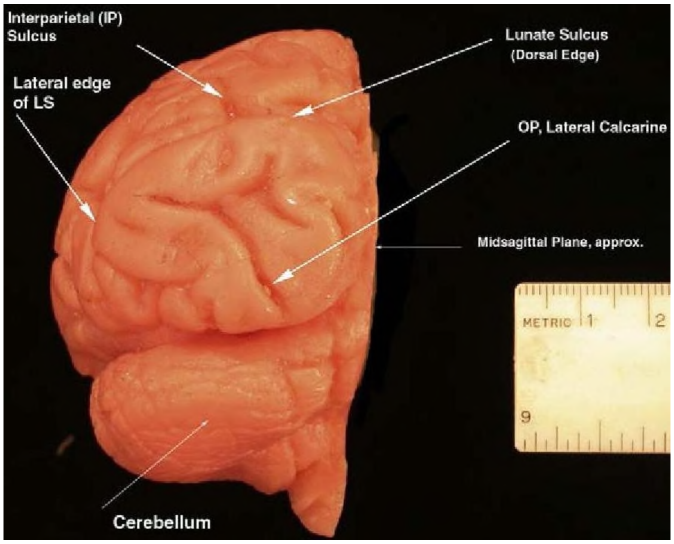
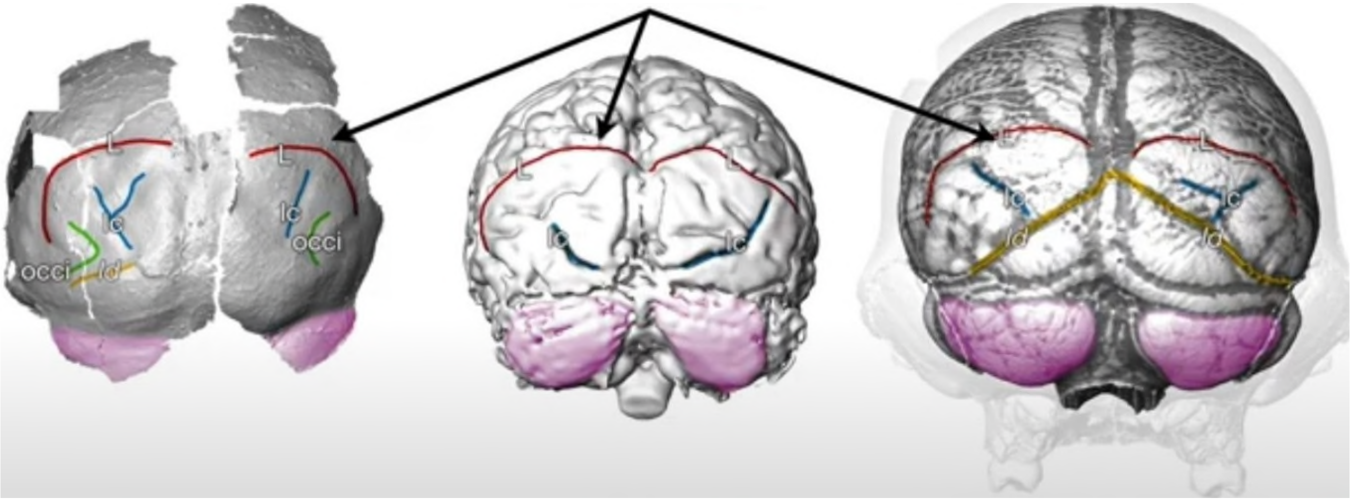


Fig. 5.21 Chimpanzee brain cast
Holloway et al. 2004:3

posterior to the lunate sulci are identified as the lateral calcarine sulci. The sulci labelled 'OCCI' in green are identified by Gunz *et al*. as the inferior occipital sulcus, which is not particularly convincing from the imagery provided, any more so than other possible occipital sulci; however, based on the scenario that Gunz *et al.* have presented - it fits with their overall suggested framework. Furthermore, these sulci do not necessarily support the identification of the lunate sulcus as Gunz *et al.* claim, but rather the identification of the *lunate sulci* supports the identification of the lateral calcarine sulcus and the inferior occipital sulcus. For this reason, the identification of the lateral calcarine sulci and the inferior occipital sulci by Gunz *et al.* is entirely subject to accepting the anteriorly placed sulci as the lunate sulci – not the other way around.



AL 162-28 Chimpanzee MRI Chimpanzee CT

Fig. 5.22 Virtual endocast of AL 162-28 with an MRI and CT scan of a chimpanzee brain. The lunate sulci are identified in red and designated by the arrows. The blue represents the lateral calcarine sulci whilst the yellow is the feature originally identified by Falk as the lunate sulcus, now believed to be remnants of the lambdoid suture. The sulci in green are thought to represent the inferior occipital sulcus. Gunz 2020 AAPA presentation: www.youtube.com/watch?v=FAIoK4mtkzM

Accordingly, the proper assessment is essentially reduced to whether or not these anteriorly-placed crescent-shaped sulci seen in the image from Gunz's AABA presentation are convincing as lunate sulci based solely on their shape, configuration and location on the AL 162-28 digital endocast. In my opinion, I believe they are, offering the most parsimonious explanation when considering there are no other particularly convincing alternatives to what the sulci in red might otherwise be, if not the lunate sulci. As a result, this new evidence affirms the lack of brain reorganisation in early *A. afarensis*. Also important is how specimens DIK-1-1, AL 333-105, and AL 162-28 can now provide appropriate baselines for comparison with later endocasts.

AL 822-1

The 822-1 cranium was found by Dato Adan, an Afar member of the Hadar Research Project, and recovered in approximately 200 fragments during the 2000 field season in the Hadar Formation KH-1 sub-member (Kimbel and Rak 2010:3366). It is approximately 3.1 million years old with small mastoid processes, thus likely representing a small adult female The cranial dimensions are small and similar to 162-28 (also believed to be female) with an estimated endocranial volume of 385 ml using mustard seed (Ibid:3367). The specimen suffered much distortion and deformation due to warping and crushing, which was corrected (to the extent possible) during reconstruction. It has an asterion notch sutural pattern and a steep nuchal plane, yet there are no compound tempo-nuchal crests. Other features of interest include a strongly prognathic face that is narrow at the midface with a gradient thickness of the supraorbital ridge, increasing medially to

Fig. 5.23 822-1 Lateral view Kimbel & Rak 2010:3367

Fig. 5.24 822-1Oblique view Kimbel & Rak 2010:3366

lateral. Following reconstruction, it is now a rare nearly complete *A. afarensis* cranium, and as a result, provides useful information regarding *afarensis* cranial morphology. Its small size again reinforces the considerable sexual dimorphism in *afarensis*. Unfortunately, there is no endocast mould, due to its fragile nature following the reconstruction process, although a digital endocast could likely be made.

AL 444-1 and 444-2

During a paleontological survey of the Kada Hadar Member sediments of the Hadar Formation in February of 1992, Yoel Rak discovered two occipital fragments at the base of a hill with Kada Hadar silts and clays (Kimbel et *al.* 2004). The lambdoidal suture on the occipital fragments had not yet fused, indicating the individual (AL 444-1) was a sub-adult. Further investigation of the upslope revealed additional hominin cranial fragments, but belonging to a second individual (AL 444-2). The following year, the entire 444 hill side was excavated, and approximately 50 cranial fragments (not including dentition) were recovered belonging to the second individual (AL 444-2), a large adult *A. afarensis* male.

The age of AL 444-2 is estimated at 3.0 ± .02 myo based on stratigraphic interpolation from the ^{40}Ar/^{39}Ar dating of the BKT-2 tephra and Kada Hadar Tuff that 'bracket' the areas where the majority of the AL 444-2 cranial fragments were recovered (Kimbel *et al.* 2004). Although there was some deformation on the right side of the cranium due to geological pressures and other factors, the cranium could be reconstructed and is mostly complete as well as sturdy enough for an endocast mould to be made. The brain was quite large for an *afarensis*, estimated between 545 and 560 ml (Holloway *et al.* 2004:45).

Unfortunately, the endocast was almost entirely devoid of any convolutional detail, and possible brain petalias could not be determined due to the distortion and missing parts. Although the lack of information from the endocast is disappointing, the skull of AL 444-2 is nevertheless an important find, providing other meaningful information in terms of the *A. afarensis* species. Its near completeness gives insight to certain cranial regions that were previously poorly represented in the fossil record, such as the frontal bones. The size of the cranium of AL 444-2 along with AL 333-45 ml (nearly 500 ml and also a male), juxtaposed to the female crania of AL 162-28 (375-400 ml) and AL 288-1 (also 375-400 ml) further demonstrate the extensive sexual dimorphism of the species.

Fig. 5.25 Artist's rendering ¾ view of AL 444-2 By Yehudit Sherman Johanson 2004:478

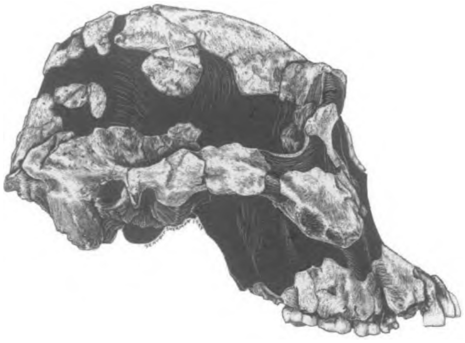


Fig. 5.26 Artist's rendering Right lateral view By Yehudit Sherman Johanson 2004:478

During the estimated life span of *A. afarensis*, several australopith-like species (or variations) appeared, three of which (*Kenyanthropus platyops*, *Australopithecus bahrelghazali*, and *Australopithecus deyiremeda*) are represented by only a few fossil specimens. As a result, there is much debate as to whether they should be considered separate species or simply radiations of taxa that derived from *afarensis* and should therefore remain classified as *A. afarensis*, considering the wide range of variation for the species (T. White 2003; Cartmill and Smith 2009; Stanford *et al.* 2017).

***Kenyanthropus platyops* (3.5 mya)**

In 1999, a highly fragmented and considerably distorted nearly complete cranium (KNM-WT-40000) was discovered by Meave Leakey's excavation team in Lomekwi, west of Lake Turkana in Kenya (M.G. Leakey *et al.* 2001). The specimen was recovered from the Kataboi Member of the Nachukui Formation, approximately eight metres below the ß-Tula Bor Tuff and twelve metres above the Lokochot Tuff, suggesting an age of approximately 3.5 myo, based on linear stratigraphic scaling (M.G. Leakey *et al.* 2001:439).

Fig. 5.27 Kenyanthropus platyops
Stanford et al. 2017:315

Additional $^{40}Ar/^{39}Ar$ dating methods were applied by McDougall and Brown to the alkali feldspars from pumice clasts within the tuffs beneath the Lokochot Tuff, which supported the date provided by Leakey *et al.* (McDougall and Brown 2008:559). McDougall and Brown add that the uncertainty regarding this date is unlikely to exceed 30k years (Ibid).

Tim White estimates that there are approximately 1,100 bone pieces in the prognathic portion of the face, held together by the natural matrix (2003:1995). Due to the severe distortion, the cranium cannot be properly measured for brain volume, but it appears to fall within the ranges of *A. afarensis* and *A. africanus* (M.G. Leakey *et al.* 2001). The cranium exhibits a combination of both derived and primitive features. For example, the zygomatic arches sit high and anterior on the face whilst the maxilla appears somewhat short, yet deep, thus producing an unusually tall and flat lower face for an early australopithecine (Cartmill and Smith 2009). However, it also has small molars as well as other characteristics more primitive than *A. anamensis* or *A. afarensis*, which prompted Leakey and Fred Spoor to give it a new genus name (M.G. Leakey *et al.* 2001:433). Many feel that the specimen is merely a local or individual variant of *A. afarensis*, and T. White in particular has taken great exception to the naming of a new species and especially a new genus (T. White 2002; T. White 2003).

T. White argues that one should first consider whether the different morphology is outside the expected range of variation for the lineage, and he points out the very wide range of variation in extant apes (2003:1995). He also notes the extreme distortion of the skull, especially the braincase, and as a result, he suggests that the original interpretation of the specimen could be in error (T. White 2002:409; T. White 2003:1997). Leakey's team responded with a study on the unusual maxilla and argues that the maxilla was not impacted by the cranial distortion and the face is substantially flatter than that of *A. afarensis* (Spoor *et al.* 2010:3387). However, one maxilla fossil alone does not make a strong case for a new species, much less a new genus. White's criticism is well-founded, especially with respect to the condition of the cranium and the wide range of variation within the *A. afarensis* species. Cartmill and Smith agree with White, and additionally note how the early hominins are likely "over-split, and that more extensive sampling in time and space would disclose continuities between populations that are currently recognized as distinct species," and they advocate for a compromise between the lumping and splitting of species (Cartmill and Smith 2009:183). At the present, it remains part of the ongoing arguments for the lumpers versus the splitters over taxonomy.

Regardless of its speciation, it is unfortunate that the KNM-WT-40000 cranium is too damaged and fragmented for even a high-resolution digital endocast, considering that the multiple fragments[1] that compose the skull are each "isolated by varying thickness of matrix fill" with as much as 24% matrix versus original bone in some places (T. White 2003:1995).

K. platyops: Correlation with Stone Tools – the Lomekwian

The earliest evidence of stone tool *production*, known as the Lomekwian, has been dated to approximately 3.3 mya and also comes from West Turkana, Kenya (Harmand *et al.* 2015). Between 2011 and 2012, 149 lithic artefacts were recovered in association with 33 hominin remains within the Lomekwian 3 (LOM3) site, located

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[1] *White estimates 4,000 fragments*

west of Lake Turkana in northern Kenya representing the same geographic and chronological range as specimen KNW-WT 38350, a paratype of *Kenyanthropus platyops* (Ibid). The LOM3 cores and flakes were deemed to have been manufactured versus 'natural' and appear to bear the characteristics of debitage products. The Lomekwian is a very simple technology, often referred to as 'pre-Oldowan' or even 'battering activities' due to their crude nature. However simple or crude, it is significant that there is evidence of stone tool production as early as 3.3 million years ago, and the only hominin recovered in the West Turkana vicinity is *K. platyops*. The cognitive features and postcranial morphologies engaged in tool-making will be discussed in Chapter 6, as well as a more detailed description of the Lomekwian.

Australopithecus bahrelghazali (3.5 – 3.0 mya)

In 1994, a hominin specimen consisting of the front of a mandible with seven teeth was recovered in the Koro-Toro[1] area of Chad (in West Africa) by Michel Brunet (Brunet *et al.* 1995). This was the first hominin fossil found in West Africa, which Brunet *et al.* named *Australopithecus bahrelghazali* for 'the hominin from Antelope Creek.' Many feel that it is either a member of *A. afarensis* or too fragmentary to justify a new species, although the 'chin' portion of the *A. bahrelghazali* fossil is more vertically shaped than that of *A. afarensis*, and the lower premolars had three roots instead of two (Cartmill and Smith 2009; Spoor *et al.* 2001; Stanford *et al.* 2017). However, these traits could simply

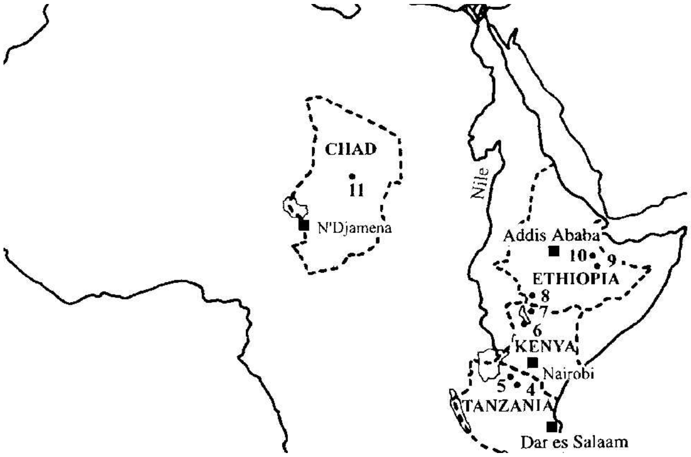

Fig. 5.28 Proximity of Chad to the East African sites
Brunet et al. 1995:273

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[1] *The Koro-Toro area is approximately 150 km from the site where Sahelanthropus was discovered.*

represent variation within the *A. afarensis* species. T. White argues that a small bit of fossil evidence is inadequate for naming a new species, and the morphology of *A. bahrelghazali* does not constitute a significant difference (2002:409). Regardless, it establishes the presence of hominins west of the Rift Valley.

Australopithecus deyiremeda **(3.5 – 3.3 mya)**

In March of 2011, a left maxilla with a few teeth (BRT-VP-3/1, holotype specimen) was found by M. Barao in the Woranso-Mille sites in Ethiopia, with additional paratype specimens found nearby (Haile-Selassie *et al.* 2015). The specimens are dated to between 3.3 and 3.5 million years ago and have been given the name of *Australopithecus deyiremeda*, which means "close relative" in the Afar language (Ibid). Other australopithecine fossil specimens have been found in the Woranso-Mille area belonging to *A. anamensis*, *A. afarensis*, and *K. platyops*. It is also where the Burtele foot fossil (not currently assigned to a species) was discovered. The Burtele specimen (BRT-VP-2/73) is dated to approximately 3.4 million years ago and is of particular interest because the hallux (big toe) of the foot is somewhat opposable indicating the ability to grasp, yet also has adaptations to provide the dorsiflexion required for bipedalism (Ibid).

According to the discovery team, *A. deyiremeda* is too derived to belong to *Ardipithecus*, primarily because of the thickness of the enamel, yet could neither be *A. anamensis* nor *A. afarensis* due to its small postcanine teeth and a differently shaped mandible (Haile-Selassie *et al.* 2015). Additionally, the zygomatic arches are more anteriorly positioned, similar to those of *K. platyops* (Ibid; Spoor 2015). However, there is again debate as to whether or not *A. deyiremeda* is, indeed, a separate species based on only a few fossil specimens. Overall, it seems more feasible that *A. deyiremeda* represents yet another variation of *A. afarensis*.

Australopithecus in South Africa

South Africa has been the most prolific region in Africa for producing early hominin fossil finds – especially from the Sterkfontein Caves, which are located in what is now a UNESCO World Heritage Site called the 'Cradle of Humankind'

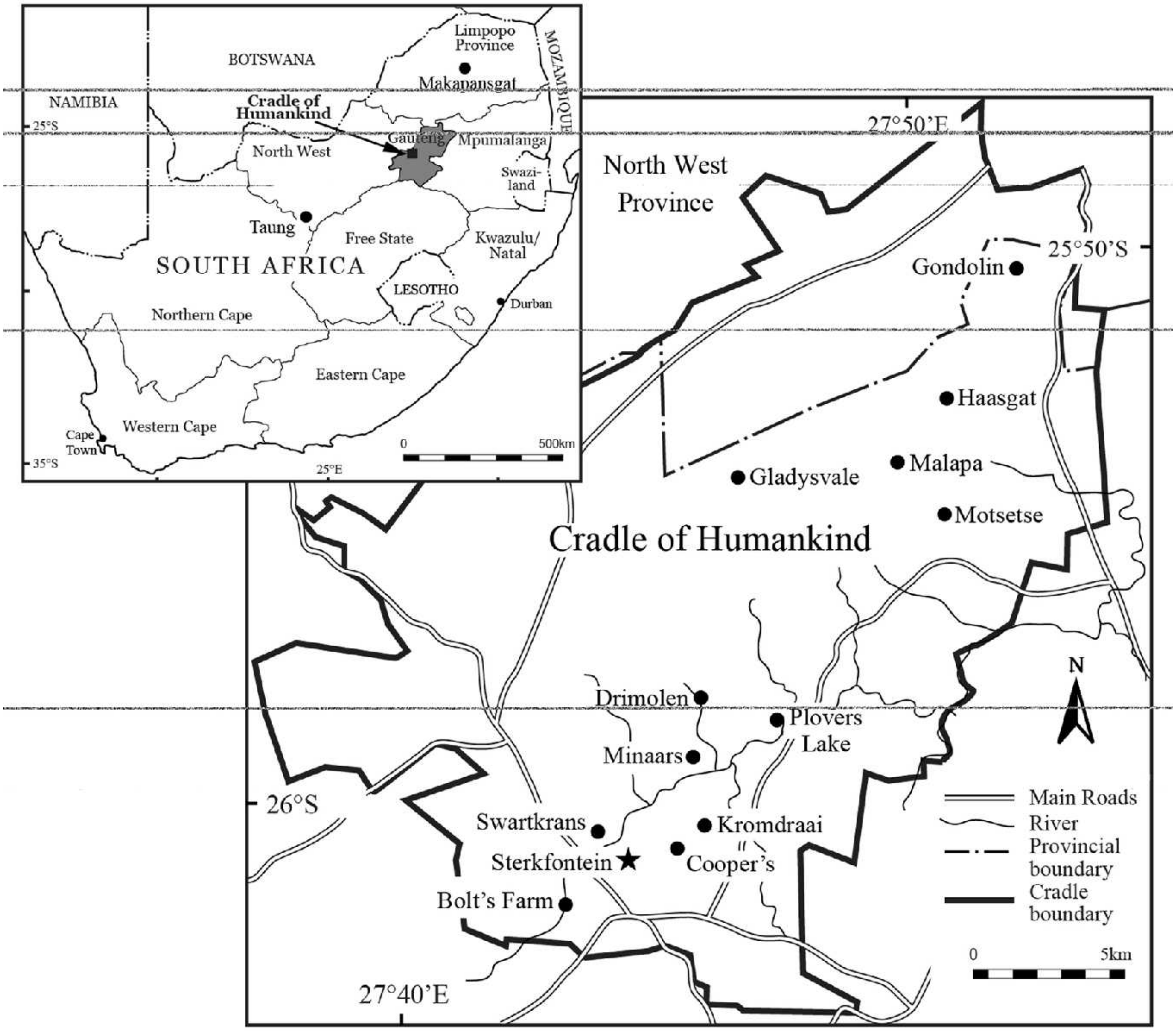

Fig. 5.29 Cradle of Humankind in South Africa
Stratford 2018:42

(Stratford 2018:40). Although the Sterkfontein Caves have been referred to as the "richest *Australopithecus*-bearing site in the world" (Ibid:39), the excavations of these caves were not due to geological research or the prescience of archaeologists in the early 20th century, but rather the importance, influence and impact of gold mining in South Africa following the initial discovery of gold in the late 19th century. In 1896, the mines on the Witwatersrand reef were the source of one-third of the world's gold supply and by 1914, they were producing two-thirds (Bonner 2007a:201). As an indirect result of the gold industry, numerous fossil-bearing sites were discovered during the mining of limestone - a crucial component for the refining of gold[1] (Ibid). During the Pliocene and Pleistocene, these underground cavern sites in the Witwatersrand Basin of South Africa occasionally had vertical shafts ('avens') which opened to the surface. Bones would accumulate in the caves either from predators eating their prey in the vicinity of the avens, whereby the bones would ultimately be washed into the avens (or over time, collapsed into the avens) or from the avens serving as 'death traps' for early hominins (Brain 1981; Clarke *et al.* 2021). They would gradually be covered by an admixture of rocks and soil, which often became sealed and hardened by calcium-carbonate water, dripping from the stalactites and forming a very hard sedimentary deposit referred to as 'breccia' (Clarke *et al.* 2021).

After mining operations uncovered the Taung child in 1924, many years would pass before another *A. africanus* specimen would be found. The years of fossil drought prompted Dart, who had moved to Johannesburg in 1922 as the new Chair of Anatomy at the University of the Witwatersrand (Bonner 2007a), to petition General Jan Smuts[2] and President J.H. Hofmeyr for their financial backing and influence with respect to increasing archaeological efforts, including support for Robert Broom's return to South Africa (Stratford 2018). Broom was a Scottish doctor who, as part of his scientific research and medical practise, had travelled extensively to the United

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[1] *The MacArthur Forrest cyanide reduction process (Bonner: 2007b:212).*

[2] *Smuts financially supported the interests of Dart, Broom, Robinson and other South African archaeologists in their archaeological pursuits, which is ironic given that Smuts also supported the Hertzog Bills which banned the teaching of evolution (Bonner 2007a:204-5).*

States, Australia and in 1897 to South Africa. In 1903, he became a Professor of Geology and Zoology at the Victoria College (later, the University of Stellenbosch),then six years later returned to medicine and science before attempting to retire in 1929. Broom was one of the first scientists to step forward in support of Dart's belief that *A. africanus* could be an ancestor to later hominins, including *Homo sapiens* (Kuykendall and Štrkalij 2007:45), so it is understandable why Dart would be inclined to work with him. In 1934, Broom was appointed Curator of Palaeontology at the Transvaal Museum after receiving an endorsement from Smuts (Ibid:44; Stratford 2018:42), and two years later visited the Sterkfontein Caves in August 1936.

Serendipitously, the mining supervisor at Sterkfontein during this time was G. W. Barlow, who had also worked at Taung when the first *A. africanus* skull was discovered. Broom asked Barlow to search for anything similar to the Taung skull and eight days later, he handed Broom the natural brain endocast of an adult *A. africanus* specimen - the first adult to be discovered[1] (Tobias 2007:229; Stratford 2018:42; Clarke 2013:105). The discovery was widely published, including articles in *Nature* and the *Illustrated London News,* and launched 80+ years of scientific exploration at the Sterkfontein Caves (Stratford 2018:42). The cranium was catalogued as TM 1511[2] by Broom and included the facial portion (albeit damaged) with many of the teeth (Kydkendall 2007:56), whilst the natural endocast was later catalogued separately as specimen Sts[3] 60 (Clarke 2013:105).

Over the next three years, Broom and his assistant Robinson recovered many craniodental specimens which Broom believed to be significantly different from the Taung child discovered by Dart (Stratford 2018). Accordingly, he designated a new genus called *Pleisanthropus*, which translates to 'near man', with the species named

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[1] *According to Broom, Barlow asked him "Is this what you are after?" (Broom 1949:21).*

[2] *The "TM" stands for "Transvaal Museum."*

[3] *Hominin fossils found at Sterkfontein prior to 1966 were designated "StS," and afterwards, "StW."*

Pleisanthropus transvaalensis (Kydkendall 2007:57; Tobias 2007:229; Clarke 2013:105; Stratford 2018:43). However, in 1954 after many more fossil specimens had been recovered allowing for detail studies, Robinson proposed reassigning the fossils to *Australopithecus africanus*, like Taung, but with the sub-species designation of *transvaalensis* (Tobias 2007), which was ultimately re-named and catalogued during the 1960s as *A. africanus* (Crawford *et al.* 2004).

Although the mining industry provided the initial means for the exploration and discovery of fossil finds, it also destroyed many specimens in the process. Additionally, the mining crews would sometimes sell or give away the fossil remains to tourists and collectors (Stratford 2018). At the time, nothing could be done about this 'double edged sword' of the mining industry due to the prevailing South African law at the time whereby "commercial interests take precedence over scientific ones in matters of this sort" (Robinson 1952:4). For example, at Swartkrans during the late 1940s whilst the archaeological team was away for a month, the limestone miners excavated a thick seam of calcite dripstone (aka stalagmite) which was forthwith sold to a toothpaste manufacturing company (Ibid).

Following this incident, the archaeologists (who consisted primarily of Broom, Robinson and several of Raymond Dart's students) made a point to perform periodic visits to the site more frequently during mining operations (Stratford *et al.* 2018). In spite of their diligent attendance, the only means allowed for recovering fossils in South Africa at that time was to rifle through the mining dumps. As a result, the provenance of the fossils recovered from the dumps was lost, making it difficult to correlate them both spatially and temporally. This tactic, nevertheless, yielded many significant specimens, although Robinson noted how the majority of the specimens were frequently "damaged and incomplete" as a result of the blasting and other mining operations (Robinson 1952:4). Furthermore, the specimens were often encased in the cement-like composition of fossilised breccia which was difficult to extract. However, one could argue that whatever negative effects the South African mining industry may have had on the quality of the fossil finds was surpassed by the sheer quantity of the numerous specimens discovered, with the majority of the hominin fossils representing *Australopithecus africanus*. However, only seven of the approximate 20 or so skulls (or skull fragments) in the fossil record are complete enough to produce somewhat meaningful endocasts.

The Issues for Dating Fossils in South Africa

Unlike East Africa, where fossils could be dated using radioisotopic dating methods to a high degree of precision, the South African caves had complex stratigraphy and no volcanic activity, thus requiring alternative means of dating (Partridge *et al.* 2003; Pickering 2011; Stanford *et al.* 2017). Furthermore, the majority of the fossils were recovered from the mining dumps, with few *in situ* discoveries until the mid-1960s. Although many techniques were attempted, most relied upon the uranium-lead (U-Pb) dating of calcium carbonate cave rocks (speleothems or flowstones), palaeomagnetic analysis, and biostratigraphic relative dating methods (Pickering *et al.* 2011; Stanford *et al.* 2017).

The biostratigraphy with fauna and hominin remains, coupled with the lithostratigraphy where the remains were found, were compared with similar rock strata from other locations, where radioisotope dating could be performed. Palaeomagnetic analyses have been useful, as there were five paleomagnetic reversals in the sequence of inter-connected calcite flowstone beds in Member 2 of the Sterkfontein Caves (Partridge *et al.* 2003:607), as well as a number of short events, some of which only lasted 3,000 to 20,000 years (Pickering *et al.* 2011:1421). Other methods, such as cosmogenic radionuclide dating, have been employed, but the complex stratigraphy and depositional environment of the South African caves presented many challenges, and as a result, much uncertainty and frequent debate over the estimated age of the specimens recovered.

The Sterkfontein Caves and *A. prometheus*

The Sterkfontein formation has exposure at both the surface and the underlying cave system from mining excavations at elevations of 1,460 to 1,480 metres (Partridge 1978). It consists of six members with Member 6 being the shallowest and Member 1, the deepest (see Figures 5.30 and 5.31). Members 2 and 3 are located within the Silberberg Grotto and consists of approximately 0.5 to 5.0 metres of light brown and red silty loam with a high concentration of bone fragments near the base (Partridge 1978:284). A continuous process of erosion and cave infilling has resulted in a complex stratigraphic relationship between and among the Members, which has contributed to the difficult process of dating the various fossil finds.

Although several *A. africanus* specimens have been recovered from Member 5, the majority of the fossil specimens came from Member 4. This member was dated in the early 1990s to approximately between 2.6 to 2.8 mya (McKee 1993; Clarke and Tobias 1995), but the range was subsequently expanded by Partridge *et al.* to between 3.0 and 2.0 mya based largely on the electron spin dating of bovid teeth and other factors (2003).

In 1966, a new excavation program began under the direction of Philip Tobias and Alan Hughes, and although the primary mission of the excavation involved detailed surveys of the cave systems as well as exploring “the possibilities of absolute dating on the site” versus searching for hominin and other fossils (Tobias and Hughes 1969:158), over the following 12 years the team recovered quite a few *A. africanus* specimens (Stratford 2018; Clarke 1998). Any specimens found within the Sterkfontein Caves from 1966 onward were given the specimen prefix “StW” to distinguish them from the specimens found prior to 1966, which were recovered primarily from the dump boxes (Stratford 2018).

Then in 1978, the team took a new direction to investigate the lower (and older) Members 2 and 3 within the Sterkfontein formation, which were exposed in the Silberberg Grotto (Clarke 1998). There were several sections of breccia and rubble left on the cave floor by the limestone workers, which Hughes had taken to the surface for the fossil finds therein to be catalogued and stored (Clarke 1998). By 1992, focus shifted to fossil extraction, and excavation (including some blasting), which began in the eastern end of the Silberberg Grotto and produced several mammalian remains, primarily Cercopithecoids (Old World monkeys) over the next two years (Ibid). However, there were no bovid fossils, which Clarke found puzzling. As a result, he searched through the dump boxes of breccia and rubble in search of bovids, but instead – he found four hominin foot bones in Dump Box #20, which would later be assigned to specimen StW 573, aka 'Little Foot' (Clarke and Tobias 1995:524; Clarke1998:460).

As is often the case with new archaeological discoveries, these four foot bones led to more questions than answers as the foot had both human and ape-like traits. There were some features that indicated habitual

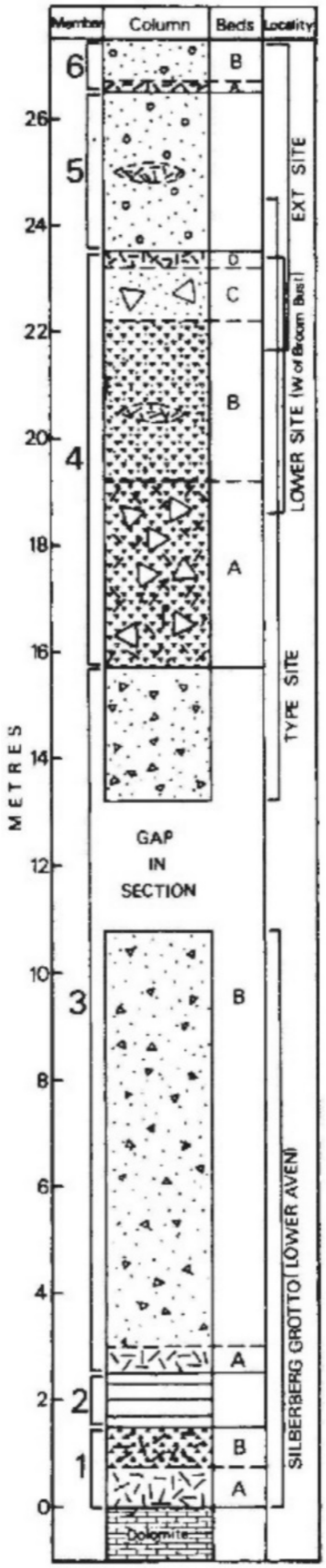

Fig. 5.30 Stratigraphic column Sterkfontein Formation Partridge 1978:285

bipedalism, whilst the medial cuneiform suggested that StW 573 may have also maintained an arboreal lifestyle. The position of the medial cuneiform as it articulates with the base of the metatarsal evinces that the hallux (big toe) abducted outward. Clarke continued to search for hominin remains from the dump boxes and by June of 1997, had ultimately recovered 12 hominin foot and leg bones, of which eight were articulated. These finds indicated that although the hallux was abducted outward, the foot was nevertheless able to produce the dorso-flexion 'push off' required for bipedal locomotion. As previously mentioned, there is debate as to whether evidence of retained arboreal adaptations are indicative of an arboreal lifestyle or perhaps simply leftover vestiges, similar to a human coccyx. As a result of this curious combination of traits, the excavation team felt compelled to search for the rest of the skeleton.

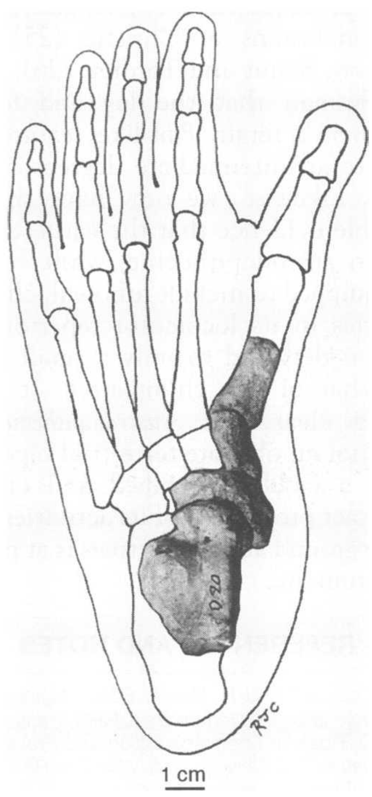

Fig. 5.31 StW 573 foot bones Clarke and Tobias 1995:523

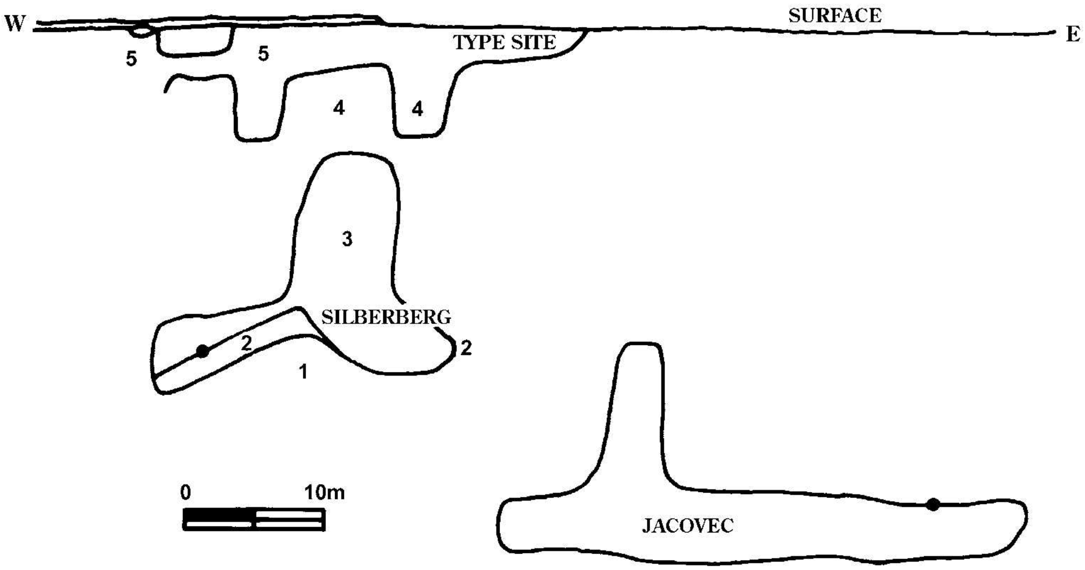

Fig. 5.32 Simplified Drawing of the Sterkfontein Formation (Clarke 2013:107)

Only one month later in July 1997, a mature adult skeleton was found encased in breccia near the bottom of the Member 2 slope at the western end of the Silberberg Grotto, which was the opposite end of where they had previously excavated (Clarke1998). This find also presented the opportunity to examine a fossil skeleton *in situ*, which was somewhat unusual for the Sterkfontein Caves given that most of the fossils had previously been recovered from the spoil dumps. The nearly complete cranium, albeit damaged, was revealed in September of the following year (Ibid:462); however, it would take more than two decades to fully recover the entire adult specimen.

Clarke noted that in addition to the foot with the outwardly abducted hallux, the cranium also had some distinctive features unlike other *A. africanus* specimens, such as a flatter face with a very prominent zygomatic arch (cheekbone), bulbous-cusped cheek teeth, a more vertical occiput, and some sagittal cresting (Clarke 1998; Clarke 2013). As a result, Clarke is convinced that StW 573 represents a species of *Australopithecus* previously unknown in South Africa, and strongly suggests that it be classified accordingly (Clarke 2013). Tim White, however, believes that StW 573 is quite possibly yet another variation of *A. afarensis*, which would indicate a greater geographic distribution for the species beyond Tanzania to the south, and White additionally notes how *A. afarensis* is considered by most to be a "suitable ancestor" for all later hominins (2002:414). Although White could well be correct regarding the status of StW 573 as another *A. afarensis*, the specimen 'pushes' the already wide range of variation with its many morphological differences, which seem more likely indicative of a plesiomorphic hominin evolving into a new species – possibly *A. africanus* or another species all together.

In 1998, Member 2 was believed to date roughly between 3.0 mya and 3.5 mya, making StW 573 the oldest hominin found in South Africa (Clarke and Tobias 1995:522; Clarke 1998:462). Yet, the subsequent U-Pb dating of the calcareous flowstones in the vicinity of the StW skeleton yielded a younger age of approximately 2.2mya (Walker *et al.* 2006:1594). During excavation, however, Clarke noticed that there were gaps in between the breccia encasement and the hand bones, suggesting that the body had been mummified in dry conditions prior to the lengthy wet period which had calcified the bones as well as the encasing sediment (Clarke 1999; Clarke 2021). Considering how the encasement occurred over an extended period of time, long after the hominin had perished, the flowstones would be younger than the skeleton. As a result, the encasing sediment of the specimen was re-dated using isochron burial dating with cosmogenic[1] aluminium-26 and beryllium-10 (^{26}Al/^{10}Be), which is based on the radioactive decay of ^{26}Al and ^{10}Be in quartz, which demonstrated that the breccia containing StW 573 did not "undergo significant reworking" similar to other areas in the caves, and thus, the deposits were likely buried at approximately 3.67 ±0.16 mya (Granger *et al.* 2015:1).

Fig. 5.33 StW 573 reconstructed
Clarke et al. 2021:135
Photo by Paul John Myburgh

Regardless of whatever species StW 573 is ultimately determined to be, she is likely a descendent of *A. afarensis* or perhaps even *A. anamensis*. Clarke *et al.* identify a number of

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[1] *Based on cosmic radiation striking rocks on the Earth's surface and producing these isotopes (aluminium-26 and beryllium-10) that have half-lives of approximately 1.0 and 1.8 million years, respectively (Cartmill and Smith 2009:191).*

morphological differences between StW 573 and *A. africanus* which include (but are not limited to): a bell-shaped outline of the posterior view of her cranium; a long nuchal plane; large canines relative to cheek teeth; and a small cranial capacity – all of which are also exhibited by the *A. anamensis* cranium MRD-VP-1/1 (2021:136). Additionally, her legs measure longer than her arms although the outward abducted hallux of the foot as well as some elements of the hand indicate both bipedal and arboreal locomotion (Ibid:138). Accordingly, there is merit to Clarke's argument for classifying specimen StW 573 as a separate species, which he has named *A. prometheus.*[1]

However, Clarke and Kuman now advocate for the reclassification of many of the other specimens currently considered *A. africanus* to *A. prometheus* (Clarke and Kuman 2019; Clarke et al. 2021). Although their argument for two species has been met with mixed reviews, the cranial comparison in Figure 5.34 presents an interesting perspective. According to *Clarke et al.,* specimen "a" represents *A. africanus* with the Sterkfontein specimen StW 53 reconstructed cranial fragments, combined with the mandible of specimen MLD 18 from Makapansgat. However, Clarke *et al.* argue that skull "b," which consists of the reconstructed cranial fragments of StW 252, combined with the mandible from Sts 36 (both from Sterkfontein), should be reclassified as *A. prometheus*. Skull "c" is the Little Foot cranium, specimen StW 573 from Sterkfontein, also argued to represent *A. prometheus* according to Clarke et al. (Ibid).

Regardless of the South African taxonomy ongoing debate, the description and discussion of the StW 573 cranium and endocast, as well as a partial cranium (StW 578) from the same time period in the Sterkfontein Caves, will be discussed here,

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[1] The name "prometheus" was initially chosen by Dart for the Makapansgat specimens with black stains, which he mistakenly misinterpreted as the use of fire (Crawford et al. 2004:45), later revealed to be manganese staining from groundwater during fossilisation (Kuykendall and Štrkalj 2007:57).

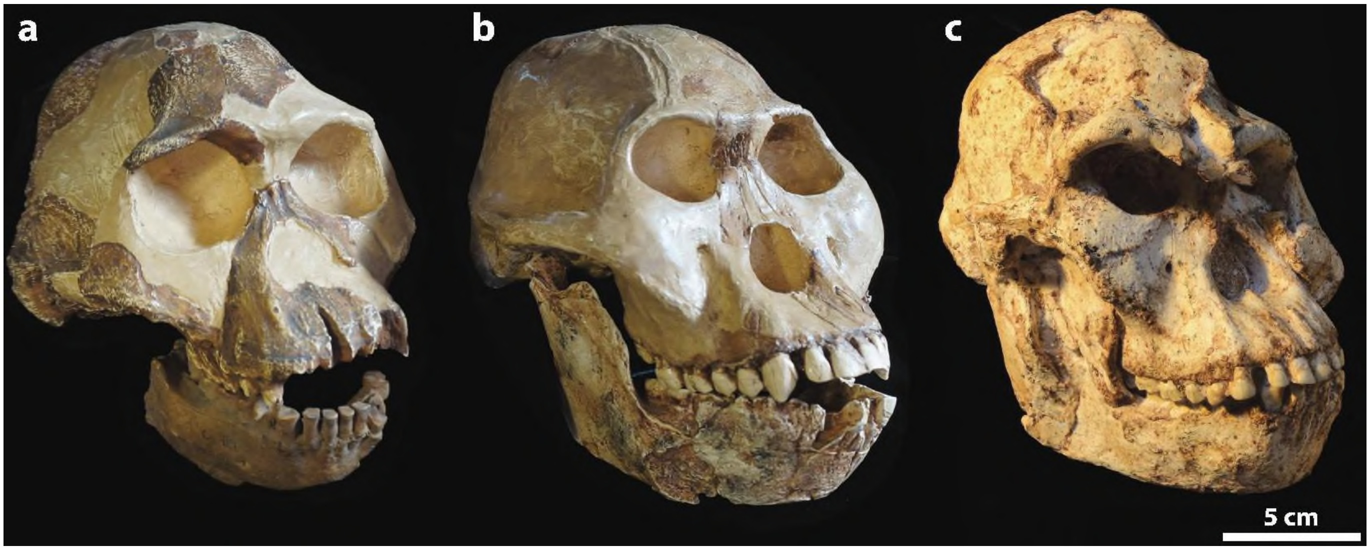

Fig. 5.34 *Comparison of A. africanus skull (a) with A. prometheus skulls (b and c)*
(a) Cranium of StW 53 from Sterkfontein, with mandible MLD 18 from Makapansgat
(b) cranium of StW 252, with mandible Sts 36,
(c) StW 573 from Sterkfontein.
Clarke et al. 2021:136

prior to the discussion of their likely descendants, *A. africanus*, instead of their chronological order in between *A. anamensis* (MRD) at 3.8 mya and the oldest *A. afarensis* specimen (Dik-1-1) at 3.3 mya.

StW 573 (Little Foot)

The skull of the likely female StW 573 is mostly complete, missing a very small piece of bone behind the foramen magnum and a few other tiny chips. The mandible remains in articulation with the rest of the cranium, fused in place by the breccia matrix (Clarke and Kuman 2019). Some breccia still needs to be removed from various cranial cavities, including the right side of the endocranial cavity. The shape of the orbitals and other regions have been somewhat crushed and compressed, displacing the lower face. There is a low sagittal crest that extends almost the entire length of the parietal bones (Ibid). Although Clarke and Kuman admit that StW 573 shares many features in common with *A. afarensis* specimen AL 444-2, such as the overall shape and zygomatic arches, they also point out the many differences such as the upper facial structure of AL 444-2 or the 'shelf' extension over her porion (near the ear canal) to join with a supra- mastoid crest, not found on StW 573 (Ibid). According to Clarke and Kuman, these discrepancies and others form the basis for their argument to split *A. africanus* into at two (if not three) species (2019:29).

The braincase of StW 573 appears to have vertical sides, but this could also be the result of the distortion. The cranium was scanned by Beaudet *et al.* using microfocus X-ray tomography, whilst the remaining breccia within the right side of the braincase was digitally removed using segmentation via Avizo v9.0 software (Beaudet *et al.* 2019:115). The endocranial brain volume was then digitally calculated as 408 ml, without adjustment/correction for skull distortion and is thus, an estimated minimum volume (Ibid). Beaudet forwarded the .ply file of the virtual endocast to Holloway, which he printed in 3D to then manually correct for the distortion. This is no easy task given that there are no other complete sample crania from the same genre to compare and contrast. Although the unreconstructed endocranial volume is only 408 ml, Holloway believes that after correcting for distortion, the volume would likely range between 450 to 460 ml (personal communication 15-Oct-2020).

Fig 5.35 StW 573 Cranium
Clarke & Kuman 2019:2

Several sulci are visible on the endocast, but some could not be definitively identified, as indicated in Figure 5.36. The lateral sulcus is visible (as is the superior temporal sulcus on the right side, not shown), but most of the sulci are 'remnants' and thus difficult to determine, such as the sulci in the interior frontal lobe, including what appears to be a fronto-occipital sulcus. However, the presence of a fronto-occipital sulcus, indicating a more primitive structure, would not be surprising for a hominin specimen dating to approximately 3.67 mya. Although the sulcus tentatively identified as the lunate sulcus (“L”) is located anteriorly with a crescent shape, Beaudet *et al.* (appropriately) consider this identification speculative as there are no other visible sulci to draw reference from (2019:118), but again, an anteriorly positioned lunate sulcus would be somewhat expected for such an early hominin (see Figure 5.37). The cranium also revealed a prominent left occipital petalia, indicating some level of brain lateralisation and a likely correlation with right handedness (previously discussed). This is a somewhat surprising example of lateralisation in such an early stage of hominin cognitive development and provides another baseline for the later hominin endocasts.

- fs – superior frontal
- fm – middle frontal
- fi – inferior frontal
- fo – orbital frontal
- r – rectus (divides the two hemispheres)
- pci – inferior precentral sulcus
- r – horizontal ramus of the pci
- c – central sulcus
- pti – inferior postcentral sulcus
- tm – middle temporal sulcus
- S – lateral (Sylvian) sulcus
- L – lunate sulcus

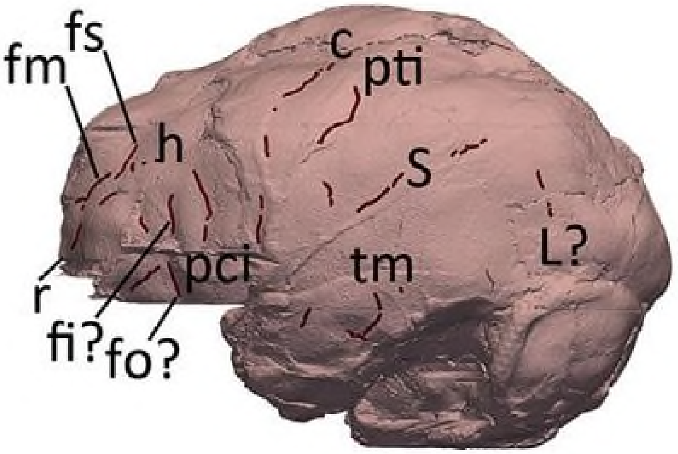

Fig. 5.36 StW 573 Endocast
Left lateral view
Beaudet et al. 2019:117

Fig. 5.37 StW 573 Endocast
Dorsal view
Beaudet et al. 2019:117
Modified by Suzi Wilson

StW 578

In August of 1995, a partial cranium was found *in situ* within the orange sediments composed of partially calcified breccia from the roof in the eastern section of the Jacovec Cavern (see Figure 5.31) (Partridge *et al.* 2003; Beaudet *et al.* 2018). Partridge *et al.* determined a date of 4.02 ± 0.27 mya for the orange breccia (and the cranium) of the Jacovec Cavern using cosmogenic ^{26}Al/^{10}Be burial dating methods, but also noted that the stratigraphically lower brown sediment found on the floor has a slightly younger burial age (2003). However, in a subsequent conversation between Beaudet and Granger, Granger cautioned Beaudet that he had reassessed this date in 2017 and as a result, he now suggests a more prudent date of 3.4 mya, which represents an "acceptable average" between the orange breccia and brown sediments (Beaudet *et al.* 2018:205).

Much of the cranial vault is preserved as well as portions of the occipitals, parietals and other small sections, but the braincase is very fragmentary (Partridge *et al.* 2003; Beaudet *et al.* 2018). Using microtomography, Beaudet *et al.* examined the specimen to measure cranial thickness as well as to possibly assess taxonomic affinity (Beaudet *et al.* 2018). Although most of the cranial vault is intact, the examination revealed no visible sulci or other landmark morphology that could help with determining the taxonomy. However, it did reveal that the frontal and posterior-superior regions of the parietal

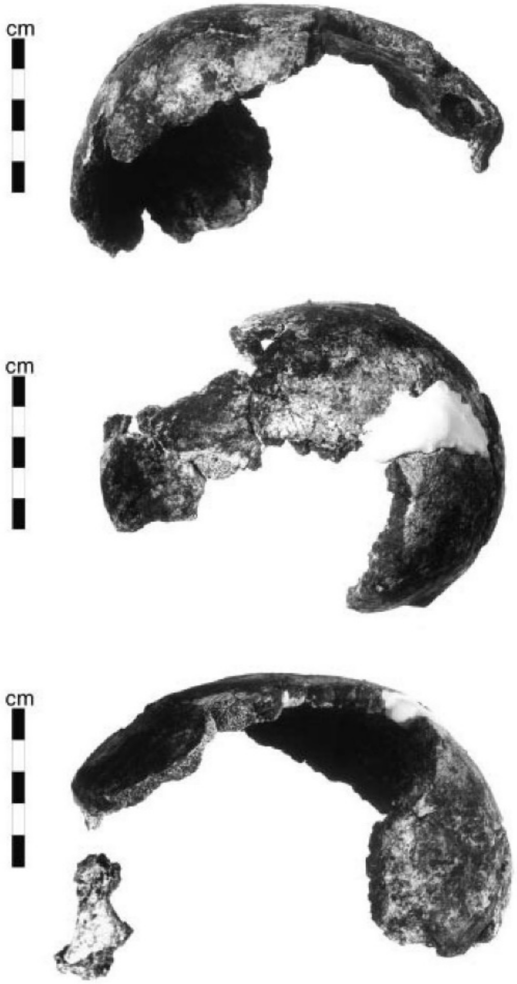

Fig. 5.38 StW 578
Calotte and facial fragment
Partridge et al. 2003:609

bone appeared to be disproportionately thicker than the comparative sample of the other Sterkfontein hominins, which is somewhat similar to the condition found in modern humans (Ibid:214). Although specimen StW 578 does not offer much in terms of cognitive evidence, the study performed by Beaudet *et al.* regarding cranial thickness is highly relative for comparative reasons, which again, provides a baseline for future research.

***Australopithecus africanus* (3.5/3.0 to <2.0 mya)**

As a result of the issues with precise dating, the range for *A. africanus* tends to be stated with caution, typically estimating the start of their time line to roughly 3.5 million years ago and extending to approximately 2.0 mya, although Stanford *et al.* believe it is possible that some of the more recent *A. africanus* fossils recovered may be much younger, dating to slightly older than 1.0 myo (2017:318). Prior to the discoveries of StW 573 and StW 578, no older hominins had been discovered in South Africa, and it is generally assumed that they likely evolved from one of the East African populations, such as *A. anamensis* or *A. afarensis* (Ibid:320).

A. africanus was small-bodied, similar to *A. afarensis,* but with less variation in terms of size for both males and females. According to McHenry, the males are estimated to have weighed between 41 and 53 kg whilst the females ranged in size between 30 to 37 kg (1992). Stanford *et al.* suggests an even smaller body type with most averages falling between a range of 29.5 kg to 41 kg for both sexes (2017). However, sexual dimorphism was clearly present in *A. africanus* at an estimated ratio between 1.35 and 1.43, less than the average ratio for *A. afarensis* estimated at 1.52 (McHenry 1992:422). Stature for *A. africanus* is estimated between 105 cm and 142 cm, which is a bit shorter than *A. afarensis* at 105 cm to 151 cm (Ward 2015).

The Crania of *Australopithecus africanus*

Whilst their postcranial morphology was very similar to *A. afarensis* in most respects, there were considerable differences in the dentition and crania of *A. africanus* (Rak 1983; McHenry 1986; Kimbel *et al.* 2004). In general, the *A. africanus* cranium is more derived than *A. afarensis* or extant apes with a more rounded (albeit low) vault with no cranial crests. The upper portion of the face is slightly less prognathic; however, the maxilla (upper jaw) exhibited 'alveolar prognathism' meaning that the alveoli (tooth sockets) protrude outward in front of the braincase (Rak 1983; Cartmill and Smith 2009). Apes also show pronounced alveolar prognathism, but in *A. africanus*, the zygomatics (cheekbones) are shifted forward relative to the jaw joint, which allows the muscles of mastication to exert stronger chewing forces through the cheek teeth (Rak 1983; Cartmill and Smith 2009). The zygomatics are anteriorly sloping with great lateral flaring, and the zygomatic process widens considerably as it approaches the zygomatic bone and attaches to the lateral flaring (Rak 1983).

Perhaps the most interesting feature of the *A. africanus* face is the presence of two pronounced 'anterior pillars' of bone flanking both sides of the nasal aperture, in line with the canine teeth, which present an unusual structure not found in extant apes or modern humans (Rak 1983). Initially, they were believed to only be present in *A. africanus,* but a later study by McKee determined that these anterior pillars, which were highly variable among the *A. africanus* specimens, are also present in some of the *Paranthropus* (robust) species, and likely served as part of a 'buttress' system to support the anterior dentition, such as the lateral incisors and first premolars (McKee 1989). As a result, the anterior pillars are not considered a defining feature of *A. africanus* (i.e., an apomorphy), yet nevertheless present an important feature to note, as changes in the morphology of cranio-dentition and masticatory systems often signal adaptations in behaviour and diet. Their dentition was more derived as the anterior teeth of *A. africanus* had become smaller, compared to *A. afarensis* and extant apes, especially the canines, whilst the molars and premolars had increased in size. There is no longer a CP_3 honing complex and accordingly, no diastema, and there are no cranial crests supporting the muscles of mastication.

Another important aspect is that the cranial base appears more flexed compared to *A. afarensis* or extant apes. The anterior and middle depressions (or 'fossae') of the cranial base act somewhat as an interface between the braincase and face (Neubauer *et al.* 2018), and greater flexure in the cranial base ultimately accommodates brain growth (although in *A. africanus*, the brain was still quite small). The supraorbital torus, which is a prominent bony ridge that protrudes along the 'eyebrow line', is considerably less defined (i.e., less robust) and the nuchal plane was more horizontal (Cartmill and Smith 2009). However, despite these derived features, the crania of *A. africanus* nevertheless remain somewhat 'ape-like' in appearance.

The Endocasts of *Australopithecus africanus*

Most (if not all) of the *A. africanus* crania suffer from damage or distortion to some extent. As a means to obtain more accurate endocranial volumes, Neubauer *et al.* digitally reconstructed several of the *A. africanus* crania to correct for distortion and missing areas. Six crania were digitally scanned and reconstructed applying mirror-imaging (of the 'good' areas) and "semi-landmark-based geometric morphometrics" (2012:499). To test the reliability of their methodology, they likewise conducted parallel computer simulations on the crania samples of extant apes and modern humans. As a result of their study, *A. africanus* average brain volume was updated to reflect a range of between 454 ml to 461 ml with a standard deviation of 66 to 75 ml (Ibid:506), representing a tighter range from previous estimates of 450 to 550 ml (Stanford 2017). Eight individual *A. africanus* crania (or partial crania) and endocasts, including those scanned by Neubauer *et al.*, are discussed in detail herein, presented in chronological order. Volumes for all *A. africanus* endocasts are based on Neubauer *et al.* 2012 except for MLD 1 and Sts 19/58, which are estimates provided by Holloway *et al.* (2004). Ages/dates are from Herries *et al.* (2013) stratigraphic analysis and study, also discussed herein.

Specimen	**Locale**	**MYA**	**Age/Sex**	**Brain Volume**	**Description**
A. Prometheus:					
StW 573	Sterk	3.67	Adult female	450-460 ml (Est)	Nearly complete
StW 578	Sterk	4.02 to 3.4	N/A	N/A	Partial cranium
A. africanus:					
MLD 1	Maka	3.0 to 2.58	Adult male	500-520 ml	Occipital / Parietal
MLD 37/38	Maka	3.0 to 2.58	Adult female	440 ml	Nearly complete
Taung child	Taung	3.0 to 2.58	3 to 4 yrs female	402-407 as child	Partial
Sts 60 (TM 1511)	Sterk	2.4 to 2.0	Adult female	391 ml	Largely complete
Sts 5 Ms. Ples	Sterk	Appx. 2.0	Adult female	475 ml	Mostly complete
Sts 71	Sterk	2.4 to 2.0	Adult female	412 ml	Right side and face, but damaged
Sts 19/58	Sterk	2.4 to 2.0	Adult	436 ml	Partial cranium

StW 505	Sterk	2.4 to 2.0	Adult	533 ml	Left side, but damaged

Makapansgat Limeworks

The Makapansgat Limeworks site is located about 12 miles east-northeast of Mokopane in the Makapansgat Valley and is known for an abundance of fossil remains, including numerous *Australopithecus africanus*[1] specimens (Crawford *et al.* 2004). In 1947, James Kitching recovered the occipital region of an australopith cranium from the Western Repository debris dumps at Makapansgat, prompting Dart to send a team of students to sort through the dumps for blocks of bone-breccia to be organized according to colour/texture, as a means to match them with the strata within the cave (Crawford *et al.* 2004; Kuykendall and Štrkalj 2007; Latham *et al.* 2007). For example, the deepest stratum (Member 5) is characterized by somewhat rounded cobbles in a dark pink matrix with lenticular gravels (Latham *et al.* 2007). In the early 2000s, a number of sequencing studies were performed, primarily biostratigraphic, and magnetostratigraphic, combined with U-Pb and stable carbon isotope analyses on faunal remains (Crawford *et al.* 2004). Accordingly, a stratigraphic succession and timeline of the fossil-bearing members on the western side of the site was approximated.

This approach indicated that most of the hominin fossils came from Member 3, which is also known as the Grey Breccia, although a few have come from Member 4, characterized by mid-to-dark pink and dolomite (Crawford *et al.* 2004; Latham *et al.* 2007). The hominin cranium MLD 37/38 was one of the rare specimens recovered somewhat *in situ* from a breccia block in 1958 (Dart 1959; Kydkendall 2007; Crawford *et al.* 2004:47). In 2013, Herries *et al.* recommended a range of dates between 3.0 and 2.58 for the Makapansgat deposits containing the *A. africanus* fossils,

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[1] *Includes the first fossils named A. prometheus by Dart or Plesianthropus by Broom.*

based on these previous studies as well as biostratigraphic and revised magnetostratigraphic analyses (2013:32).

MLD 1

In 1947, a partial cranium with the occipital and most of the parietal bones was recovered from a Makapansgat Limeworks dump box, which Bone and Dart had as an adult male (1955), although Conroy *et al.* suggest that the specimen probably belonged to a sub-adult male (1990).

Fig. 5.39 MLD 1 Cranium, occipital view
Courtesy of John Hawks web blog (2015)

The endocast does not reveal any sulcal markings, but there appears to be a very slight right occipital petalia, and some elements of the sagittal sinus drainage system are visible. The left transverse sinus seems to be more robust on the left side than the right, and near the right cerebellar lobe is a small protrusion, which could possibly be an enlarged marginal-occipital sinus, but Holloway advises that the protrusion could also be the result of cranial damage versus a true sinus (Holloway *et al.* 2004). In my opinion, this protrusion is likely damage considering that no other *A. africanus* endocast, except possibly for Taung (which remains questionable), displays an enlarged marginal-occipital sinus. Accordingly, this indicates that by the time of *A. africanus*, the cranial venous drainage network had better adjusted to the gravitational effects of bipedalism, now likely draining from the sagittal sinus to the left and right transverse sinuses (as it does in modern humans), thus gradually eliminating the need for a large marginal-occipital sinus, as previously explained. The endocranial value is large, estimated at 500 to 520 ml by Holloway *et al.* using the partial endocast method (Ibid).

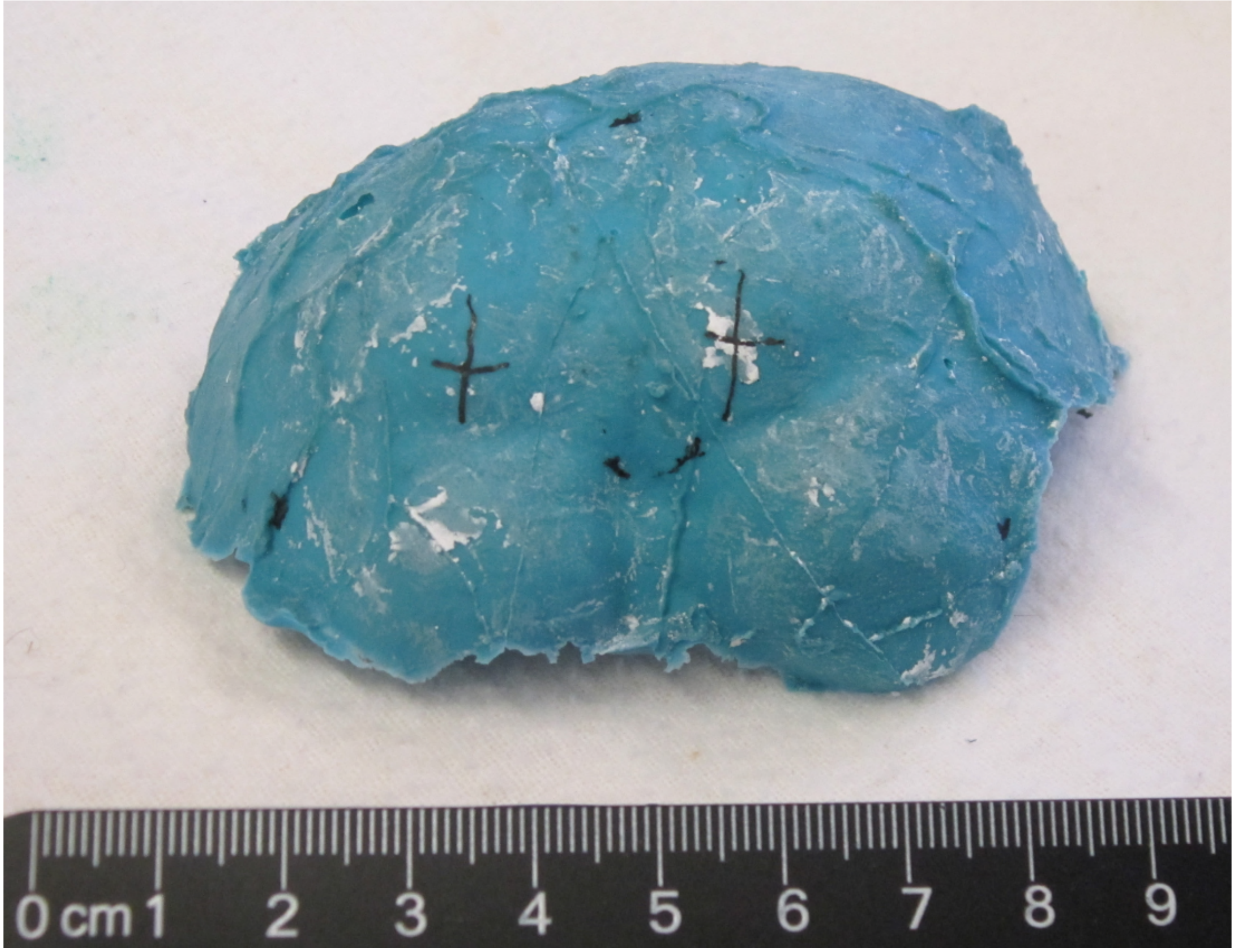

Fig. 5.40 MLD 1 Endocast, occipital view
Photo by Suzi Wilson

MLD 37/38

In 1958, Kitching recovered another *A. africanus* cranium, this time from the pink breccia dump that lay between the two main quarry mouths (Dart 1959). The pink colour indicates that it originated in the layer where the red silts from Member 2 are interspersed with the grey dolomite of Member 3 (Crawford 2004). The skull had been split laterally (catalogued as MLD37 and MLD 38), but both sides were found and re-articulated to form a nearly complete braincase, missing only the face and most of the area anterior to the coronal suture (which contains the frontal lobes).

According to Dart, the fused sphen-occipital suture had closed, thus indicating that the individual was at least 25 years of age, and possibly older based on the wear

Fig. 5.41 MLD 37/38 Cranium
Photo by Suzi Wilson

of the third molars (Dart 1962). The cranium was filled with stone matrix, forming a natural endocast that would be impossible to remove without damage. Prior to the technological advances in CT technology, endocranial volume had been estimated by Conroy *et al.* at 425 ml in 1990, based on the 2-D and 3-D CT imagery that was available at the time (1990:839), whilst Holloway *et al.* calculated a volume of 435 ml based on cranial measurements and regression analysis (2004:63).

In 2004, Neubauer *et al.* created a digital endocast of MLD 37/28 by first making a CT scan of the cranium using an Mx8000 scanner at the Sunninghill Hospital in Johannesburg, which produced high resolution images with a slice thickness of 1.3 mm. The stone matrix inside the crania was then digitally removed via segmentation, and the missing cranial areas were reconstructed using cranial morphological data from another female *A. africanus* specimen (Sts 5, also scanned at a local hospital) with eight anatomical landmarks as well as 455 semi-landmarks to serve as control points (see Figure 5.42). Neubauer *et al.* then applied a thin-plate spline[1] warping program to interpolate a smooth surface connecting the landmarked data points, which calculated an endocranial volume estimate of 440 ml for the entire braincase (sans meningeal vessels), very close to the Holloway *et al.* estimate of 435 ml (Neubauer *et al.* 2004:274).

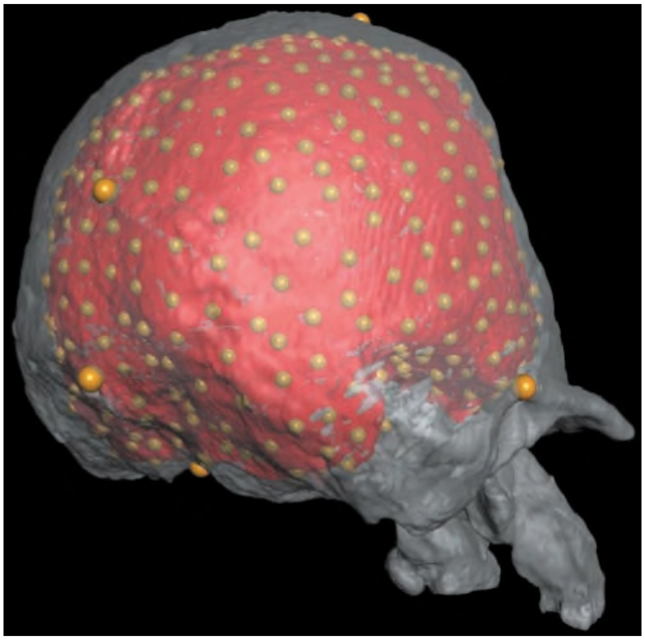

Fig. 5.42 MLD 37/38 virtual endocast
Digital reconstruction of missing area
Neubauer et al. 2004:274

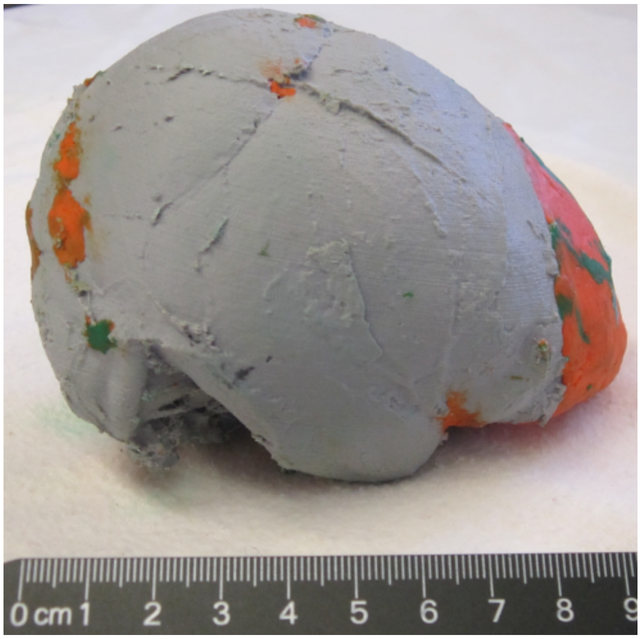

Fig. 5.43 MLD 37/38 endocast mould
Orange section designates missing area
Photo by Suzi Wilson

Although Neubauer *et al.* were able to digitally remove the stone matrix to calculate the endocranial volume, only a few impressions of the endocast were visible following segmentation, including the sagittal and lambdoid sutures, but no sulci or gyri. However, the cranial venous drainage system was recovered, which did not indicate an enlarged occipital-marginal sinus (Neubauer *et al.* 2004), thus again evincing the cranial blood flow adjustment to bipedalism.

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[1] *The term "thin-plate spline" likely derives from the industrial bending of a thin sheet of metal.*

Taung

The skull of the small juvenile discovered in 1924 (previously mentioned) was filled with stone matrix, creating a natural brain endocast. Dart had estimated the child's age at death as approximately six years based on modern human dental development, which he had incorrectly presumed to be similar (1925). Later studies by Bromage revealed that the development pattern of *early* hominin dentition was likely more similar to extant living apes than modern humans (1987:271). The eruption of the first molars had occurred but not moved into functional occlusion

Fig. 5.44 Taung child
Photo by Suzi Wilson

(Mann 1975; Bromage 1987;McCarthy and Zimel 2020). Accordingly, Taung's age at his time of death was revised to between 3.3 and 3.9 years of age (Bromage1987:265; McCarthy and Zimel 2020:3). The skull was encased in limestone, which Dart removed using his wife's knitting needles (Holloway 2014:13023; Falk 2019:41, likely causing additional damage to the cranium in the process. The majority of the right side is intact, except for a very small portion of the frontal lobe, and there is also a portion of the left side intact. In the late 1960s, Holloway made a mould of the natural endocast to create a 'hemi' plaster cast of only the right hemisphere as a means to measure volume. His measurements yielded a brain volume of between

Fig 5.45 Taung child natural endocast exposed
Photo by Suzi Wilson

202 and 205 ml, which thus results in a total endocranial estimate of between 404 and 410 ml (Holloway *et al.* 2004:96). As an adult, Holloway believed that the brain would grow to approximately 440 ml, which was considerably less than Dart's original estimate of 520 ml (Ibid). The study by Neubauer *et al.* produced a similar endocranial estimate for the child between 402 ml to 407 ml (2012:507), although Neubauer *et al.* assumed that Taung had already reached between 96% to 100% of its adult brain size (Ibid:508), which is an interesting assumption considering that the child was no more than 3.9 years old. McCarthy and Zimel, on the other hand, estimated a range between 404 ml (child endocranial volume with no increase) and 430 ml as an adult (2020:5), and they further suggest that Taung was female, considering how the endocranial volume was at the lower end of *A. africanus* variation (2020).

It was Dart who first observed a sulcus he identified as the lunate sulcus on the occipital lobe of the Taung natural endocast, which he believed had derived into a more posterior, 'human-like' position (1925). This observation was first brought into question by Sir Arthur Keith (1931), with LeGros Clark also casting doubt on Dart's identification of the lunate sulcus which he initially believed to be an imprint of the lambdoid suture, as often seen on the brains of chimpanzees (Clark 1936), but later argued that it simply could not be determined (Clark 1947). Broom and Schepers supported Dart's observations in their 1946 book, but the debate over the occipital position of the Taung lunate sulcus, including whether or not it was visible at all, particularly escalated during the 1980s between Falk (1980, 1983, 1985b, 1989) and Holloway (1975, 1981, 1984, 1985, 1988). Falk took the position that the lunate sulcus was located in a more anterior position, similar to modern apes (see the white slash mark in Figure 5.6), whilst Holloway argued that although he could not positively identify a lunate sulcus on the Taung endocast – it could not be in the position asserted by Falk due to other sulcal morphology (e.g., distance from the occipital pole, etc). Like Clark, Tobias shared the view that the position of the lunate sulcus in Taung could not be determined (Tobias 1991).

One of the problems with interpreting any potential landmarks on the Taung natural endocast is that although it appears to contain several convolutional details, it is damaged from both the initial mining blast as well as Dart's extrication from the limestone via knitting needles. More problematic is that it also contains many calcite crystal deposits on its surface, that partially obscure the morphological features which might otherwise be detected. As a result of these contributing factors, it is very difficult to identify and differentiate among what appears to be a landmark or semi-landmark on Taung as well as the relative positions of these sulci to one another, including what might (or might not) be an imprint of the lambdoid suture, which is also very difficult to locate/identify with any degree of confidence. Falk acknowledges that the quality of the occipital portion of the natural endocast is poor and damaged in several areas (Falk 1980), yet she has remained adamant that evidence of brain reorganisation was not present in Taung.

Holloway has five endocasts of the Taung child in his lab made from different materials and in different colours as a means to hopefully better discern sulcal landmarks, which unfortunately were not as useful as I had hoped. I examined each of them, and the most pertinent observation I made was that it was highly unlikely for anyone to be absolutely certain of which feature might be the lambdoid suture, although I am slightly leaning toward Clark's interpretation of the feature on the 'hemi' endocast of Taung (directly posterior to the white dotted line in Figure 5.46). Yet, this feature does not seem to have the appearance of a suture but rather a sulcus, so I remain in doubt with respect to the proper location of the lambdoid suture, if an imprint is even present. Most likely, the debate over the Taung lunate sulcus will remain unsettled unless and until a high-resolution CT scan is conducted which reveals additional information. However, it does seem possible that *some* expansion of the parietal lobes may have occurred in Taung, perhaps resulting in the more globular shape of the *A. africanus* cranium.

I also observed the sigmoid sinus on the right side of the endocast but did not notice an enlarged marginal sinus. Kimbel had made note of the absence of an enlarged marginal sinus on Taung in his 1984 paper on cranial venous system patterns in early hominins (1984:252). Tobias and Falk, on the other hand, disagree with Kimbel and argue that there is an enlarged right marginal sinus near the very end of the sigmoid sinus impression (Tobias and Falk 1988). Without a high-resolution scan, I question how well one can differentiate between a tiny semi-landmark feature and an impression resulting from damage or calcite deposits. Additionally, none of the other *A. africanus* crania/endocasts show any evidence of an enlarged marginal sinus, which Tobias and Falk acknowledge (1988).

Fig. 5.46 Occipital (posterior) view of the Taung Child right hemi-endocast
The anteriorly placed white slash mark is Falk's identification of the Lunate sulcus
The dotted white line is Holloway's approximation for where the Lunate sulcus is found in apes
Photo by Suzi Wilson

Furthermore, in vivo studies have demonstrated that the transverse sinus in modern human embryos initially arises as a *secondary* channel during development then moves into a more caudal 'adult' position during the third month of foetal development (Kimbel 1984:244), and Aurboonyawat *et al.* stress that morphological changes in the venous sinus system continue to develop in modern human neonates after delivery (2007:341). Although the venous sinus system in modern human children matures by three years of age (the estimated age of the Taung child), it seems likely that the venous sinus drainage pattern would be influenced by the age at which quadruped 'crawlers' became fully bipedal toddlers. Therefore, it is also possible that Tobias and Falk may be correct in their identification of the feature in question as an enlarged marginal sinus, but one which would have ultimately given way to the transverse sinuses after its full development was prompted by habitual upright posture.

Sts 60 (TM 1511)

The specimen, now catalogued as Sts 60, is two-thirds of a natural brain endocast of the first adult South African australopithecine discovered, handed to Broom by the mining supervisor (Barlow) of the Sterkfontein Caves in 1936 (Broom 1936a). It is one of five natural endocasts discovered in South Africa, which Broom initially named *Australopithecus transvaalensis* because he believed it represented a different species from the Taung Child (Broom 1938). Over the following three years, he and his assistant Robinson recovered

Fig. 5.47 TM 1511 and natural endocast (Sts 60)
Photo by Jason Heaton in Heaton et al. 2016
Scientific American Online
Modifications by Suzi Wilson

many more fossils from the Sterkfontein Caves, and Broom decided that these specimens not only deserved their own species but also their own genus (Broom 1938). Accordingly, he renamed them Plesianthropus[1] transvaalensis. However, by the mid-1960s, Robinson[2] consolidated them into the species africanus, with Homo as the genus, then ultimately back to Dart's original genus/species name of *Australopithecus africanus* (Tobias 1967; Crawford 2004).

The specimen had been blasted out of one of the caves in Member 4, just a few days prior to Broom's arrival (Broom 1936a; Beaudet *et al.* 2018; Partridge 1978). After an extensive search, parts of the badly damaged cranium were found, such as the top of the head (embedded in the cave wall), most of the skull base, the upper part of the face and the right maxilla still containing three teeth, as well as a detached third upper molar (Broom 1936b). During the latter excavations led by Tobias and Hughes in the 1960s, additional teeth of TM 1511were found in Dump Box #18 (Stratford 2018). The initial blast had destroyed a good portion of the cranial vault, but a large part of each parietal was preserved as well as a portion of the occipital bone.

The natural hemi-endocast constitutes approximately two-thirds of the anterior portion of the brain, missing the occipital pole, the posterior cerebellar lobe, and parts of the temporal pole on its left side. Additionally, parts of the frontal pole region are missing. The dorsal surface appears to offer impressions of the coronal and sagittal sutures. On the right side, only small regions are preserved, including most of the frontal lobe and medial portions of the parietal lobe.

Holloway *et al.* made an endocast, which reconstructed the missing parts and estimated a brain volume of 400 ml using water displacement (2004:73), whilst Neubauer *et al.* created a digital endocast with an estimated average volume of 391

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[1] *Plesianthropus is Greek for "close to human" (Cartmill and Smith 2009:132).*
[2] *Robinson was clearly a 'lumper*

ml, with a range of between 384 to 398 ml (2012:501). Neubauer *et al.* applied the digital processes previously discussed using Avizio 9.0 software to replace its missing parts, also using existing portions of the natural endocast as well as input from 60 extant chimpanzee brains and *A. africanus* endocast Sts 5, which is of similar size (2012:507).

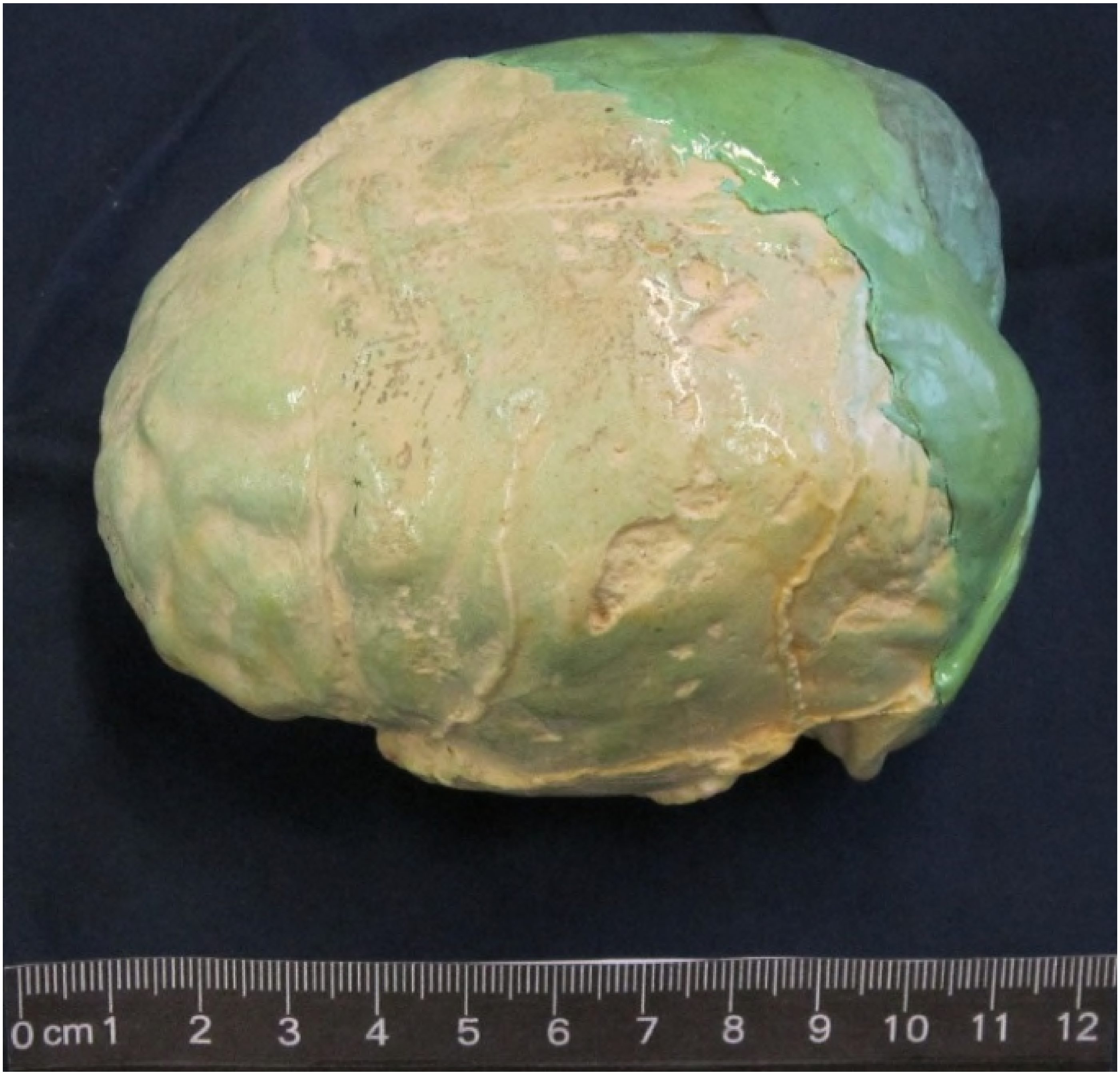

Fig. 5.48 Sts 60 Reconstructed endocast
Photo by Suzi Wilson

Although it is not particularly visible on the lateral view of the endocast mould in Holloway's lab, Hurst argues that a fronto-orbital (fo) sulcus is evident on a digital endocast he obtained, courtesy of the Transvaal Museum in Pretoria (Hurst 2017: 114,121). The endocast in Figure 5.49 is a basal view, from the bottom looking upward. As previously mentioned, the presence of the fronto-orbital (fo) sulcus indicates a more primitive structure.

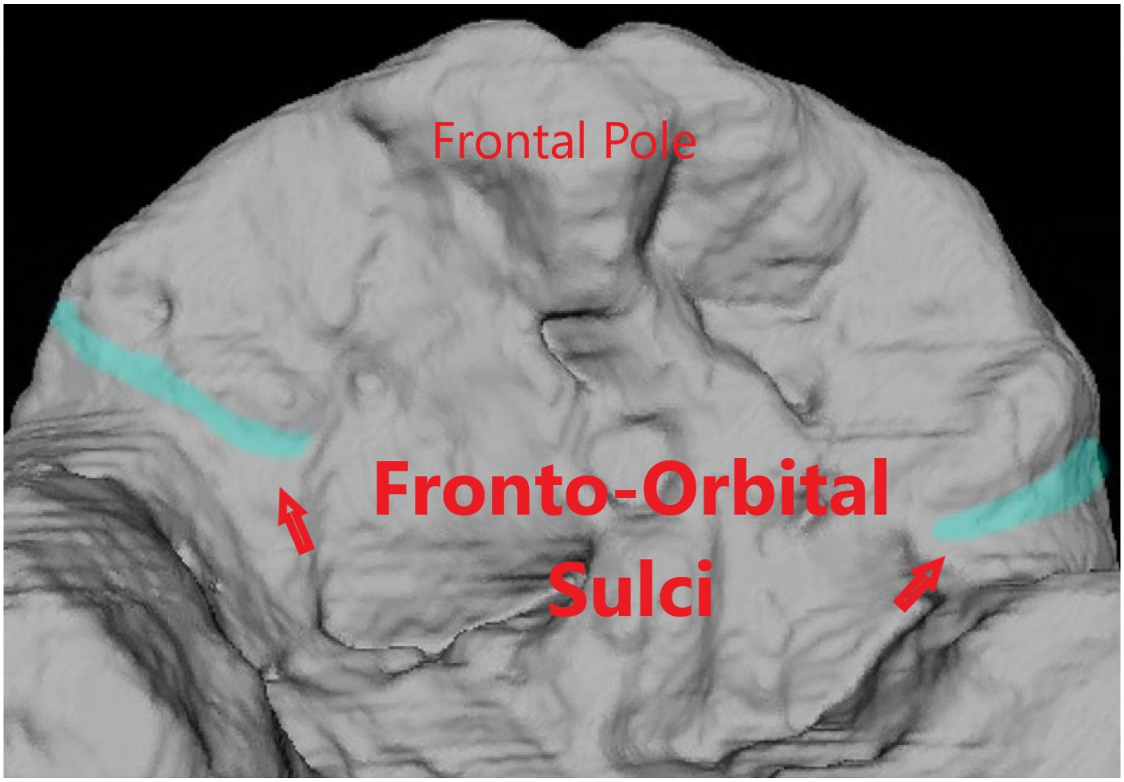

Fig. 5.49 Sts 60 fronto-orbital sulcus, indicating a more primitive condition
Blue modifications by Hurst 2017:121
Red modifications by Suzi Wilson

Sts 5 (Ms. Ples)

On April 18th of 1947, a block of breccia was blasted open in Member 4 of Sterkfontein to reveal a nearly complete cranium (Broom 1947; Broom *et al.* 1950; Beaudet *et al.* 2018). The blast had split the skull horizontally around the widest part of the brain case, and the cavity of each half was lined with between 1/16th and 3/8th inch of crystalline limestone deposit (Broom 1950:12). It was missing the mandible as well as the maxillary teeth, but the alveoli remained intact. Because the sockets were small in size (and a few other factors), Broom and Robinson believed the skull belonged to an elderly[1] female (Broom 1947). Broom catalogued the cranium as *Plesianthropus transvaalensis* #5 (later reclassified as *A. africanus* Sts 5), giving rise to her nickname 'Mrs. Ples'. However, Broom's age/sex assessment of Sts 5 as an older female has been challenged by Thackeray *et al.* who argued that Sts 5 was an adolescent male, based primarily on facial morphology (2002).

Fig. 5.50 Sts 5 cranium
Grine et al. 2012:594

The proper age/sex identification of the Sterkfontein fossils is important for evaluating the taxonomic significance of the variable craniodental features found in *A. africanus* (Kimbel and White 1988; Lockwood and Tobias 2002; Grine *et al.* 2012). However, it is not quite so crucial for the aims of this thesis. Nevertheless, it should be noted that the more recent literature on this debate reflects that there is insufficient evidence to contradict Broom's initial identification of Sts 5 as an older female, due to the prevailing evidence of suture closures with respect to age (Grine *et al.* 2012; Villmoare *et al.* 2013). The suture closures indicate that Sts 5 could not have been an adolescent, and if the specimen does not represent an adolescent - then the small alveoli indicate it is most likely a female.

The natural endocast consists largely of a travertine mixture, which was moulded by the inside of the skull. Schepers described the endocast as "elongated[2] and narrow towards the posterior half, but well-formed anteriorly" with a prominent

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[1] *Broom does not provide an age, but 'elderly' in the Palaeolithic might refer to someone in their 40s.*
[2] *Indeed, Broom described the cranium as "extremely dolichocephalic" (1947:672).*

rostral projection (Schepers 1950:100). He acknowledged that "the convolutional markings are inadequately preserved" (1950:101), but then described the "prominent sulci" in detail (Ibid) which, in my opinion, could not be seen on the endocast made by Holloway. Falk, however, offers a possible explanation for what seems to be likely exaggerations by Schepers. According to Falk, Schepers employed several different methods for identifying sulci on endocasts, such as rubbing soot on the endocasts or using a pencil to shade the grooves and depressions, which may have resulted in sutures and meningeal vessels being mistaken for sulci (1980). The endocast made by Holloway in Figure 5.51 produced a large endocranial volume of 480 ml using water displacement (Holloway *et al.* 2004:72), whilst a digital endocast

Fig. 5.51 Sts 5 Endocast mould, left lateral view
Photo by Suzi Wilson

created by Neubauer *et al.* likewise revealed a large volume of 475 ml, slightly less than Holloway's endocast (2012:506). The surface area of the endocast mould is poor, making it difficult to identify even the sinuses or meningeal vessels, much less convolutional details. Indeed, Holloway *et al.* referred to Sts 5 as "one of the ugliest brain endocasts we have seen" (2004:72).

Sts 5 nevertheless yields a few noteworthy observations. The area in the Broca's cap region, just anterior to Broca's Area, is distinctly larger on the right side than the left. There is also a left occipital/right frontal petalia, indicating some degree of brain lateralisation and likely right-handedness. However, other than its large size and indications of brain lateralisation, the Sts 5 endocast mould does not provide very much in terms of convolutional details. Regardless, the cranium is mostly complete with very little distortion, making it useful to compensate for missing parts among the other Sterkfontein specimens.

Sts 71

The cranium was recovered from Member 4 on November 13, 1947, and catalogued as *Plesianthropus transvaalensis* Skull #7 by Broom (Broom et al. 1950; Partridge 1978; Thackeray and Gommery 2002). According to Broom *et al*., more than half of the face was preserved, along with almost the entire right side of the braincase (1950). However, the lower parietal/upper temporal portion was subject to crushing and distortion, and the occipital bone is considerably deformed. Endocranial volume, as corrected for distortion, was estimated at 428 ml by Holloway *et al.* using traditional methods at the time (2004:73). Sts 71 was one of the six crania re-measured by Neubauer *et al.,* digitally, which produced an endocranial volume of 412 ml (2012:507). However, Neubauer *et al.* note that this estimate might be slightly too low if the cranium had been subject to anterior-posterior compression

(Ibid), which is quite possible considering the length of the Sts 71 cranium compared to the elongated cranium of the Sts 5 specimen from the same period and Member.

Fig. 5.52 Sts 71 cranium
Photo by Suzi Wilson

Schepers describes the natural endocast as “magnificently preserved in the frontal lobe” and he further notes that it is a “pity that crushing and distortion of the skull opposite the parietal and upper temporal regions should have interfered with identification of the sulci and gyri [in this region]” (1950:101). Neither Holloway nor I can discern these “magnificently preserved” sulci described by Schepers, and it seems likely that Falk was correct regarding how Schepers methods may have deceived him. There is, however, a distinct segment of the inferior frontal sulcus (which offers little information), and the anterior portion of the middle temporal sulcus can also be identified. A large portion of the posterior sinus drainage system is also visible.

Fig. 5.53 Sts 71 Endocast mould, right lateral view
Photo by Suzi Wilson

Sts 17, Sts 19/58, Sts 20

These specimens represent partial crania or cranial fragments which were recovered during the latter part of 1947 and identified by Broom as Skulls VI, VIII, and IX, respectively (Thackeray and Gommery 2002; Grine *et al.* 2012). However, they provide little information that would contribute to the aims of this thesis. They should, nevertheless, be mentioned, and a few factors noted. For example, the pieces appear to be undistorted, and the left temporal lobe piece of Sts 19/58 displays both the middle and inferior temporal sulci as well as the sigmoid and transverse sinuses. Using traditional methods, Holloway *et al.* estimated an endocranial volume of 436 ml (2004:73) for Sts 19/58.

StW 505 2.4 to 2.0 mya

In early 1989, a very large cranium was found *in situ* from Grid Square H/42 in the Member 4 formation (Lockwood and Tobias 1999). Although specimen StW 505 was recovered in two parts (identified as 505a and 505b, respectively), their association was based on similar size, preservation and morphology (Ibid). Much of the skull has been preserved, but there is also severe distortion, deformation, and damage to various areas - especially on the right side, which is largely missing, as well as the neurocranium.

Fig. 5.54 StW 505 Cranium
Photo by Suzi Wilson

There are several defining traits that identify StW 505 as an *A. africanus* – primarily the morphology of the infraorbital region, which includes the distinctive anterior pillar of *A. africanus*, previously discussed. The position and shape of the zygomatic process is also characteristic of *A. africanus*, and Lockwood and Tobias observe that "when the total evidence is considered, StW 505 presents a combination of features found only in *A. africanus*" (1999:657). The endocast consists primarily of the left side, which is mostly complete but missing the cerebellum as well as the occipital region directly above the cerebellum, including the occipital pole. There is also a small portion of the right prefrontal lobe and a bit of the medial temporal lobe.

Holloway has made several endocasts of StW 505, each of which I examined in his lab. The braincase is quite large, which Holloway estimated at roughly between 550 to 560 ml, based solely on visual examination with estimates to account for the damage and distortion (2004:74). In 2012, Neubauer *et al.* produced an endocranial volume with a likely average of 533 ml (530 – 538) after creating a virtual endocast and performing digital reconstruction (2012:507). It is unfortunate that so much of the cranium has been damaged/distorted because specimen StW 505 presents what appears to be a definitive crescent-shaped sulcus having the shape and appearance of a lunate sulcus, located just superior to what appears to be the left transverse sinus (see the red crescent in Figure 5.55). Although the lunate sulcus does not typically resemble other sulci, the shape and even direction of the occipital sulci can be highly variable. As a result, Falk believes that the sulcus in question is the lateral calcarine sulcus.

As mentioned, the lateral calcarine sulcus in chimpanzees appears in a pronounced 'y' shape, whilst in modern humans, it is only visible in roughly 69% to 70% of the population and when present, only as a small "fish-tail" sulcus near the occipital pole (Iaria *et al*. 2008; Ribas 2010; El Mohamad *et al.* 2019), but the occipital pole is missing on specimen StW 505.

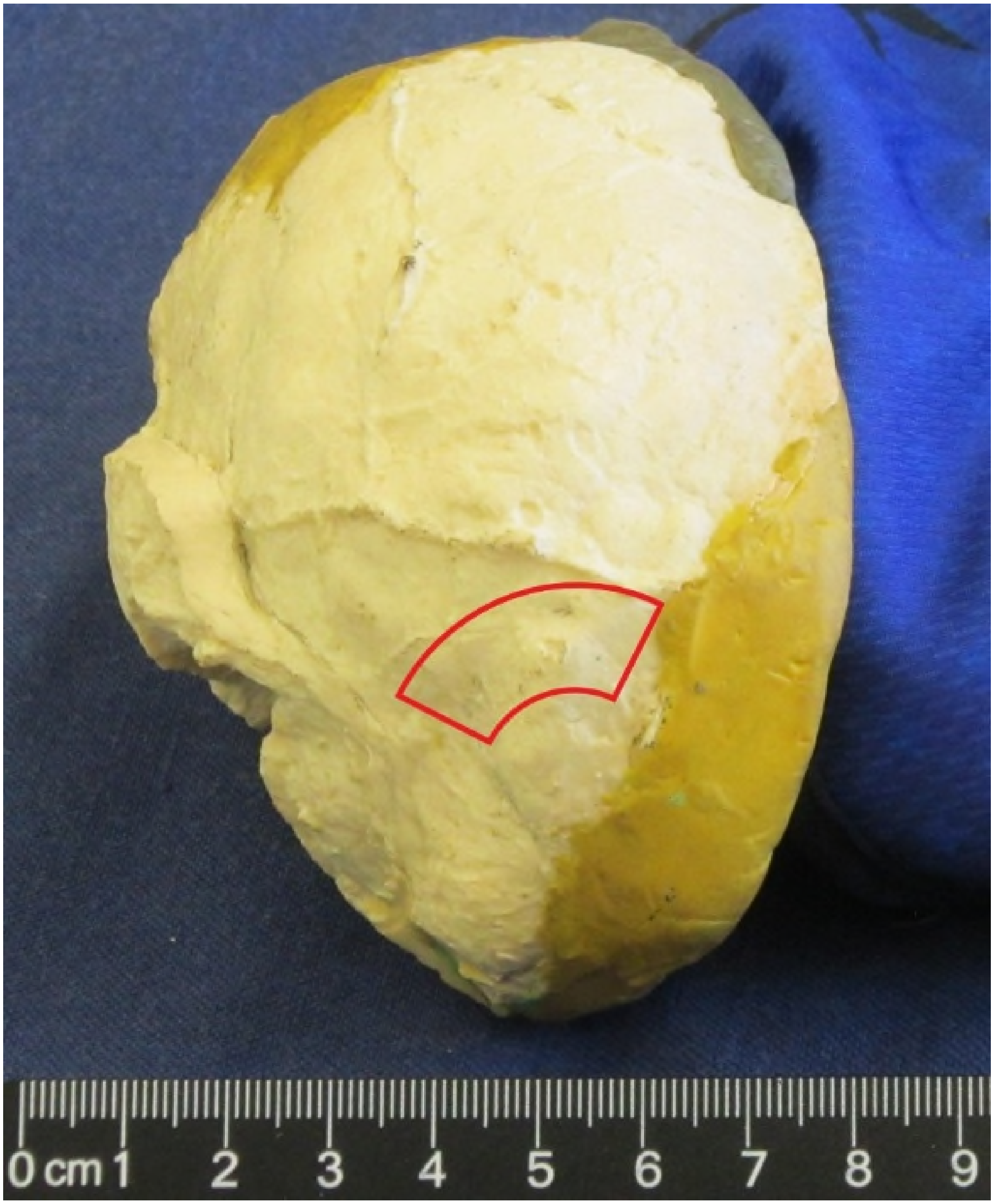
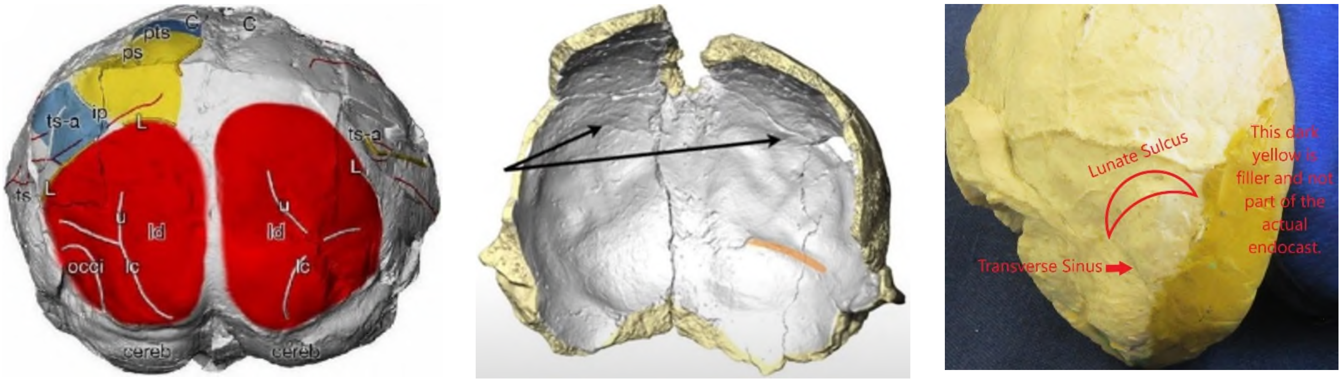


Fig. 5.55 StW 505 endocast, posterior view
Photo by Suzi Wilson

The sulcus highlighted in orange on the 162-28 endocast in Figure 5.56 (initially believed by Falk to represent a lunate sulcus) was identified by Gunz *et al.* as the lateral calcarine sulcus (previously discussed). Compared to the lunate sulci in the digital endocasts of *A. afarensis* DIK-1-1 and AL 162-28, the crescent-shaped sulcus in StW 505 is smaller and positioned significantly more posteriorly than the lunate sulci in DIK-1-1 or AL 162-28, and it does somewhat resemble the sulcus argued by Gunz *et al.* to be the lateral calcarine sulcus on the AL 162-28 endocast. Accordingly, the more advanced cyto-architecture of a posteriorly placed *lunate sulcus* in StW 505 would have only had a maximum period of roughly 1.2 million years to derive to this posterior position, which may not be feasible for such a measure of a neurological change. At present, there is no high resolution digitally reconstructed virtual endocast of the StW 505 specimen that would highlight the occipital sulci and potentially provide more conclusive evidence.



DIK-1-1 Colour-coded endocast
DIK-1-1 digital endocast
Gunz et al. 2020:4

AL 162-28 endocast from Gunz et al. 2020 AAPA Presentation
www.youtube.com/watch?v=FAIoK4mtkzM

StW 505 endocast magnified
Possible lunate sulcus?
Photo by Suzi Wilson

Fig. 5.56 Comparison of DIK-1-1, AL 162-28 and StW 505 occipital regions from endocasts

A. africanus **Phylogeny**

The South African mining industry that began in the early 1900s not only produced numerous fossils, it also launched the search for early hominins throughout the region. Although the early specimens found prior to 1966 could only be recovered from the dump boxes, the excavations that began in 1966 by Tobias and Hughes produced many *in situ* finds, including the nearly complete skeleton and cranium of the oldest Australopith in South Africa – specimen StW 573 (aka 'Little Foot'), dated to approximately 3.67 mya. In 1981, T. White *et al.* published an analysis regarding the position of *A. africanus* in hominin phylogeny. The various traits of modern chimpanzees, *A. afarensis*, *A. africanus*, *A robustus* (Paranthropus) and *H. habilis* were compared, and the authors concluded that *A. afarensis* should replace *A. africanus* as “the most suitable known ancestor” for the latter australopithecine species as well as for *Homo*, based on the available fossil record at that time (T. White *et al.* 1981:467).

It also proposed *A. africanus* as the exclusive ancestor to *P. robustus* and *P. boisei*, and they additionally argued that these phylogenetic links would persist even in the event it is determined that *A. afarensis* and *A. africanus* overlap based on the prevailing relevance of morphology over time (Ibid). Lockwood and Tobias stressed how an uncertain phylogenetic position of *A. africanus* presented implications for this period with respect to variation and diversification (Tobias 1980; Skelton and McHenry 1992; Strait *et al* 1997; Lockwood and Tobias 1999). Thus, if the only descendants of *A. africanus* were *P. robustus* and *P. boisei*, who became extinct without any known descendants, then *A. africanus* is left at a phylogenetic dead end.

However, these hypotheses required reassessment when two new species were discovered in East Africa (*A. garhi* and *P. aethiopicus*), as well as a new South African species (*A. sediba*) with morphology most similar to *A. africanus*, all contributing to the phylogenetic possibilities.

***Australopithecus garhi* (2.5 mya)**

On November 20, 1997, an associated set of australopithecine cranial fragments were found by Haile-Selassie in the Ethiopian Middle Awash Valley on the eastern side of the Bouri peninsula (Asfaw *et al.* 1999). More specifically, the fossil remains were recovered from the Hatayae (‘Hata’) Member, at the base of the Bouri Formation within the Awash paleoanthropological study area Bouri Vertebrate Palaeontology locality 12 (aka BOU-VP-12), and dated to approximately 2.5 mya via biochronology, ^{40}Ar/^{39}AR radioisotope dating, and magnetostratigraphic methods

(Asfaw *et al.* 1999: 630; de Heinzelin *et al.* 1999:625).

Fig. 5.57 Bouri, Ethiopia
Dalton 2006:15

The Bouri Formation consists of three members, together forming a thickness of approximately 80 metres (de Heinzelin *et al.* 1999). The Hata consists of approximately 40 metres of "variegated silty clay and paleosols, zeolitic, and bentonitic tuffs, paedogenic carbonates, sandstone with bivalve and gastropod shells, and mudstone," and these units were primarily deposited by fluvial processes associated with a shallow fluctuating lake (Ibid:625). Over 400 vertebrate fossil specimens were collected from the Hata Member, the majority of which came from an area within three metres of the Maoleem Vitric Tuff (MOVT), dated to approximately 2.5 mya (Ibid). Above the Hata Member is the Dakanihylo ('Daka'), which is about 30 metres thick with early Acheulean artefacts, hominins and fauna (discussed in Chapter 7), whilst the Herto is the youngest member, where both late Acheulean and Middle Stone Age assemblages have been found, as well as *Homo sapien* fossils dating between 160K and 154k via ^{40}Ar/^{39}AR dating (de Heinzelin *et al.* 1999:625; J.D. Clark *et al.* 2003:747).

Although the African record is replete with hominin remains representing the time period from approximately 4.0 to 3.0 million years ago, the subsequent period between 3.0 and 2.0 mya is relatively sparse in East Africa. As a result, the trajectory of the hominin diversification into different adaptive patterns, which had commenced by 2.7 mya, has been difficult to trace due to the lack of evidence (Asfaw *et al.* 1999). Additionally, this million-year dearth of evidence in East Africa has contributed to the uncertainty regarding hominin phylogenies and possible *Homo* origins, especially when considering that *Homo* may have emerged during this time period. As Tim White states, "You go into this period with, in essence, bipedal big-toothed chimps and come out with meat-eating large-brained hominids. That's a big change in a relatively short time. We'd really like to know more about what happened there" (Fox 1999). As a result, these hominin finds are highly relevant.

Fig. 5.58 A. garhi cranial fragments
Asfaw et al. 1999:630

The cranial remains represent portions of the frontal and parietal bones as well as the maxilla (with dentition), and the specimen was catalogued as BOU-VP-12/130. The discovery of this partial cranium, particularly the maxilla, is of particular interest for two reasons: (i) the dating of the specimen; and (ii) the unusual combination of traits presented by the dentition.

Hominin teeth in the more gracile species have tended to derive larger posteriorly (post-canine)and smaller anteriorly, yet all of the BOU-VP-12/130 teeth are quite large (Asfaw *et al.* 1999). As a result, it is distinguished from its likely ancestor *A. afarensis* primarily due to its large postcanine teeth, and it is also distinguished from later and concomitant australopith species (as well as *Homo*), due to its primitive frontal, facial, palatal, and sub-nasal morphology. Accordingly, it was designated as a new species called *Australopithecus garhi*[1] (Ibid).

Other post-cranial remains were recovered within relatively close proximity to the *A. garhi* cranial specimen, thus indicating other individuals, but only post-cranial

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[1] *The name "garhi" means "surprise" in the local Afar language (Fox 1999), or "the unexpected southern ape from the Afar" in context (Stanford 2017:316).*

remains, which can be definitively associated with the BOU-VP-12/130 cranium, are considered *A. garhi* at this time. These include arm and leg bones which suggest, according to T. White, that the specimen was approximately 1.2 metres (a bit taller than *A. afarensis*) and male (Asfaw *et al.* 1999; Fox 1999). The lower portion of the face is prognathic (with alveolar prognathism, similar to *A. africanus*), and the premaxillary surface is convex-shaped and separated from the nasal floor by a ridge. The dental arcade is U-shaped, and the parietal bones have a well-formed anteriorly positioned sagittal crest (Asfaw *et al.* 1999).

Fig. 5.59 BOU-VP-12/130 Endocast mould, left lateral view
Photo by Suzi Wilson

Holloway made an endocast mould based on the arc and measurements of the cranial fragments, and estimated the endocranial volume as approximately 450 ml using water displacement (Holloway 2002:86; Holloway *et al.* 2004:41). There were no sulci or other impressions on the cranial fragments.

A. Garhi – Association with Stone Tools

In addition to the various fossil finds recovered at Bouri, the team also found evidence indicating the use of stone tools to butcher large mammal carcasses (de Heinzelin *et al.* 1999:625). The Bouri site is only about 96 km south of the Gona site, which produced surface and *in situ* Oldowan artifacts dated to between 2.6 and 2.5 mya via a combination of radio-isotopic dating and magnetic polarity stratigraphy (Semaw 1997:333), discussed further in Chapter 6. Although no significant lithic technologies have been recovered from the Hata Member (other than a few random cores and flakes), the evidence for hominin modification, both cutting and percussive, to various mammal bones is significant. The bones show clear indications of cut marks (possibly made by a sharp stone flake), chop marks and hammerstone impact scars as well as conchoidal scars. There is also evidence for the dismemberment and filleting of a Hipparion (horse) femur (de Heinzelin *et al.* 1999:627). Furthermore, there are indications to suggest that in addition to the disarticulation and de-fleshing of the large mammals, their long bones were broken open presumably for marrow extraction. Although the animal butchery and use of stone tools cannot be definitively associated with *A. garhi*, it is currently the only recognized hominin taxon recovered from this region.

Australopithecus sediba

On August 15, 2008, the right clavicle of a hominin was discovered near a 'de-roofed' cave site in Malapa, approximately 15 kilometres north- northeast of the Sterkfontein, Swartkrans and Kromdraai sites in South Africa and where some limited limestone mining had occurred prior to Broom's exploration and excavation of the area in the mid-1930s (Berger *et al.* 2010; Berger 2012). The fossil was encased in a block of stone that had likely been tossed out of the cave by the miners and much later found by nine-year-old Matthew Berger, Lee Berger's son (Berger *et al.* 2010). Other hominin remains, including a partial cranium, were recovered and catalogued as individuals MH1 and MH2.


Fig. 5.60 MH1 cranium
Berger et al. 2010:195

The cranium was associated with specimen MH1, identified as a sub-adult male based largely on sexual dimorphic features (e.g., a pronounced supraorbital region), with an estimated age of between 12 and 13 years old based on the epiphyseal closure patterns, the erupted second molars, and the developed yet unerupted third molars (Berger *et al.* 2010; Carlson 2011). However, Kimbel and Rak have suggested the possibility that MH1 is a female and argue that there are not enough fossil samples among these newly discovered individuals to indicate the extent of sexual dimorphism and hence, the sexual dimorphic features characterised (2017). Although both the mandible and skeleton of MH2 are smaller than those of MH1, MH2 is an adult, which strongly suggests that MH2 is a female and MH1 is a male. (Berger *et al.* 2010).

The fossil remains of these two individuals, both cranial and postcranial, display an unusual combination of both primitive and derived features. As a result, a new species was established by Berger *et al.* named *Australopithecus sediba*[1] (Berger *et al.* 2010). Independent labs in Switzerland and Australia performed U-Pb radiometric dating from cave deposits immediately below the fossils, which yielded

[1] *The word "sediba" means "fountain" or "wellspring" in the Sesotho language (Berger et al. 2010:195).*

dates of 2.024 mya and 2.026 mya (respectively) and with error margins of ± 62k (Dirks *et al.* 2010). However, paleomagnetic studies suggested that the stratum containing the fossils was deposited between approximately 1.95 and 1.78 mya, verified by a number of animal bones[1] found with the hominins (Dirks *et al.* 2010; Stanford *et al.* 2017). Dirks *et al.* have argued their case for a date of between 1.95 to 1.78 mya, whilst geochronologist Paul Renne[2] agrees that the fossils are no more than 2 million-years-old, based on the credible reputations of the two U-Pb labs (Dirks *et al.* 2010). Dirks *et al.* stress that the U-Pb dating represents a maximum age limit and the dates between the two methods are negligible when considering the margin of error (2010:207). After additional geological studies, Berger's team refined the depositional date to a slightly older range of between 1.98 to 1.977 mya (Pickering *et al.* 2011; Berger 2012).

Overall, the body size of *A. sediba* is small with long upper limbs, similar to other australopithecines[3]. In general, the femur and tibia fall within the range of variation associated with *A. africanus*. However, the ilium, hip joints and other areas of the pelvis have derived in ways very similar to *Homo* (Berger *et al.* 2010; 2012), possibly suggesting an intermediate/advanced stage of bipedal locomotion prior to the emergence of the highly efficient walking and running observed in *Homo erectus*. Oddly though, the ankle and foot were relatively primitive, further contributing to the amalgamated anatomy of both derived and primitive traits.

The female MH2 was associated with a nearly complete right hand and wrist bones, which indicated some interesting manipulative abilities (Kivell *et al.* 2011). Although the distal phalanx of the thumb (i.e., the tip) is small, it has an expanded apical tuft similar to those of contemporary and later hominins (Ibid). At the same

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[1] *According to Dirks et al., 209 nonhuman fossil specimens were collected (2010:207).*
[2] *Berkeley Geochronology Center in California*
[3] *The postcranial remains of three additional individuals have also been recovered.*

time, the shaft of the phalanx is more narrow and taller than those of *all* other hominins (including modern humans). Kivell *et al.* additionally stress how MH2 has a "clear ungual fossa, a well-developed ridge distal to a deeply excavated proximal palmar fossa, and a distinct proximal border to the apical tuberosity," thus suggesting that the MH2 thumb had a well-developed flexor pollicis longus (FPL) muscle, based on this combination of fosse and tuberosity (Ibid:1412). The FPL muscle extends from the radius of the lower arm, crosses over three joints and inserts into the distal phalanx of the thumb, to provide the flexion of the thumb at the interphalangeal joint, essential for gripping. This evidence of a well-developed FPL muscle combined with what appears to be a human-like palmer pad suggests she was capable of tool production. However, other muscles were poorly developed. MH2 had fingers that were shorter than other hominins, which would have hindered arboreal locomotion, so it is also possible that the long muscular thumb may have derived as a means to

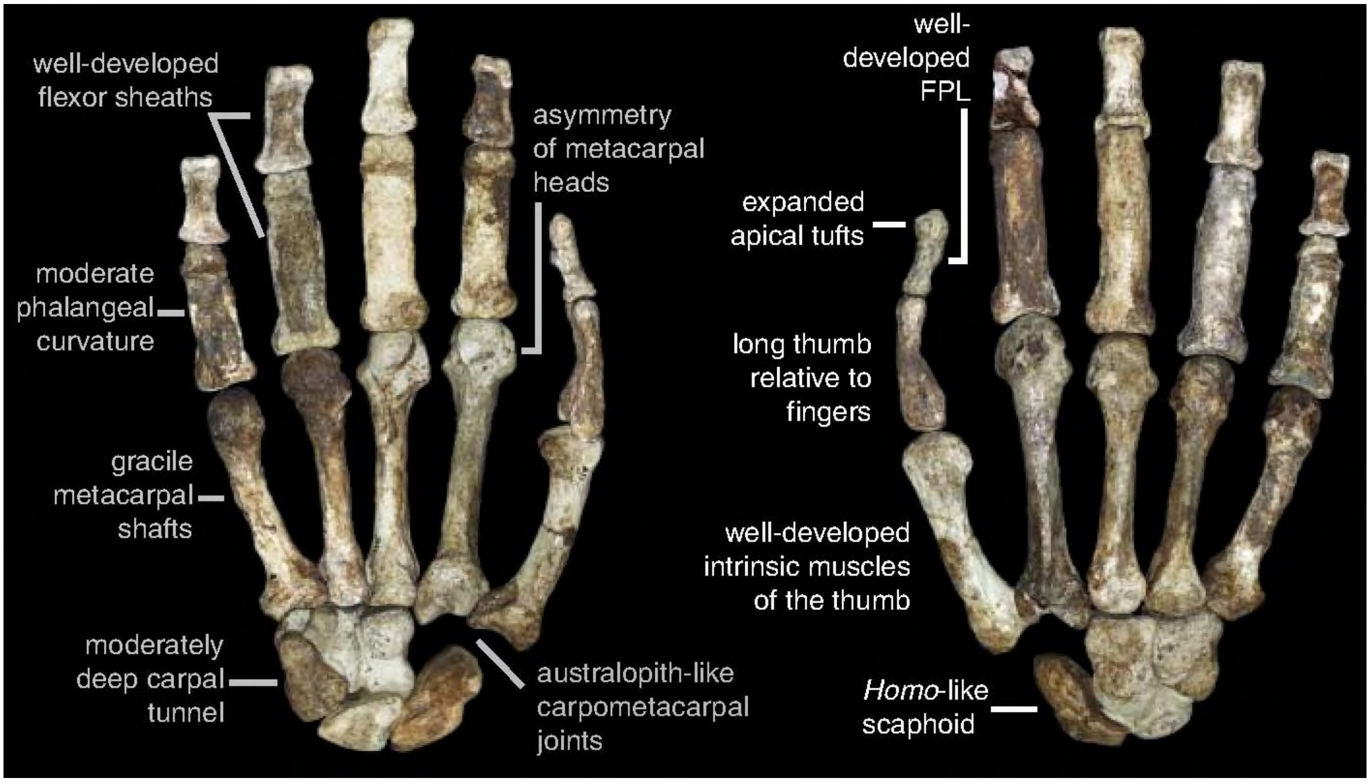

Fig. 5.61 A. sediba right hand. Left photo is palm up (palmar) / right photo is palm down (dorsal). Kivell et al. 2011:1412

compensate for the shorter fingers when engaging in arboreal activities. Dunmore *et al.* point out that the phalanges were moderately curved with well-developed flexor sheath ridges, which are useful for arboreal locomotion (2020), and Kivell *et al.* agree that *A. sediba* regularly engaged in arboreal locomotion (2011). Although the features of the thumb suggest a manipulative hand, Dunmore *et al.* believe that the structure of the MH2 metacarpals indicate that these derived features developed for arboreal locomotion versus the manipulation or grasping of objects (2020). The evolution of the various muscles and bones of the hand with respect to making stone tools will be discussed further in Chapter 6.

MH1 Endocast

An endocast mould of MH1 was made by Holloway (see Figure 5.62) whilst a virtual endocast of the MH1 partial cranium was digitally scanned by Carlson *et al.* using phase contrast x-ray synchrotron microtomography at the European

Fig. 5.62 MH1 Endocast mould, left lateral view
Photo by Suzi Wilson

Synchrotron Radiation Facility (2011:1402) to create a virtual endocast, which has captured several interesting sulci features in the frontal portion of the endocast. It is missing the right hemisphere posterior to the coronal suture, as well as posterior portions of left occipital and temporal lobes, and also missing the cerebellum. Although the shape of the endocast could not be fully recognised due to the missing parts, in general it seems similar to the elongated shape of Sts 5 and modern humans versus the mediolateral wider shape of Sts 60 and extant chimpanzees (Carlson *et al.* 2011).

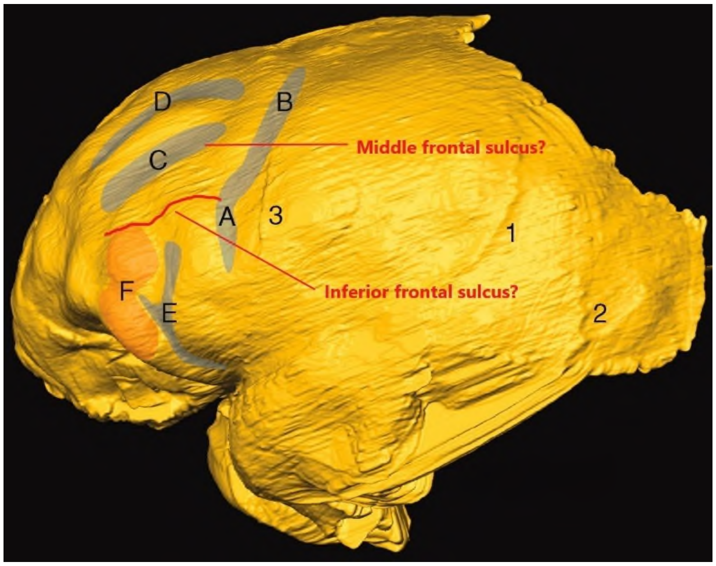

Fig. 5.63 Virtual endocast of MH1 (left lateral)
Carlson et al. 2011:1403
Modifications by Suzi Wilson in red

At 12 to 13 years of age, MH1 is believed to have reached roughly 95% of his adult brain size (Berger 2010:195). After the missing parts were virtually reconstructed, an additional 5% of brain growth was calculated for the presumed growth to adulthood, and the endocast yielded an estimated cranial capacity of 420 ml (Berger 2010:196; Carlson *et al.* 2011:1402). This is a somewhat surprising small-sized brain on the lower end of the spectrum for australopithecine variation, at such a late date between 1.98 and 1.977 mya, when australopith brain size had previously been trending upward. However, the digital endocast from Carlson *et al.* in Figure 5.63 shows a number of sulci/gyrus features, including a few derived indicators. The visible sulci and features[1] are identified as follows:

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[1] Features 1 and 2 represent two meningeal arteries, whilst feature 3 is believed to be the coronal suture (Carlson 2011:1403).

A & B-Precentral sulcus; C-Inferior frontal sulcus; D-Superior frontal sulcus; E-Fronto-orbital sulcus; and F-Inferior frontal gyrus. Although Carlson *et al.* believed that feature "C" represented the inferior frontal sulcus, Falk has argued that feature "C" instead represents the middle frontal sulcus (Falk et al. 2014:8), and I agree. The inferior frontal sulcus (fi) would be located just below, identified as the sulcus in red, joining the precentral sulcus, and cresting just above Carlson's identification of the inferior frontal gyrus.

There is also an apparent fronto-orbital (fo) sulcus labelled "E," indicating that it had not yet been swallowed by the operculum (as described in Chapter 2), thus evincing a more pleiomorphic state. However, the operculum appears to be in the process of forming over the insula in MH1, and Hurst notes the presence of posterior lateral OFC thickening on the left side of the MH1 endocast, suggesting early lateralisation (2017). A right frontal petalia also appears to be present, possibly indicating right-handedness. Although the *A. sediba* endocast is small with most convolutional patterns similar to other australopiths, the orbitofrontal cortex seems to be transitioning in the area behind the nose and above the maxilla where the ethmoid is located (Carlson *et al.* 2011). The olfactory bulbs, which sit on the cribriform plate of the ethmoid bone, have shifted to a more posterior position, which likely signals a decrease in the posterior orbitofrontal cortex (OFC), whilst the anterior portion of the OFC seems to be expanding (Carlson *et al.* 2011; Hurst 2017). The reduction of the posterior OFC is consistent with a decreased posterior orbitofrontal area in modern humans, which would also be consistent with the anterior extension of the temporal poles in modern humans (Carlson *et al.* 2011). Although the temporal poles do seem to have expanded anteriorly in *A. sediba*, they are, at the same time, similar to other australopithecine temporal poles, except that they do not appear to project as much laterally, as also noted by Carlson *et al.* (2011), and as I was able to observe on the endocast mould in Holloway's lab (Figure 5.62).

The decrease of the posterior OFC in modern humans accommodates an expansion in the anterior region of the frontal lobes where high-level cognitive processing occurs, such as BA 10 and 11, and Hurst believes the MH1 endocast exhibits the "perfect example" of a transitional stage in the expansion of the OFC toward a more 'human-like' condition (2017:119).

Berger *et al.* believe that *A. sediba* descended from *A. africanus* based on morphology, location, and age, with some features more derived (toward *Homo*) than *A. africanus*, *A. garhi* or *A. afarensis* (2010). *A. sediba* lacks the suite of traits typically characterized by the more robust species, such as the extreme megadontia (big teeth) and prognathic face, as well as anterior sagittal cresting, yet also lacks the anterior pillars, alveolar prognathism, and pronounced lateral flaring of the zygomatics, which characterize *A. africanus*. Regardless, I agree that its morphology seems closest to *A. africanus*, thus suggesting an ancestral relationship. For example, although the cranium is small, it is relatively vaulted with somewhat vertical parietal walls and expanded temporal lines. Most significant is that *A. sediba* appears to have the least amount of orbital constriction of all the australopithecines (Berger *et al.* 2010), and orbital constriction tends to decrease as brain size increases, although MH1 had a relatively small brain. According to Berger *et al.*, *Homo habilis* had greater orbital constriction whilst the orbital constriction in *A. sediba* is more similar to what is seen in *Homo erectus* (Ibid).

Berger *et al.* have argued that *A. sediba* might represent a 'transitional' species, likely ancestral to the *Homo* genus and possibly even the direct ancestor of *H. erectus* (vs. *H. habilis*) based on the morphologies it seems to share with *H. erectus* such as the adaptations for more efficient locomotion and brain reorganisation. However, the partial cranium of a *H. erectus* child, recently recovered from the Drimolen Quarry in South Africa and dated to between 2.04 and 1.95 mya (Herries *et al.* 2020), has ruled out *A. sediba* as an ancestor to *H. erectus*. Furthermore, these very broad evolutionary hypotheses based on limited evidence have been referred to by Tim White as "fossil-free speculation," and White additionally argues that *A. sediba* and *A. africanus* were most likely 'chronospecies' (contemporaneous 'sister' species) where a lineage of the original species evolves specific morphologies into a somewhat different form but is nevertheless the same species (Cherry 2010; Berger 2012:122).

Fred Grine has criticized Berger and his team for not undertaking "any competent analysis of variation within *A. africanus* – something [he does] not understand in the context that three further skeletons have been found by the same team at Malapa" (Cherry 2010). It does seem that Berger and team have focused solely on the sub-adult male MH1, and considering how morphology changes as the body matures – both Grine and T. White assert that phylogenetic assertions will have to wait until more complete adult remains have been excavated and analysed (Cherry 2010). Additional analyses were published by Berger in 2012, where he insisted that the morphological mosaic with derived features places *A. sediba* outside of the variation seen in any *A. africanus* samples (2012). He also argues how *A. sediba* shares many derived characters with *H. erectus* but also agrees that there are several possibilities regarding the phylogenetic position of *A. sediba* (Ibid).

Kimbel and Rak contested the evidence presented by MH1 as "failing to provide convincing morphological evidence for a 2.0 [myo] ancestral species of the *Homo* clade" (Kimbel and Rak 2017:105), although Rak[1] has insisted that whilst specimen MH1 is neither *Homo* nor ancestral to *Homo*, specimen MH2 *does* represent a member of the *Homo* clade, based primarily on the morphology of her mandible (Rak and Been 2014; Kimbel and Rak 2017:105). Ritzman *et al.* refuted Rak and Been's 2014 claim regarding the MH2 mandible and insisted that the mandible is attributed to *Australopithecus* variation, yet agreed that it is not the result of ontology or sexual

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[1] *Although Rak's argument for MH2 as Homo is reiterated in his 2017 article with Kimbel, Rak makes note that Kimbel does not agree that MH2 is Homo. (Kimbel and Rak 2017:105).*

dimorphism (2016:63). However, Rak *et al.* recently conducted a study comparing the two mandibles with each other, as well as other *Homo* species, including *H. sapiens* (2021). They demonstrate the differences between MH1 and MH2, particularly in the mandibular (sigmoid) notches, and argue that the specimens not only represent different taxa but also cannot be ancestral to *Homo*, based on the earliest *Homo* finds dating to 2.8 mya and 2.4 mya (2021). Berger and team had previously acknowledged that the specific Malapa fossils were not likely the ancestors of *Homo*, but alternatively suggested that the *A. sediba* taxon had evolved much earlier, and as a result - the Malapa individuals represent late-surviving members of the *A. sediba* lineage (Berger 2012).

Although Berger has received some rather harsh criticism with respect to his possibly premature assumptions based on little fossil evidence, no one denies that the Malapa discoveries are significant finds. Berger and his team have also received a great deal of support from other researchers such as Fred Spoor, currently at the Natural History Museum in London, who notes the traits that are, indeed, similar to *H. erectus*, but Spoor also stresses the need for more fossil evidence (Spoor 2011). As is usually the case with new hominin discoveries, the sample size is too small to draw any definitive conclusions, especially when considering the wide range of variation throughout the australopithecine genus. However, *A. sediba* has nevertheless provided much information amid a time period (3.0 to 2.0 mya) during which the more gracile hominin fossils have not been well represented, thus presenting several possible interpretations worth considering. Most importantly, the MH1 cranium presents a transitional morphology which strongly suggests the early stages of re-organisation in the orbitofrontal region of the brain.

Summary/Conclusion

Aside from early instances of lateralisation in the form of brain petalias and/or development in the Broca/Broca cap's regions, the australopithecine endocasts offered little, prior to the recovery of the *A. sediba* cranium in Malapa. However, the 149 lithic artefacts representing the Lomekwian technology and dated to 3.3 mya suggest that something in the brain had occurred to facilitate the cognitive portion of tool-making, although the postcranial morphology left much to be desired. Although the toolkit was simple and crude, it nevertheless indicates that these australopiths had the wherewithal to come up with the idea and strategy for making tools versus searching for tools to use, even though that strategy may have only been to simply bang stones together and hope for the best.

Over a million years later, the Malapa MH1 endocast presents some significant transitional evidence regarding the likely start of the re-positioning/re-organisation of the orbito-frontal cortex around 2.0 mya. The further development of this region (and others) can continue to be traced in some of the early *Homo* crania in the chapters to follow, and the production of stone tool artefacts expanded considerably after 2.0 mya, offering another perspective for assessing cognitive abilities and/or advancement.

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Chapter 6: Paranthropus, Speciation, and Oldowan Stone Tools

Man alone has succeeded in impressing his stamp on nature. He has accomplished this primarily and essentially by means of the hand. But step by step with the development of the hand went that of the brain.

~Friedrich Engels 1896

In June of 1938, a young South African schoolboy[1] found a partial hominin cranium with a few teeth near the top of a hill, located just a short distance from the Sterkfontein Caves (Broom 1938; Kuykendall and Štrkalj 2007). Upon hearing this news, Robert Broom tracked the boy down at his school to 'interview' him as well as retrieve the four hominin teeth the boy was carrying in his pocket. After recovering additional skull pieces from the hillside, Broom cleaned the fossils and initially identified his finds as "a large ape, larger than most male chimpanzees and nearly as large as most female gorillas" yet at the same time, the specimen was quite different from any extant apes as well as the *A. africanus* specimens recovered from the Taung site and the Sterkfontein Caves (Broom 1938:378).

It had a shorter face than *A. africanus*, smaller anterior teeth yet large square premolars and flatter molars (Broom 1938; Ward 2015; Stanford *et al.* 2017). Considering the unusual morphology of the face and other cranial features, Broom gave it the name *Paranthropus cressidus* as a new 'man-ape' genus/species *(later assigned to Paranthropus robustus)*, although he often referred to it as the Kromdraai skull, referencing the locale where it was found (Broom 1938:379). Based on the geological conditions where the specimens were recovered, Broom estimated the age as being older than the fossils found at Sterkfontein (Ibid:378); however, it would ultimately be determined that *P. robustus* was younger than the other hominin remains found at Sterkfontein, with the oldest *P. robustus* fossil specimen (the DNH 152 cranium found at Drimolen, South Africa) dating to approximately 1.95 mya

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[1] *Gert Terblanch*

Fig. 6.1 P. robustus from Swartkrans Kuykendall and Štrkalj 2007:43

(Herries 2020:14) whilst the youngest estimate for their last known appearance dates to approximately 1.5 mya, based on geomagnetic polarity and biostratigraphy (Suwa *et al.* 1996:276; Hunt 2015:115; Stanford 2017:324). In the decades following the Kromdraai discovery, additional *P. robustus* specimens would be recovered, including postcranial fossils which would indicate a body size roughly the same size as *A. africanus*. The crania all had short faces, flaring zygomatics, anterior pillars[1] and other distinctive *P. robustus* traits, recovered from other South Africa sites, such as Swartkrans, Drimolen and Gondolin (Rak 1983; Cartmill and Smith 2009; Stanford 2017).

The most prominent features of the paranthropines are the highly specialised cranial morphologies which enabled them to chew hard and fibrous food sources such as fibrous vegetation, low quality grasses/sedges and hard-shelled nuts, earning them the nickname 'Nutcracker Man.' Although these specialisations included the very big molars and premolars (with thick enamel), it was the overall masticatory system that was so impressive. The power of the mandible and maxillae was enabled by very large muscles for chewing and grinding, primarily the temporalis and masseter, which had adapted in terms of their size and mechanics in order to produce maximum force and efficiencies. The anteriorly-placed sagittal crests on the tops of their skulls served as an anchor for the large temporalis muscles, which had also extended anteriorly in order to apply stronger force for lifting the mandible against the maxillae. The masseter muscles, which attach to the zygomatics, likewise increased in size to assist the temporalis with lifting the mandible, and together,

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[1] *Rak notes how the width and degree of the upward extension of the anterior pillars toward the frontal bone in P. robustus are somewhat larger than those found in A. africanus (1983:32).*

these muscles (along with the lateral and medial pterygoid muscles) moved the jaw from side-to-side for grinding (Gray 1974; Stanford *et al.* 2017). The size and anterior placement of these muscles resulted in extreme postorbital constriction as well as the lateral flaring of the zygomatic arches, which together, produced a ‘dished-in’ face, whereby the cheeks extend further anteriorly than the nose. As previously mentioned, postorbital constriction is the narrowing of the skull behind the eye sockets. Whilst a small amount of postorbital constriction is typically indicative of a large brain (or room for a large brain), a great amount of constriction usually signals a large muscle. They also had a highly flexed cranial base, which further accommodated their eating mechanics. Although their cheek teeth were quite large, their anterior teeth were very small, likely an indication of their lack of importance for dietary concerns.

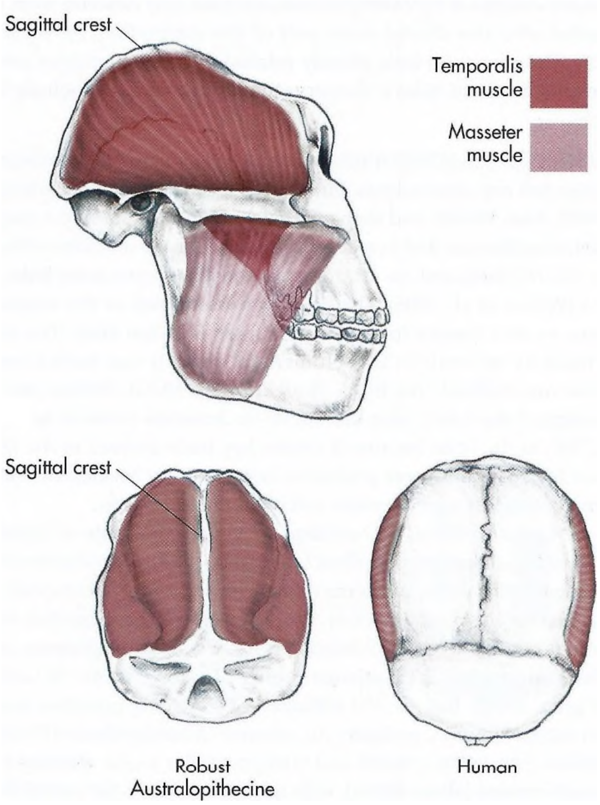

Fig. 6.2 Paranthropus muscles of mastication
Stanford et al. 2017:321

These highly specialized chewing adaptations of the robust australopithecines is the crux of the argument for assigning them to a separate genus, and whether or not this suite of morphological traits justifies the argument – it demonstrates just how different and extraordinary their masticatory system had developed. As previously noted, the name *Paranthropus* seems to be the more common nomenclature employed today when referring to these australopithecines and serves to distinguish these robust eating machines from the more gracile/less robust species. The hyper-masticatory system derived by the paranthropines is believed to have been an adaptation in response to major changes in the Pliocene environment.

During the 1980s, Vrba stressed how "physical environmental change is required to initiate most speciations, extinctions and distribution drift," as part of her Turnover Pulse Hypothesis (1988:410). She additionally noted how these physical environmental changes, which act as evolutionary drivers, typically come from either local tectonic changes and/or global climate change (1988:407), and she argued that a high concentration of speciation and extinction events (hence, "turnover") within relatively short periods of time occurred as the result of environmental change – especially around 2.5 mya (Vrba 1988:449; Potts 1998:108). A period of cyclical glaciation, which began approximately 3.0 mya, became increasingly intense throughout the Pleistocene and there seemed, indeed, to be a great deal of variation as well as a substantial number of extinctions among the mammalian species as they struggled to adapt and survive. At the time Vrba published her hypothesis, most agreed that this increased level of variation and number of extinctions were, at the very least, heavily influenced by the cyclical glaciation fluctuations, which became particularly severe at 2.5 mya (Vrba 1993; Stanford *et al.* 2017).

More recently, Antón *et al.* have presented an approach that integrates the environmental evidence from multiple indicators rather than solely focusing on global cooling, which includes increased aridity in Africa and C_4 (secondary) grass dominated open habitats (2014). Their argument for the synergistic effect of these amalgamated environmental elements, which produced 'habitat unpredictability,' focuses primarily on the period following 2.5 mya, and thus will be discussed further herein and in Chapter 7. Between 3.0 and 2.5 mya, the biggest challenge facing these hominins and other mammals was the likely decrease in usual food sources, resulting from the environmental changes. It is commonly said that during this period, hominins either had to 'think their way out or chew their way out' in order to survive.

Thus, greater orbital constriction provided the means for larger cranial muscles whilst reduced orbital constriction provided room for an expanded brain. By deriving a hyper-masticatory system, the paranthropines gained access to alternative food sources thereby reducing the competition for food between themselves and the more gracile australopithecine species with whom they lived contemporaneously during this time. Although the paranthropine feeding adaptations may have saved them in the short term, it is likely that these extreme eating specialisations were ultimately the cause of their demise in the longue durée, as food sources continued to change or disappear, resulting in the end of their lineage.

Whilst they have been ruled out as a possible ancestor to *Homo*, they are nevertheless of interest to the aims of this thesis because of their potential association with stone tools. The paranthropines had a derived thumb anatomy, similar to the other hominins known to make tools (as well as modern humans), whilst *A. afarensis* had a more primitive thumb (Stanford *et al.* 2017). This alone does not signal that the paranthropines made tools nor does it mean that *A. afarensis* could *not* have made tools, but rather that the derived thumb would have been more accommodating for tool-making, as discussed later in the chapter.

Following the first discovery of a paranthropine in 1938, many other *P. robustus* fossils were recovered in South Africa. However, none had been knowingly[1] found in East Africa until July 17, 1959, when Mary Leakey found a broken cranium (specimen OH5) with specialised eating adaptations, at the FLK[2] site in Bed I of Olduvai Gorge and within close proximity to where some Oldowan tools were previously recovered during the 1931-32 field season (L. Leakey 1960a; Napier 1962b; Walker and R. Leakey 1988).

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[1] *The first P. boisei fossils (two teeth) were actually found in 1955 at Olduvai Gorge, but their taxonomy could not be determined until OH5 was discovered (Wood and Constantino 2007:107).*

[2] *Named for Frida Leakey, who discovered the site and, 'K' for 'korongo' (Swahili for 'gully').*

At the time, these artefacts represented what was believed to be the earliest evidence of stone tool production, dated to slightly older than 1.8 mya, as the Gona Oldowan (2.6 and 2.5 mya) would not be discovered until the early 1990s, whilst the Lomekwi pre-Oldowan toolkit (3.3 mya), would not be found until 2011 (T. White 1988; Semaw *et al.* 1997; de Heinzelin *et al.*1999; Asfaw *et al.* 1999; Harmand *et al.* 2015). Because the OH5 skull was found within relatively close proximity to the stone tools and debitage previously recovered from FLK, *P. boisei* was understandably believed to represent the first toolmaker (L. Leakey 1960a).

Fig. 6.3 P. boisei specimen OH5
Photo by Suzi Wilson

Although OH5 displayed the enhanced eating mechanisms, its facial morphology was different from that of *P. robustus*, with regard to the shape of the supraorbital torus (brow bridge) and nasal bones, as well as the lack of anterior pillars. In many respects, OH5 appeared as a somewhat 'hyper-robust' version of *P. robustus* with exaggerated features (Cartmill and Smith 2009). As a result of these and several other differences, the Leakeys assigned the specimen to not only a new species, but also a new genus based on Louis Leakey's specifications, which they named *Zinjanthropus boisei*[1] (L. Leakey 1959; L. Leakey 1960a). Robinson, however, assessed Leakey's list of 'major differences,' and immediately refuted the vast majority of Leakey's claims by referencing "nearly 200 specimens of *Paranthropus*," thereby suggesting that Leakey was unfamiliar with the range of variation (Robinson 1960:458). Robinson objected to the new genus name, which in his opinion, was "unwarranted and biologically unmeaningful," and instead proposed the name *Paranthropus boisei* which was ultimately accepted[2] (Ibid). Although the discovery of OH5 represented the first evidence of paranthropines in East Africa, additional *P. boisei* specimens would be found including postcranial remains, which indicated a slightly larger body than *A. africanus* and *P. robustus*, ranging between 34 and 49 kg and dating between 2.5/2.3 mya to as late as possibly 1.4 mya (Antón *et al.* 2014:45; Stanford *et al.* 2017: 445). These fossils were found across several other sites in East Africa, including the Omo-Turkana basin (Walker and R. Leakey 1988; Hunt 2015).

The Omo-Turkana basin

The Omo-Turkana basin developed during the early Pliocene within part of the East African Rift (in the northern section of the Kenya Rift) and extends roughly 500

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[1] *The name "Zinj" is an ancient Arabic name for East Africa, whilst the name "Boisei" is a tribute to a Mr. Charles Boise, a financier for the Leakeys' endeavours (L. Leakey 1959:491, 1960a:77).*

[2] *This could not have been an easy feat for Robinson, considering the numerous debates over the naming of new genera and species.*

km in length from southern Ethiopia to northern Kenya and approximately 100 km in width, with Lake Turkana accounting for a large percentage of this area (McDougall and Brown 2006; McDougall and Brown 2008). It includes the formations surrounding Lake Turkana in northern Kenya as well as several formations from the lower Omo Valley in southern Ethiopia and has produced an extensive collection of hominin fossil specimens (Feibel 1989). The 'Omo Group' portion includes the Mursi, Nkalabon, and Usno formations, found in the northernmost reach of the Omo basin near the Usno River in Ethiopia, whilst the Shungura formation is found a bit further south along the Omo River (Howell *et al.* 1987; Feibel *et al.* 1989; de la Torre 2004). The Koobi Fora and Nachukui formations on the eastern and western borders (respectfully) of Lake Turkana in Kenya are generally referred to as the 'Turkana Group,' which also typically includes the Kibish and Galana Boi formations, as well as other undifferentiated sediments (Feibel *et al.* 1989).

The sediments of the basin were mainly deposited by the 'proto' Omo River, which originated in the Ethiopian Highlands to the north, and the exposed thickness of the sediments total approximately 800 m, which were deposited primarily between 4.2 and .07 mya during the Pliocene-Pleistocene (McDougall and Brown 2006:205). The volcanic centres that produced the tephra throughout the region are believed to have been located in the Ethiopian portion of the Rift, or possibly the highlands to the west, although these origins are uncertain. The sediments in the lower Omo portion of the basin were initially recorded in 1896 by a geologist (M. Sacco) with the Bottego Expedition, and the first collections of vertebrate fossils were made by du Bourg de Bozas expeditions in the early 1900s (Howell and Coppens 1974:1; Alemseged 2003:452). However, it was during the 1932-1933 Mission Scientifique de L'Omo led by Professor Camille Arambourg that systematic palaeontological investigations had truly commenced via the documentation of nine species of fish, six species of reptiles and 29 species of mammals (Howell and Coppens 1974; Alemseged 2003).

In 1966, the Omo Research Expedition was created under the direction of Howell, Arambourg,[1] and R. Leakey, to investigate the age and consistencies of the various geological formations, as well as the possible presence of older hominins over the course of an initial geological reconnaissance season followed by several subsequent field seasons from 1966 through 1976 (Howell 1968; Howell and Coppens 1974; Suwa *et al.* 1996; Alemseged 2003). During this period, thousands of vertebrate fossils, including over 200 hominins (mostly teeth), were discovered (Suwa *et al.* 1996; Alemseged 2003), whilst another group, led by L. Leakey and R. Leakey, worked in the northern portion of the Turkana-Omo basin in Kenya. By 1974, nearly 80 localities had reported the recovery of hominin fossil remains (Howell and Coppens 1974).

Over the next several decades, the sedimentation of the Omo-Turkana basin would be studied, mapped, dated, and redated, during which it was confirmed that the various formations within the basin were correlated with one another, and thus composed a single depositional system (Cerling *et al.* 1979; Brown and Feibel 1986; Brown *et al.* 2006; McDougall and Brown 2006). Prior to the mid-1980s, the stratigraphy was based largely on biostratigraphic zones from the vertebrate and molluscan studies in concert with dating from the rhyolitic tuffaceous beds, which had produced conflicting reports and miscorrelations between sections, according to the palaeomagnetic polarity readings. As increasingly more hominin fossils and stone tool artefacts were recovered from the basin, a greater demand was placed on reconciling these miscorrelations and employing better technologies for properly determining the dates of the volcanic tuffs. In 1985, McDougall initiated a new study whereby $^{40}Ar/^{39}Ar$ dating methods were employed using the alkali feldspar crystals

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[1] *Arambourg was replaced by Coppens in 1968 (Alemseged 2003:452).*

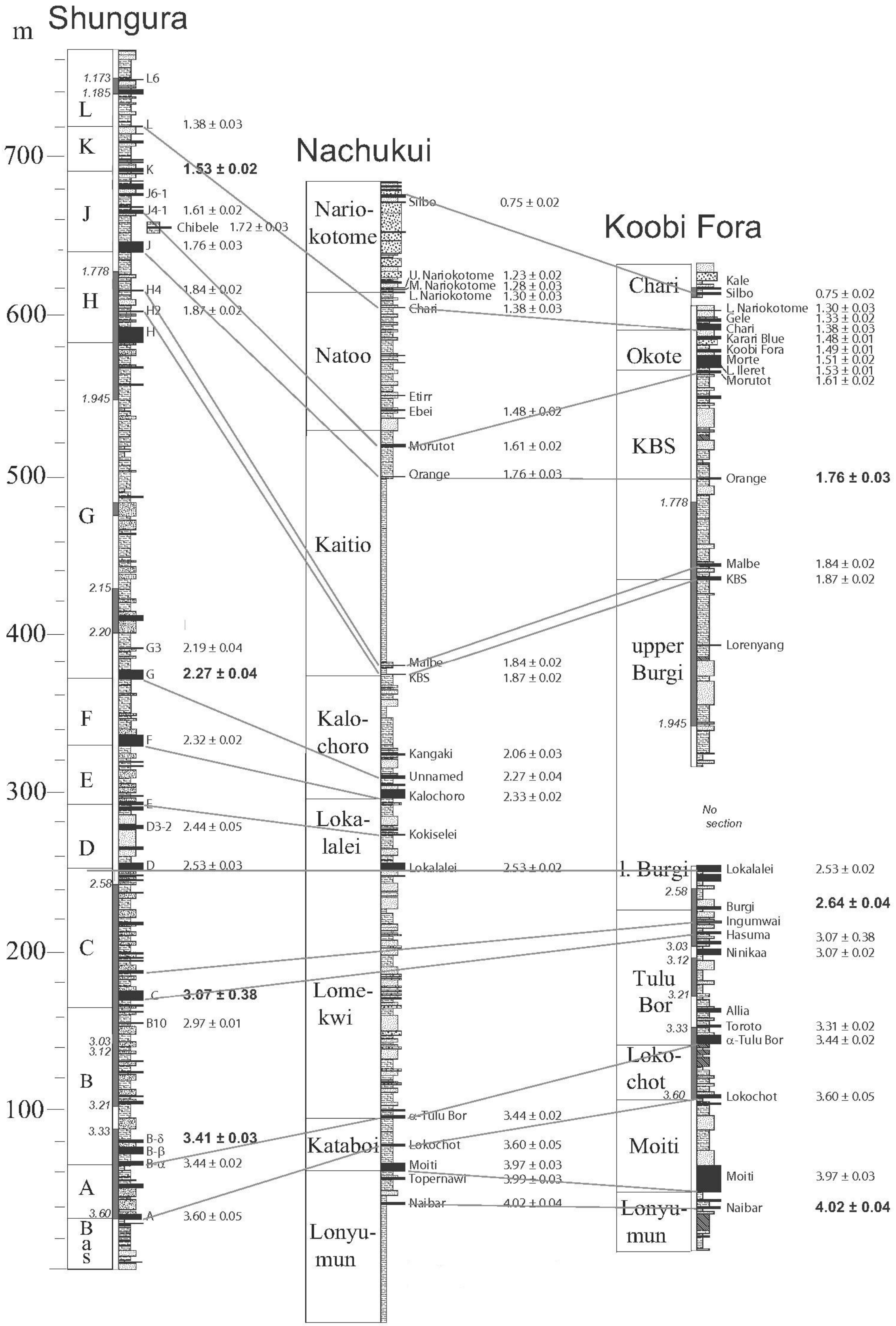

Fig. 6.4 Temporal correlational diagram for the Shungura, Nachukui, and Koobi Fora formations. McDougall and Brown 2012:215

separated from the pumice clasts found within the tuff beds, the results of which were published in 1985[1] (McDougall 1985).

The Shungura, which was initially mapped by de Heinzelin (who published his findings in 1983), is divided into 12 members[2] starting with the Basal Member followed by Members A, B, C, D, E, F, G, H, J, K, and L (no 'I'), with each Member corresponding to a volcanic tuff designated by the same letter and covering a period between approximately 3.6 mya to 1.16/1.3 mya (Alemseged 2003:453; de la Torre

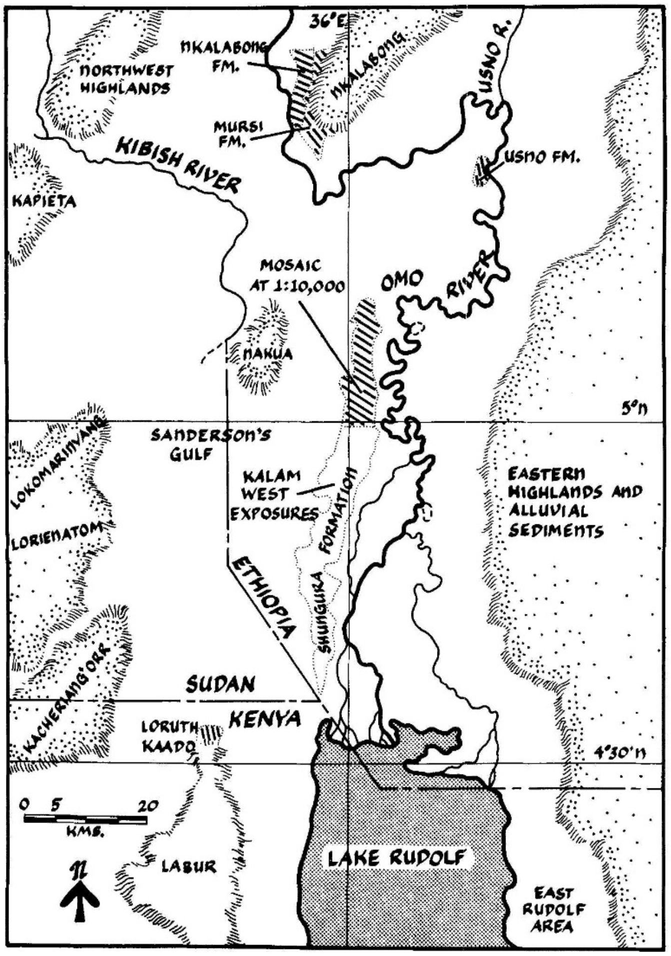

Fig. 6.5 Lower Omo Basin. Note that Lake Rudolf in Kenya is now known as Lake Turkana
Howell and Coppens 1974:2

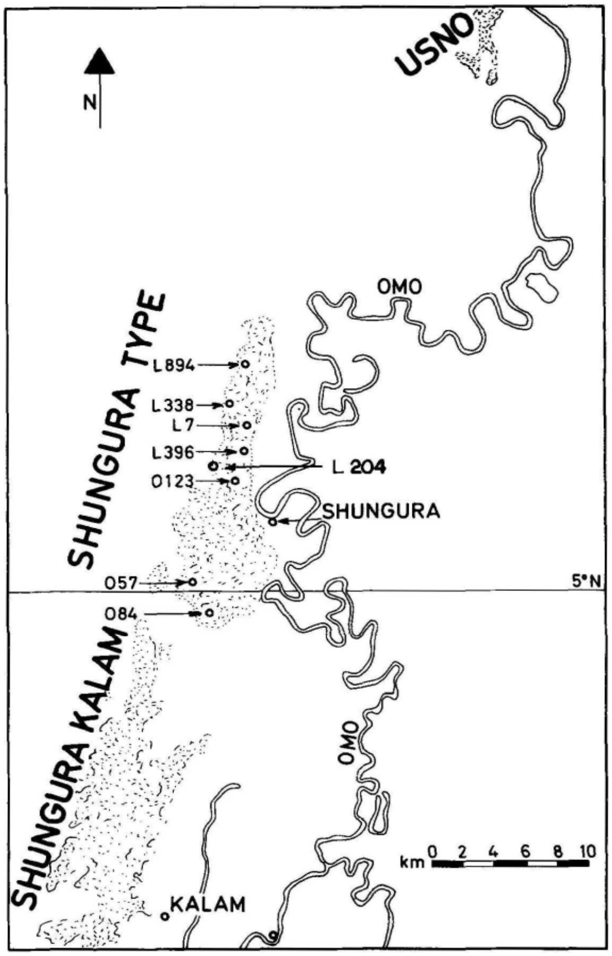

Fig. 6.6 Shungura Formation and some other localities of interest
Howell et al. 1987:671

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[1] *McDougall decided against K-Ar dating in his 1985 study due to the tendency of altered glasses to leak argon (1985:161).*

[2] *There has been some confusion in the literature regarding the number of members (12 or 13, including the basal). This is likely due to some authors not realizing there is no "I" member.*

2004:440; Plummer *et al.* 2015:109). Most of the hominin remains and artifacts (choppers, flakes, etc.) have been recovered from Members E and F; however, the oldest hominin remains are relatively gracile[1] and found in Member B, whilst fossils from *A. aethiopicus*, another robust australopithecine (to be discussed), have been found in Members C through the lower portion of Member G (Howell *et al.* 1987; Suwa *et al.* 1996; Alemseged 2003; de la Torre 2004). Although specimens representing both *P. boisei* and *Homo* were also found at the base of Member G, it should be noted that *Homo* may have also existed during the period represented by Member E, as discussed in Chapter 7 (Howell *et al.* 1987; Suwa *et al.* 1996; Alemseged 2003).

Older *Paranthropus*

In 1967, an older mandible with primitive features (specimen Omo-18-1967-18) was recovered from submember C-8 of the Shungura Formation in Kenya, roughly dated to between 2.6 and 2.75 mya (Arambourg and Coppens 1968; Walker *et al.* 1986; R. Leakey and Walker 1988; Wood and Constantino 2007; Cartmill and Smith 2009). Although the crowns of the mandible teeth had been broken off, the roots suggested that the specimen (presumed female) had diminutive canines and incisors yet very large molars (Arambourg and Coppens 1968; Walker and R. Leakey 1988; Cartmill and Smith 2009). Although all of the paranthropines had large cheek teeth, the anterior teeth of the Omo-18-1967-18 mandible were substantially reduced in size, and there were other peculiarities such as the shape of the mandible, which indicated a more prognathic face than the other two paranthropine species (Arambourg and Coppens 1968; Walker and R. Leakey 1988; Cartmill and Smith 2009).

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[1] *Evidence of gracile australopithecines has also been found in other nearby formations, including the Usno Formation (Suwa et al. 1996:247; Alemseged 2003:453; de la Torre 2004:440).*

As a result, Arambourg and Coppens argued that the specimen was so significantly different from any other australopithecine mandibular fossils that it should not only be designated as a new species but a new genus as well, proposing the name: *Paraustralopithecus aethiopicus* (1968:59; Wood and Leakey 2011:270, 279). Although Omo-18-1967-18 did appear to be considerably different from the mandibles of other Australopithecine taxa as Arambourg and Coppens described, it was nevertheless the only known specimen of its kind at the time. As a result, some believed it belonged in *A. africanus* (Johanson and White 1979) whilst others suggested the mandible was more representative of *P. boisei* (Chamberlain and Wood 1985).

Fig. 6.7 Specimen KNM-WT-17000
P. aethiopicus (aka the 'Black Skull')
Photo by Suzi Wilson

During 1985, however, two important specimens with similar mandibles were recovered from the Lokalalei Member of the Nachukui Formation, west of Lake Turkana in Kenya. The first was another hyper-megadont mandible (KNM-WT-16005) while the second was a massive cranium with a protruding face (KNM-WT-17000) (Walker *et al.* 1986; Feibel *et al.* 1989; Suwa et al. 1996; Wood and R. Leakey 2011). The shape of the face and other features indicate that the specimen would have had a massive mandible that was at least "as big as the largest [*P.*] *boisei*[1] ever found" (Walker and R. Leakey 1988:249). The cranium, presumed male, was found within deposits contemporaneous with Tuff D (see Figure 6.4) and thus dated to approximately 2.5 mya based on the potassium/argon chronology of the formation and palaeomagnetic polarity, whilst the mandible was dated to roughly 2.41 ± 0.05 mya given its location approximately 19 metres above Tuff D (Feibel *et al.* 1989:610).

Most of the traits that distinguish the KNM-WT-17000 cranium from *P. boisei* and *P. robustus* crania are all plesiomorphic (primitive) in nature - the most obvious being the alveolar prognathism of the lower face (Walker *et al.* 1986; Cartmill and Smith 2009). Compared to the *P. boisei* specimen OH5 from Olduvai Gorge, which has roughly the same size palate and cranial base, the mid and lower facial region of KNM-WT-1700 is considerably more prognathic. The facial region of the later paranthropines is typically so orthognathic that only a small part of the incisor region projects past the supraorbital tori (eyebrow line), which appear somewhat 'twisted' in KNM-WT-17000 (Walker *et al.* 1986). Additionally, the brain case is unexpectedly small compared to the later paranthropines with an endocranial volume of roughly410 ml - nearly 25% smaller than that of the *P. boisei* specimen OH-5, which is believed to have had about the same body size (Walker *et al.*1986:519; Walker and R. Leakey 1988:253; Holloway *et al.* 2004:102. Furthermore, the occipital region is

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[1] *Specimen KNM-ER-3230*

wide and low, whilst the temporal bone is lacking a well-developed articular tubercle[1] at the front of its mandibular fossa, whilst the latter paranthropines crania have distinct tubercles (Cartmill and Smith 2009).

Walker *et al.*, however, characterized the specimens as likely "part of the *A. boisei* clade" and attributed their differences from the younger *boisei* specimens as the result of being older/more primitive or "part of normal intraspecific variation . . . or both" (1986:521). They suggested that additional finds in the future would dictate whether or not these three specimens are within the range of expected variation or should be classified as a separate species (Walker *et al.* 1986; Walker and R. Leakey 1988). Today, the consensus is that the cranium and mandible from the Nachukui Formation, along with the Omo-18-1967-18 mandible and a few other jaw/cranial fragment specimens dating to between 2.7 and 2.3 mya demonstrate sufficient differences to be designated as a separate species, *Paranthropus aethiopicus*, which is believed to have begun an anagenetic evolution into *P. boisei* around (or prior to) 2.3 mya (Kimbel *et al.* 1988; Kimbel and White 1988; Walker and R. Leakey 1988; Suwa 1988; Suwa *et al.* 1996; Cartmill and Smith 2009).

Based on these timelines, there appeared to be temporal overlaps between and among the paranthropines as well as some of the gracile australopithecine species, referred to as 'sympatric species.' Furthermore, two early *Homo* species (*H. habilis* and *H. rudolfensis*) began to emerge in eastern Africa, possibly as early as 2.4 mya for *habilis* and 2.0 for *rudolfensis*, presenting additional sympatric possibilities for the hominins occupying the same geographical areas in eastern and southern Africa. This situation would have presented considerable competition for food during a time when sources were scarce, likely contributing to the extreme eating adaptations of the paranthropines, previously discussed, and also possibly spurring the Palaeolithic

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[1] *Tubercles are small 'bumps' on bone, indicating the attachment of a muscle or tendon.*

industrial revolution for stone tool production as a means to assist with both the acquisition and processing of food, or perhaps even as a weapon to defend food resources. Accordingly, this leads to the question as to which species may have produced tools and more importantly - what physical morphologies and neurological abilities would be required to devise and successfully execute a tool-making process.

Hand Morphology for Making Tools

About a year after recovering the *P. boisei* cranial specimen OH5 at Olduvai Gorge, Mary Leakey found two partial parietals alongside 15 hand bones and a gracile mandible in FLK NN1, roughly 20 feet below Tuff IF, the uppermost limit of Olduvai Bed I, dated to 1.803 ± 0.002 mya (McHenry *et al.* 2020:3; Njau *et al.* 2021:4; Deino *et al.* 2021:17). These new finds, catalogued as specimen OH7, were also within close proximity to an assemblage of stone tools previously recovered, which were assumed to be the product of OH5 at the time of discovery. However, these newly recovered hand bones exhibited a much more 'human-like' morphology, and the gracile mandible likewise strongly suggested that OH7 was not the same species as *P. boisei* OH5 (L. Leakey 1960b; L. Leakey *et al.* 1964). The hand bones of specimen OH7 appeared quite capable of making the associated stone tools at Olduvai and was thus given the new species name *Homo habilis*, (meaning 'handy man' or more literally 'man having ability') at the suggestion of Raymond Dart, whilst the stone tools were attributed to the Oldowan[1] Industry (Napier 1962a; L. Leakey *et al.* 1964; Marzke and Marzke 2000).

Oldowan tools are rather simple, described by Stout and Chaminade as merely "sharp-edged stone flakes produced by striking one cobble (the core) with another (the hammerstone)" (2007:1091). Kathy Schick and Nick Toth prefer an expanded

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[1] *Oldowan comes from 'Oldoway,' which was the name the Germans gave the gorge during their early explorations (de la Torre 2011:1029).*

definition characterising them as simple core forms dated to at least a million years ago which demonstrate patterned conchoidal fracture, produced by hard hammer percussion either via bipolar knapping, where the core is struck against a stationary 'anvil,' or by freehand knapping using both hands (Schick and Toth 2006:3; Toth and Schick 2018:4). However simple, the earliest evidence of making a tool from another tool nevertheless demonstrates a cognitive adaptive threshold, which would have assisted these early tool-makers in 'thinking their way out' and gaining access to additional food sources, including high-quality proteins from meat (Ambrose 2001).

Although some of the OH7 hand bones at Olduvai suggested an ape-like pattern, curved with a strong flexion ability of the fingers, the thumb was very similar to a human thumb with respect to its length, stoutness, greater range of motion, and the ability to flex firmly at the tip (Napier 1962a; Marzke and Marzke 2000). Unfortunately, the OH7 specimen was missing both the first metacarpal and proximal phalanx, as well as a few other bones, making it very difficult to thoroughly compare manual or thumb proportions (Alba *et al.* 2003). Although soft tissue does not survive the fossil record, the origin and insertion[1] points of muscles can often be found on the bone specimens. As a result, it is possible to determine the presence and often the size of certain muscles, tendons and ligaments, and there was a clear impression on the OH7 hand bone for the insertion of the flexor pollicis longus muscle (Napier 1962a; Marzke and Marzke 2000), which provides flexion of the thumb at the interphalangeal joint (of the thumb), essential for gripping.

Over the years that followed, there has been much debate over *Homo habilis* regarding the use/making of tools, the evolution of the hand, and whether or not *H. habilis* was more of an advanced australopithecine than a primitive *Homo*, which continues to this day and will be discussed further in Chapter 7. The hand of modern

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[1] *The point where a muscle attaches to a bone is referred to as an 'insertion' if the bone moves during an action. If it is immobile, the point is referred to as an 'origin.'*

humans has 27 major bones and (typically) five sesamoid bones, which are small cartilaginous nodules, often within tendons which act somewhat as 'pulleys' (V. Wood1984; White *et al.* 2012). The major bones are typically divided into three categories: (i) phalanges, which are the furthest (most distal) extended half of the fingers; (ii) metacarpals, which are the bottom half of the fingers; and (iii) the carpals, which consists of eight wrist (carpus) bones that bear a strong resemblance to a set

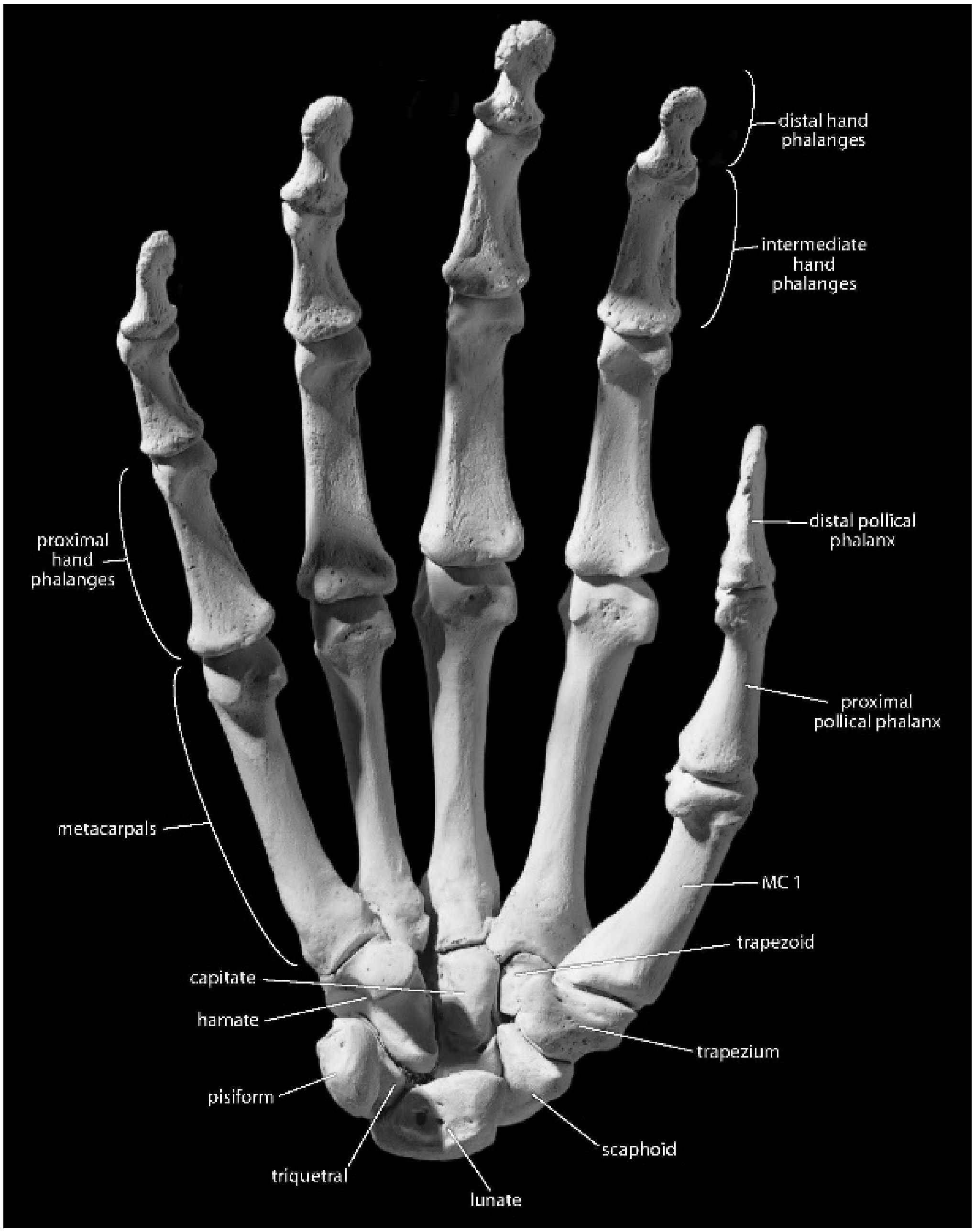

Fig. 6.8 Palmar (palm-side up) view of modern human hand
T. White et al. 2012:200

of uneven marbles or rocks, especially to those with an untrained eye. These semi-round carpal bones are divided into two rows, with the top (or distal) row containing the trapezium (also called the greater multangular), the trapezoid (lesser multangular), the capitate, and the hamate, listed in order from radial (thumb-side) to ulnar (little finger-side), whilst the bottom row consists of the scaphoid, the lunate, the triquetral, and the pisiform, again in the order of radial to ulnar. Although early hominin hands and even extant ape hands contain the same carpal bones as modern human hands, it is the *shape* and features of these carpals that set them apart – especially the trapezium and capitate, as well as how they evolved over time to facilitate precision grasping capabilities.

Also important for the ability to make stone tools are thumb length, flexibility, and rotational abilities, which are crucial for dexterity and manipulation. Compared to the hands of extant apes, modern human hands have longer thumbs and shorter hands/fingers (Alba *et al.* 2003; Almécija *et al.* 2015), which is considered to be a matter of evolutionary selection favouring manipulation for early bipedal hominins versus locomotion for the apes. Ambrose argues that the 'locking' mechanism which protects the wrists from overextension during knuckle-walking (thus limiting rotation) would hinder the capability for tool-making versus a 'mobile' wrist that affords dexterity for precision (2001). The agility, strength, and length of the thumb bone, proportionate to the finger bones, is especially important for hand control when grasping and/or manipulating objects, as well as facilitating forceful precision grips (Marzke and Marzke 2000; Marzke (2013). The control enabled by these forceful "pinch grips" minimize injury to the fingers during tool-making (Marzke 2013:1). Napier recognized this issue from his study of

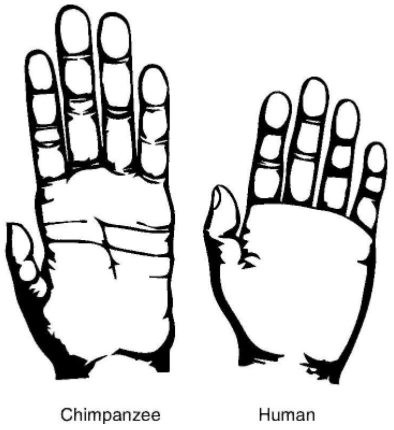

Fig. 6.9 Modern Chimpanzee and Human hands Almécija et al. 2015:2

apes manipulating objects, where he concluded that the apes were limited by their short weak thumbs as well as the great distance between their short thumbs and their long distal fingertips, considering how this ratio greatly affects the ability to control objects (Napier 1962b; Marzke and Marzke 2000).

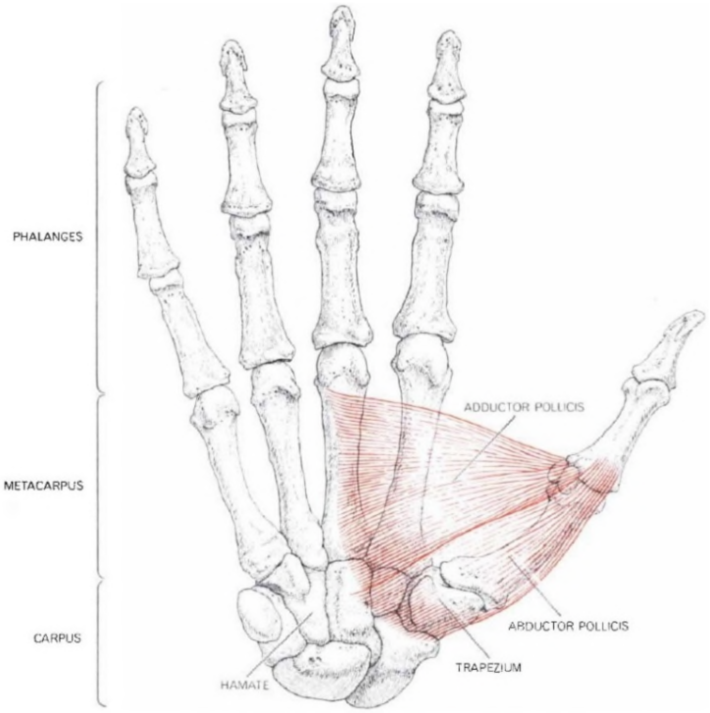

Fig. 6.10 Modern human hand Napier 1962b:57

Additionally significant are the adductor pollicis, the abductor pollicis, and the flexor pollicis longus muscle. The adductor pollicis and the abductor pollicis move the thumb toward and away from the palm whilst the saddle joint, where the trapezium of the wrist articulates with the thumb, enables the thumb to rotate 45 degrees in all directions and can thus be placed in opposition to any of the fingers (Napier 1962b). This 'opposability' of the thumb to the other fingers – especially the index finger - is important for what Napier referred to as a "precision grip," verses a "power grip" which engages the power of the palm and is used when a strong grip is required and precision is not essential (1962a:410; 1962b:58).

According to Napier, there are certain "essential osteological correlates" of the precision grip; however, he also notes that a precision grip was not required for the production of the Oldowan tools or 'Chellean[1]' handaxes (1962a:410). In fact, Napier stressed how the toolkits from the stratum at Olduvai Gorge that date to a period

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[1] *The Chellean is/was a debated classification for the earliest hand axe culture in Europe (de la Torre 2011:1029), although an Olduvai Chellean was also proposed (de la Torre 2016:3). Today it has been subsumed into the Acheulean by most authors.*

prior to the emergence of *Homo habilis* and even prior to *Paranthropus boisei* are "little more than pebbles modified in the simplest way by striking off one or such more flakes to produce a chopping edge" (1962b:62). As a result, he believed that such a technology would require neither an advanced hand with modern human proportions nor a "particularly large brain" (Ibid). Accordingly, his assessment provides some perspective with respect to the early stone tools found at Gona, and especially the Lomekwi toolkit from 3.3 mya.

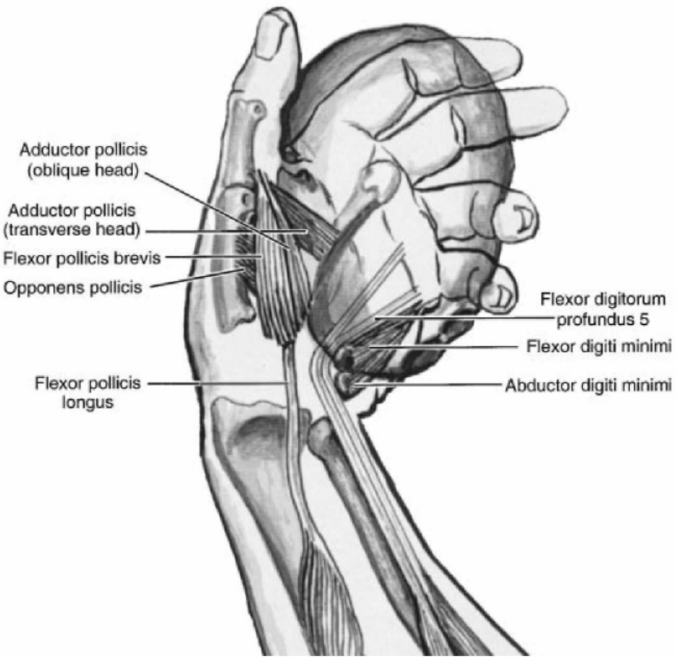

Fig. 6.11 Muscles of the modern hand/arm
Marzke and Marzke 2000:133

During the 1990s, one of the most relevant features for the inference of tool-making was deemed to be a muscle insertion point on the distal pollical phalanx, indicating the presence of the flexor pollicis longus tendon (Marzke and Marzke 2000:124). Research for this tendon had been somewhat lacking for early hominins until 1998, when Marzke *et al.* revealed via electromyography[1] (EMG) studies that a hollow in the phalanx, which was previously believed to receive the tendon, was actually an accommodation for a sesamoid bone in the distal interphalangeal joint capsule when the distal phalanx is flexed (1998; Marzke and Marzke 2000). The sesamoid has the effect of essentially elongating the flexor pollicis longus tendon movement arm, thus providing additional leverage, and the presence of these two features together indicate a possible enhancement to torque capability for the muscle. This morphology, however, can

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[1] *EMG measures the electrical signal produced by muscle response either during a specific activity or as prompted by nerve stimulation.*

also be found on other nonhuman primate specimens (Marzke and Marzke 2000). Additionally, Marzke and Marzke note that EMG experiments for the flexor pollicis longus have indicated that it may not be as crucial for precision grips as previously thought, but it does contribute substantially to squeeze grips (Marzke and Marzke 2000; Marzke 2013). Marzke and Marzke also advise that there are some limitations and short-comings to the type of information obtained through the use of EMG studies (2000), including (but not limited to): (i) the size of the EMG signals, primarily with regard to how the signal size does not reflect the relative importance of the muscle in the activity; and (ii) 'cross talk' whereby an electrode picks up a signal from a neighbouring muscle. However, Marzke and Marzke also make suggestions for reading the signals and comparing patterns.

Following Napier (albeit 15 years later), Lewis also studied the various aspects of the modern human hand compared to both apes and early hominins, with a focus on the human ability to 'cup' the hand, primarily enabled by features of the carpometacarpal and metacarpophalangeal joint regions, which include: (i) the trapezium, trapezoid and capitate wrist bones which facilitate pronation of the metacarpal; (ii) the asymmetry of the 2nd and 5th metacarpal heads which provide the index finger with the ability to rotate toward the 5th finger with both flexion and abduction (as well as reciprocal rotation of the 5th finger); and (iii) a saddle joint between the base of the 5th metacarpal and hamate, which contributes to the 5th finger rotation toward the index finger and thumb (Lewis 1977, 1989; Marzke and Marzke 2000). Like Napier, Lewis also stressed the importance of the trapezoid providing full opposition between the thumb and fingers but additionally noted how the anterior articulation between the trapezoid and the capitate accommodates greater stress/force/weight between the thumb and fingers when manipulating objects (Ibid).

Other important features of the human hand include the styloid process on the third metacarpal and behind the capitate[1], which helps to stabilise the bone against large external forces in the palmar region (Marzke and Marzke 2000). Accordingly, it is believed that the styloid process would have assisted with the use of hammerstones, among other capabilities, and it is interesting to note that a third metacarpal from Sterkfontein (*A. africanus* specimen Stw 64) is the earliest known fossil specimen to display this feature, although it is distinctively shorter in this specimen (Ricklan 1987; Marzke and Marzke 2000).

H. habilis hand at Olduvai

According to Napier, the Olduvai hand bones bear a greater resemblance to those of adult humans and *juvenile* gorillas than they do the adult great apes (1962a:409). Some of the similarities these hand bones share with modern humans include: (i) a trapezium with a broad saddle-shaped surface which provided full opposition between the thumb and fingers; (ii) broad distal phalanges; and (iii) a cavity on the distal phalanx of the thumb suggesting the insertion of the flexor pollicis longus muscle (found in the morphology of *A. sediba*, as discussed in Chapter 5) – all suggesting that *H. habilis* was able to grasp objects with 'modern human-like dexterity' (Napier 1962a:411; Napier 1962b:62; Marzke and Marzke 2000:122). Although primates also have a broad saddle-shaped surface on the trapezium as well as the flexor pollicis longus muscle for the thumb, apes are not able to control objects by the palmar pads of the thumb and fingers as well as humans due to the long distance between the fingertips and the thumb tip (Marzke and Marzke 2000:122).

The crux of hand control, especially when grasping objects, relies largely on the strength and agility of the thumb (Ibid). However, despite lacking some of the bones to properly gauge the length of the thumb bones proportionately to the finger bones,

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[1] *The capitate also provides an 'assist' to the styloid process with its bevelled dorsal radial corner.*

Napier concluded that the Olduvai hominins were capable of making the associated tools given the simplicity and primitive nature of the Oldowan toolkit, which did not particularly require a longer agile thumb in order to produce (Napier 1962b:62; Marzke and Marzke 2000:122), and has been demonstrated in experiments whereby extant apes have been taught to knap (Wright 1972).

Additionally, Marzke and Marzke stressed how the manufacture of both Oldowan (*and* Acheulean) tools did not "elicit the grip requiring full opposition of the distal thumb and index pads exclusively," and agreed with Napier that it is possible this grip did not evolve until the Upper Palaeolithic (Napier 1965:548; Marzke and Marzke 1997:98). Napier further argued that early hominins likely did not require *advanced* cognition, given the simplicity of the Oldowan toolkit (Napier 1962b:62); however, the cognitive ability to conceive the idea for using a tool to create another tool from a stone, as well as a plan and the means to do so, required visuomotor skill and a basic understanding of stone fracture properties (Ambrose 2001). It also suggests that perhaps some form of brain re-organisation had already occurred, as well as possibly the development of the neural substrates engaged in the tool-perceiving/tool-making process, considering how brain volumes were still relatively small during this time.

Tool-Making Brain

As previously explained and demonstrated in Chapters 1:35; 2:87-88; and 3:108, the physiological adaptations of the hand would have had corresponding changes in the premotor cortex of the brain, but it would also have an effect on the way early hominins interacted with the environment, as well as each other. John Barrett particularly notes how grip and manual dexterity during this phase of evolution would have allowed for "a more complex exploration of the attributes of materials" than what was previously possible (Barrett 2013:11). Indeed, neurologists Rizzolatti and Strick stress how the evolution of the prehensile hand played a crucial role in primate behaviour, and thus “greatly enriched the development of cognitive capacities" (Rizzolatti and Strick 2013:420, 412). According to Rizzolatti and Strick, when the cerebral cortex expanded during hominin evolution, the three most likely impacted regions of the brain were:

Brain Region	**Location**	**Function**
Prefrontal Cortex	Anterior portion of the frontal lobe	Higher order functions such as working memory, problem solving, social interaction and conscious motor actions
Posterior portion of inferotemporal cortex	Posterior portion of temporal lobe	Visual processing, crucial for recognizing objects and faces
Posterior portion of the parietal lobe[1]	Posterior portion of parietal lobe	Planned movements, spatial reasoning and attention

(2013:419)

Yet, early hominins somehow managed to make stone tools prior to major brain expansion, which suggests they already possessed the necessary neural substrates to do so. The identification of these areas would thus provide useful information in determining the neurological capabilities involved, if not required, for making simple tools like the Oldowan Industry versus those demanded by the more complex tools of the Acheulean.

In 2007, Stout and Chaminade conducted an experiment where they collected brain activation imagery via PET scans on six inexperienced right-handed subjects (three male/three female) prior to an Oldowan tool-making practice session and afterwards (in four weekly one-hour sessions) to explore the neural foundations for simple tool-making. Their study was far from ideal considering the small sample size, in addition to how modern human brains likely differ considerably from early

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[1] *Most likely, they are referring to the most posterior portion of BA 7 and the angular gyrus (BA 39).*

hominin brains. For example, Stout and Chaminade reported brain activation in Brodmann Area 7, which contains (among other cortical areas) the praecuneus in modern human cytoarchitecture. As mentioned, it is believed that the praecuneus only recently evolved within the past 150,000 years (Bruner *et al.* 2017; Bruner *et al.* 2018). Additionally, the cerebellum was incompletely scanned in four of the six subjects so any information involving the cerebellum was inconclusive. Nevertheless, their study provided a good working sense of the neurological areas engaged in simple tool-making by amateurs (in modern humans). The areas activated along with a brief identification of the Brodmann area function are listed below:

Oldowan Toolmaking Brain Activity with Novices

Activated Areas	Hemi	BA	Brodmann Area Function
Frontal Cortex:			
Postcentral gyrus (Pre-practice scans only)	Right	3	BA areas 1,2, and 3 of the postcentral gyrus are part of the primary somatic sensory cortex (aka S-I), responsible for sensory reception, receiving the bulk of tactile sensory input.[1, 2, 3]
Postcentral gyrus /Parietal operculum	Left	43	At the most inferior border of the postcentral gyrus and within the parietal operculum is BA 43. It abuts the primary somatosensory cortex and is thus referred to as the secondary somatosensory cortex (aka S-II), where pain and other senses are received/felt. It also responds to pressure on the eardrum and oral intake (e.g., food).[1,4]
Dorsal premotor cortex	Left	6	BA 6 is divided into at least five sub-regions, all of which are involved in various aspects of the planning and control of motor actions for different body parts. The medial portion is important for the update of verbal
Medial premotor cortex	Right	6	

Ventral premotor cortex	Left	6	representations, and also corresponds with the supplementary motor area (SMA). Lateral portion involved in the update of spatial representations and relates to the premotor area. Other functions include motor learning, planning, and motor activation of the hand. BA 6 is part of the dorsolateral frontal cortex (DLFC), thus connected to working memory and strategic action planning. Left anterior BA 6 relates to object manipulation, whilst the ventral premotor cortex (PM_v) is believed responsible for selecting 'grasps' employed. The most inferior region of BA 6 borders BA 44, part of Broca's area. [1, 5, 6, 7, 13]
Central Sulcus	Right	3/4/6	BA 3 & BA 6 discussed above. BA 4 is also a part of the precentral sulcus and serves as a main source of motor activation.[1]
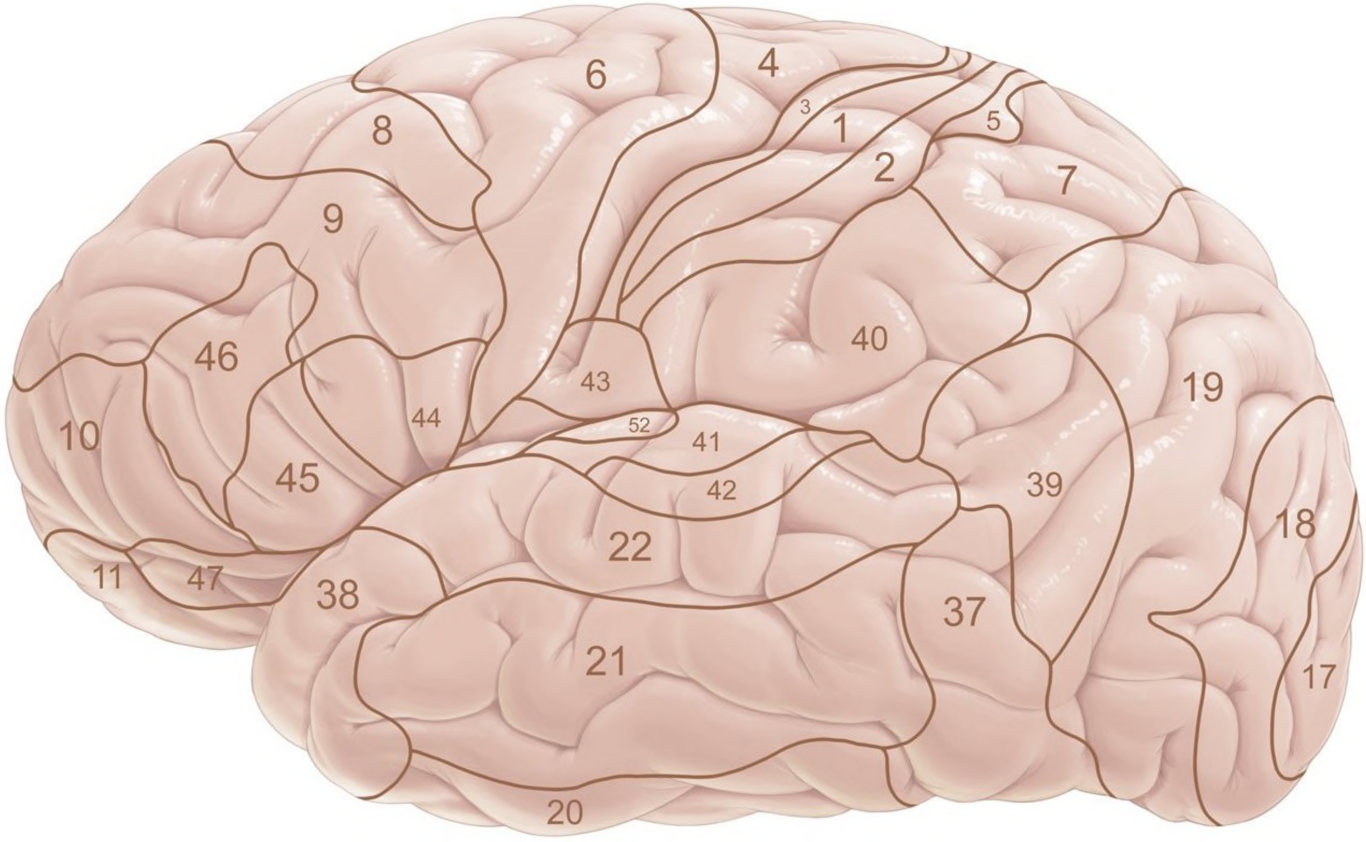			
Fig. 6.12 Lateral view of Brodmann areas *Image courtesy of ©KenHub, www.kenhub.com (Illustrator: Paul Kim)*			

Parietal Cortex:			
Superior Parietal Lobule	left	7	Part of the somatic sensory cortex, BA 7 includes the superior parietal lobule laterally and the praecuneus medially. Also relates to mathematics (in the dominant hemisphere) memory retrieval and visuospatial processing, but more so in the nondominant hemisphere. Sensory info is received and processed to program and guide hand/arm movements toward objects within peri-personal space in order for the hand to touch or grasp. [1,8]
Intraparietal Sulcus	Left	7/40	The intraparietal sulcus separates BA 7 (superior parietal lobule) from BA 40 (inferior parietal lobule). These Brodmann areas are bounded anteriorly by the postcentral gyrus, and this most anterior region of the intraparietal sulcus is known as the anterior intraparietal sulcus (AIP), important for hand/grasping information. [7, 8] BA 40 contains the supramarginal gyrus which interprets language by converting graphics to letters, and plays a role in phonological processing (spoken and written). It additionally interprets numerical functions, emotional responses, tactile sensory data, and calculates depth perception for the visuo-guidance of limb movement or planning object-related movements. It is involved with tasks involving tools, including the grasping and manipulation of tools. It is also a part of the mirror neuron system in that it identifies the postures and gestures of others. [1, 9, 12]
Intraparietal Sulcus	Right	7/40	Same as above, but should be noted that the *right* supramarginal gyrus also plays a major

			role in extending empathy to others as well as egocentrism.[10]
Occipital Cortex:			
Calcarine Sulcus	Left and Right	17	BA 17 serves as the primary visual cortex (PVC), which includes the calcarine sulcus and occipital pole and is responsible for visual perception. It is the initial cortical region of the visual hierarchy to receive visual input. [1, 11]
Superior Occipital Gyrus	Left and Right	18	BA 18 is part of the secondary visual cortex which interprets colour and motion recognition and also includes a portion of the medial occipitotemporal (aka fusiform) gyrus. However, Stout and Chaminade noted that the portion of this gyrus that was activated in their study was the portion located in BA 19, described below.[1, 6]
Calcarine Sulcus	Right	18	
Inferior Occipital Gyrus	Left	18	
Lingual Gyrus	Right	18	
Middle Occipital Gyrus	Left and Right	19	BA 19 is a pre-occipital area and also a part of the secondary visual cortex. It additionally includes a portion of the medial occipitotemporal/fusiform gyrus and represents a higher order visual area, including object and face recognition.[1, 6]
Fusiform Gyrus	Right	19	

[1] Strotzer 2009:182, 184; [2]Sanchez-Panchuelo et al. 2012:15815; [3] Zilles and Amunts 2010:144; [4] Job et al. 2011:2; [5]Tanaka et al. 2005:500; [6]Stout and Chaminade 2007:1095, 1096; [7]Stout 2010:163; [8] Rizzolatti & Kalaska 2013:871,875; [9]Stoeckel et al. 2009:1094-1095; [10] Silani et al. 2013:15475; [11]Hinds et al. 2009:915; [12]Johnson-Frey et al. 2005:692; [13]Scott and Kalaska 2021:819.

The most highly activated regions were the anterior intraparietal sulcus (AIP), the ventral premotor cortex (PM$_v$) and the high order visual areas, but not the dorso-lateral frontal cortex. This is somewhat surprising yet confirms that whilst it was previously believed the perception of space and complex cognitive acts were *only* represented in higher-order sensory and association areas of the cerebral cortex - it now appears that the premotor areas may also have cognitive functions (Stout and Chaminade 2007:1092; Rizzolatti and Strick 2013:413). Although these results provide some interesting aspects as to the neural correlates for amateur toolmaking in modern humans, the tools made by the novices did not reflect the more "well-controlled, systematic and productive flaking" (Stout *et al.* 2008:1939-1940) as seen from Oldowan sites such as Lokalalei 2C and Gona. Accordingly, a follow-up experiment was launched employing the same methodology but with expert toolmakers as the subjects.

Oldowan Toolmaking Brain Activity with Experts

There were only three subjects in the follow-up study, likely because it is not easy to find volunteers with 10+ years of expert stone toolmaking, willing to be injected (via a venous catheter to a vein in the foot) with a radioactive isotope tracer for three days in a row. The demographics of the three subjects (two males/one female between ages 30 and 55) suggests the subjects may have been Stout and his two advisors, Nick Toth and Kathy Schick. The first day was simply a 'control' session, which consisted of banging rocks together without intent. On the second day, Oldowan tools were knapped, and Late Acheulean handaxes were made on the third day. (The Acheulean results will be discussed in Chapter 7.) Although there was much overlap of the Brodmann regions between the Oldowan novices and experts, there were also a few notable differences.

The only regions from the novice study which were not engaged in the expert study were BA 3 and 43, both relating to the somatosensory cortex, described above. Although the inferior temporal gyrus was not engaged during the novice Oldowan study, it was activated in the expert Oldowan study. The Brodmann areas associated with the inferior temporal gyrus are described below:

Temporal Cortex	**Hemi**	**BA**	**Brodmann Area Function**
Inferior temporal gyrus	Right	20	Primarily involved with visual association processes, such as emotions associated with colours or facial expressions[1]
Inferior temporal gyrus	Right	21	Includes the middle temporal gyrus and is involved in higher-order audition process and speech reception whilst the posterior division belongs to the visual association cortex.[1]
Inferior temporal gyrus	Right	37	An occipito-temporal area that houses visual and language functions such as word and object recognition and face recognition[1]

[1] Strozer 2009:183-184

Also interesting is the high level of activation for the supramarginal gyri (SMG) in the inferior parietal lobules (Brodmann area 40) and the superior parietal lobules (Brodmann area 7) in both hemispheres during the expert study. In the 2007 study, the supramarginal gyrus in the left inferior parietal lobule (BA 40) was more activated than the right, which would be anticipated considering how the left hemisphere is typically dominant for tasks with familiar tools, regardless of which hand is involved (Lewis 2006). Likewise, only the left superior parietal lobule (Brodmann area 7) was engaged during the novice Oldowan toolmaking. However, during the expert Oldowan sessions, activation was strongly bilateral with the supramarginal gyri heavily engaged, as well as the bi-lateralisation activation of both superior parietal lobules (Stout *et al.* 2008:1944). Stout *et al.* believe that the unexpected activation of the right SMG resulted largely from the design of the task.

Left-hand dominant behaviour in the brain is more active during conceptual planning (or imagery) and less so during the actual physical use of tools (Lewis 2006:217; Stout *et al.* 2008:1945), particularly with respect to the SMG (Johnson-Frey *et al.* 2005:687). However, the activation of the right SMG may have also indicated the importance of the left hand controlling the placement and orientation of the core on the left thigh. In this respect, Stout *et al.* consider the exercise (per design) as bi-manual, with different yet complementary tasks for both hands, although the dominant hand would play a more prominent role (2008:1945).

Stout *et al.* also note how expert performance is supported/enhanced by past experience in tool making (2008:1945), which includes a body of knowledge with respect to fracture mechanics and reliable expected responses to actions taken by the arm and hand, which in turn, is based on observed patterns in toolmaking. Stout *et al*. refer to this as the "tool+body system" which is consistent with the bilateral SMG activation (Ibid). More simply, it is the 'muscle memory' provided by experience that enables us to perform certain tasks without particularly having to plan/think about what we are doing, which would otherwise require more work on the part of the left SMG (Johnson-Frey *et al.* 2005). Stout *et al.* suggest that bilateral SMG activation in experts (compared to novices) emerges after substantial practice has enabled adept bimanual coordination, including left-hand support (2008:1946). In other words, it is not so much a matter of greater activation in the right SMG, but rather that there is considerably less activation in the left SMG, simply because detailed planning is no longer required at the expert level.

Tool Use, Tool Modification, and Tool Making

Cognitively, it is important to distinguish between tool-making and tool use, which tend to rely on different sets of neural substrates. There are a number of animals in today's world that are known to *use* tools, but the cognitive means to conceptualize and create a *stone* tool has been (thus far) limited to the hominins[1] (Stanford *et al.* 2017:325). Although the early toolkits were simple in both design and construction, their invention and production implied a shift in cognitive abilities. Indeed, de la Torre notes how the hominins at the Omo sites only had marginal raw

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[1] *The great apes were found to have tool-modifying capabilities during the 1960s; however, they do not make stone tools in the wild (Stanford et al. 2017:325).*

materials for tool production possibilities, yet they somehow managed to "make cores and flakes out of this mediocre material; [something] a chimpanzee never could" (2004:456). As discussed in Chapter 5, there is evidence of tool-making among the australopithecines as early as 3.3 mya with the Lomekwian toolkit, and by 2.0 mya, tool use and tool making had become ubiquitous among the hominins (Stanford *et al.* 2017:326).

The brain's ability to focus on objects in both peri-personal (within arm's reach) and extra-personal space[1] (beyond arm's reach) (Kandel 2013:374) is germane to the study of cognition[2] and tool making/tool use. In the late 1970s, psychologist James J. Gibson presented his ideas concerning a notion which he referred to as 'affordances' (Gibson 1979; Rizzolatti and Strick 2013; Rizzolatti and Kalaska 2013). Gibson was interested in the cognitive interaction of perception and action as focused on information in the environment, which is another role of the parietal lobes. Rizzolatti and Strick note how Gibson's theory suggests that "the sight of an object in the environment triggers an immediate and automatic selection of those properties of the object that allows one to interact with it. These properties or affordances, are not the visual aspects of the object (shape, mass, colour, etc.) but the *pragmatic opportunities* that the object affords the observer" (Rizzolatti and Strick 2013:421, my emphasis).

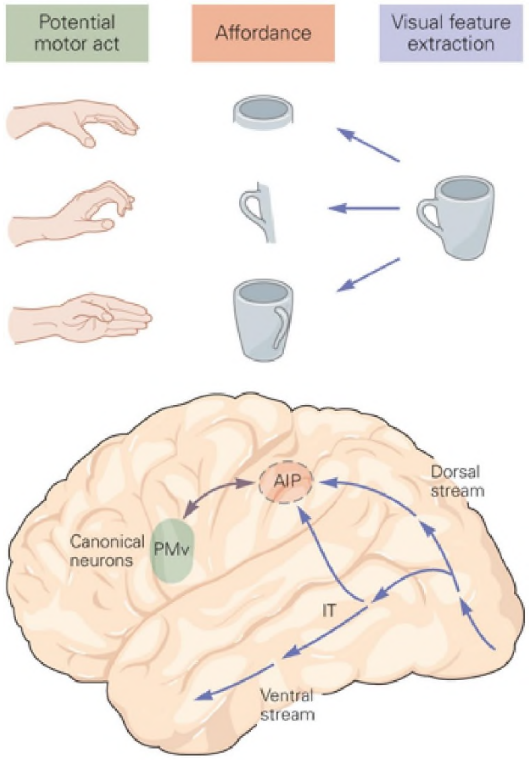

Fig. 6.13 Neural Informational Pathways Rizzolatti and Strick 2013:422

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[1] *Whilst personal space is on the surface of the body (Kandel 2013:373).*
[2] *According to Neisser, "The term 'cognition' refers to all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered and used" (Neisser 1967:3; Kandel 2013:371).*

For example, suppose an early hominin sees a piece of flint from which s/he would like to make a tool. First, s/he would consider the raw material itself followed by how to reach for it and grasp it with the hand. As s/he observes the piece of flint, visual information from the eyes is collected in the primary visual cortex (in the occipital lobe), which is then sent to the anterior portion of the intraparietal sulcus (AIP), a visual-motor association area considered crucial for "visually guided grasping" (Stout 2010:163). Assuming the piece of flint is located within peri-personal space, spatial information is also collected and calculated in order to guide and coordinate the reaching arm and grasping hand to the piece of flint. This information is sent to the anterior intraparietal sulcus to help determine the proper grip to employ. The potential grasp choices (i.e., affordances) are then sent from the anterior intraparietal sulcus (AIP) to the ventral pre-motor cortex (PM_v) (see Figure 6.13). The PM_v then chooses which grasp to employ, based on available information and constraints, then sends its decision back to the AIP, which then discards the un-selected grasp choices (Stout 2010:163; Rizzolatti and Strick 2013:421). The PM_v then executes the action utilizing the selected grasp and other associated actions such as holding, flexing, etc. (Ibid). More specifically, Rizzolatti and Strick describe the process as follows:

> "Based on the extensive elaboration of an object's properties in the extrastriate visual areas of the dorsal stream beginning in V_2, the visual-dominant and visual-and-motor neurons in the *anterior intraparietal cortex* are able to encode the object's affordances. This information is then sent to F5 neurons that encode potential motor acts. An F5 neuron can transform a given affordance into an appropriate potential motor act because of the congruence of its response to the affordance and the motor act it controls (2013:421)[1]."

[1] *V_2 refers to Visual Area 2 (in Brodmann area 18) of the visual cortex (see also Chapter 2), while F5 neurons (in the frontal lobe) discharge during specific goal-directed actions (such as grasping). Many of them fire selectively during particular types of grips, and some (canonical neurons) become active simply when viewing objects (Rizzolatti and Strick 2013:420).*

Essentially, affordances equate to the available possibilities for the brain to choose from, whether the raw materials available for knapping a tool, or an affordance of the body, such as how to grasp and hold it with one hand while knapping with the other. The previous example demonstrates some of the various thought processes and brain mechanics involved in the actions of seeing an object and reaching for it. Clearly, these cognitive and motor processes increase in complexity when employing both hands, and even more so when the hands are performing separate tasks.

There are many species in the animal kingdom other than humans who are known to use tools, including but not limited to: crows, dolphins, elephants, otters, apes and beavers (Goodall 1964:1264; Haslam *et al.* 2009:343; Alba *et al.* 2003:226). Some of these animals have also been observed manipulating or modifying a tool for a specific purpose. For example, Hunt observes how New Caledonian crows create hooks from twigs and leaves in order to assist with food procurement (1996), and Weir *et al.* have studied how these crows can bend straight wire with their beaks in order to fashion a hook to better suit their needs (2002). During her time in Gombe (Tanzania), Goodall witnessed several examples of chimpanzee tool use, including an adolescent stripping the leaves off a stick to act as a lever in his attempts to open a banana box (1964).

The manufacture of tools from raw materials, however, is a more complex process requiring a certain degree of both anatomical and cognitive competence, if not prowess. There have been many tool-using/tool-making studies of both captive and free-living extant apes, which examine the capabilities – both cognitively and anatomically – required to make tools. In this respect, extant apes can provide insight into an early tool using/tool making culture through the observation of their learning processes and anatomical struggles, more so than what the early toolkits alone can offer (Toth and Schick 2009). In Chapter 5, it was noted that although extant apes are not proxies for early hominins, the organisation of their brains did provide a marginal level of interest when considering how hominin brains *might* have derived/re-organised over the course of evolution. As previously discussed, much of this analysis is speculative because neither early ape brains nor early hominin brains survived the fossil record. However, the skeletal remains of hands do survive, providing the ability to compare the morphology and proportions among extant apes, early hominins and modern humans. Although the cognitive assumptions may remain hypothetical, there is now scientific evidence to better understand the evolution of tools in concert with the evolution of the hand.

Whilst Goodall spent three years observing the Gombe chimpanzees in Tanzania, she not only documented the various natural objects they used as tools, she also described *how* they used these tools. Aside from using sticks, stalks, stems and twigs for accessing insects or insect products (e.g., honey) or using leaves or fruit to clean themselves, she additionally noted how they had also developed a 'throwing culture' that was sometimes playful, yet sometimes an aggressive means to intimidate (Goodall 1964). Additionally, it has been observed how they throw rocks to crack open nuts, but they are also known to use two stones for a hammer and anvil technique for nut cracking (McGrew 1992, 2004; Toth and Schick 2009; de la Torre and Hirata 2015). However, they are not known to *intentionally* 'knap' tools in the wild nor do they knap in captivity unless taught to knap by a modern human (Alba *et al.* 2003; Toth and Schick 2009).

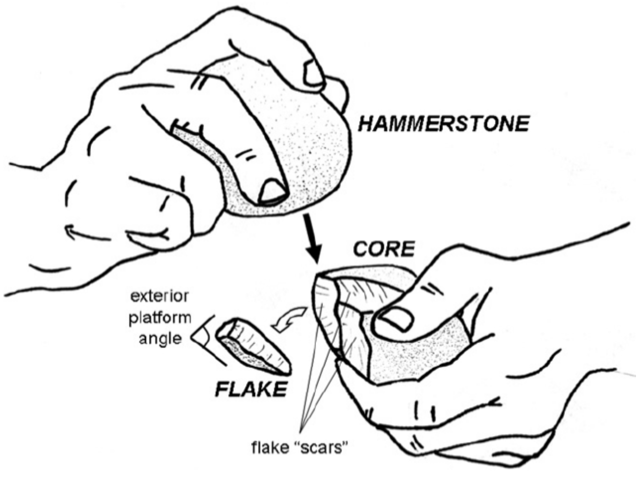

Fig. 6.14 Freehand knapping from Stout 2007:1092

[1] *Sometimes, as part of the 'throwing culture' observed by Goodall, apes and monkeys deliberately break stones. As a result, sometimes sharp flakes are unintentionally created during this process, which are then sometimes used by the apes or monkeys (Proffitt et al. 2016:85).*

As mentioned, Oldowan tools are simple core forms made by either bipolar knapping (where the stone core is struck against a stationary 'anvil') or by freehand knapping, which involves grasping a 'percussor' (aka an 'indenter' or 'hammerstone' or 'billet') with the dominant hand and striking the core (aka 'nucleus' or 'cobble') held in the other hand, in order to carve off a chip or a 'flake.' When the percussor is another hard object (such as a stone) employed to 'hammer' the core (hence 'hammerstone'), the percussion itself is referred to as 'hard-hammer' percussion versus 'soft-hammer' percussion which involves the use of a less rigid percussor, such as bone or wood. In early toolmaking, the goal was not the end-product tool reduced[1] and sculpted from the core itself, but rather the flakes to be used as cutting instruments (Toth 1985; Cotterell and Kamminga 1987). Indeed, flakes ejected from the core during knapping typically have sharp edges making them very useful in this context.

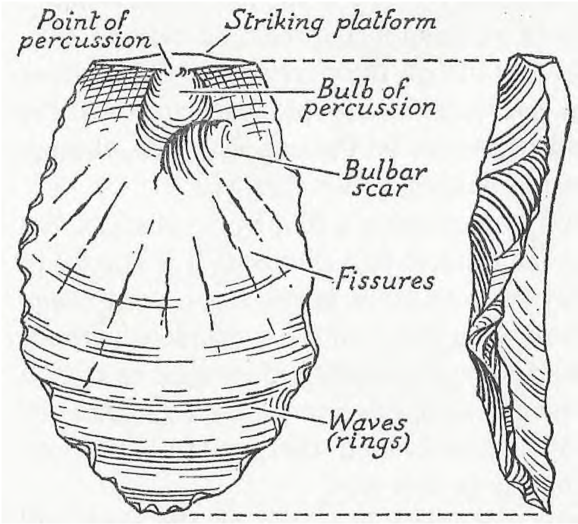

Fig. 6.15 Knapped Flake with Scars
Sheperd 1972:151

Regardless of whether the knapping goal was to produce a tool from the core or to produce flakes as cutting tools or scrapers, the whole flakes and flaking debris produced during the knapping process is typically referred to as 'debitage' in accordance with the terminology outlined by M.D. Leakey (1971; Semaw 2006); however, the term *débitage* is also occasionally used in its original meaning as a process and as defined by Inizan *et al.* as the "intentional knapping of blocks of raw material, in order to obtain products that will either be subsequently shaped or retouched, or directly

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[1] Reduction is the process of 'reducing' the core in an efficient manner in order to either make the best use of the core to produce the most flakes or to best reduce the core with the intent of making a larger tool from the core itself (or both).

used without further modification. [It] refers also to the tangible results (debitage products) of this action" (1999:138). When the desired end product is the tool made by reducing the core, the process defined by Inizan *et al.* is called 'shaping' which refers to a "knapping operation carried out for the purpose of manufacturing a single artefact by sculpting the raw material in accordance with the desired form" (Ibid:155).

Flakes are knapped from a flat surface on the core (either naturally flat or made flat by breaking off a piece of the core), referred to as the striking platform (Sheperd 1972), although the earliest industries do not show evidence of platform preparation. In freehand knapping, a percussor is then used to strike the platform at about a right angle (Ibid:150). The point of impact is referred to as the 'point of percussion,' which is recognized by the small impression bead the force leaves behind on the core, whilst the entire portion of the core effected by a percussive act is known as a flake scar. Immediately below this tiny bead is the hole or depression left in the core where the flake was detached, which is often referred to as the 'bulb' of percussion. If the core was struck properly at a near right angle with enough force and control (and using a hard percussor such as a hammerstone), the bulb will display concentric semi-circles radiating outward. As a result, this is referred to as conchoidal fracture, so-named for the semi-circles' resemblance to a conch shell, but also resembling the image made from a projectile hitting glass (Pelegrin 2005). Likewise, the inner surface of the detached flake also has the appearance of concentric semi-circles (Cotterell and Kamminga 1987). These flakes and flake-scars can indicate both the point of origin as well as the directional orientation of percussion, and it is also possible to determine the sequential order of the adjacent flakes knapped if their scars overlap (Pelegrin 2005).

There are three common knapping styles as well as variations of each. Freehand knapping, as previously described, is the most complicated of the three because the right and left hands are performing completely different tasks, thereby requiring some level of brain lateralisation with the dominant hand operating the hammerstone whilst the recessive hand secures the core. In a passive hammer approach, the core is secured either in the ground or to an anvil whilst both hands (and arms) perform the same motion together to strike the core, thereby requiring little or no brain lateralisation, which is very similar to the means employed by chimpanzees to crack nuts. In bipolar knapping, one hand secures the core on the anvil whilst the other hand strikes the core with the hammerstone, thereby likely requiring more brain lateralisation than the passive hammer approach, but not as much as freehand knapping. Accordingly, if we are able to determine the knapping style of the earliest hominin tool-makers, it could provide some insight regarding potential cognitive development in terms of brain lateralisation.

In 1971, Wright conducted an experiment with an adolescent (5.5 years) orangutan named Abang to determine whether or not orangutans could be taught to knap a sharp flake then use it as a cutting tool (1972). An orangutan was not his first choice[1] but given the constraints due to housing and pregnancy at the Bristol Zoo, it was the only species he could access. As mentioned, extant apes have shorter thumbs than humans which negatively impacts their precision abilities to manipulate objects, and orangutans have even shorter thumbs than gorillas or chimpanzees (1972:298). Wright's aim was to teach Abang (via imitative learning) to strike a flake from a flint core using a hammerstone, then use the flake to cut a cord, thereby opening a box with food as a reward (Ibid).

The experiment commenced on March 5th, 1971 and included ten sessions consisting of a total 48 episodes (of varying length), and on April 6th, 1971 - Abang finally achieved success, but not without some human influence aside from the initial

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[1] *Not only do orangutans have the shortest thumbs of the great apes, they are also the least sociable, typically living in groups of only one to two individuals.*

teaching sessions. The core was strapped down securely, providing the orangutan with the option to use both hands to flake. Abang was not particularly a willing participant so at one point, his caregiver was asked to withhold his last meal prior to a knapping session in order to provide additional motivation.

It was challenging for Abang to manipulate the flake with his short thumb, and during one episode he cut himself on the flake. Perhaps for this reason, he tried to cut the cord with the flake in his teeth a few times. Ultimately, however, he managed to complete the task, cut the cord, and retrieve the food reward, after which he promptly walked back to the core and urinated on it before enjoying his meal, thus exhibiting his distaste for Wright's experiment. Cognitively, Wright believes that Abang's adaptive learning was more than him simply mirroring the actions of humans, and he stressed how Abang would attempt new strategies other than what he was taught, such as attempting to cut the cord with his teeth versus using the flake (Ibid:305).

At the time of Wright's experiment, neither the Lomekwi nor the Gona toolkits had been discovered so it was generally believed that the australopithecines were incapable of making tools. Yet, Wright argued that his experiment with Abang demonstrated how it was unlikely that the australopithecines were prevented from making stone tools by any "deficiencies in their intelligence or manipulative skills" (1972:305). Furthermore, the hominin innovation to create a tool knapped from stone in the first place signalled an important watershed, cognitively, and the australopithecines had neither the advantage of a 'strapped-down' core to flake from nor the benefit of modern humans as models to imitate.

Following up on Wright's experiment, Toth and Schick[1] began a three-year study in 1990 to investigate if a 9-year-old male bonobo named Kanzi could be taught

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[1] *In collaboration with cognitive psychologists Sue Savage-Rumbaugh, Duane Rumbaugh, and other colleagues from the Language Research Laboratory of Atlanta and the Great Ape Trust of Iowa.*

to knap in a more natural setting versus a controlled lab, then use the tool he created, again to access a food reward (Toth *et al.* 1993:81; Toth and Schick 2009:297). In this environment, freehand knapping with hard-hammer percussion was demonstrated by human models flaking cobbles of quartzite, quartz, lava, and chert. Kanzi would then select the raw material to use as his core, which would be held in one of his hands (and not strapped down, as it was for Abang), whilst he used the hammerstone in the other hand to strike the core (i.e., freehand knapping). The goal was to produce a sharp flake for either cutting through the membrane of a drum or cutting a cord to access one of the food rewards.

However, Kanzi had some advantages that Abang did not. He was raised in captivity at the Language Research Center in Atlanta, where he had become proficient at using lexigrams to communicate with humans as well as adept at understanding human instructions/cues (Toth *et al.* 1993), and as a result - he had been socialised as a human and had likely already grown accustomed to mimicking their actions. It is therefore not surprising that after observing a human tool-maker for a period, Kanzi needed little encouragement for attempting to knap over long periods of trial-and-error learning, on his own.

Fig. 6.16 Kanzi freehand knapping
Photo courtesy of:
Great Ape Trust of Iowa
Toth and Schick 2009:C-2

He experimented with the various choices of raw materials provided and ultimately showed a preference for the finer-grained, more easily flaked (and sharper) chert. After 18 months, Kanzi had mastered the basic skills for extracting flakes from stone cores as well as attempting some innovation of his own by throwing cobbles against a hard surface (i.e., an ‘anvil’) to fracture and produce flakes (Ibid). Over time, he developed a preference for throwing the hammerstone against the core to create flakes, thereby increasing the force of the impact, and he even deduced how to target the thrown hammerstone to hit near the edge of the core for more successful flake production (Schick *et al.* 1999:831).

Schick *et al.* believed that he developed this 'throwing' technique to compensate for his lack of control/power in hitting the core in one hand with the hammerstone in the other, but they also acknowledge that there was likely some motivation on Kanzi's part to avoid hitting his fingers with the hammerstone, which was a common occurrence (Ibid). Since the experiment, Kanzi continued to improve his knapping skills and has even taught his younger half-sister (Panbanisha), who learned to flake from observing only Kanzi and not human models, which is relevant to note. However, despite Kanzi's learning curve and progress, his technical skill set remained considerably lower compared to what the hominins had achieved, especially at Gona and Lokalalei (Toth *et al.* 1993:89; Schick *et al.* 1999:831). Pelegrin gave a harsh critique of Kanzi's work, which he described as the detachment of some "splinters," which included a few "conchoidal-looking flakes," likely by accident, and assessed that Kanzi was far from controlling conchoidal fracture, and thus, unable to produce anything particularly relevant (2005:25).

Although the studies involving Abang and Kanzi have demonstrated that extant apes can be taught to freehand knap by mirroring a human model, it seems that both apes showed a preference to either throw the percussor against a core or use a hammer-and-anvil technique (bi-polar knapping) rather than freehand knap, possibly due to the limitations presented by their arm and hand morphology. Furthermore, although their tools might be adequate in terms of function, they are considerably crude in form and design.

According Lewis and Harmand, as well as Hovers, successful and efficient knapping largely depends upon: (i) the ability to understand basic fracture mechanics with respect to the properties of available raw materials; (ii) a physical morphology that can provide the dexterity and strength required for applying both the proper force and precision in order to most accurately strike flakes without breakage and without damaging the core, unnecessarily; and (iii) a competent level of depth perception and the ability to recognise the best locations and angles at which the core should be struck, as well as the amount of force to be applied (Lewis and Harmand 2016:2; Hovers 2009:137).

The required cognitive abilities (i) and (iii) of the earliest tool-making hominins can be assessed through the artefacts they produced, which might be further supported by the evidence retrieved from brain endocasts. As for the postcranial morphology required for (ii), the modern 'human-like' hand did not derive until *Homo habilis*. Although we cannot be certain of the precise nature of early hominin hand morphology given the small sample size in the fossil record, we know that whilst they had some measure of limitations (to be further discussed), at the very least they had begun to derive more flexible mobile wrists as 'stiff wrists' were no longer required for knuckle-walking locomotion.

The Lomekwian – the Earliest Toolkit (3.3 mya)

The Nachukui Formation, one of the formations surrounding Lake Turkana in northern Kenya, is approximately 730 metres thick and consists of eight members ranging between 4.3 and 0.7 million years and with 43 volcanic tuffs, over half of which overlap with the Koobi Fora and Shungura Formations (Harris *et al.* 1988a:27; Harris *et al.* 1988b:5; Delagnes and Roche 2005:437). The Nachukui is highly relevant both archaeologically and anthropologically due to the early tool kits it has yielded, as well as the fossil remains of the multiple hominin species that occupied the region between approximately 3.3 and 0.70 mya. The correlations between and among the Turkana formations are illustrated in Figure 6.4. For example, the lower portion of the Lomekwi Member of the Nachukui compares in age to the lower portion of the Shungura formation Member B. The Lomekwi Member measures 159 metres in thickness and refers to the strata between Tulu Bor Tuff (=B Shungura) in the Nachukui column (see Figure 6.4) and the Lokalalei Tuff (=D Shungura) (Harris *et al.* 1988a:28; Harris *et al.* 1988b:14; McDougall and Brown 2012:215).

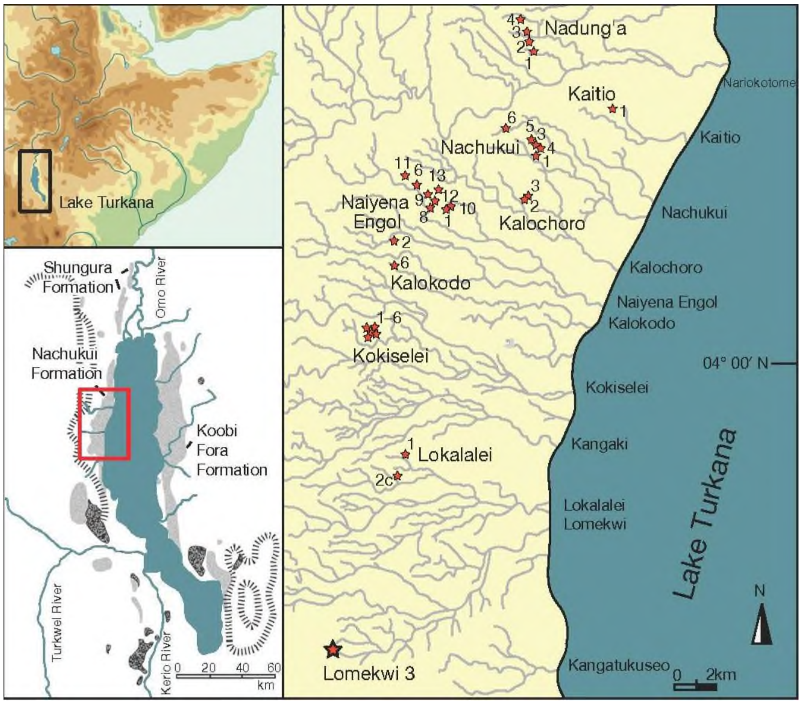

Fig. 6.17 Geographic proximities of Lake Turkana formations, including Lomekwi and Lokalalei sites Harmand et al. 2015:311

The Lomekwi strata consists of two contrasting associations: one, with volcanic conglomerates and sandy siltstones, and the other, with quartz-rich sandstones that grade upward into the siltstones and sandy claystones (Harris *et al.* 1988a). The Lomekwi Member dates to between 3.36 and 2.52 ± 0.05 mya and has been sub-divided into sub-members LOC1 through LOC10 (aka I through X), each identified by its proximity to the nearest Tuff (Harmand *et al.* 2015:310).

During the 2011 and 2012 field seasons by the West Turkana Archaeological Project (WTAP), 149 lithic artefacts were recovered in the LOC3 sub-member of the Lomekwi and dated to 3.3 mya, via $^{40}Ar/^{39}Ar$ dating and magneto-stratigraphy (Harmand *et al.* 2015:310; Lewis and Harmand 2016:2). The assemblage, discovered both as surface finds and *in situ*, consists of 83 cores, 35 flakes (whole and broken), seven passive elements (possibly anvils), seven percussors (whole, broken or potential), three worked cobbles, two split cobbles, and 12 indeterminate fragments/pieces (Harmand *et al.* 2015:312; Lewis and Harmand 2016:2). The sediments in LOC3 are fine-grained, and one of the flakes found could be re-fitted onto the core from which it was made, thus indicating it is unlikely that these tools accumulated via fluvial processes (Callaway 2015; Hovers 2015).

However, the *in situ* nature of the stone tools has been challenged by Domínguez-Rodrigo and Alcalá based on their interpretations of the published site photographs. In their critique, they made clear that they were not denouncing the chronology of the assemblage as "false," but rather "insufficient" and thus requiring more evidence (2016:52). Harmand *et al.* vigorously defended their analysis of the Lomekwi site and argued that Domínguez-Rodrigo and Alcalá ignored both the geological and taphonomic details provided in the literature from Harmand *et al.* 2015 as well as Lewis and Harmand 2016, and as a result - had misinterpreted the geological conditions in the photographs and mispositioned the lithics (2019:180). Although the defence from Harmand *et al.* is compelling, Toth and Schick advise how "critical" it is that Harmand *et al.* fully demonstrate that these stone tools are, indeed, "clearly in situ" and not "more recent artefacts redeposited against the older sediments" in order to fully substantiate their 3.3 mya date (Toth and Schick 2018:6). More recently, Archer *et al.* have questioned the 'in situ' recovery of some of the artifacts, primarily with respect to how it could impact their dating of 3.3 mya (2020). Key to their argument is the true provenance of a core, identified as specimen LOM3-2011-116-3 and an anvil, identified as LOM3-2011-K18-2, both of which Lewis and Harmand consider to be in situ (2016) but without providing the proper contextual information that Archer et al. deem

Fig. 6.18 Surface core from LOC3
Hovers 2015:294

necessary (2020). Toth and Schick further note that even if the site is definitively proven to be *in situ*, the question remains as to whether these stone tools warrant their own industry or if they should be considered part of the "Oldowan Industrial Complex" (Ibid). Both the Lomekwi and Oldowan are simple toolkits, but the Lomekwi lithics present some interesting differences in terms of both size and quality.

The Lomekwi cores are much bigger than the Oldowan artefacts, described by Toth and Schick as "unusually large," with some weighing as much as 15 kg (Callaway 2015; Hovers 2015; Toth and Schick 2018). This is somewhat puzzling considering that hominins during this time only weighed, on average, about 45 kg, and it suggests greater upper body strength than would be expected. Although numerous blocks of all sizes were available within 100 metres of the site, these early hominin tool-makers consistently selected the larger cobbles for knapping (Lewis and Harmand 2015). Most likely, the goal was to produce flakes, and it was probably easier to knap the larger cobbles if these hominins had a more primitive hand and arm morphology. It is also possible they may have had some cognitive limitations for tool-making, as Wynn has strongly advocated that precise visuo-spatial skills did not fully develop until *H. erectus* (Wynn 1979, 1995, 2002). However, three-dimensional spatial adeptness is common in the animal kingdom and well evinced among insects, fish and birds – especially humming birds (Holbrook and de Perera 2011; Davis *et al.* 2014; Healey *et al.* 2022). It thus seems unlikely that advanced visuo-spatial perception would have been lacking in the Lomekwi toolmakers; however, it is possible that the dorsolateral frontal cortex had not yet developed enough to help these hominins formulate a strategic plan of action for creating the kind of tool envisioned. On the other hand, it is also possible that the simple tools made by the Lomekwi toolmakers were all they required at 3.3 mya, which would have represented a major technological improvement over perhaps sticks, for example.

The majority of the cores had flat natural surfaces and consisted of either basalts (34.9%) or phonolites (34.23%), but there were also a number of 'trachy-phonolite' cobbles (Harmand *et al.* 2015). According to Harmand *et al.,* the toolmakers likely employed a passive hammer and/or bipolar approach based on flake scars and replication experiments, although freehand knapping could not be ruled out (Harmand *et al.* 2015; Lewis and Harmand 2016). The flakes were removed primarily from a single striking platform and in the same direction, although a few cores evidenced multi-directional flaking whilst a few others were worked bifacially.[1]

Fig. 6.19 Unifacial core (with refitting flake) with a series of percussive marks prior to flake removal, suggesting that the core may have additionally been used for other purposes. Harmand et al. 2015:313; Lewis and Harmand 2016:5

There were a significant number of knapping accidents evident on the Lomekwi cores recovered, and the percussive marks suggests that these early tool-makers experimented with different knapping techniques (Harmand *et al.* 2015; Lewis and Harmand 2016). The Lomekwi knappers apparently had the wherewithal to provide sufficient force in order to detach series of unidirectional flakes and then either rotate or invert the core and continue knapping (Harmand *et al.* 2015:313). However, the scars on the cores indicated that the majority of the flakes terminated early (i.e., 'short' and incorrectly) as either hinges or step fractures[2], and there were

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[1] *Worked on both sides of the core*

[2] *A step fracture leaves a scar that resembles a series of small steps, whilst a hinge leaves a hole.*

impact marks indicating a number of 'failed blows' where the core platform was struck too far from the edge in order to produce fracture (Ibid). Hinges typically occur when a flake forms near the surface of the core and too much pressure is applied to the sides, which prevents the flake from ejecting properly, whilst a step fracture can be caused by a number of issues, including: (i) a hammerstone that is too light; (ii) striking the core platform in an incorrect position (i.e., too far from the edge); and (iii) applying insufficient strike force to remove the flake properly (Hovers 2009). This suggests that their limitations were primarily with respect to their postcranial morphology, rather than cognitive ability.

Lomekwi Toolmakers

During this time period, the only known hominin species living in the region where the Lomekwi tools were discovered were *Australopithecus afarensis* and *Kenyanthropus platyops*, as discussed in Chapter 5. *Australopithecus deyiremeda* was approximately 1,000 kilometres to the northeast and thus, an unlikely candidate. The 3.5 myo cranium of *Kenyanthropus platyops* was found at LO-6N within close proximity to the tools, as well as other fossil remains including a temporal bone, two mandibles, two partial maxillae and a number of teeth, which Meave Leakey *et al.* have argued is evidence "that multiple species occupied the Lomekwi between 3.0 and 3.5 mya" (M.G. Leakey *et al.* 2001:434). However, M.G. Leakey *et al.* are likely referring to the "multiple species" of *A. afarensis* and *K. platyops* as a means to bolster their argument for *K. platyops* as a separate genus/species. Although it seems likely that the *K. platyops* cranium was a variation of *A. afarensis*, it is also possible that this specimen had begun to develop a morphology that would ultimately evolve into *P. aethiopicus* in another 700 to 800k years, considering the early *Paranthropus* fossils which have also been recovered in this region. However, this is purely conjecture given the lack of evidence and, unfortunately, no hominin hand bones or other postcranial remains have yet been recovered at LO-6N.

The first criterium for successful and efficient knapping as described by Hovers (2009:137-140) does not necessarily imply that one should *only* choose resources that would respond best to the knapping process, as this choice would also likely be influenced by the end-use product desired. The bonobo Kanzi realised early on that of the four options offered, the chert was more easily knapped and produced sharp flakes, and this is what he preferentially chose. However, it is unclear if the raw materials employed by the Lomekwi hominins, which were consistently the larger stones available (based on the conglomerate surveyed), were purposely selected based on the properties of the raw materials for the end-product or based on size in order to find large flat surfaces to use as a striking platform – probably the latter. Criteria (ii) and (iii) present constraints based largely on hand morphology for manipulation and accuracy; arm/shoulder morphology for force/velocity; and cognitive capabilities for the ability to determine or learn (from trial-and-error) the proper fracture mechanics to employ.

Although no *A. afarensis*, *K. platyops*, or any other early hominin hand bones have yet been recovered from the Lomekwi site, an extensive bivariate and multivariate morphometric statistical analysis by Alba *et al.* was performed in 2000-2001 on a composite *A. afarensis* hand consisting of bones recovered from several individuals in the 333/333w locality in Hadar (Ethiopia). Their goal was to investigate the manual proportions of the composite hand and assess where these proportions fell on the spectrum between modern humans and extant apes. Since the early 1980s, Stern and Sussman have argued that the *A. afarensis* hand was "ape-like" with a "chimpanzee-like thumb" (Stern and Sussman 1983:284; Sussman 1995:589), whilst Marzke has contended that the *A. afarensis* thumb "was longer relative to the index finger than it is in the chimpanzee" and overall, *A. afarensis* had several features more similar to human hands than extant apes (Marzke 1983:199; Marzke1997:108).

The statistical analysis by Alba *et al.* confirmed that not only are the thumb/hand proportions greater in *A. afarensis* than chimpanzees, but they are much closer "if not equal" to the condition found in modern humans (2003:241), as well as their overall manual proportions (2003:243). Alba *et al.* additionally note that the manual proportions of *A. afarensis* would have most likely provided for "pad-to-pad human-like precision grasping" (2003:250), although Domalain *et al.* argue that the lack of development in the 'fifth ray' (little finger) would have limited the amount of force exerted onto large stones like those at Lomekwi (2017). According to Marzke, the fifth finger supports the squeeze grip applied in handling cylindrical tools (such as a hammerstone) and is also important for stabilizing the core between the thumb and fingers during hard hammer percussion (2013). Thus, even though their hands may have been closer to modern humans on the proportion scale, there was nevertheless the retention of some primitive features that may have presented at least *some* level of difficulty whilst knapping tools. Although these physical constraints would not have *prevented* them from making stone tools, as demonstrated by Wright's study involving the orangutan Abang, it is also not unexpected that the earliest toolkits would be rife with flaws and experimentation as the result of a less optimal hands, arms, and shoulders for tool-making.

However, Napier stresses that "it is in the elaboration of the central nervous system and not in the specialization of the hand that we find the basis of human skill" (1956:913). Accordingly, these numerous failed knapping attempts suggests that in addition to a 'less than optimal' hand/arm morphology, the Lomekwi hominins also lacked a basic understanding of physics and fracture mechanics, as well as the ability to learn quickly (if at all) from trial-and-error experimentation in order to reassess and make corrections. However, at 3.3 mya, the Lomekwi hominins were nevertheless ultimately able to successfully knap stone tools for their needs, despite any cognitive or morphological shortcomings.

Although we have not been able to determine definitively exactly what developments had evolved in the brain by 3.3 mya (other than brain size), it seems likely that at least *some* level of advancement/reorganisation had occurred as the mere presence of these early stone tools suggests. It is especially noteworthy that these early hominins had the *innovation* at 3.3 mya to create a stone tool from a stone by using another stone as a tool – something that an extant ape in the wild has never *intentionally* done. Others, however, have been less impressed, refuting the possibility that the making of simple stone tools may have signalled a noteworthy cognitive achievement. This sentiment was especially apparent during the 1980s with respect to the Oldowan toolkit, discovered long before the Lomekwi tools were found.

During the 1980s whilst Sussman insisted that the Oldowan toolmakers had an ape-like hand with a chimpanzee-like thumb, Wynn and McGrew similarly believed these hominins had an ape-like brain in terms of mental competency and spatial concepts (Wynn 1981; Wynn and McGrew 1989). Wynn and McGrew asserted that the "minimal competence" needed to make Oldowan tools was no greater than what extant chimpanzees possess (1989:384), and they further argued that chimpanzees in the wild do not intentionally flake stone tools likely because they do not need stone tools to process their food and/or other culture (Ibid:390). True, chimpanzees have managed to process their food by modifying sticks and other means, but to suggest that chimpanzees (like the early hominins) also had the cognitive ability to come up with the idea to make stone tools but deliberately decided against doing so seems unlikely.

Wynn's assessment of early hominin intelligence was based on Piaget's psychological theories of cognitive development in children, which focused on four stages (Wynn 1981). During the 1980s and early 1990s, neural science had not yet acquired the imaging technologies providing easy access for observing the various regions of the cerebral cortex of living conscious humans whilst engaged in a particular thought process or task. It is therefore not surprising that Wynn and others turned to psychological theory during this time as a means to *hypothesize* the neurological capacities and understandings of hominin brains using the brains of modern human children as proxies, which alone is problematic for the obvious reasons.

Wynn argued that early hominins were only able to cognitively process what Piaget refers to as "*pre-operational thinking*" versus concrete "*operational thinking*," and could only conceive simple spatial concepts (1981:532, 535; 1985:34,36). According to Piaget's four stages of cognitive development: (i) the *sensorimotor period* characterizes infants' understanding of the world from their physical interaction with it and represents the period from birth to two years old; (ii) in *pre-operational thinking*, which typically occurs when children are between two and seven years old, children begin to use symbols to represent objects and events, and; (iii) the concrete *operational period* develops between seven and ten years of age, whereby children acquire logical structures that enable them to perform many various mental operations and can conceptualize them also in reverse; (iv) during the *formal operational period* between the ages of 11 and 15, children essentially develop adult thinking with the ability to conceptualize abstract thinking and expectations regarding the future instead of only living in the present (Klahr 2012).

Piaget was a strikingly influential developmental psychologist during his time, especially after his works were translated into English in the late 1950s. Although his work was highly acclaimed from the 1960s well into the 1980s and early 1990s, modern child psychology has since moved beyond Piaget's stage theory to more of a 'spectrum' approach, which considers other factors involved in children's ability to learn, thus moving away from Piaget's broad, general explanations that now seem unlikely (Spencer *et al.* 2006; Klahr 2012). Furthermore, Esther Thelan argued that for both infants and adults, action and cognition cannot be separated as "cognition is inextricably linked to perception and movement," (Spencer *et al.* 2006:1529). Piaget was also criticized for his use of small sample sizes and lack of random sampling (e.g., using his own children) for his observations[1] and statistical analyses (Klahr 2012).

Wynn has acknowledged that Piaget's sample size was small but argues that for this reason, it is an ideal application for analysing the cognitive abilities (or lack thereof) of early hominins, considering how the cranial fossil record is also represented by a small sample size. This is essentially arguing that two wrongs make a right. Psychological hypotheses rely heavily on the observation and/or experimentation of a large sample size of *living* subjects, repeated over a substantial period of time in order to determine whether or not a significant statistical probability exists. Not only is Piagetian stage theory an inappropriate application for (hypothetically) assessing the cognitive capabilities of early hominins for these reasons, but also because modern human children are not acceptable substitutes for early hominin brains, any more than extant apes.

Finally, Wynn also suggests that early hominins struggled with spatial concepts which, he believes, did not develop until the Acheulean (Wynn 1979, 1995, 2002). Although this claim cannot currently be supported or dismissed from the scientific evidence in the cranial fossil record (i.e., endocasts), the postcranial fossil record suggests that early hominins still spent a high percentage of their time in the trees, which would likely require adept depth perception. Thus, it is more reasonable to assume that their limitations were linked mostly to postcranial deficits, such as the under development of grip strength in the index pads, which may have not *fully*

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[1] *Additionally, there are no available audio or video tapes of his observations, which is not unexpected considering that he began his research in the 1920s.*

developed until the Upper Palaeolithic, as previously suggested (Napier 1965:548; Marzke and Marzke 1997:98). Currently, there is no evidence in the fossil record to prove or dis-prove any of his psychological hypothesis, which Wynn concedes.

Not only does Wynn acknowledge the shortcomings in his various psychological arguments, but he also admits that "there is no way logically to eliminate the possibility that prehistoric Einsteins were making crude stone tools while speculating about general relativity" (1985:33). Although it is highly unlikely that the Lomekwi hominins were 'Einsteins contemplating the Theory of Relativity' whilst making poor quality stone tools, Wynn's point is well-taken in that we cannot possibly know what was happening in their *minds* based on psychological theory that typically observes/studies the behavioural *actions* of *living* subjects. Yet Wynn has, nevertheless, stood firm in both his views as well as his approach (e.g., using Piaget) even somewhat recently (Wynn 2002; Wynn *et al.* 2011; Coolidge, *et al.* 2015). Although the cognitive information extracted from brain endocasts is sparse and often ambiguous, it is nevertheless based on neural science, and the study of neural science informs us of the neurological structures that would have likely (or unlikely) been in place in order to produce stone tools. Although these neurological developments can be subject to interpretation, it is nevertheless interpretation based on the scientific neurological evidence provided by PET and fMRI brain scans, as well as other technologies.

Harmand *et al.* argue that the Lomekwi hominins not only possessed "substantial" motor control in their hands, but they also demonstrated how "the reorganization and/or expansion of several regions of the cerebral cortex (for example, somatosensory, visual, premotor and motor correct), cerebellum, and of the spinal tract could have occurred before 3.3 [mya]" (2015:314). Whilst I am not convinced that the motor control of their hands was, indeed, "substantial" as Harmand *et al.* insist, I concede that it is *possible* – especially if the parietal lobes had expanded and/or there was brain re-organisation by this date, as they suggest. Furthermore, even if their manual motor control was lacking, they were likely competent enough to compensate for whatever shortfalls may have been present in their hand/arm morphology, at least on some level (as did Abang and Kanzi).

However, the questions remain as to whether or not these early stool tools *effectively demonstrate* that the Lomekwi hominins were capable of: (i) choosing the proper raw materials for their end goals; (ii) determining the appropriate hammerstone for successful flaking; (iii) applying enough force with the hammerstone to the core; and (iv) learning where to strike the core platform in order to produce a successful flake for their needs; or if they were simply banging rocks together and hoping for the best. Considering the high percentage of failed flaking attempts among the Lomekwi tools, it is unlikely that they had developed any solid sense of fracture mechanics. Yet these early hominins were nevertheless experimenting with the production process, and although they did not appear cognitively astute in interpreting their mistakes and making corrections – they somehow had the innovation to come up with the idea of making stone tools for their needs and execute that process without the advantage of having an experienced tool-maker to observe and learn from, as did Abang and Kanzi. Regardless of how crude the end product may have been, it was nevertheless a better product than what Abang and Kanzi managed to produce with the benefit of teachers.

At this juncture in hominin evolution, brain size was only marginally larger than today's extant apes, ranging between 380 and 450 ml[1] (Holloway *et al.* 2004; Kimbel and Delezene 2009:20; Lewis and Harmand 2015:5; Toth and Schick 2018:7), thus, any cognitive innovation advancement, such as the idea to make tools from stone as well as the strategy to put that idea into action, was likely enabled by some form of brain reorganisation. Although the 2020 CT study by Gunz *et al.* provides

[1] *The Kenyanthropus Platyops cranium could not be measured, due to distortion.*

convincing evidence that the *lunate sulcus* had not yet relocated posteriorly in the occipital lobe in early Australopithecus, there are several other forms of brain reorganisation, including lateralisation, for example, which may have occurred. Additionally, there could be other development/reorganisation which occurred deeper within the brain, thus not capable of leaving evidence on the internal table of bone inside the cranium. The table in Figure 6.20 provides some examples of

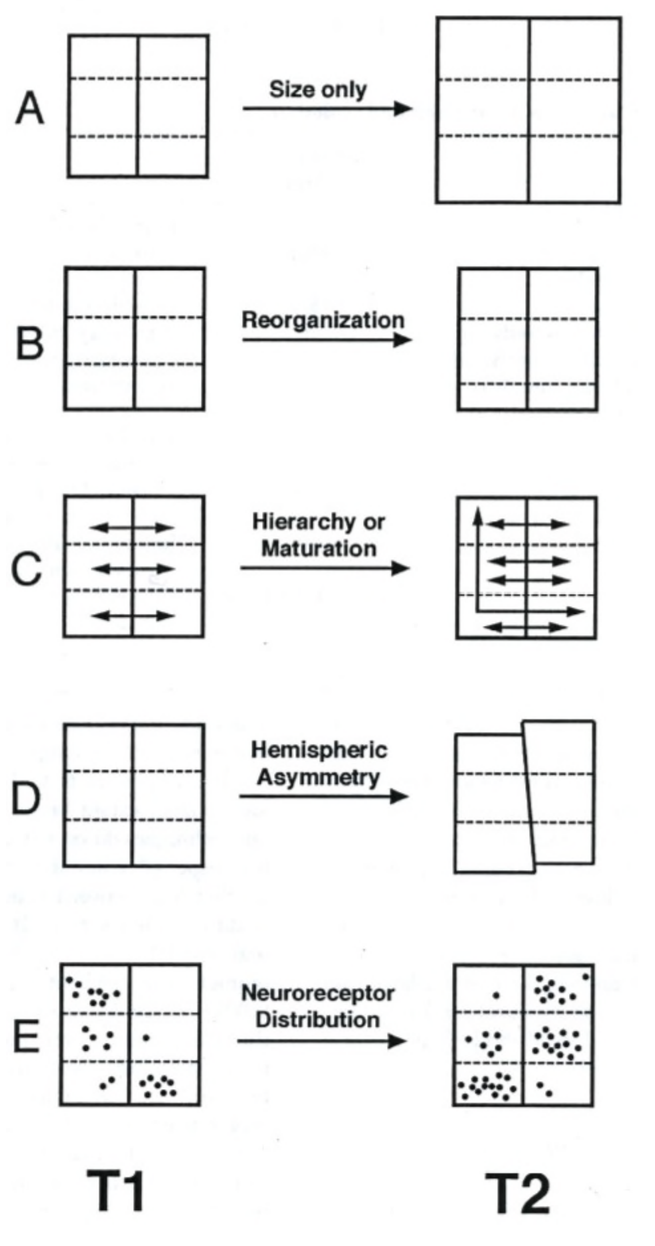	A. Increase in absolute size (isometric or allometric) without any other changes B. No change in absolute brain size, but change in size of components (i.e., some components expand whilst others contract.) C: No change in absolute brain size, but changes in neural fibre development, either maturing at different rates and/or increasing in number between cortical regions D: No change in absolute brain size, but a more an asymmetrical petalia pattern emerges hemi-spherically (i.e., left occipital, right frontal). E. No change in absolute brain size, but there is a redistribution of neuroreceptors.

Fig. 6.20 Evolutionary possibilities for neural changes, developments, and reorganisation. Holloway et al. 2004:6

cognitive development/reorganisation which may have occurred at some point during the evolution process.

Unfortunately, no toolkits have been recovered representing the period between 3.3 mya and 2.6/2.5 mya. Thus, the next assemblage found would be the Gona Oldowan.

The Earliest Oldowan Toolkits[1] – Gona at 2.6 mya

Although the stone tools along the Kada Gona River (a tributary of the Awash River) were first recognized in the 1970s (Semaw *et al.* 1997; Quade 2004; Semaw 2006), the artefacts were not recovered or dated until the early 1990s, when archaeological excavations commenced in 1992 (Semaw *et al.* 2003). The Gona sites lie within the Afar Triangle of Ethiopia, adjacent to the Hadar region. The dating and other elements of the Hadar Formation Members were discussed in Chapter 5, which focused on the lower portion of the formation where many *A. afarensis* fossil remains were recovered (Quade et al. 2004; Stanford *et al.* 2017; Johanson *et al.* 2004; Kimbel *et al.* 2006).

In the early to mid-2000s, the uppermost portion of the Kada Hadar Member was re-classified as the "Busidima Formation," which is roughly 80 metres thick and dated to between 2.9/2.7 mya to 0.6 mya, whilst the Kada Hadar Member now encompasses stratigraphy dated between 3.18 and 2.9 /2.7mya (Quade *et al.* 2004:1531). The strata associated with the Gona sites comprise three sedimentary intervals within the Busidima Formation, and the sites have been dated to between 2.6 and 2.5 mya using magnetic polarity stratigraphy in combination with the ^{40}Ar/^{39}Ar dating of two corresponding vitric tuffs (Semaw 1997; Quade *et al.* 2004).

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[1] *Early Oldowan artifacts have also been recovered from Ledi-Geraru, Ethiopia dated to between 2.61 and 2.58, which may ultimately prove to be the oldest Oldowan following further studies to definitively identify the locally Gauss-Matuyama Chron transition.*

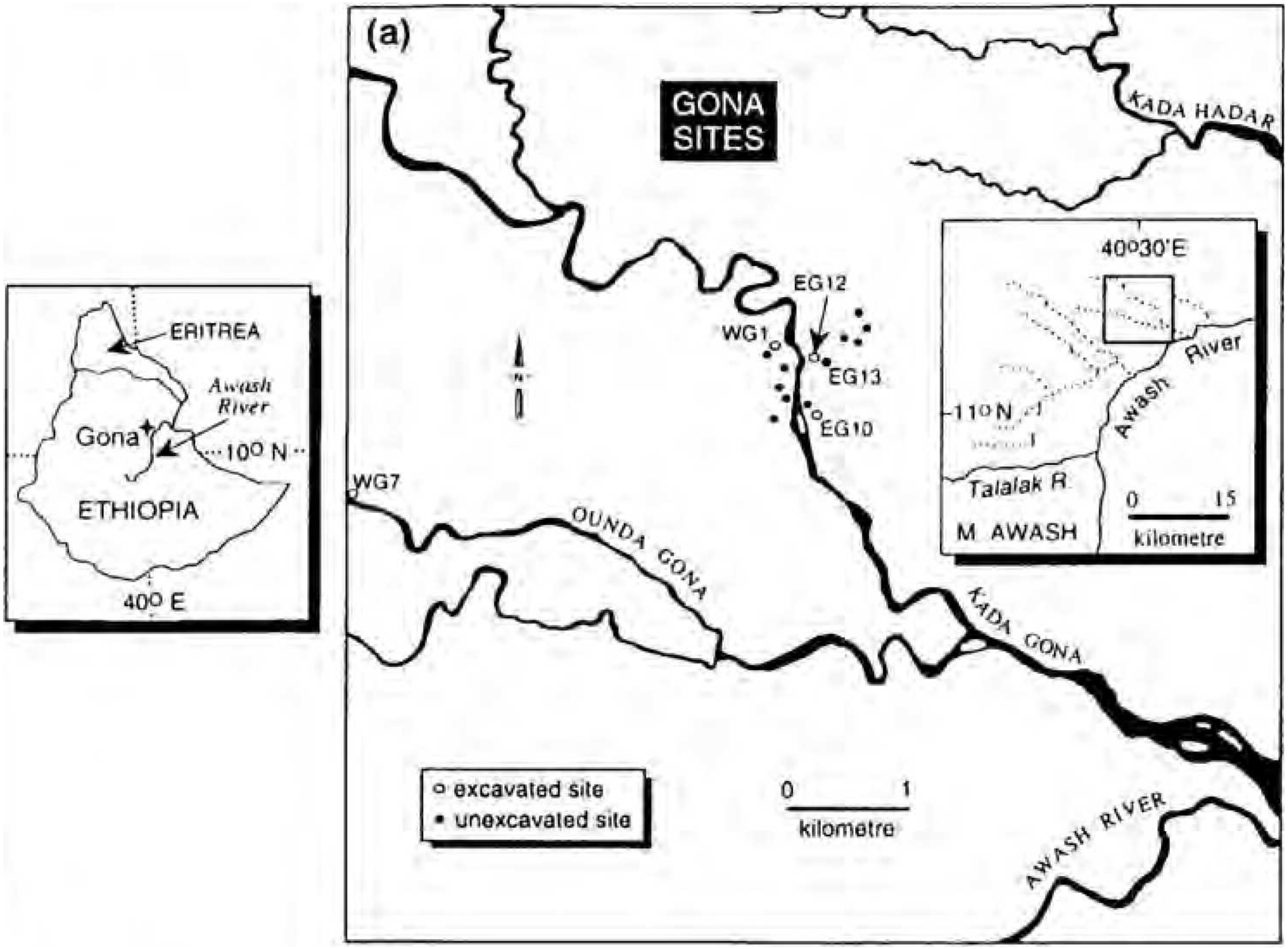

Fig. 6.21 Map of the Gona River basin with the locations of the archaeological sites Semaw et al. 1997:333

Between 1992 and 1994, over 3,000 surface and *in situ* artefacts were recovered from sites EG10 and EG12 with over 97% of the *débitage* consisting of whole flakes, broken flakes, and flaking debris (Semaw 1997; Semaw 2006). Most of the cores had numerous flake scars and had been predominantly flaked unifacially, but at least 35% of them were also bifacially flaked, with some of the cores being significantly reduced (Semaw 1997:335; Semaw 2006:69). Whole flakes were classified as those with obvious platforms, diagnostic bulbs of percussion and clear release surfaces, and such specimens number 110 (25%) from EG10 and 58 (34%) from EG12 (Semaw 2006:59). The majority (80%) of the whole flakes from EG10 were made from trachyte and the rest from rhyolite, basalt and other materials,

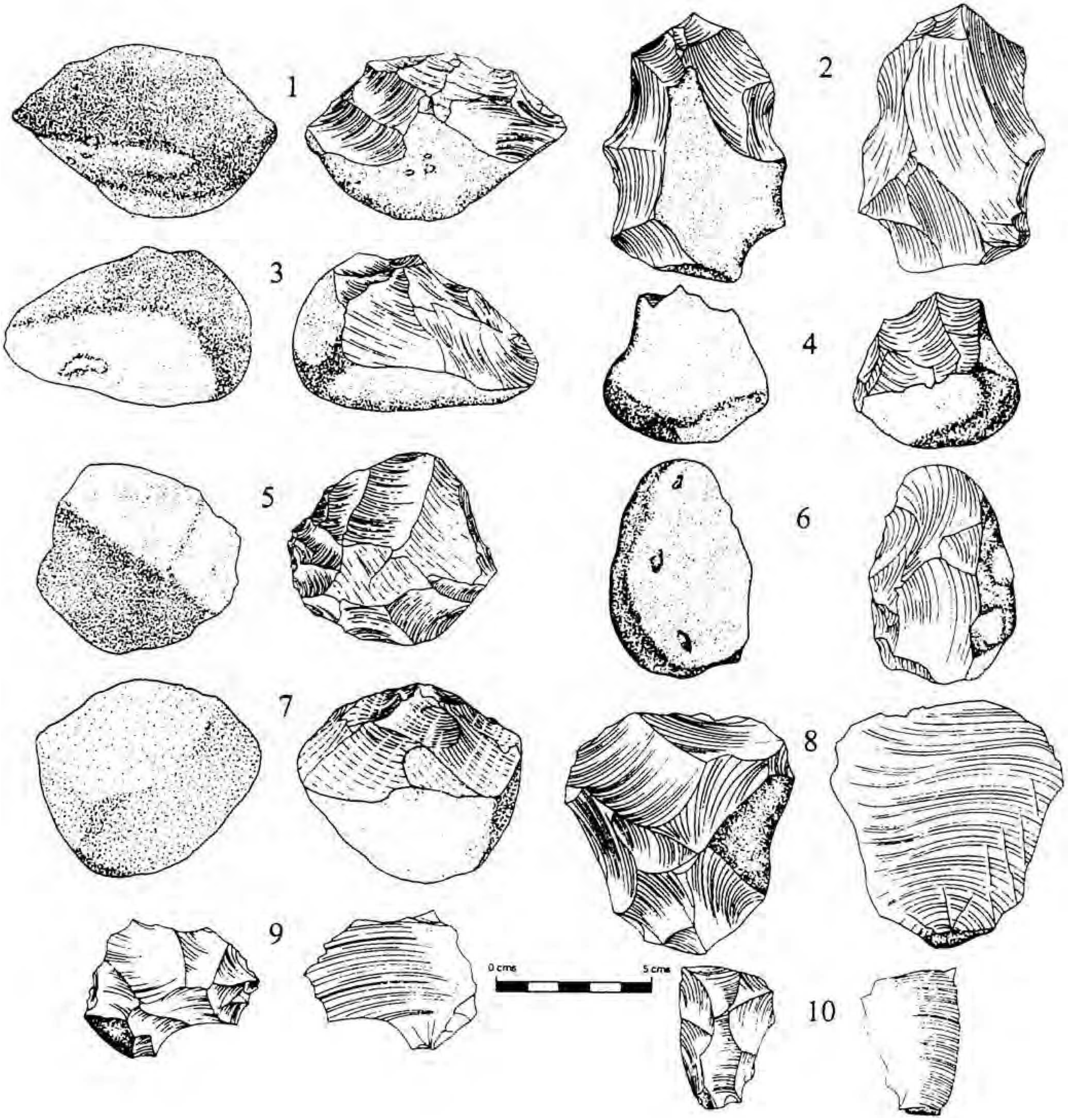

Fig. 6.22 Renderings of the Kada Gona tools from Sites EG10 and EG12
(1) Unifacial side chopper, (2) discoid, (3) unifacial side chopper, (4) unifacial end chopper,
(5) partial discoid, (6) unifacial side chopper, (7) unifacial side chopper, (8 – 10) whole flakes
Semaw 2006:61

Note: Although these renderings depict greater detail which would probably not be revealed in a photo, it is nevertheless questionable if unintentional enhancement may have occurred in the process.

whilst the whole flakes from EG12 were also made primarily (69%) from trachyte, 17% from rhyolite and the remainder from basalt and other materials (Ibid).

Semaw notes how most of the whole flakes exhibited very prominent bulbs of percussion, and he argues that the toolmakers had "excellent coordination and control over the core reduction processes" (Ibid). However, there were also a number of knapping accidents with at least one step/hinge termination on nearly 80% of the cores (Semaw 2006). Unfortunately, no hominin nor fauna fossils were found in association with the lithic artefacts (Ibid:69).

Nearby sites OGS-6 and OGS-7 in the Ounda Gona South, which are separated by approximately 300 metres, were excavated in 2000 and also yielded a number of interesting finds. Faunal fossils associated with the lithics, including rib fragments, were recovered *in situ* at OGS-7, whilst site OGS-6 produced artefacts but no bones, other than a fragment with cutmarks (Semaw *et al.* 2003). The OGS-7 assemblage includes seven cores – all bifacial and heavily reduced, 76 whole flakes, five side choppers, two end choppers plus 182 items of flaking debris (Semaw *et al.*2003). The largest core had a maximum dimension of 70 mm, and the average maximum

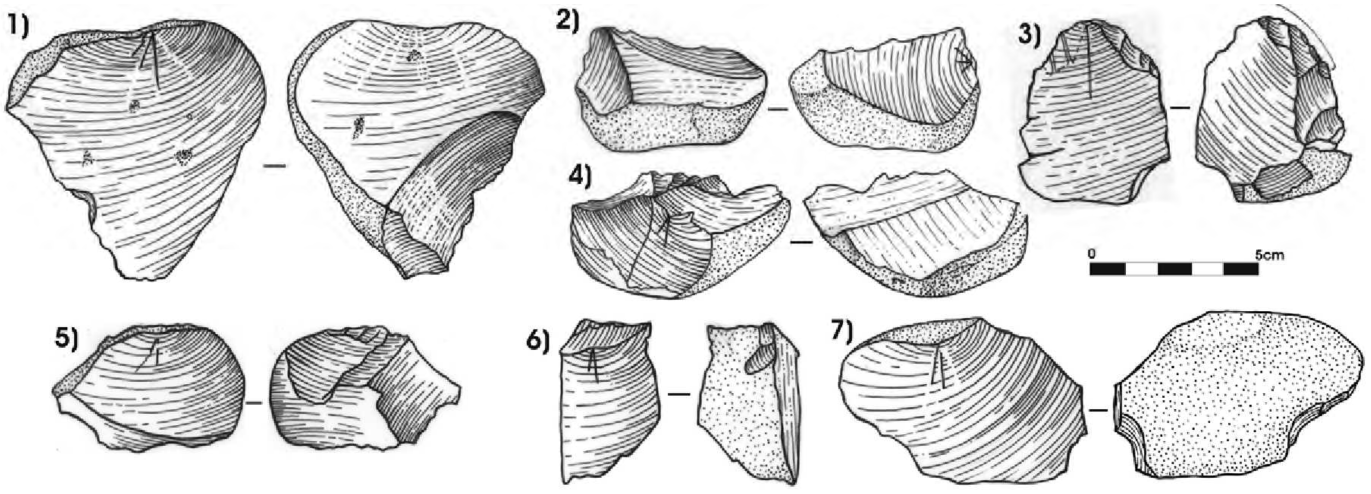

Fig. 6.23 Renderings of the Ounda Gona lithics from Site OGS-7
Drawings (2) and (4) are heavily reduced cores while the rest are whole flakes
Semaw et al. 2003:174

Fig. 6.24 Photos of the Ounda Gona lithics from Site OGS-7
The top three are cores whilst the bottom three are flakes
Photo by S. Semaw in Toth & Schick 2009:C-1

dimension was 63mm. They were a bit on the large size, but not as large as those recovered at EG-10 and EG-12, and certainly not as large as the cores found at Lomekwi. The raw materials employed at OGS-7 were primarily latite (29%) and trachyte (20%), although rhyolite, chert and others were also used (Ibid:175).

Like the Kada Gona sites, the Ounda Gona sites date to between 2.6 and 2.5 mya (Ibid:169-170). A volcanic tuff approximately seven metres directly above OGS-7 was dated by $^{40}Ar/^{39}Ar$ to 2.53 ±0.15 mya, whilst a geomagnetic polarity transition was traced immediately beneath the excavation to the Gauss-Matuyama, which is dated to approximately 2.6 mya (Ibid). Although the Gona tools were simple in design and construction, there were several well struck flakes with distinct 'bulbs of percussion' as well as some deliberately retouched pieces, demonstrating that these early

Oldowan toolmakers had an understanding of conchoidal fracture mechanics and thus, had become more adept at tool-making compared to their Lomekwi predecessors. Additionally, the Gona toolkits seem to demonstrate more intense and uniform reduction sequences as well as greater accuracy in knapping than the tools found in Olduvai Bed I, which are roughly 500,000 years *younger* than the Gona toolkit (Stout and Semaw 2006; de la Torre 2011).

Wynn *et al*., however, remain unimpressed with the Oldowan toolkit, insisting that the manufacture of these tools only served to "push" the standard of ape cognitive capabilities, concerning what he terms "ape grade adaptations," versus exceeding them, and they argue that the Oldowan should be considered more as a variation on an old theme (ape tools), rather than a new standard or grade (2011:195). Wynn *et al.* also stress how the Oldowan is only marginally more impressive than what extant apes accomplish through their use and modification of tools, and although they acknowledge that apes do not intentionally knap tools in the wild – they nevertheless do not consider tool manufacture by early hominins to be a "crossing of an evolutionary Rubicon" (Ibid:182). However, Wynn *et al.* do concede two advantageous characteristics of the early hominins over apes: (i) early hominins regularly carried tools a greater distance than extant apes; and (ii) early hominins competed both directly and indirectly with other carnivores (Ibid:195). I find it puzzling that Wynn *et al.* view neither the idea to make a stone tool using another stone nor the manufacture of the stone tools themselves as a significant cognitive development in hominin evolution.

Sussman, on the other hand, feels that "chimpanzee tool use [and tool modification] falls short of toolmaking of the kind we see in the residues of the Oldowan Industrial Complex" (Sussman 1995:589), whilst Toth and Schick further stress how "a variety of archaeological and paleo-neurological evidence indicate that Oldowan hominins represent a state of technological and cognitive complexity not seen in modern great apes transitional between a modern ape-like cognition and that of later *Homo*" (2018:3). It is possible that the views of Wynn *et al.* are influenced by a concept of 'humanness,' suggesting that perhaps they are measuring early hominin behaviour with a 'humanness' yardstick, in terms of context, and through this lens - the early Oldowan hominins fall woefully short of their standard for 'humanness.' For example, Wynn *et al.* insist that the "Oldowan was not a proto-human technology" and argue that there was nothing "humanlike" about it, and they additionally suggest that "human" should not be defined as the "ability to knap invasive flakes" (Wynn *et al.* 2011:195).

Although the importance they seem to place on a standard of 'humanness' is interesting, it is not a goal of this thesis to define 'humanness' nor measure cognitive change as a semiotic index of 'humanness' but rather to research, identify, and discuss the various transitions throughout hominin evolution that demonstrate evolutionary cognitive development through either the scientific and/or behavioural evidence. Furthermore, these possible cognitive developments appear to be better interpreted as occurring on a 'spectrum' versus a punctuated adaptation or 'crossing of the Rubicon,' perhaps to reach Wynn *et al.'s* definition of 'humanness' on the other side.

Gona Tool-makers

As mentioned in Chapter 5, the fossil record for early hominins in East Africa is rather sparse between 2.0 and 3.0 mya. Currently, the hominin with the closest association to the Gona tools, both spatially and temporally, is *Australopithecus garhi*, whose cranial fragments were recovered in the Bouri Formation, approximately 96 km south of the Gona site (Toth & Schick 2018; Wynn 2011). As a reminder, the entire *A. garhi* species is represented by these cranial fragments and a few postcranial remains, which date to approximately 2.5 mya (see Chapter 5). Although

96 km is not an infeasible distance, it remains possible that the tools were made by another yet-to-be-discovered hominin species. *A. garhi* is considered the most likely candidate for the tool-maker simply because it is currently the *only* known hominin candidate within reasonable proximity to the tools. The endocranial volume for *A. garhi* measured 450 ml, which is within the same range for *A. afarensis* albeit on the higher end of the range, but the endocast yielded no visible landmarks. As a result, there is no evidence to suggest any cognitive development other than the behavioural evidence of the Gona tools themselves, assuming that *A. garhi* is, indeed, their maker.

The Lokalalei LA1 and LA2C Toolkits – 2.34 mya

The Lokalalei archaeological area of interest consists of several site complexes within the Kalochoro Member of the Nachukui Formation in Kenya, some of which have yielded stone tool assemblages (Roche *et al.* 2003). The Kalochoro Member is comprised of the strata that lie between the base of the Kalochoro Tuff and the base of the KBS Tuff, and these strata correspond with Members of both the Shungura and Koobi Fora Formations (see Figure 6.4). The Kalochoro is approximately 87 metres thick and can be divided into three sections (lower, middle, and upper) based on sediments (Harris *et al.* 1988b; Tiercelin *et al.* 2010). The Kalochoro Tuff, which is "compositionally indistinguishable" with Tuff F of the Shungura, has been dated to 2.34 (± 0.02 to 0.04) mya (Harris *et al.*1988b:20; Feibel et al.1989:604; Tiercelin *et al.* 2010:161) whilst the KBS Tuff is dated to 1.88 ± 0.02 mya (Feibel *et al.* 1989:608; Tiercelin *et al.* 2010:161). The lower section of the Kalochoro, which is approximately 40 metres thick and consisting of sandstones and claystones, contains the two oldest Lokalalei sites where stone tools have been recovered and which are correlated by a mollusc-packed sandstone beneath both sites (Harmand 2009; Tiercelin *et al.* 2010).

In 1981, a research and survey team from the National Museums of Kenya, accompanied by geologists Frank Brown and John Harris, visited these areas West of Lake Turkana in order to undertake a geological mapping and palaeontological documentation program, which began in 1983 (Harris *et al.* 1988a; Harris *et al.* 1988b). A few years later, the Lokalalei 1 site (aka LA1 or GaJh5) was discovered by Brown and Harris, and test excavated in 1987 (Harris *et al.* 1988a; Kibunjia 1994; Kibunjia 1998). Lokalalei 1 is situated along the northern branch of the Lokalalei dry channel (Kibunjia 1992; 1994; 1998). Hence, the site was named for the Lokalalei ephemeral stream and not the Lokalalei Member of the Nachukui Formation, which coincidentally lies just below the Kalochoro Member (Kibunjia *et al.* 1992:435). The site is near the base of the Kalochoro Tuff (nine metres above) and was therefore dated to approximately the same age (2.34 ± 0.02 to 0.04), albeit slightly younger (Kibunjia 1992:432). In 1991, a team led by Mzalendo Kibunjia[1] extensively excavated Lokalalei 1 and recovered 392 lithics over an area of approximately 60 square feet, (Kibunjia 1998:41: Harmand 2009:92-93).

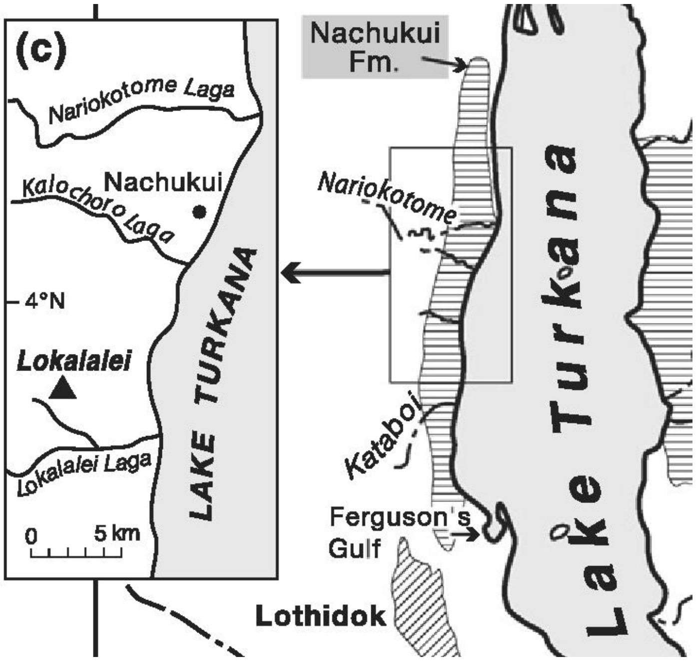

Fig. 6.25 Lokalalei, West of Lake Turkana
Tiercelin et al. 2010:159

The assemblage consists primarily of very crude cores of fine-grained lava (medium diameter = 120 mm), unmodified split cobbles, hammerstones, and flakes made mostly from trachyte and phonolite (Kibunjia 1992, 1998; Harmand 2009). Instead of round cobbles, the cores were prismatic in shape (Kibunjia 1994), and

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[1] *as part of Kibunjia's PhD studies at Rutgers University*

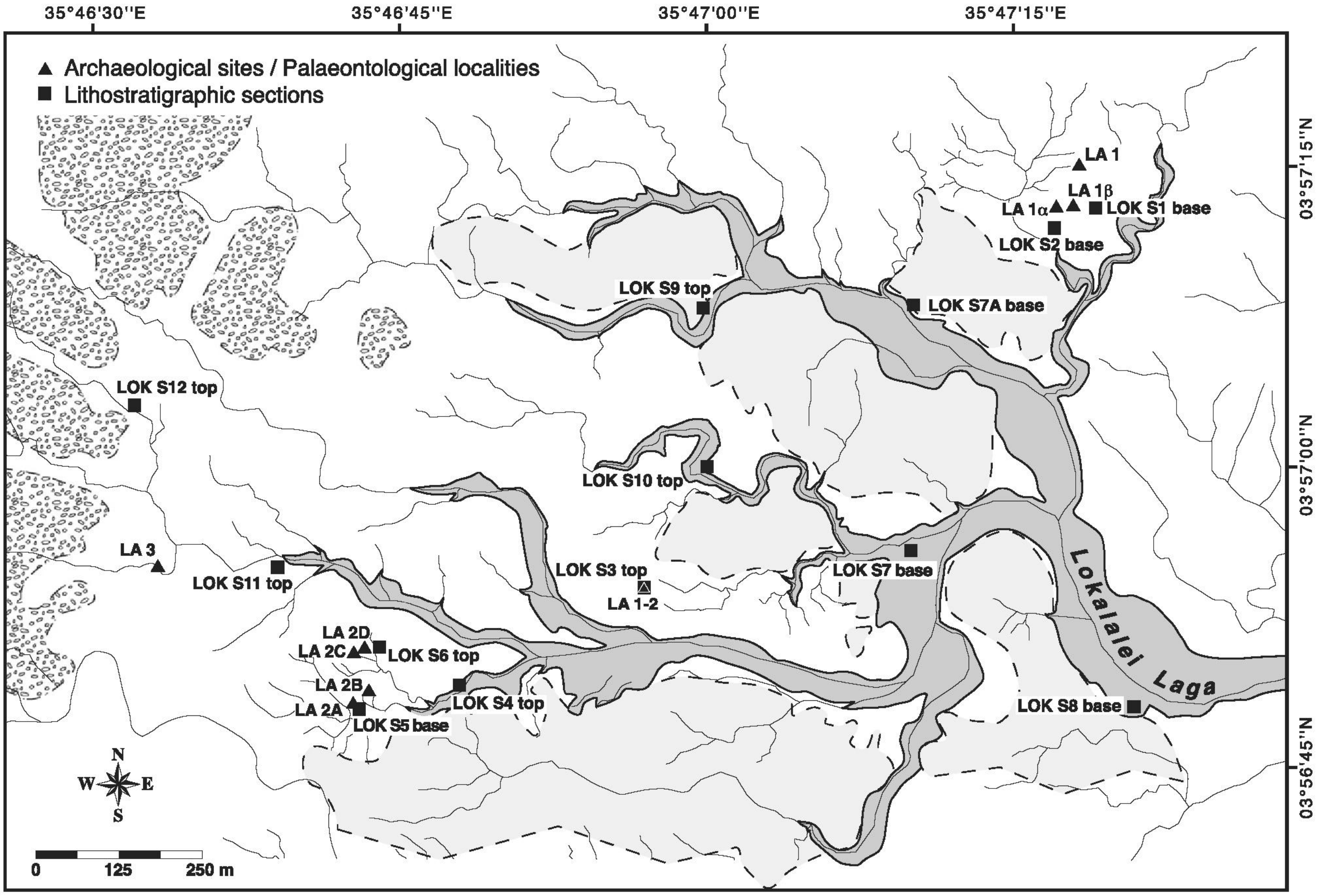

Fig. 6.26 Lokalalei Site Complex
Tiercelin et al. 2010:160

according to Harmand, 71% of the on-site cobbles surveyed had very few natural surfaces that would have served as a proper striking platform (2009). She additionally notes that there was no evidence of preparation on these less-desirable cobbles to create a suitable striking plane, which likely had a negative impact on the reduction sequences and flake production. As a result, only a relatively small number of acceptable whole flakes were found, and the majority of successful flakes (63) came from medium-grained phonolite while 47 flakes came from other rocks (Ibid). Whatever negative influence the poor raw materials may have had on the overall process, the cores were also poorly knapped, rife with flaking accidents and crude workmanship with randomly applied blows and sometimes with several different directions of percussion. It appears that the goal was (again) to produce flakes versus a tool created by core reduction as there was no shaping of the core and no cutting edge.

Most of the flakes produced were small, poorly formed and/or broken, and the cores exhibited between five and 20+ flaking scars, whereby removal often ended in step or hinge fractures (Kibunjia 1992). According to Kibunjia, the skill set was very poor and the overall practice appeared un-organized and random (Ibid). In general, the toolkit is unimpressive and not significantly more advanced than those found at Lomekwi. However, it is of particular interest not so much as an example of another early toolkit but rather because a more advanced, if not impressive, toolkit was found at another Lokalalei site within close proximity and dating approximately 74,000 years later.

During 1996 and 1997, the West Turkana Archaeological Project, which is a joint research organisation formed between the National Museums of Kenya and *Mission Préhistorique au Kenya* in 1996, excavated Lokalalei site 2C (aka LA2C or GaJh6) located approximately one kilometre away from LA 1 and slightly higher, stratigraphically (thus younger), in the Kalochoro Member (Roche *et al.* 1999; Harmand 2009). Initially, it was believed that 2C was only "marginally younger" than LA 1 (Delagnes and Roche 2005:439), but shortly after the 2C discovery, Brown and Gathogo argued that based on the higher position of 2C in the stratigraphy (11.2 metres above LA 1) as well as other geological conditions, 2C was likely closer to 100,000 years younger than LA 1 (2002:701). However, additional information obtained by Tiercelin *et al.* via researching and combining independent field data (including high-resolution lithostratigraphic studies), as well as estimating age differences based on sedimentation rates, indicated that the temporal difference between the two sites is approximately 74,000 years (2010:181), thus dating Lokalalei 2C to roughly 2.266 mya.

Nearly 3,000 finds were recovered of which the majority (2,624) were lithics, including 60 sets of "complementary matching" stone artefacts (Roche 1999:57; Delagnes and Roche 2005:437; Harmand 2009:87). This large sample set recovered from an area of approximately 17 square metres, reveal a number of interesting attributes with respect to the tool-makers. The lithics consisted primarily of cores, hammerstones and flakes plus a small number of unmodified split cobbles (Roche 1999; Delagnes and Roche 2005). Over 185 cobbles (or cobble fragments) were transported to the 2C site, of which between 90 and 95 were flaked, with 55 of these demonstrating an organised sequential knapping practice (Delagnes and Roche 2005), which resulted in the "extensive production" of a number of well-struck flakes (Harmand 2009:91). Although the end goal of these early tool-makers was the production of flakes, Delagnes and Roche believe that "core tools" may have sometimes served as a by-product, possibly as a means for processing local sustenance on site (2005:46). It is also likely at least some of the flakes were also used on site, based on evidence of retouch on 22 pieces.

According to Harmand, the medium-grained phonolite was favoured, which constituted approximately 52% of the on-site raw materials in Harmand's study on raw materials at Lokalalei 2C (2009). Harmand notes how phonolite has a natural 'foliation' and fractures easily along the foliation plane, thereby providing the knappers with a mechanical predictability in terms of fracture orientation (2009). Additionally, Delagnes and Roche argue that the 2C toolkit exhibited a more advanced knowledge of fracture mechanics than previously seen (2005). For example, ample force was applied with a great deal of accuracy with blows striking not too far/close to the edges at an ideal less-than-90^0 angle, and Delagnes and Roche further stress how the toolkit overall evinces the makers' manual dexterity, planning capabilities and consistency in their flaking process (Ibid).

Delagnes and Roche divide the artefacts into two sets based on either simple or organised technology ("simple *débitage*" versus "organised *débitage,*" as per the Inizan definition of *débitage*, previously discussed), whereas the simple set constitutes a small number of flakes and cores demonstrating simple technology (as well as split and unmodified cobbles), whilst the organised set demonstrates planning, strategy, fracture mechanics, dexterity, etc. as substantiated by the refitting group studies they performed[1] (2005). According to Delagnes and Roche, the refitting studies revealed that the organised *débitage* at 2C appeared to abide by a set of technical 'rules,' where flaking was performed on the largest available natural platform and sustained throughout reduction (Ibid). The natural platform was struck with sufficient force and at angles just under 90^0, and reduction was maximized by the knappers utilizing the entire perimeter of the platform. The knappers typically struck from the longest available edge, producing proportionately long flakes, and the number of flakes produced per series averaged between two and five, although there were examples of as many as 11 per series. Through "conscious planning" (according to Delagnes and Roche), the flaked surface of the core remained flat throughout the process until the core was abandoned (Ibid:466).

Although knapping accidents such as step fractures and hinges occurred, it appears that the knappers would often strike the core from the opposite direction as a means to correct any disfigurement (Ibid). Delagnes and Roche also stress how the manual dexterity of the 2C knappers was evident in the hammerstones, which show "highly circumscribed" battering marks from precise, recurrent motions (Ibid). Likewise, Harmand stresses that although raw material procurement/selectivity by the Lokalalei 1 knappers was largely limited to the quality available, the Lokalalei 2C knappers nevertheless displayed a much higher degree of planning and foresight

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[1] *Fewer artefacts were recovered from L1, thus refitting could not be established (Delagnes and Roche 2005:467).*

with respect to the procurement of quality raw materials, as well as strategies regarding how these raw materials would be deployed for extended reduction processes (2009).

Lokalalei Toolmakers

The disparity in technology between the two toolkits recovered at LA 1 and LA 2C is a bit perplexing, especially considering that the sites are separated by only one km and 74,000 years. Harmand offers two possible explanations for such a wide range of expertise when comparing the two toolkits. On one hand, it is possible the Lokalalei 1 knappers were primarily interested in rapidly producing a number of sharp cutting edges for their immediate needs (Harmand 2009), thus a goal of 'quantity over quality.' On the other hand, however, it is also possible the two toolkits were produced by two different species with different morphologies and cognitive abilities. Among the known hominin species in East Africa at the time, there are several potential candidates who may have been responsible for one or both of the toolkits at Lokalalei.

Although *A. garhi* is a possibility, only a few fossil specimens belonging to a single individual were recovered at Bouri, which is over 1,000 kilometres from the Lokalalei sites (see Figure 6.27). As discussed, *A. garhi* has been characterised as dating to roughly 2.5 mya with an endocranial volume of approximately 450 ml. It was recognised as a separate species due to: (i) its postcanine teeth, which are much larger than *A. afarensis* or *A. africanus*; and (ii) its primitive frontal, facial, palatal and sub-nasal morphology, which distinguish it from later or contemporaneous species (Asfaw *et al.* 1999:631). Significantly closer to both Lokalalei sites, the two *P. aethiopicus* specimens (mandible KNM-WT-16005 and cranium KNM-WT-17000) recovered from the Lokalalei Member of the Nachukui, date to 2.41 ± 0.05 mya and 2.5 mya, respectively, whilst the Lokalalei 1 and 2C toolkits date to approximately

2.34 and 2.266 mya, respectfully. The mandible and cranium specimens were found within relatively close proximity to the north of the Lokalalei site complex (see Figure 6.27), thus establishing the presence of *P. aethiopicus* in the area. As mentioned, it is believed that *P. aethiopicus* began to derive anagenetically into *P. boisei* around 2.3 mya, if not sooner. However, there are not enough *P. aethiopicus* specimens to better estimate when this process occurred. Although it is possible that *P. aethiopicus* made *both* toolkits; it is also possible that (i) the anagenetic evolutionary process began sooner, and *P. boisei* made both toolkits; or (ii) *P. aethiopicus* or a plesiomorphic form of *P. boisei* made the first toolkit at LA 1, and 74,000 years later – a more derived *P. boisei* made the second toolkit at LA 2C; or (iii) the toolkits were made by a different species all together.

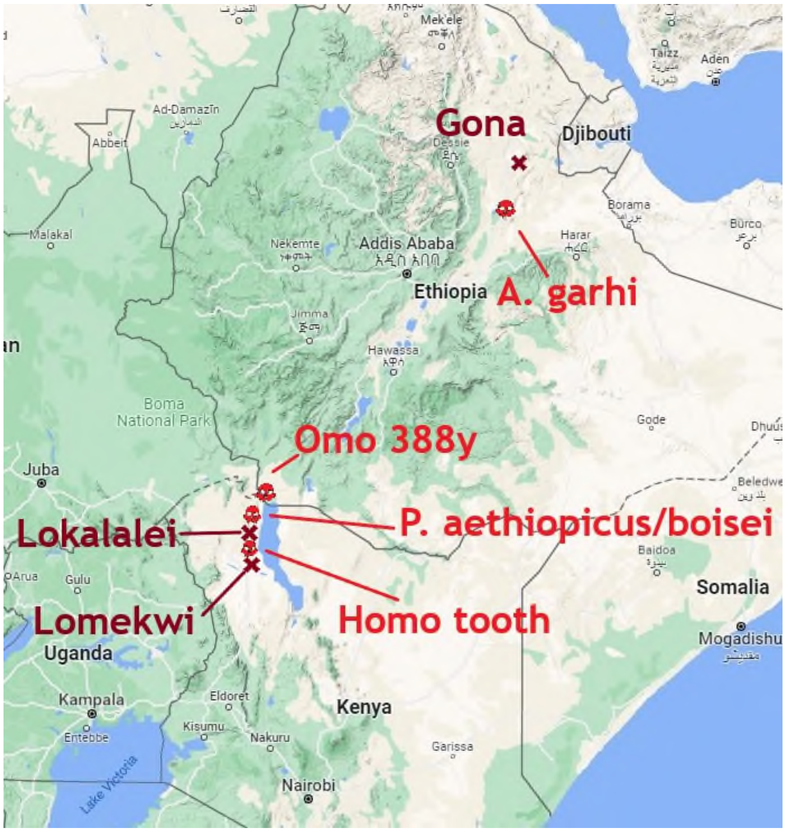

Fig. 6.27 Tool-making sites and hominin fossil sites
Not to scale: The Paranthropus specimens and Homo tooth are within close proximity of the Lokalalei site complex
Map downloaded from Google maps
Modification with sites by Suzi Wilson

Although we cannot conclusively determine who made the tools recovered from Gona or Lokalalei 2C, it is apparent that these toolkits demonstrate a significant technological improvement over the Lomekwian toolkit as well as those found at LA1, if not most of the Oldowan toolkits from other sites (including Olduvai Gorge at 500,000 years younger), suggesting some form of cognitive advancement and possibly some postcranial development in the hands, arms and shoulders, as well.

The toolmakers clearly possessed a good working knowledge of fracture mechanics, and selected raw materials which could be knapped with a reasonable expectation of predictability.

Blows were applied accurately with sufficient force and at the proper angle. When mistakes were made, the knappers would attempt to correct the core by striking it from the opposite direction, then continue working the surface through an organised reduction process until the core was abandoned. These hominins did not just come up with an idea then haphazardly attempt to bring it into fruition. There was clear planning, first from selecting cores with naturally flat planes from raw materials, known to fracture well and with predictability, followed by a strategy for reduction which was executed with a precision not previously seen. These toolkits were significantly better than the Lomekwian industry and far superior to 'ape-grade.'

Endocasts of the Potential Toolmakers

An endocast was made from the *P. aethiopicus* KNM-WT-17000 cranium, which unfortunately provides no markings in terms of sulci and gyri to observe. However, endocranial volume was measured as approximately 410 in volume, which is less than *A. garhi* but within the range expected for the earlier australopithecines (Walker *et al.* 1986:519, 253; Walker and R. Leakey 1988:253; Holloway *et al.* 2004:102). Other than endocranial volume, the KNM-WT-17000 endocast yields little other information other than what appears to be a slight left occipital/right frontal petalia, suggesting some level of brain lateralisation.

Evidence of another hominin from East Africa within reasonable proximity of the Lokalalei toolkit sites and dated slightly earlier, was recovered by de Heinzelin toward the end of the 1969 field season from locality 338y within Member E (E-3) of the Shungura Formation, which is approximately 90 km to the north of the Lokalalei

Fig. 6.28 KNM-WT-17000 Endocast mould, right lateral view
Photo by Suzi Wilson

site complex (Rak and Howell 1978:345). The partial cranium (specimen L338y-6) consists of both parietals and occipital bone, which belonged to a juvenile hominin aged to between eight and twelve-years-old, based on the absence of spheno-occipital synchondrosal fusion (Ibid:346).

At the time of its discovery, the specimen was dated to between 2.1 and 2.2 mya and believed by most (including Rak and Howell) to be *P. boisei*, based largely on the (interpolated) age of Member E in the Shungura, from the potassium/argon dating of the volcanic tuffs of Members D and F, above and below. During the late 1980s, however, the formations of the Omo-Turkana basin were more precisely dated using new technologies[1] (see following page), and Member E was determined to represent a somewhat older age range of between 2.40 ± 0.05 (Tuff E) and 2.32 ± 0.02 (Tuff F) (Feibel *et al.* 1989:605), thus corresponding with the upper portion of

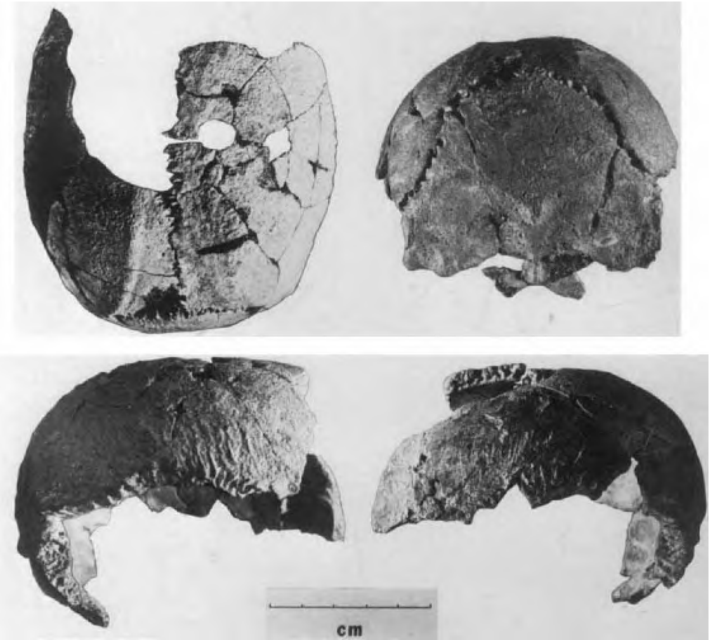

Fig. 6.29 Partial Cranium Omo L338y-6
Rak and Howell 1978:348

the Lokalalei Member and the lower portion of the Kalochoro Member of the Nachukui Formation. Specimen Omo L338y-6 was recovered from submember E-3 and was therefore re-dated to between 2.4 and 2.36 mya (Feibel *et al.* 1989:617; Wood and Constantino 2007:112), thus making it another potential candidate as the tool-maker for either (or both) assemblages. Holloway reconstructed the cranium to make an endocast, which measured 427 ml in volume via water displacement (Holloway 1981:110). Had Omo L338y-6 lived to adulthood, Holloway predicted that endocranial volume would be approximately 448 ml (Ibid:118). The cerebellum lobes appear somewhat rounded and there are a few sulcal impressions on the endocast, but there is a slight left occipital petalia. Unfortunately, the corresponding right frontal section of the skull was missing.

There is also what appears to be a small segment of the interparietal sulcus and posterior to that, there is a small depression which is likely an indention caused by the edge of the parietal bone. If so, this feature would support Rak and Howell's original taxonomy assessment of the specimen as *P. boisei* considering that one of the defining traits of both *P. aethiopicus* and *P. boisei* is the overlapping and striated

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[1] *By 1989, Feibel, Brown and McDougall had partially resolved a variance between previous dating and the boundaries of the magnetic polarity time scale using lithostratigraphy, geochemical correlation, paleomagnetic stratigraphy and isotopic dating (1989:595) with a focus on the relationships between depositional, eruptive and magnetization ages as well as taking into account the time lag between a volcanic eruption and the time that eruptive products are transported back to the basin and deposited (1989:601).*

Fig. 6.30 Omo L338y-6 Endocast mould, posterior view
Photo by Suzi Wilson

squamosal suture pattern (as well as a heart-shaped foramen magnum) (Rak and Howell 1978; Walker and R. Leakey 1988; White and Falk 1999). The possibility also exists that it could be a portion of the *lunate sulcus*; however, there are too few sulcal markings to support this feature, and the parsimonious explanation is that the depression was made by the lip of the parietal bone, considering that this trait is known to exists in two of the possible toolmaking candidates. Neither Holloway nor I could find any evidence of an enlarged occipital marginal sinus, but White and Falk insist that an enlarged occipital marginal sinus is present (1999:405). Whilst the presence of an enlarged occipital marginal sinus does not particularly offer any relevant information regarding cognition or brain re-organisation, it does play an important role with respect to the species controversy over Omo L338y-6.

Although Rak and Howell initially believed it was likely a *P. boisei* specimen, it has been very difficult to conclusively confirm its taxonomy, in part because it is a juvenile, and cranial features change and develop with age. Additionally, no dentition or mandible has been recovered, making it even more difficult to identify a juvenile species during this period with such wide variation within and among species. Holloway has argued that Omo L338y-6 specimen was more likely a gracile australopithecine, similar to *A. afarensis* or *A. africanus* for several reasons, but particularly because the brain volume was so much lower (nearly 25% lower) than the later *P. boisei* specimens (Holloway 1981; Walker and R. Leakey 1988). He also suggests that the cerebellar lobes are more rounded than the paranthropines, thus more similar to the gracile australopithecines, and he additional notes the absence of occipital and/or marginal sinuses in other robust specimens such as OH5 (Holloway 1981).

Finally, Holloway argues that the meningeal patterns on Omo L338y-6 present further similarities between the specimen and the gracile species, based on Saban's 1978 study of meningeal patterns (Holloway 1981:117). Holloway acknowledges that none of his assessments, individually or as a whole, would justify refuting Rak and Howell's classification of L338y-6 as a *P. boisei* nor conclusively confirm the taxonomy of the specimen as one of the gracile species (Ibid), but his observations nevertheless highlight some of the issues in assessing taxonomy during a time when there is so much variation (and speciation), especially when the specimen in question is a juvenile with no fossil dentition.

In 1988, Walker and R. Leakey agreed with Rak and Howell's initial taxonomic assessment, arguing that Omo L338y-6 is a *P. boisei* based on cranial morphology, namely the overlapping striated squamosal suture and a heart-shaped foramen magnum, which are unique to the *P. aethiopicus* and *P. boisei* lineage, and they additionally noted the similarities between Omo L338y-6 and KNM-WT-1700 crania, arguing that KNM-WT-1700 should also be considered within the variation of *P. boisei,* unless and until future finds demonstrate otherwise (1988). In contrast, Kimbel *et al.* argued for the validity of *P. aethiopicus* as a separate species and noted that the KNM-WT-1700 cranium has retained several primitive traits in common with *A. afarensis* whilst sharing only two derived characters with *P. boisei* (and Omo L338y-6), which are the heart-shaped foramen magnum and the squamosal suture overlap at the asterion (1988).

Others agree with Walker and R. Leakey on the similarities between the two crania, but argue that both specimens should be considered *P. aethiopicus* – not *P. boisei* (Suwa *et al.* 1996; Wood and Constantino 2007; Wood and M.G. Leakey 2011). More recently, Holloway shared that he is "more convinced more than ever" that Omo L338y-6 is *A. africanus* (personal conversation June 2021). The debate over its taxonomy will likely not be resolved anytime soon, unless and until additional fossil specimens are recovered. The argument over the significance of the various morphological features of specimen Omo L338y-6 provides an excellent example of the variation and speciation that occurred during this time period, which will be seen in other potential tool-making hominins in Chapter 7. Although the taxonomy of Omo L338y-6 cannot be conclusively determined, it nevertheless remains a potential candidate as the maker of at least one of the Lokalalei toolkits along with one final possibility.

In June 2002, a new palaeontological site was identified (Lokalalei α) within the Lokalalei complex and located just 100 metres south of Lokalalei 1. The new site is part of a yellow-beige clay siltstone near the top of the LOKS1 lithostratigraphic section at the base of the Kalochoro Member of the Nachukui and dated to 2.34 ± 0.04 mya based on the K/Ar and ^{40} Ar/^{39}Ar dating of the various East African tuffs, as well as estimated sedimentation rates (Prat *et al.* 2005). During the recovery of several *Cercopithecoid* fossils (old world monkeys) and other fauna, a well-preserved permanent right lower first molar belonging to a hominin was discovered and classified as specimen KNM-WT 42718.

A detailed metrical and morphological comparative study was performed where the specimen was measured and examined against data from *Homo*, *A. africanus*, *A. afarensis*, *A. anamensis*, and *P. boisei* samples. After a lengthy comparative process and evaluation, the molar was ultimately determined to belong to early *Homo* based on:

> "the relative small size of the crown, the existence of marked mesio-distal elongation and bucco-lingual reduction, the verticality of the buccal and lingual faces, the more triangular shape and relative position of the cusps, the lack of C6 [of the mandibular molars], and the mild expression of the protostylid [an accessory cusp on the buccal surface] reinforced by the results of the posterior probabilities [which] point to the distinctiveness of this tooth . . . and its similarity to early *Homo*" (Prat et al. 2005:238).

Thus, there are now four possibilities for the two Lokalalei toolkits. Although it is possible that one of these four species could have made at least one of the toolkits, it is also possible that the tools were made by an entirely different, even unknown, species. This discussion highlights how there were several species living within relatively close proximity to one another during a challenging period, marked by climate and other environmental changes and fluctuations, as well as disappearing food sources for all the mammalian species, which would have heavily impacted variation, speciation, and certainly extinction. Likewise, new species and genera emerged during this time as the result of new adaptive strategies.

Summary / Conclusion

Following alternating seasons of wet and dry periods since 5.0 mya, a long-term trend toward increasingly arid (and more variable) conditions began shortly after 3.0 mya, which peaked between 1.8 and 1.6 mya (de Menocal 2011:541). Also occurring around 3.0 mya, a cyclical glaciation period commenced which became quite severe at 2.5 mya (Vrba 1993; Stanford *et al.* 2017). As a result, the East African grasslands (i.e., C_4 or 'secondary' grasses) were expanding and creating more open landscapes, and this expansion continued until at least 1.8 mya (Reed 1997; de Menocal 2011; Bobe and Behrensmeyer 2004). Antón *et al*. argue that it was a "synthesis" of these and other factors which caused a variable and dynamic environment, particularly in East Africa, which created a changing landscape with "fluctuating moisture and aridity, shifting resource regimes, and spatial heterogeneity" as well as a wide diversity for vegetation in this setting (2014:7). These factors contributed to the competition for resources and sustenance (among all mammals), and likely served as the evolutionary drivers for the high concentration of variation, speciations, and extinctions that seemed to culminate around 2.5 mya (2014:7).

These and other studies indicate that whilst the early hominins (up to *P. aethiopicus*) had remained largely in closed forested environments, later *Paranthropus* expanded to slightly more open habitats with wetlands (Reed 1997; Antón *et al.* 2014). However, it was not until the emergence of early *Homo* that hominins adapted to live in a wider range of environments, whilst only later *Homo* (i.e., *erectus*) had acquired the ability to live in extremely arid and open landscapes (Reed 1997:318; Antón *et al.* 2014:8-10). Thus, these hominins truly had to either (i) 'eat their way out,' by adapting a megadontia eating machine, powered by the impressive muscles of mastication, thus enabling them to eat otherwise difficult foods to chew/consume; or (ii) 'think their way out' by developing a better tool technology to help them procure, process and protect food sources. Although the Oldowan artefacts were not particularly pretty or impressive, they nevertheless provided sharp cutting tools that fulfilled hominin needs at the time. Furthermore, there were a few exceptional examples of quality Oldowan tools, such those from Gona and Lokalalei 2C. These artefacts demonstrate that their knappers employed a higher degree of planning and foresight (than previously seen) for the procurement of quality raw materials, as well as how to best use these materials for extended reduction processes whereby they maximized the entire perimeter of the core, which remained flat throughout reduction until abandoned. Although mistakes occurred, they tried to correct them by striking the core from the opposite direction.

We may not be able to identify the species who made these tools, but these knappers would have likely had more derived hands and arms to deliver the blows with such manual dexterity. Their conscious planning also suggests that cognitively, there was some form of development or reorganisation in their frontal cortex, their motor cortices, and the areas in the parietals for visuo-spatial expertise, giving them the ability to better procure resources and sustenance with their Oldowan tools and avoid extinction. At 2.5 mya (approximately), *A. afarensis* was extinct, *A. aethiopicus* had likely begun the process of anagenetically evolving into *A. boisei*, *A. africanus* was still in the picture, *A. garhi* had appeared in Bouri in East Africa, and early *Homo* was emerging in the forms of *H. habilis* and *H. rudolfensis.* Although many believe that *Homo* may have begun to derive as early as 3 mya, there is little in the fossil record to trace/evince this provenance, other than a few *Homo* dentition fossils (including a partial mandible) recovered in Ethiopia, dating to between 2.6 and 2.9 mya (Villmoare 2015; Simpson 2015; Stanford *et al.* 2017). This provenance, as well as whether or not the earliest *Homo* specimens evinced the derived morphological to warrant a new genus, will be discussed further in the following chapter.

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Chapter 7: The Rise of *Homo*

In the presence of Chris Stringer and Mark Lewis of the Natural History Museum we matched, for the first time in 150 years, the photograph with the [Acheulean handaxe] artefact. It was immediately apparent that this was the stone that shattered the time barrier. *~Gamble and Kruszynski (2009:469)*

The Emergence of *Homo* (sensu lato)

The general morphology that separates early *Homo* from *Australopithecus* includes a larger braincase with a smaller, more orthognathic (i.e., 'flatter') face, as well as smaller teeth. Early *Homo* bodies were larger and better adapted to bipedalism than the australopithecines, but their locomotion was not as fully developed as the *H. erectus* striding gait. As discussed in Chapter 6, there was an increase in variation, speciation and extinctions which began around 3.0 mya and peaked at about 2.5 mya, roughly around the time of the emergence of early *Homo*, although many believe that *Homo* may have begun to emerge as early as 2.8 mya, if not sooner (Villmoare *et al.* 2015:1352; Simpson 2015:143; Stanford *et al.* 2017:333).

Also discussed in Chapters 5 and 6, it is often difficult to accurately identify a plesiomorphic hominin who is in the process of evolving into a new species, especially among a small sample size, and thus, there has been and continues to be, a great deal of debate over the proper zoological classification(s) for early *Homo* given their wide range of variation. For example, *H. rudolfensis* had a much larger brain than *H. habilis*, yet some feel that *H. habilis* and *H. rudolfensis* represent one species with substantial sexual dimorphism, which would account for the difference in brain size, allometrically (Mayr 1950; Wolpoff 1971), whilst others argue they are separate *Homo* species (R. Leakey and Walker 1976; Wood 1986; Stringer 1986; Lieberman *et al.* 1988; Falk 1983; Rightmire 1993; Blumenschine *et al.* 2003). Still others believe that these pre-erectus hominins are australopithecines and thus refer to them as "habilines" or "*Australopithecus habilis*" (Cartmill and Smith 2009; Hunt 2015), whilst

Robinson insisted that OH7 and the other hominins in Olduvai Bed I represented *Australopithecus africanus* (1960, 1965, 1966). Wood and Collard argue that despite the somewhat expanded braincase, more rounded cranial vaults, flatter faces, and smaller jaws/dentition, early *Homo* is far from the extensive cranial and postcranial growth seen in *H. erectus* (1999). Indeed, early *Homo* is still fairly ape-like in a number of ways, and none of the specimens present a *significantly* different postcranial morphology than the later australopiths. There is also debate over what to call/classify the early/plesiomorphic *Homo erectus* fossils, which similarly exhibit a great deal of variation. These issues will be discussed further in the examinations of the individual specimens.

Sympatric Hominins between 1.88 and 1.4 mya

The first pre-sapien *Homo* fossils, other than the Neanderthal remains found in Germany, were found on the East Java province of Trinil in Indonesia by former Dutch army surgeon Eugène Dubois in 1891 and 1892 (Dubois 1896:241). Dubois considered the fossil finds, which consisted of a calvaria, a femur, and two molar teeth, to represent a species in between man and the apes, and thus named it *Pithecanthropus*[1] *erectus* (also called 'Java Man') meaning 'erect ape-man' (Dubois 1896:241), which would later be subsumed into *Homo erectus* (Mayr 1944, 1950; Antón 2003).

Homo erectus fossils would not be found in Africa until April of 1949, when Robinson recovered a slender mandible with small molars in the same Transvaal cave near Swartkrans, where he and Broom had recovered *Paranthropus robustus* fossil specimens (Broom and Robinson 1949). The specimen SK 15 is indeed more gracile than the mandibles of the australopiths and/or paranthropines, leading

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[1] *The name Pithecanthropus was coined earlier by the German zoologist Ernst Haeckel*

Broom and Robinson to refer to it as 'more human,' and thus giving it the name *Telanthropus capensis* (man from the Cape), which was also later subsumed into *Homo erectus* (Broom and Robinson 1949; Mayr 1950; Robinson 1953; Antón 2003; Cartmill and Smith 2009). However, it was debated during the 1970s whether the SK 15 mandible truly represented *H. erectus* versus a young or female (or both) *Paranthropus*, and there were also questions regarding its initial dating of between 2.0 and 1.5 mya (Tobias 1978). Following the discovery of OH7 at Olduvai, the debate was expanded to include the possibility SK 15 mandible might represent *H. habilis* (L. Leakey *et al.* 1964). Meanwhile, additional *Homo erectus* fossil specimens would continue to be found in Africa, Asia and other areas, which ranged in age from as early as 2.04 to 1.95 mya (with the recent discovery of Drimolen cranium DNH 134 in South Africa) to as late as 100 kya and possibly as recent as 50,000 kya in Asia (Feibel *et al.* 1989; Swisher *et al.* 1996; Antón 2003; Herries *et al.* 2020). Yet, the 'almost human-like' morphology of *Homo erectus* seemed quite the evolutionary leap from the ape-like morphology of the australopithecines. Thus, when the *Homo habilis* specimen OH7 was recovered from the uppermost portion of Bed I of Olduvai Gorge by the Leakey team in 1960 and dated to approximately 1.8 mya, it was evident that this juvenile gracile skeleton, comprised of a mandible with teeth, parietal bones, and 15 hand bones (described in Chapter 6) was not the same species as the other hominin (*P. boisei* OH5) also found in Bed I. Yet, it was also clear that the OH7 postcranial morphology was not nearly as derived as *Homo erectus* (L. Leakey 1960b; Napier 1962a; L. Leakey *et al.* 1964; Tobias 1991).

The OH7 dentition reflected an age of approximately 12 to 13 years old, with an adult endocranial volume estimated at roughly 680 ml[1] (Tobias 1991:535; Cartmill

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[1] *In 1991, Tobias had estimated 674 ml as an adult whilst in 2004, Holloway et al. estimated 687 ml (Holloway 2004:144).*

and Smith 2009:217; Holloway *et al.* 2004:144). More recently, Spoor *et al.* have provided an adult estimation of between 729 and 824 ml, based on digital reconstruction and measurement (2015:83). Regardless of the revised (and increased) endocranial volume produced by Spoor *et al.,* even the earlier, smaller estimate of 680 ml would indicate a substantially larger brain than previously seen in any of the earlier hominin species prior to *H. erectus*. Its mandible was gracile, the cheek teeth were small and the P_3 premolars appeared closer in appearance to modern bicuspids than the large 'molarised' appearance of the australopith teeth (Cartmill and Smith 2009). Finally, the tip of the thumb was observed to be fully opposable to the tip of the index finger and with a full range of motion, which provided the juvenile specimen OH7 with what Napier and Leakey *et al.* referred to as a "precision grip" (Napier 1962a:411; Leakey *et al.* 1964:7).

Although the stone tools found in association with OH7 may have played a role in the classification of the new species *Homo habilis*, the designation of any new taxon should depend upon the nature of the morphological adaptations and not collateral behavioural adaptations (Stanford *et al.* 2017:333). However, the increase in brain size, smaller teeth/face and the dexterity of the OH7 hand seemingly presented a reasonable argument for the new taxon, yet many scholars disagreed (and continue to disagree) based on the primitive post-cranial morphology of early *Homo*. There has also been debate over the methods employed for estimating the considerably larger endocranial volume of OH7.

Wolpoff insisted that cranial capacity cannot be measured reliably when based on cranial fragments (1969, 1970) and additionally argued (along with Brace) that both parietals had been found "crushed flat" thus providing no evidence for calculation (Wolpoff and Brace 1975:62). In response, Holloway argued that they were not "crushed flat" and had, in fact, retained their curvature, thus providing arcs for estimating volume (1980:271). Although most of the Olduvai crania suffered

Fig. 7.1 OH7 Cranium, anterior view
Photo by Suzi Wilson

from some level of distortion or damage, the image in Figure 7.1 shows the condition and shape of the OH7 parietals, which were clearly not flat as Wolpoff and Brace maintained. Holloway corrected for the distortion via stereo-plotting, calculated a new range of estimated endocranial volume between 700 and 750 ml and additionally expressed his belief that the specimen belonged to the *Homo* genus (Holloway 1980:273). In spite of the evidence, Wolpoff continued to argue that the parietals were too flat to measure, criticised a number of Holloway's methods and insisted that the cranial volume for OH7 was overstated (1981).

However, present-day digital technology, such as that employed by Spoor *et al.* (2015) for OH7, is not only capable of measuring endocranial volume to a high degree of accuracy but also for correcting distortion, which has confirmed that substantial brain growth in *H. habilis* OH7 indeed occurred, based on their calculated estimate of between 729 and 824 ml. Irrespective of brain volume, the debate over how these early *Homo* hominins should be phylogenetically classified continues. Wood and Collard argue that a genus "should be defined as a species, or monophylum, whose members occupy a single adaptive zone" (1999:66), but the issue for early *Homo* (as well as early *H. erectus*) remains just how and where to *recognize* the 'adaptive zone' and thus, the origin of the genus, especially when considering how these traits most likely evolved in a mosaic fashion (Antón 2012:S279).

The individual crania, endocasts and associated stone tools of interest will be presented somewhat chronologically (to the extent practical) and/or regionally, versus by species, and as based on relevance with respect to potential cognitive abilities for making stone tools. Some, but not all, of the paranthropine specimens will be included as reference points for comparative purposes, during the period between 1.88 and 1.5 mya when *P. boisei*, *P. robustus*, *H. habilis*, *H. rudolfensis* and *H. erectus* lived contemporaneously in Africa. The co-existence of these sympatric hominins likely created a competitive environment for resources and thus, prompted various adaptations as a means to survive. However, by 1.5 mya, *P. robustus* had gone extinct, followed shortly thereafter by *H. habilis/H. rudolfensis* at approximately 1.44 (Hunt 2015:115). The last paranthropine, *P. boisei,* managed to survive until 1.4 mya, leaving *H. ergaster/erectus*[1] as the last man standing (Toth and Schick 2018:9).

The phylogenetic identification issues discussed above, as well as the difficulty in interpreting morphological features for species specific traits among a small sample size, is well illustrated by the following five crania recovered from the Koobi Fora Formation:

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[1] *The name H. ergaster has been used to designate early H. erectus forms found only in Africa. Recent literature more commonly uses the name H. erectus for both, as will this thesis moving forward.*

Specimen	**Location**	**MYA**	**Age/Sex**	**Brain Volume**	**Description**
H. rudolfensis KNM-ER 1470	Koobi Fora	2.03		750 to 775 ml	Over 150 reconstructed fragments
H. habilis KNM-ER 1813	Koobi Fora	1.88	Possibly female	509 ml	Mostly complete but fragmented
H. rudolfensis KNM-ER 3732	Koobi Fora	1.88		750 to 800 ml	Right parietal, left & central portion occipital
H. rudolfensis KNM-ER-1590	Koobi Fora	1.88	juvenile	800 to 850 ml	Dorsal portion
H. habilis KNM-ER-1805	Koobi Fora	1.8 to 1.55		582	Calvaria and facial portion

Koobi Fora Formation

The first European to explore the region east of Lake Turkana was Count Samuel Teleki, an Austro-Hungarian geographer, who originally named the lake "Rudolf" in 1888 for Emperor Franz Josef's son (Walker and R. Leakey 1978). During the 20th century, geological investigations were initiated in 1969 as part of the National Museums of Kenya expedition that began in 1968, largely at the behest of R.E.F. Leakey after he had noticed the potentially fossil-bearing terrain while flying over it in 1967, and shortly after he had become the Director of the National Museums of Kenya (Bowen and Vondra 1973; Walker and R. Leakey 1978). The initial description of the sediments in this region were provided by Ana Behrensmeyer in 1970, whose work was continued in the early 1970s by Bowen and Vondra in collaboration with Ian Findlater (Walker and R. Leakey 1978; Brown and Feibel 1986).

The Koobi Fora Formation lies east of Lake Turkana, across the lake from the Shungura and Nachukui Formations to the northwest and west, respectively. As previously mentioned, these formations compose a single depositional system in the Omo-Turkana basin and correlate with one another (see Figure 6.4 in Chapter 6). The Koobi Fora Formation is approximately 560 metres thick, subdivided into eight members and exposed over an area of roughly 80 km by 40 km, consisting primarily of sands, silts and clays (Cerling and Brown 1982; McDougall 1985; Brown and Feibel 1986; McDougall and Brown 2006), of which approximately 800 square kilometres were deemed to be fossil-bearing sediments (Walker and R. Leakey 1978). It is overlain by what was originally known as the Guomde Formation, which included the strata from the top of the Chari Tuff on the Ileret ridge to the grey tuffaceous siltstones (up to 40 metres thick in segments), whilst a lower formation, previously referred to as the Kubi Algi, lay beneath the Koobi Fora Formation (Bowen and Vondra 1973; McDougall 1985). Both the Guomde and Kubi Algi formations were later subsumed within the Koobi Fora Formation.

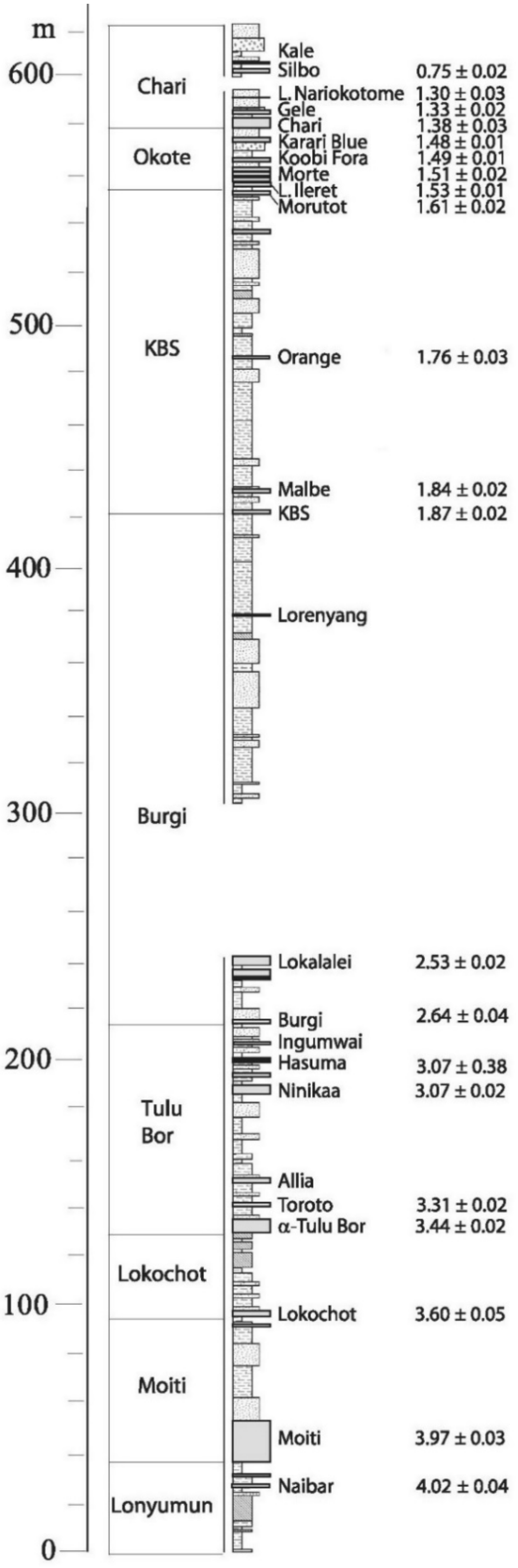

Fig. 7.2 Revised Koobi Fora Formation
Lepre and Kent 2015:101

Following McDougall's work (1985), whereby he dated the alkali feldspar crystals within the tuffs as a means to resolve the correlation issues among the Omo-Turkana formations (see Chapter 6), Brown and Feibel revised the stratigraphy of Koobi Fora by further defining and correlating the intervals of the strata in between the volcanic ash layers via the chemical fingerprinting of the distinctive chemical composition volcanic glasses (1986; McDougall and Brown 2006). Chemical fingerprinting is a process which analyses a test sample for a particular combination of elemental and isotopic characteristics that would link that pattern (aka 'fingerprint') to a geological formation (Kamber 2009:1075). As a result, the volcanic tuffs were correlated to provide stratigraphic boundaries between the members. The eruptive age of the Lokochot Tuff was estimated as 3.956 mya, based on the mean ages of feldspars from three pumice clasts, which is supported by its horizon below the Gilbert-Gauss Chron boundary, with an estimated age of 3.57 ± 0.05 mya (McDougall and Brown 2008). In 2012, McDougall *et al.* further improved the Omo-Turkana time scale with new ages for the Naibar and Orange Tuffs in Koobi Fora and Tuff K in the Shungura, and also provided revised age estimates for many of the hominin specimens (McDougal *et al.* 2012).

KNM-ER 1470 - *H. rudolfensis* 1.88 mya

The cranial fragments of specimen KNM-ER 1470 were collected from Area 131 of the Koobi Fora Formation during the 1972 field season of the Koobi Fora Research Project (KFRP) (Day *et al.* 1975). Area 131 consists of approximately 30 square kilometres of lacustrine and fluvial sediments with several volcanic tuffs within its vicinity, the lowest of which are the Tulu-Bor Tuff (not exposed, but outcropping nearby) and the KBS Tuff at a slightly higher elevation (Day *et al.* 1975; R. Leakey 1973). The fragments were found by Bernard Kgeneo, a Kenyan member of the KFRP team, who noticed a large assemblage of bone fragments washing down the sloped side of a gully (R. Leakey 1973). Over 150 fragments were recovered to reconstruct the cranium, which was initially dated to 2.9 mya, based on what was (at that time) believed to be the "secure dating" of the KBS volcanic tuff at 2.6 mya (R. Leakey 1973:447). However, following the subsequent stratigraphic studies mentioned above, the dating for the KBS Tuff was revised to 1.87 ± 0.02 mya (McDougall and Brown 2006; McDougall *et al.* 2012), and the age for specimen KNM-ER 1470 has been revised to 2.03 mya based on its lower horizon from the KBS Tuff (McDougall *et al.* 2012).

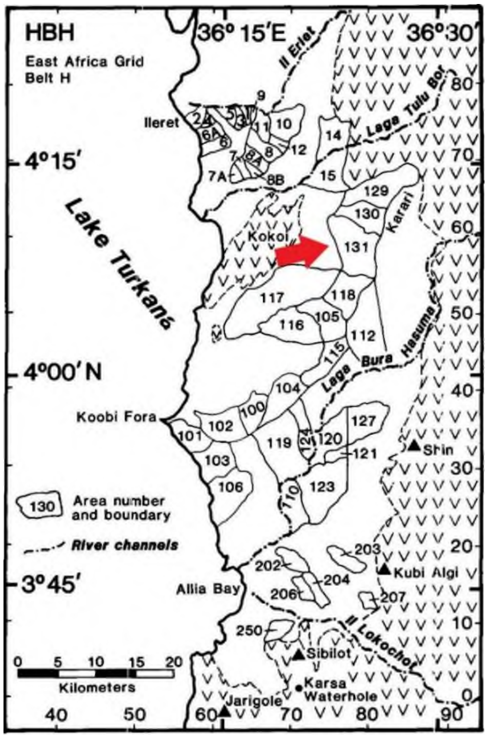

Fig. 7.3 Area 131 of Koobi Fora
McDougall 1985:160

The orientation of the face is somewhat uncertain due to distortion (especially on the right side) and missing pieces, but it appears to be more orthognathic compared to the projected prognathic faces of the earlier hominin species, and the supraorbital ridges are not particularly prominent (R. Leakey 1973; Day *et al.* 1975). The cranial vault is domed with steeply sloping sides, although there are parietal eminences (i.e., rounded elevations or *tuber parietale*) at their centres. No teeth were recovered but several of the roots have been preserved (Day *et al.* 1975). According to Day *et al.*, the canine and second molar (M^2) roots appear fully closed, and "the extensive pneumatisation of the frontal and maxillary air sinuses, together with the developed mastoid air cells" indicate an adult (1975:465).

Fig. 7.4 KNM-ER 1470 face
Leakey 1973:449

Walker initially calculated the endocranial volume as approximately 810 ml using water displacement (R. Leakey 1973:449). However, based on later measurements and correction for distortion, it is more likely between 750 and 775 ml – still a big brain at 2.03 mya (Day *et al.* 1975:461; Holloway *et al.* 2004:123; Antón 2012:335; Stanford *et al.* 2017:335). Unfortunately, no meaningful postcranial fossils associated with KNM-ER 1470 were recovered for estimating body size and thus, how much of this brain size was allometric with a potentially large body. Although the specimen was initially assigned to *H. habilis*, it was later given its own designation as *H. rudolfensis* (to be discussed).

Fig. 7.5 KNM-ER 1470 Cranium, left lateral view
Photo by Suzi Wilson

The endocast has several features of interest. First, a fronto-orbital sulcus cannot be detected, and the Broca's area is more developed in the left hemisphere, as it is in 95% of modern humans. Although difficult to discern, there do appear to be ascending sulci ('southeast' of the green dot in Figure 7.6) which may be delineating the boundaries of BA 45 in Broca's area, also observed by Holloway and Falk (Holloway *et al.* 2004:123-124; Falk 1983:1072). Falk describes this derived configuration as very similar to the same Broca pattern found in modern humans, although she also points out how the anterior ascending ramus of the lateral fissure (aalf) and the horizontal ascending ramus of the lateral fissure (half),[1] which

Fig. 7.6 KNM-ER 1470 Endocast mould, left lateral view
Photo by Suzi Wilson

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[1] *Technically, she referred to them as the "horizontal and ascending branches of the Sylvian sulcus" (R' and R, respectively), the common terminology in the 1980s.*

delineate the pars triangularis (aka BA 45), appear slightly narrower than the condition typically seen in modern humans, but she also acknowledges that a great deal of variation in Broca's area is not uncommon (1983:1073).

Additionally, it appears that the operculum has now covered more of the insula compared to what was seen in *A. sediba* (Figure 7.7) and there is a visible Sylvian notch (Figures 7.9 and 7.10), initially detected by Hurst (2017:127). Regarding the variation of the sulci in the Broca area among modern humans today, recent medical studies indicate that there are at least three typical sulci patterns, which are illustrated in Figure 7.11 (Sprung-Much and Petrides 2018, 2020; Wang *et al.* 2022). In addition to the 'aalf' (in orange in Figure 7.11) and 'half' sulci, which delineate the pars triangularis (BA 45), there are also the sulcus diagonalis (in purple), which lies within the pars opercularis, and the sulcus triangularis (labelled 't' or 'ts' and anterior to the aalf) which lies *within* the pars triangularis – both of which are not always visible on modern humans (Sprung-Much and Petrides 2018, 2020). Thus, it is often very difficult to accurately define which sulcus is which, especially during their evolution in hominins, as well as during foetal development.

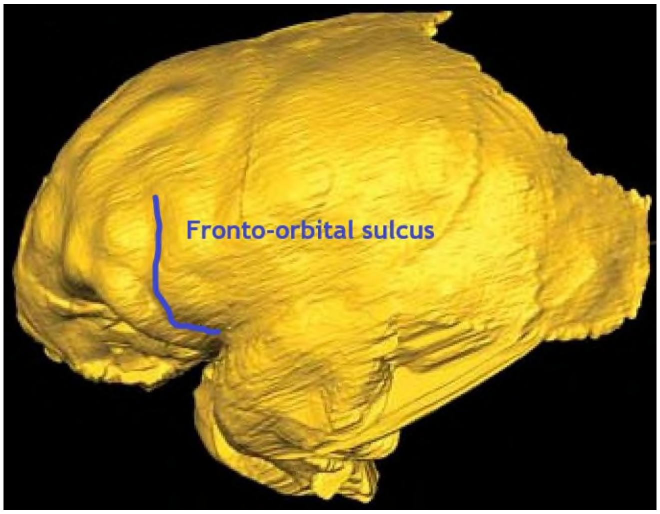

Fig. 7.7 MH1 A. sediba endocast
Remaining fronto-orbital sulcus
Carlson et al. 2011:1402
Modifications by Suzi Wilson

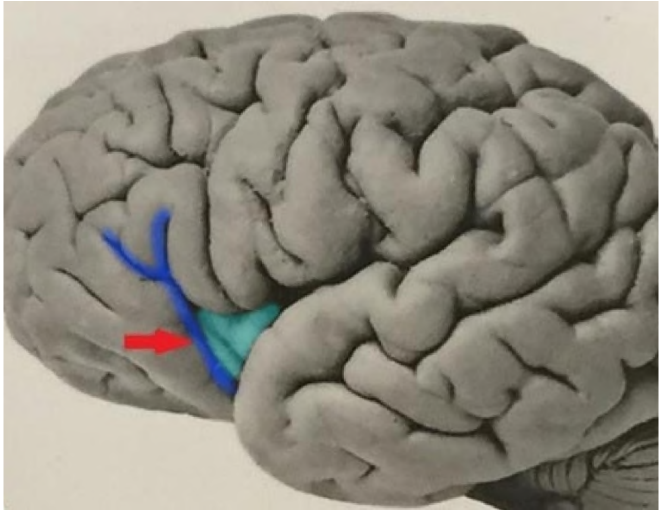

Fig. 7.8 Human foetus (eight months)
Fronto-orbital sulcus and Sylvian notch
Hurst 2017:125 (from Retzius 1896)
Modifications by Hurst

Fig. 7.9 KNM-ER 1470 Endocast mould of left lateral view without labels/modifications
Photo by Suzi Wilson

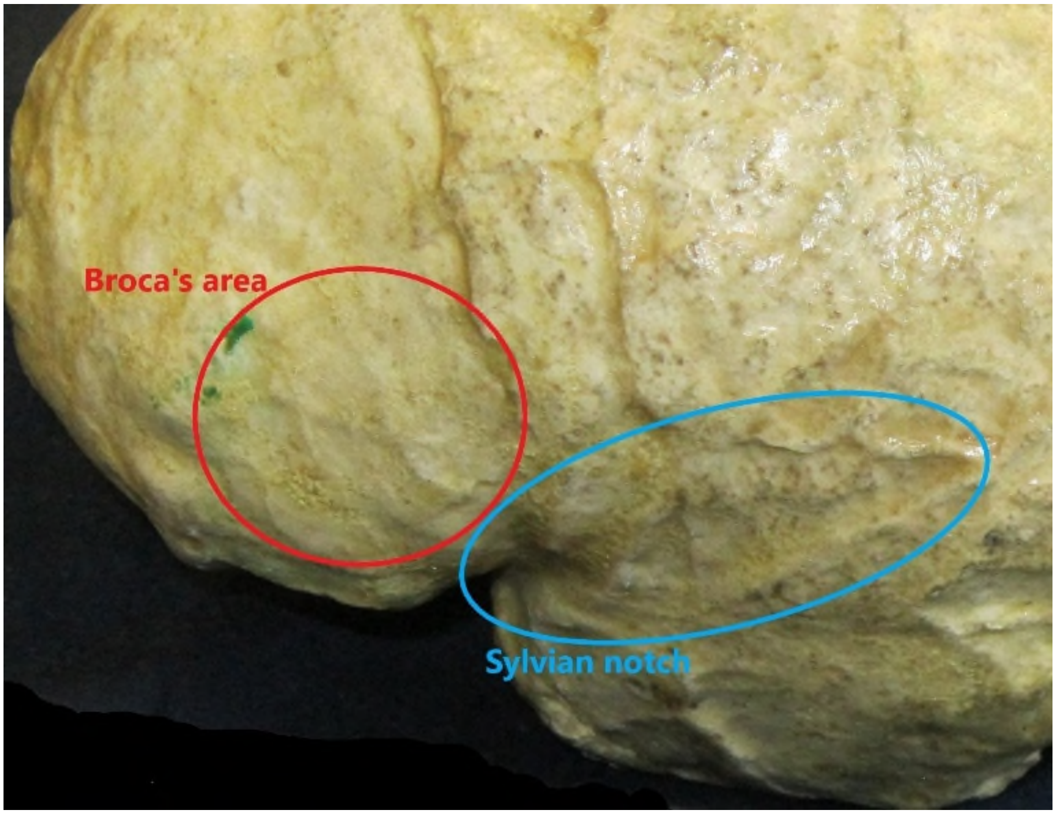

Fig. 7.10 KNM-ER 1470 Endocast mould, *BA 45 sulci and Sylvian notch*
Photo/modifications by Suzi Wilson

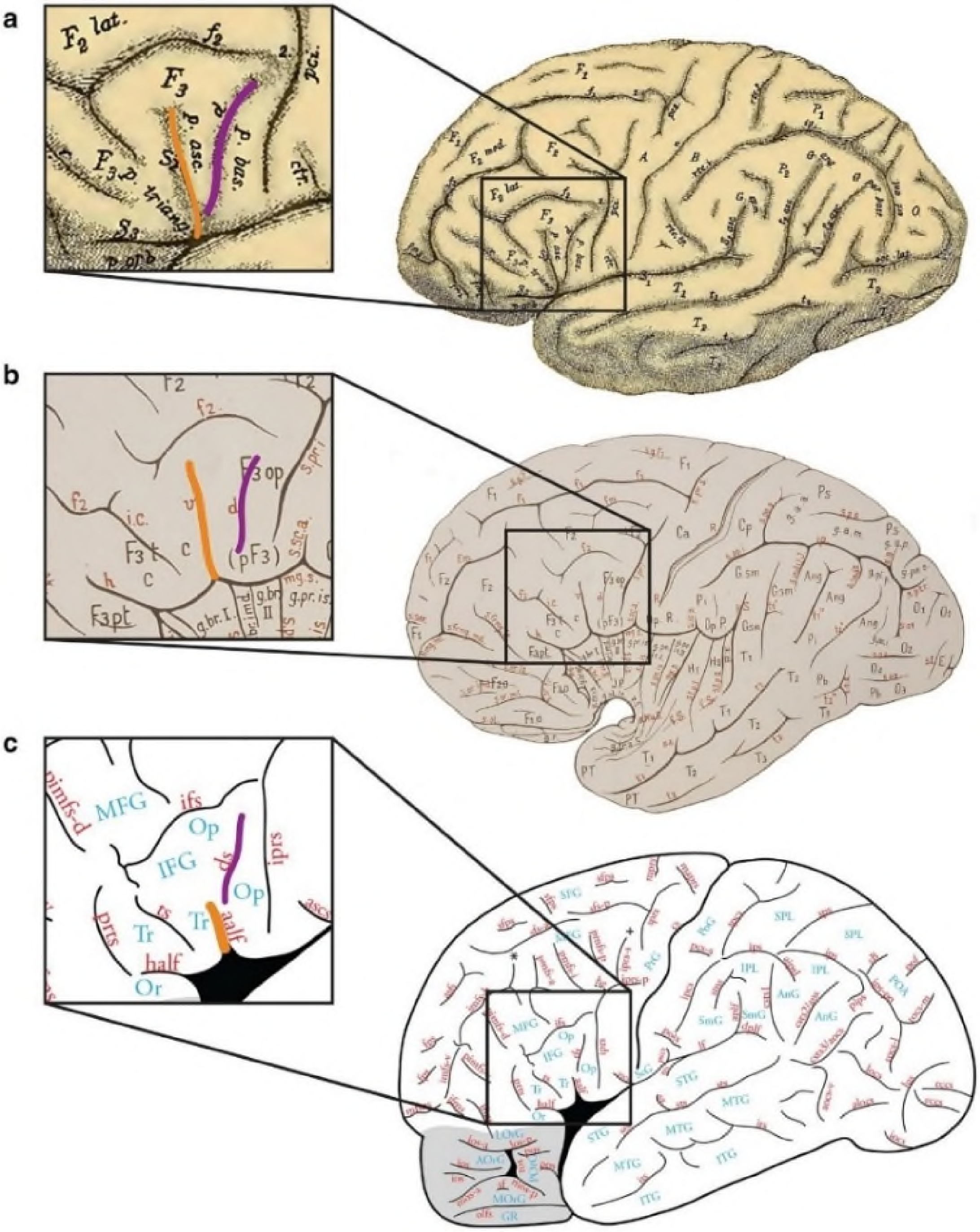

Fig. 7.11 Variation in the Broca region sulci patterns
Sprung-Much and Petrides 2018:4126

Finally, there is also a very evident left occipital/right frontal petalia in both width and projection, suggesting right-handedness.

KNM-ER 1813 - *H. habilis* 1.8 to 1.55 mya

Specimen KNM-ER 1813 is another fragmented cranium, found by Kamoya Kimeu with the KFRP *in situ* in Area 123 (south of Area 131 in Figure 7.3) of the Koobi Fora Formation (R. Leakey 1974). The frontal bones are curved and the teeth are small, most of which have been preserved. The endocranial volume was estimated at 500 ml and later measured as 509 ml by Holloway via water displacement, although Benazzi *et al.* calculated a lower volume of 478 ml via digital reconstruction (R. Leakey 1974:655; Holloway *et al.* 2004:125; Benazzi *et al.* 2014:158). Either way, this endocranial volume is not much larger than the later australopithecine brains.

Fig. 7.12 KNM-ER 1813 Cranium (reconstructed)
Photo by Suzi Wilson

Although initially dated to 1.88 mya, the stratigraphic chronology of Area 123 was revised in 2006 by Gathogo and Brown, who believe that KNM-ER 1813 is a younger hominin dated to 1.65 mya (2006a:473). If so, this would make KNM-ER 1813 the youngest *Homo habilis* at Koobi Fora and possibly contemporary with *Homo erectus* specimen KNM-ER 3733. However, Suwa *et al.* caution that the Gathogo and Brown revisions assume a constant depositional rate for a composite section and advise how it is not uncommon for gaps of ~400k years to occur with "no obvious erosional unconformities" when comparing to sequences with more continuous depositional records (2007:136). Accordingly, they suggest a conservative range for KNM-ER 1813 between ~1.8 and 1.55 mya.

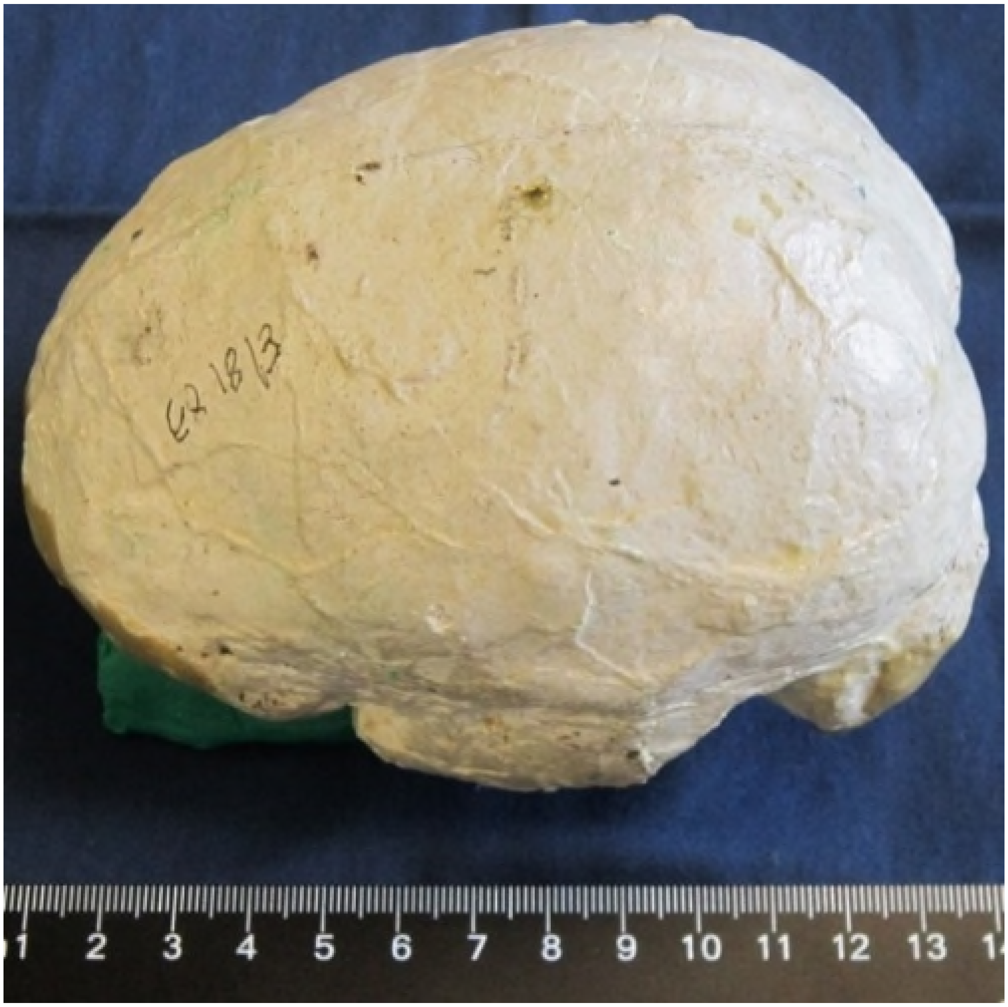

Fig. 7.13 KNM-ER 1813 Endocast mould, left lateral view
Photo by Suzi Wilson

For *Homo*, this is a small brain at 1.8 mya, and even more so at 1.55 mya, if Gathogo and Brown are correct. Plus, its small dentition (similar to later *Homo*) coupled with a small-sized brain (similar to the australopiths) has presented a bit of a conundrum for scholars regarding the taxonomy of KNM-ER 1813. *H. habilis* specimen OH7 (at 1.8 mya) would be the same age and more likely older than KNM-ER 1813, yet the adult endocranial volume for OH7 is about 50% larger, estimated between 729 ml and 824 ml, based on the recent digital reconstruction and re-measurement by Spoor *et al.* (2015:83). However, some believe that KNM-ER 1813 may be a female, which would support the speculation that *H. habilis* exhibited extreme sexual dimorphism and thus, a small female (compared to a much larger male) would have a small brain size, allometrically (Stringer 1986; Wolpoff 1999; Antón 2012, 2014). The endocast provides little information. There is a slight bulge in the Broca area, but with the right side missing, the two Broca regions cannot be compared.

KNM-ER 3732 - *H. rudolfensis* 1.88 mya

The specimen is a highly distorted cranial fragment found *in situ* during the 1974/1975 field seasons (R. Leakey 1976). It is primarily the dorsal surface, including part of the frontal region and left orbital margin. Holloway *et al.* have estimated the endocranial volume to between 750 and 800 ml (2004:127), and R. Leakey described it as "striking similar to" specimen KNM-ER 1470 (1976:575). There is a well-developed Broca's region on the left side of the endocast with some sulci detail, but without the *Sylvian Fissure* or other landmarks - it is difficult to interpret. This endocast, as well as KNM-ER 1470 and several others, would benefit greatly from a high-resolution scan to better observe the convolutional details, especially in Broca's area.

Fig. 7.14 KNM-ER 3732 Endocast mould, lateral view
Photo by Suzi Wilson

KNM-ER 1590 - *H. rudolfensis* 1.88 mya

The specimen represents the dorsal portion of a fragmented cranium belonging to a juvenile, which was recovered in Area 12 about 12 metres below the KBS Tuff at Koobi Fora during the 1972-73 (R. Leakey 1974; Day *et al.* 1976). It consists of most of the parietals, parts of the vault and a small portion of the frontal bone, along with several teeth (Ibid). R. Leakey notes that although the parietals show some deformation, they suggest that the cranium was wide, possibly with a sagittal keel (1974:654). There are no visible convolutions on the endocasts, and the endocranial volume has been roughly estimated to between 800 and 850 ml (Holloway *et al.* 2004:127).

KNM-ER 1805 - *H. habilis* 1.85 mya

The partial cranial specimen was found by Paul Abell with the KFRP *in situ* during the 1973 field season in Area 130 of Koobi Fora, which is adjacent to Area 131 where the KNM- ER 1470 cranium was recovered (Day *et al.* 1976). It consists of three main pieces that fit together to form a mostly complete calvaria with a somewhat deformed facial portion and an almost complete mandible, including some

Fig. 7.15 KNM-ER 1805 Partial cranium and front part of face (w/teeth)
Photo by Suzi Wilson

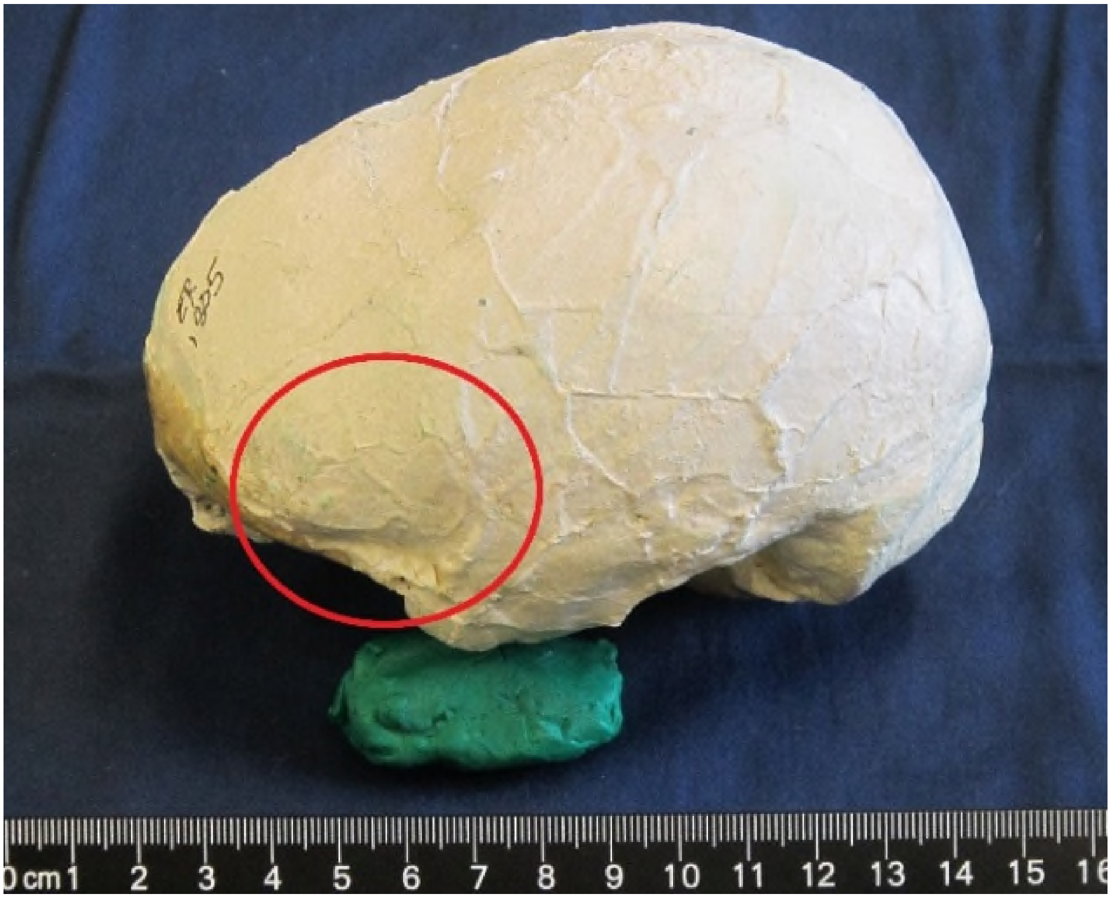

Fig. 7.16 KNM-ER 1805 Endocast mould, left lateral view
Photo by Suzi Wilson

teeth. Endocranial volume has been estimated at 582 ml (Day *et al.* 1976:387;Holloway et al. 2004:125). There is, what appears to be, some derived patterning in both Broca regions, yet too nondescript to definitively define the individual Brodmann areas. There also appears to be a small Sylvian notch, but again – it is difficult to fully delineate on the mould. This is yet another endocast which would benefit greatly from a digital scan. Overall, it is very symmetrical, including both Broca areas, although there might be a very slight left occipital petalia.

Speciation versus Variation/Sexual Dimorphism

These five crania/partial crania were all found below the KBS Tuff at Koobi Fora during the early 1970s and date from roughly 2.03 to 1.8/1.55 mya. During this time, these and the other non-robust *Homo* specimens recovered were often lumped together as either *H. habilis* or simply *Homo*, despite morphological differences. However, as additional hominin specimens were recovered exhibiting a wide range of diversities, it became increasingly difficult to explain their morphology as merely variation or sexual dimorphism. Regardless of how many species these fossils may have represented or how they should be classified, most scholars during this time agreed that there were at least two species, which conflicts with the 'single species hypothesis.'

The single species hypothesis argued that it would be extremely unlikely for two or more hominin species to have existed sympatrically (Mayr 1950; Wolpoff 1971), although today, it is abundantly clear that they did. According to Wolpoff, the single species hypothesis was based on how the nature of culture ("structured learned behaviour") prompts adaptation, and because of cultural adaptation, all hominins were assumed to occupy "the same, extremely broad, adaptative niche" (Wolpoff 1971:601). As a result, allopatric hominin species become sympatric because competition would force the survival of only one hominin lineage (Ibid).

Those who argue for a single species among these cranial fossils from this period attribute the apparent morphological differences to sexual dimorphism (Mayr 1950; Brace 1967; Wolpoff 1971), whilst the 'multiple species' stance insists that the evidence of variation would be considerably wider than expected from male and female conspecifics – even more so than extant gorillas (Leakey and Walker 1976; Wood 1985; Stringer 1986; Lieberman *et al.* 1988; Falk 1983; Rightmire 1993).

In 1975, Groves and Mazák proposed dividing the fossils into *H. habilis* and *H. ergaster* with KNM-ER 992, a 1.5 mya mandible, as the type specimen for *H. ergaster/erectus* (Groves and Mazák 1975; Liebermann *et al.* 1988). Although this suggestion was not met with a great deal of enthusiasm, it re-opened the door for discussion regarding the speciation issue. A few years later, Alan Walker argued (in a paper with Richard Leakey) that the KNM-ER 1470 specimen was likely an australopithecine, whilst R. Leakey argued (in the same article) that it belonged in *Homo* (Walker and R. Leakey 1978:66). They concluded that it would be acceptable to place it in *H. habilis*.

Over the following years, most of the early *Homo* specimens became designated as *H. habilis* until Bernard Wood pointed out how different the KNM-ER 1470 specimen was from both *H. habilis* and *H. erectus* (Wood 1985). Valery Alexeev agreed and proposed the name *Pithecanthropus rudolfensis* for specimens like KNM-ER 1470, whose name was later informally changed to *Homo rudolfensis* by Groves (Alexeev 1986; Groves 1989). Wood formalised the species name in a 1992 article, but was later criticised by Kennedy in 1999 for not following standard procedures with respect to zoological nomenclature, which he promptly rectified (Wood 1992; Kennedy 1999; Wood 1999).

The arguments for at least two species generally define the morphological criteria for separation based largely on brain size (and body size, allometrically), but these pre-*erectus Homo* specimens also differ in a number of other ways that focus on the *shape* of morphological features such as crania, faces, palates, mandibles and teeth. As a result, Antón *et al.* have presented a different perspective that examined the morphological differences without focusing on brain size and employed a new informal nomenclature for what they considered to be 'like-kind' early *Homo* non-*erectus* specimens. Basically, they placed the specimens most resembling type specimen KNM-ER 1470 into what they call the 1470 group, whilst those resembling type specimen KNM-ER 1813 were placed into the 1813 group (2014:1236828-1,2).

The 1813 group has a more primitive facial architecture with a rounded palate whilst the 1470 group has a more derived face, which is relatively tall and flat with upper third premolars forming the corner of the anterior palate (Antón *et al.* 2014:1236828-5). For the fossil specimens which were unclear, Antón *et al.* categorized them as "likely" (for one of the two groups) or "unknowns," meaning that they either could not be determined or might belong to an as-of-yet unrecognised/undefined species (Ibid). Accordingly, this analysis by Antón *et al.* illustrates just how difficult it is to differentiate between speciation and variation and/or sexual dimorphism during this period and further demonstrates the importance of these adaptations as a means to survive in a challenging competitive environment. Hence, the capability to find and consume adequate sustenance via adaptations in masticatory morphology, digestive systems, and/or cognition, such as the ability to devise better tools for acquiring/processing sustenance, became crucial for survival.

Oldowan Tools

As described in Chapter 6, Oldowan tools are simple core forms with conchoidal fracture produced by bipolar or freehand knapping (Schick and Toth 2006; Toth and Schick 2018). Despite their simplicity, the Oldowan was a considerable improvement over the Lomekwi tools, and some Oldowan tools were likewise more advanced (Gona, Lokalalei 2C, Olduvai Bed II) than others (Olduvai Bed I, Lokalalei 1), as discussed in Chapter 6. Schick and Toth note that although freehand knapping was not required for the Oldowan technology, there is much evidence of it in the Oldowan fossil record (2006:4).

Mary Leakey distinguished between the tools recovered from Bed I at Olduvai Gorge, which were predominantly choppers, as "Oldowan" and those from Bed II, which consisted of mostly spheroids/retouched flakes, as "Developed Oldowan A and B" (M. Leakey 1975:484). The difference between 'A' and 'B', according to M. Leakey, is that whilst there are no true bifaces in 'A,' there are a greater proportion of "proto-bifaces" in 'A' than seen in the basic Oldowan and less choppers, whilst 'B' contains true bifaces, albeit small and poorly made (Ibid). Glynn Isaac, however, combined them all into the 'Oldowan Industrial Complex' (Isaac 1976; Schick and Toth 2006; Toth and Schick 2018), although at the time, many felt that the Developed Oldowan B deserved its own classification (possibly as early Acheulean). Whilst the Developed Oldowan B is very similar in form, if not size, to the earliest Acheulean assemblages, it is somewhat akin to the plesiomorphic hominins previously discussed, where the adaptations of an ancestral species have begun to step outside their typical range of variation, yet have not fully evolved (enough) to be accepted as a new derived species. Accordingly, the 'lumping' of the DOB into the Oldowan Industrial Complex by Glynn Isaac has now been generally accepted by most (de la Torre and Mora 2014; de la Torre 2016).

Some prefer Grahame Clark's term for these simple technologies as 'Mode I industries' or other classification systems such as those developed by (Biberson (1967), Isaac (1997), Toth (1982, 1985) or Shea (2013), yet Mary Leakey's typological system remains the most popular (Schick and Toth 2006:6). Although she did not distinguish between the cores and the heavy-duty tools, it appears that most of the time, the worked cores were included in the "tools" category whist the minimally flaked cores were placed in the category for "cobblestones, nodules and blocks" (Schick and Toth 2006:9).

The prominent localities in Africa yielding either Pre-Oldowan or Oldowan artefacts are listed below. Most of the sites in East Africa were found in fluvial or lake environments whilst the South African sites were typically inside limestone caves. The tools found at the Ain Boucherit site (in the northern part of Algeria) roughly date to between 2.4 and 1.9 mya (Sahnouni and van der Made 2009), yet the closest known hominin site to Ain Boucherit is nearly 3,000 km to the west in Chad, where fossils of *A. bahrelghazali* (arguably *A. afarensis*) were found, dating to approximately 3.5 mya (see Chapter 5). Also of interest are other Oldowan assemblages from Algeria, dating younger than 1.4 mya, during a time when the only known surviving hominin species was *H. erectus*.

Locality/Site	**Country**	**Age[1] (Mya)**	**Possible Toolmakers (w/in reasonable proximity)**
Lomekwi	Kenya	3.3[(a)]	*K. playtops*
Ounda/Kada - Gona	Ethiopia	2.6 to 2.5[(b)]	*P. aethiopicus*; *A. garhi*
Ledi-Geraru[2]	Ethiopia	2.61 to 2.58[(c)]	*P. aethiopicus; A. garhi*
Middle Awash	Ethiopia	2.5[(d)]	*P. aethiopicus*; *A. garhi*
Omo Valley	Ethiopia	2.4 to 2.3[(e)]	*P. aethiopicus*; *P. boisei*
Ain Boucherit	Algeria	2.4 to 1.9[(f)]	Unknown
Lokalalei 1A & 2C	Kenya	2.34[(g)]	*P. aethiopicus*; *P. boisei*; *A. garhi*; early *Homo*
Hadar	Ethiopia	2.3[(h)]	*P. boisei*; early *Homo*
Swartkrans	So. Africa	2.22[(i)]	*P. robustus; early Homo*

Kanjera	Kenya	2.2(j)	*P. boisei*; early *Homo*
Olduvai Gorge	Tanzania	2.0 to 1.35(k)	*P. boisei; early Homo; H. erectus*
Sterkfontein	So. Africa	2.18 (l)	*P. robustus*; early *Homo*
Kromdraii	So. Africa	2.0 to 1.0(m)	*P. robustus*; early *Homo; H. erectus*
Fejej	Ethiopia	1.96(n)	*P. boisei*; early *Homo*; *H. erectus*
Koobi Fora	Kenya	1.9 to 1.3(o)	P. boisei; early *Homo*; *H. erectus*
Ain Hanech	Algeria	1.8(p)	Unknown
El-Kherba	Algeria	1.8(p)	Unknown
Konso Gardula	Ethiopia	1.7(q)	*P. boisei*; early *Homo*; *H. erectus*
Melka Kunture	Ethiopia	1.7(r)	*P. boisei*; early *Homo*; *H. erectus*
Gona No. - Dan Auole	Ethiopia	1.6 to 1.5(s)	*P. boisei*; early *Homo*; *H. erectus*
Peninj	Tanzania	1.6 to 1.4(t)	*P. boisei*; early *Homo*; *H. erectus*
Nyabusosi	Uganda	1.5(u)	*P. boisei*; early *Homo*; *H. erectus*
Gadeb (early tools)	Ethiopia	1.45(v)	*P. boisei*; *H. erectus*
Chesowanja	Kenya	1.42(w)	*P. boisei*; *H. erectus*
Busidima North - Gona	Ethiopia	1.26(x)	*H. erectus*

[1] *Dating from: (a)Harmand et al. 2015, Lewis and Harmand 2016; (b)Semaw et al. 1997, 2003; (c)Braun et al. 2019; (d)Clark et al. 1984; (e)de la Torre 2004; (f)Sahnouni and van der Made 2009; (g)Delagnes and Roche 2005; (h)Kimbel et al. 1996, Hovers 2009; (i)Kuman et al. 2021; (j)Braun and Harris 2009; (k)M. Leakey 1971, Blumenschine et al. 2012; (l)Granger 2015; (m)Isaac 1997; (n)Kuman 2003; (o)Isaac 1997; (p)Sahnouni et al. 2002; (q)Suwa et al. 1997; (r)Gallotti and Mussi 2015; (s)Semaw et al. 2020; (t)Domínguez-Rodrigo et al. 2002; (u)Texier 1993, 1995; (v)de la Torre 2011; (w)Harris and Gowlett 1980; (x)Semaw et al. 2020.*

[2] *It is possible that Ledi-Geraru may ultimately be proven to be older than Gona, once dating issues have been resolved.*

Olduvai Gorge

In 1911, a German entomologist (Kattwinkel) was exploring the Serengeti plains of Tanzania, currently under German rule as part of German East Africa, and came across what would later be known as the Olduvai Gorge (L. Leakey 1954). As he descended the canyon, he collected some Hipparion fossils embedded in the steep slope, which he brought back to Berlin. As a result of these finds, a German geologist (Reck) spent three months in Olduvai Gorge where he recovered hundreds of fossil specimens, many of which were previously unknown species and genera (Ibid:67). However, exploration of the gorge ceased with the onset of World War I, after which the British gained control of the territory. This worked quite well for Louis Leakey who then visited Reck in Berlin and invited him to join him on a new expedition of the gorge in 1931, primarily to

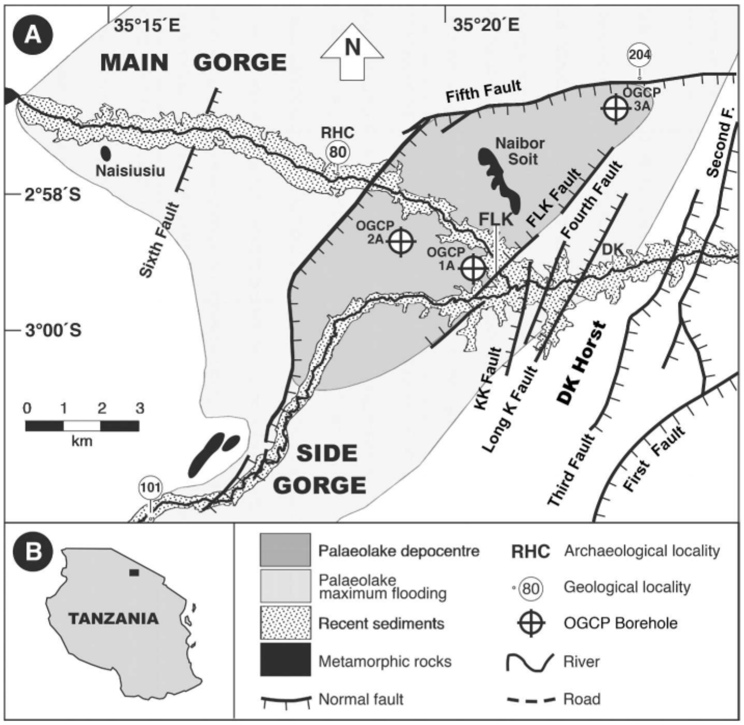

Fig. 7.17 Olduvai Gorge
Njau 2021:3

search for ancient stone tools[1] (Ibid). Leakey found hand axes on the same day they made camp, and over the years to follow, thousands of artefacts and fossils representing various species and genera have been recovered, including those of hominins. Olduvai Gorge is approximately 20 kilometres long, running somewhat east-northeast to west-southwest, located in between the Serengeti Plains and the Ngorongoro Crater (Walter 1992; McHenry 2012; Deino *et al.* 2021). The Gorge consists of two main branches (Main Gorge and Side Gorge) that meet in what is referred to as the central 'Junction' area, exposing approximately 100 metres of late Pliocene to Holocene strata along its course (M. Leakey 1971). Reck had originally divided the sediments of the gorge into five formations, which he referred to as beds, the lowest of which sits on a tuff of trachyte (an ancient lava flow referred to as the Naabi Ignimbrite), whist the youngest Bed V consists mostly of windblown sand (L. Leakey 1954; M. Leakey 1971).

Reck's nomenclature for the bed divisions has continued over the years, yet the divisions themselves have been revised, initially by Hay (1971, 1976) and more recently as geotechnical investigative dating methods have improved the Olduvai stratigraphy database, including the 2014 core drilling by the Olduvai Gorge Coring Project[2] ('OGCP') at three locations in Olduvai Gorge (see borehole locations in Figure 7.16). The cores recovered more than 575 metres of sedimentation, more than doubling the known stratigraphy, and now includes additional older formations (Njau *et al.* 2021; Deino *et al.* 2021). The OGCP employed ^{40}Ar/^{39} Ar dating methods (of the tuffs and lavas), magnetostratigraphy, and tephrostratigraphy to assess and correlate the information retrieved from the core drills, and sometimes used

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[1] *Reck considered Leakey's quest for stone tools foolish, as Reck was convinced none were present. Leakey bet him ten pounds that he would find evidence of stone tools within 24 hours of making camp, and found the hand axes less than 100 yards away that same afternoon (L. Leakey 1954:67-68).*

[2] *The OGCP commenced drilling in late 2014, and is jointly conducted by researchers from Indiana University/Stone Age Institute (Toth, Schick, and Njau) and the University of Liverpool (Stanistreet).*

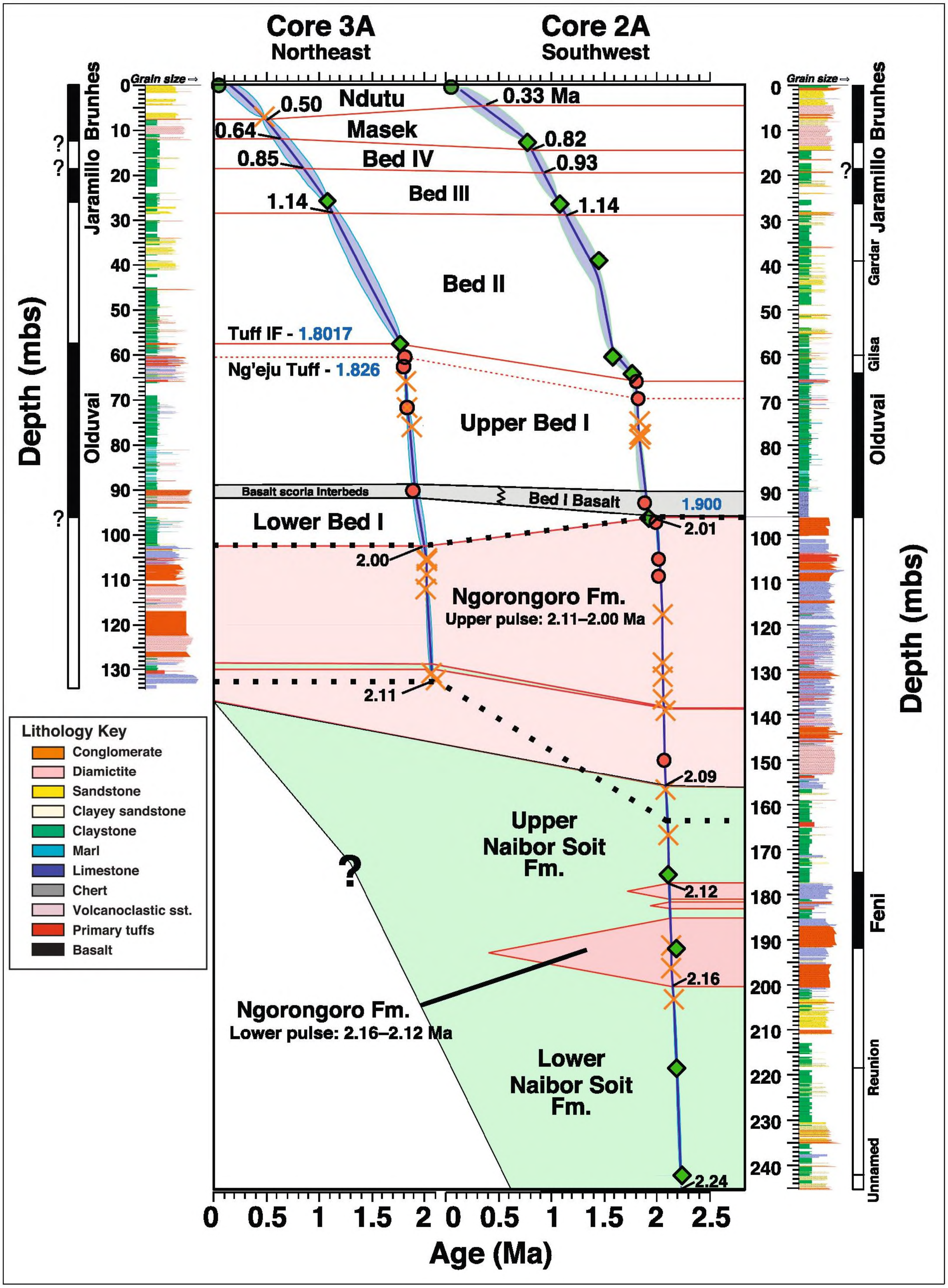

Fig. 7.18 Revised Stratigraphy at Olduvai Gorge
Deino 2021:14

Bayesian statistical age modelling, as a means to better estimate core levels with realistic confidence intervals (Deino *et al.* 2021). Accordingly, some of the stratigraphy and estimated dates have been revised and continue to be revised, especially at the upper and lower levels, to reflect these calibrated adjustments.

The Naabi Ignimbrite Formation is now considered part of the Ngorongoro Formation, which interfaces with another formation known as the Naibor Soit (see Figure 7.18), and the boundary between the uppermost Ngorongoro and the lower limit of Bed I has been dated to roughly 2.0 mya (Njau *et al.* 2021; Deino *et al.* 2021). The dating of both the very lower levels and upper beds has been arduous for a number of reasons, which include detrital contamination and faulting complications (Walter *et al.* 1992; Deino 2012), but the most challenging issue appears to have been the inconsistencies between the paleomagnetic ages and radiometric dating (Deino 2012). For example, Tuff IA is a thick vitric tuff exposed only to the west of the Fifth Fault and lying approximately six metres above the lower bound of the normal Olduvai Subchron interval in Locality 67 (Walter 1992:37; Tamrat *et al.* 1995:280; Deino 2012:253). In 1992, Walter *et al.* applied single crystal laser-fusion with $^{40}Ar/^{39}Ar$ dating to produce an age of 1.976 ± 0.004 mya for Tuff IA (Walter *et al.*1992:37). In

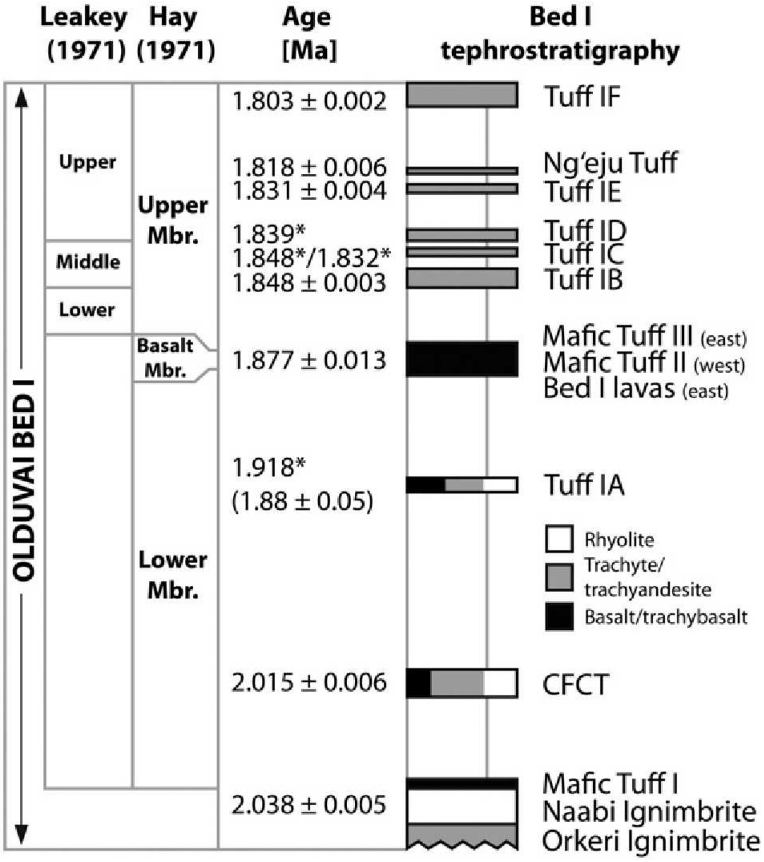

Fig. 7.19 Olduvai Bed I Tuffs
** Indicates interpolated*
Habermann et al. 2016:117

2004, however, the base of the Olduvai Subchron was determined to date to 1.945 mya based on the Astronomically Tuned Neogene Timescale,[1] which conflicts with Tuff IA having an older date given that it lies above the base of the Olduvai Subchron (Lourens *et al.* 2004; Deino 2012).

In 2012, Deino re-dated the stratigraphy in Olduvai using ^{40}Ar/^{39}Ar on the phenocrystic potassium feldspar from the interbedded marker tuffs, as a means to resolve some of the anomalies in the Bed I chronostratigraphy. Although Deino revised the date for Tuff IA to 1.88± 0.05 mya based on these measurements, he also characterised the date as "relatively imprecise" yet in agreement with a projected date of 1.92 mya, which he based on magnetostratigraphy and sedimentation rates from the Bed I base (Deino 2012:272). Additional studies by Habermann *et al.* in 2016 now refer to the dating of Tuff IA as 1.918 mya "interpolated" and 1.88 ± 0.05 mya "as measured" (2016:117). The boundary between Bed I and Bed II is delineated by Tuff IF, dated to 1.803 ± 0.002 mya, whilst the upper boundary of Bed II/lower of Bed III extends to 1.14 ± 0.05 mya with Bed IV beginning at .93 ± 0.08 (McHenry *et al.* 2020:3; Njau 2021:4; Deino *et al.*2021:17). Bed V has been revised to reflect the Ndutu/Naisiusiu Beds which represent the uppermost stratigraphy with the Masek Beds directly below (Stanistreet *et al.* 2020; Deino *et al.* 2021).

However, it should be noted that although the designation of tuffs as markers is popular among archaeologists for establishing chronostratigraphic boundaries, this practice is frowned upon by geologists as it causes problems and inconsistences with lithostratigraphic correlations when considering how formations can 'migrate' across temporal planes, thus presenting a diachronous dilemma. It should additionally be noted that from the initial geological studies by Reck in 1931 through the Olduvai revisions in the 1970s, proper stratigraphic nomenclature had not yet been codified and thus, there were rarely distinctions between and among chronostratigraphy,

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[1] *ATNTS2004*

biostratigraphy and lithostratigraphy[1] (Stanistreet *et al.* 2018:20). This was not particularly an issue in Olduvai Bed I, but the 'temporal migrations' presented some difficulties for Mary Leakey's excavations of Bed II (M. Leakey 1989).

Olduvai Bed I Toolkits

Prior to the discoveries of the Oldowan tools at the Ethiopian sites of Gona and Ledi-Geraru, the oldest Oldowan stone tools were believed to be those found by Mary Leakey's team at the Douglas (Leakey) Korongo ('DK') site, located approximately 2.5 km east of the Junction within Locality 13, in the Bed I eastern basin and just below the IB Tuff, dated to 1.848 ± 0.003 (Deino 2012; Stanistreet *et al.* 2018; Stollhofen 2021). Beneath the toolkit is the basalt lava layer, dated to 1.877 ± 0.013 (Deino 2012; Stanistreet *et al.* 2018) thus providing the oldest potential age for time-bracketing the DK tools. Although the OGCP recently uncovered an older Olduvai assemblage in Trench 168 in the western basin of Olduvai, dating to between 2.0 mya (CFC Tuff) and 1.9mya[2] (Tuff IA), the toolkit is not significantly different from the previous early Oldowan tools discussed, nor were any hominin specimens found in association with the tools. Nevertheless,

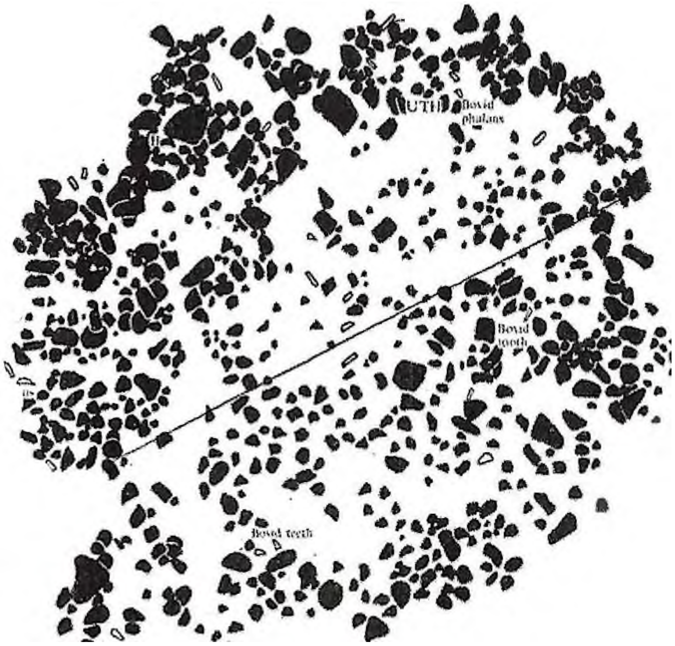

Fig. 7.20 Olduvai Bed I Stone Circle
M. Leakey 1971: Appendix, Fig. 7

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[1] *Although Hay often employed incision surfaces as sequence boundaries.*

[2] *Found appx. 2.7 metres above the CFC Tuff dated to 2.015 ± 0.006 mya (Deino 2012:255) and ten metres below Tuff IA dated to roughly 1.9 mya as discussed above (Habermann et al. 2016:117).*

this newly discovered assemblage is of interest in that it provides a temporal marker between the Gona Oldowan tools and the Olduvai DK Oldowan.

The DK toolkit has been thoroughly documented by Mary Leakey (1971), whose team also found the remnants of a loosely piled circle of lava block stones nearby (at DK IA), which present some interesting possibilities in terms of human behaviour. The stone circle measures approximately 14 feet in diameter from east to west and 12 feet from north to south (M. Leakey 1971). The basalt blocks ranged in size with the plurality at approximately four to six inches in average diameter, but there were also smaller blocks, as well as bigger blocks measuring ten inches or more in diameter (Ibid). Leakey suggested that the stone circle resembled those built by modern nomadic tribes as a wind shelter or as a base for a larger structure (Ibid), whilst Stanistreet *et al* speculate that it might have encircled a large tree that provided shade (2018).

The DK site consists of three levels, which together amount to a depth of roughly between 1.67 and 1.8 metres, suggesting a relatively short deposition period (M. Leakey 1971). The artefacts collected by Leakey's team included 124 artefacts (47 choppers, 32 polyhedrons, 27 discoids, ten heavy-duty scrapers, eight 'knife-like' sundry tools); 55 battered percussors (48 hammerstones and 7 subspheroids), 23 re-touched flakes (including three burins), and 894 pieces of debitage, based on Leakey's classification (Ibid). Also recovered from the DK site were three anvils, 20 cobbles and 79 nodules/blocks, the majority of which were believed to represent manuports[1] although only five broken cobbles of basalt could be definitively confirmed as imports (Ibid). The tools, *débitage* and other materials found at the DK site were predominantly sourced from lava, whereas quartz and/or quartzite were the favoured material employed at all the other sites in Beds I and II, except for EF-HR, an early Acheulean site (M. Leakey 1971:24). All of the scrapers, save one, were

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[1] A manuport is a natural raw material, moved from its original location for tool or tool-making use.

bifacially flaked, yet otherwise crude in construction as assessed by Leakey, possibly due to the poor quality of the raw materials sourced - namely the vesicular lava (M. Leakey 1971).

However, Leakey noted that when fine-grained stones were used, the quality of the choppers was greatly improved, if not indistinguishable, from those recovered in the upper beds (Ibid), but the tools made from vesicular lava did not compare favourably, even with the much older tools found at Gona as they neither demonstrated the same level of accuracy nor did the reduction sequences appear as uniform or intense, as mentioned in Chapter 6 (Stout and Semaw 2006; de la Torre 2011). This observation illustrates why ability should not be assessed solely on the toolkit alone, without also taking into consideration the quality of the available resources and/or the affordances they offered. Although Kanzi the chimpanzee was capable of deducing in relatively short order that the chert was the best option for knapping over the other materials provided, he was was offered affordances from which he could choose.

Olduvai Bed I Hominins

The FLK and FLK NN sites are also located in Bed I of the eastern basin, where Mary Leakey recovered the *P. boisei* broken skull (OH5) in Level 3 of FLK, and the *H. habilis* skull (OH7) in Level 3 of FLK NN, both found roughly six metres below the uppermost limit of Bed I (L. Leakey 1959; L. Leakey 1960a; L. Leakey 1960b; L. Leakey 1962; Walker and R. Leakey 1988), albeit the OH5 specimen was found approximately one-half metre higher in the stratigraphy than the OH7 skull (Tobias 1991). Levels 1 through 3 of the FLK and FLK NN sites are found between Tuffs IB, dated to 1.848 mya, and Tuff IC, dated between 1.848 ± 0.008 and 1.832 ± 0.003 mya (Blumenschine *et al.* 2012; Deino 2012; Habermann *et al.* 2016), whilst Level 4 is just below Tuff IB (M. Leakey 1971).

As briefly discussed in Chapter 6, the OH5 cranium was initially believed to be associated with a number of stone tools, *débitage,* and animal bones, some which had been broken open, presumably to obtain the marrow (L. Leakey 1959; L. Leakey 1960b). Following further faunal discoveries, it now seems more likely that although hominins were probably responsible for some portion of animal bone assemblage, the majority were accumulated by large felids and hyenas (Blumenschine and Peters 1998; Sánchez-Yustos 2021).

Below are four *H. habilis* crania and one *P. boisei* cranium (OH5) found at Olduvai in Beds I and II, with respective dating provided primarily by the OGDP literature cited and discussed herein, unless otherwise noted:

Specimen	**Olduvai Location**	**Appx. MYA**	**Age/Sex**	**Brain Volume**	**Description**
H. habilis OH24	Bed I	1.88 to 1.85	Adult	590 to 594 ml	Damaged partial cranium
P. boisei OH5	Bed I	1.85 to 1.83	Adult	498 to 530 ml	Damaged partial cranium
H. habilis OH7	Bed I	1.85 to 1.83	12 to 13 yrs.	729 to 824 ml (as adult)	Parietal bones
H. habilis OH16	FLK II Bed II	1.80	Late Adolescent	638 (as adult)	Crushed/Highly fragmented
H. habilis OH13	MNK Bed II	1.67 to 1.65	Late Adolescent Female	650 to 673 (as adult)	Parietals and partial occipital

OH5 - *P. boisei* 1.84 to 1.83 mya

Following the reconstruction of the damaged OH5 nearly complete cranium (Figure 6.3 in Chapter 6), an endocast was made with an estimated volume of between 520 to 525 ml, according to Holloway *et al.* (2004:66). Falk *et al.* estimated a lower volume of 500ml (2000:708) whilst Tobias calculated a volume of approximately 530 ml (1963:744). The endocast lacks any meaningful convolutional detail, and the sphenoid bones on both sides of the cranium were badly damaged, hence missing the areas where Broca's cap might be present. However, there seems to be a slight, albeit convincing, left occipital petalia, possibly indicating right handedness.

About a year after the discovery of the OH5 cranium, Jonathan Leakey recovered some dentition and other fossil specimens (OH 6) with more '*Homo*-like'

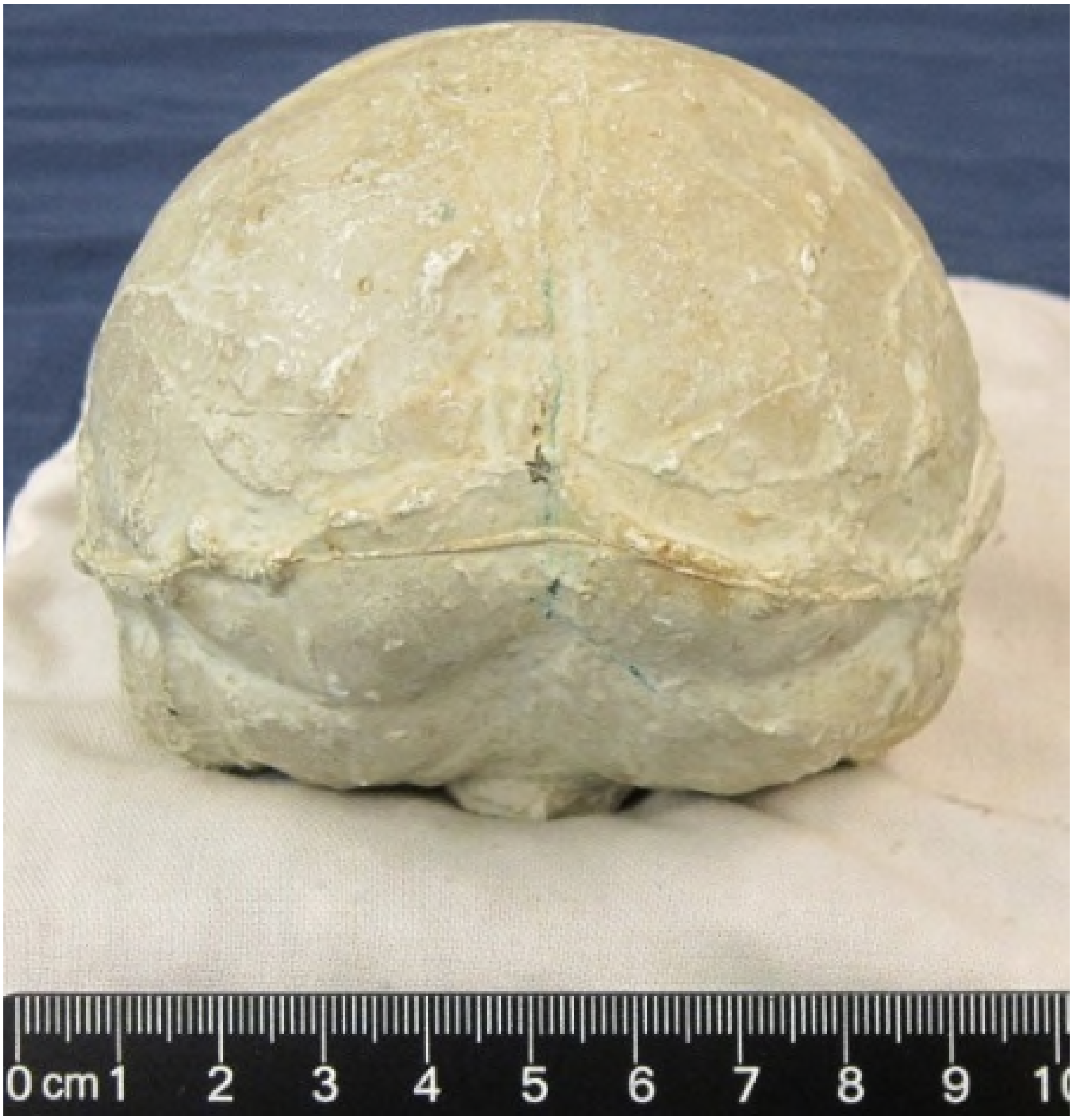

Fig. 7.21 OH5 Endocast mould, posterior view
Photo by Suzi Wilson

traits, also near the uppermost limit of Bed I. Shortly thereafter, the *H. habilis* juvenile OH7 fossil specimens were recovered at the FLK NN site, also within close proximity to some animal bones and what L. Leakey believed to be a bone tool ('lissoir') for working leather (L. Leakey 1960b; Napier 1962a; Napier 1962b; L. Leakey *et al.* 1964; Blumenschine *et al.* 2012). The recovery of hominin fossils in association with stone tools continued in both the upper portion of Bed I and the lower/middle portion of Bed II, which led L. Leakey *et al.* to believe that *H. habilis* was the true maker of the toolkits previously recovered and not the *P. boisei* specimen OH5 as originally thought, who L. Leakey *et al.* suggested may have been a "victim" of *H. habilis* (1964:9).

Although L. Leakey *et al.* (1964) were no doubt very pleased to have finally discovered what appeared to be early *Homo* specimens at Olduvai, there is really no way of knowing with certainty which species made the Oldowan tools, although it does seem that *H. habilis* would have had an advantage based on its hand morphology and larger brain. In total, 2,470 artefacts and 96 manuports had been recovered from Level 3 of FLK prior to Mary Leakey's 1971 book going to press (M. Leakey 1971:51). For the most part, none of the assemblages from the lower beds are particularly advanced or any more significant than those found at Gona in terms of requiring any special cognitive abilities, other than the very important innovation of coming up with the idea to make a sharp stone tool in the first place. In general, with the exceptions of Gona and Lokalalei 2C, the Oldowan Industry is only slightly more advanced than the earliest known tools made by the australopiths, who somehow managed to bang rocks together and create simple toolkits with their small brains. It thus continues to be relevant to examine these brain endocasts to search for any morphological changes in the features of the cerebral cortex for whatever evidence (however little) they might offer, as well as to track marked increases in brain volume. However, the thresholds of cognitive development may be more readily indicated by the behavioural evidence offered by the toolkits.

OH24 - *H. habilis* 1.88 to 1.85 mya

The OH24 skull (nicknamed 'Twiggy') was found in 1968 by the M. Leakey team, embedded within a solidified mass of hard lime, which had preserved the

Fig. 7.22 OH24 (Twiggy) cranium
Photo by Suzi Wilson

specimen yet also crushed it over time. Following reconstruction to correct for the damage and high distortion, Tobias estimated its endocranial volume at 594 ml (1991:707) whilst Holloway's reconstruction produced a similar value of 590 ml (Holloway *et al.* 2004:144). M. Leakey believed that the teeth of specimen OH24 as well as the skull itself, resembled other *H. habilis* specimens recovered (M. Leakey 1969), and both Tobias and Holloway agreed (Tobias 1991; Holloway *et al.* 2004). The reconstructed endocasts from both Tobias and Holloway suggest a left occipital/right frontal petalia pattern, but Holloway *et al.* warn that due to the extensive distortion, one cannot be certain of the skull shape nor any of the few sulci/gyri markings (2004). Unfortunately, the endocast specimen has gone missing from the Holloway lab at Columbia University, and I was, thus, unable to examine it for myself.

OH7 - *H. habilis* 1.85 to 1.83 mya

The debate regarding the OH7 crania and volume of the OH7 endocast has already been discussed. With respect to convolutional details, Tobias documented/described a number of gyri and sulci that he was able to discern from the endocast he made, such as the posterior portion of the superior frontal gyrus, the right interparietal sulcus and the Sylvian fissure (1991). However, the OH7 endocast in Holloway's lab does not illustrate these details, except for perhaps a small section of the Sylvian Fissure on the right side, and Tobias did not provide any high-resolution photographs or diagrams of such (to my knowledge). However, assuming these convolutional details existed as Tobias has reported, they are not particularly useful for providing any insight with respect to brain re-organisation, brain lateralisation or handedness (petalias) due to the missing and/or damaged areas in the frontal, temporal and occipital areas. At present, the only useful scientific evidence from the OH7 endocast is the estimated adult endocranial volume between

Fig. 7.23 OH7 Endocast mould
Photo by Suzi Wilson

729 and 824 ml as provided by Spoor *et al.* (2015).

In 2010 and 2011, new trenches 152, 153, and 154 were excavated by the Olduvai Landscape and Palaeoanthropology Project ('OLAPP') near the Leakey trenches DK I, DK IA, and DK IB, whilst new trenches 160, 161, 164 and 166 were excavated in 2012 to create a northwest by southeast cross-section (Stanistreet *et al.* 2018). The purpose was to further investigate the effects of a thick lahar lava mudflow (1.2 metres in trench DK 9) which buried the stone circle, tool assemblages and hominin remains (including the OH24 and OH56 partial crania), thereby preserving them, yet also damaging them whilst transporting them in the process (Stanistreet *et al.* 2018). Accordingly, Stanistreet *et al.* believe that the actions of the lahar explain why some of the fossils and artefacts were recovered at a higher stratigraphy than the level of the original assemblage, and thus propose that the OH24 cranium should be associated with the DK assemblage (and OH56 with Taliwawa Hill) and dated accordingly (Ibid).

Indeed, the DK assemblage was found sitting partially on volcaniclastic sandstone and partially on the basalt ridge, yet the small and gracile cranial specimen OH24 was recovered slightly higher in DK East (M. Leakey 1969:756) and approximately 300 metres east of the original site, less than a metre above the basalt layer (dated to 1.877) and beneath Tuff IB (dated to 1.848) (Stanistreet *et al.* 2018:28). Similarly, the OH56 parietal fragments recovered in 1977 near the original site in Locality 24-DK were also found slightly higher in the stratigraphy and with the remnants of a sandy matrix attached to them (Stanistreet et al. 2018; Sánchez-Yustos 2021).

Olduvai Bed II – More *H. habilis* and the Developed Oldowan

In addition to the Bed I sites (DK, FLK, FLK North, FLK NN), hominin fossils and other Oldowan toolkits were also recovered from the Bed II sites, such as HWK[1] East site at the base of Bed II and the MNK[2] Skull site in what M. Leakey considered the lower part of middle Bed II (1975), which has now been revised to lower Bed II, later discussed. The industry she described as Developed Oldowan A was recovered largely from the lower section of Bed II whilst the Developed Oldowan B was found primarily in the upper horizons of Bed II, although some 'basic' Oldowan tools, such as those sourced from the MNK Skull site and found in association with fossil remains assigned to *H. habilis*, were recovered within stratigraphy higher than the Developed Oldowan at HWK east (Ibid:482). M. Leakey noted that although there are no true bifaces in the Developed Oldowan 'A,' there are a greater proportion of "proto-

[1] *Henrietta Wilfrida Korongo*
[2] *Mary Nicol Korongo*

bifaces" and less choppers than seen in the Oldowan, whilst the Developed Oldowan 'B' contains what she considers to be true bifaces, yet small and poorly made (Ibid:484).

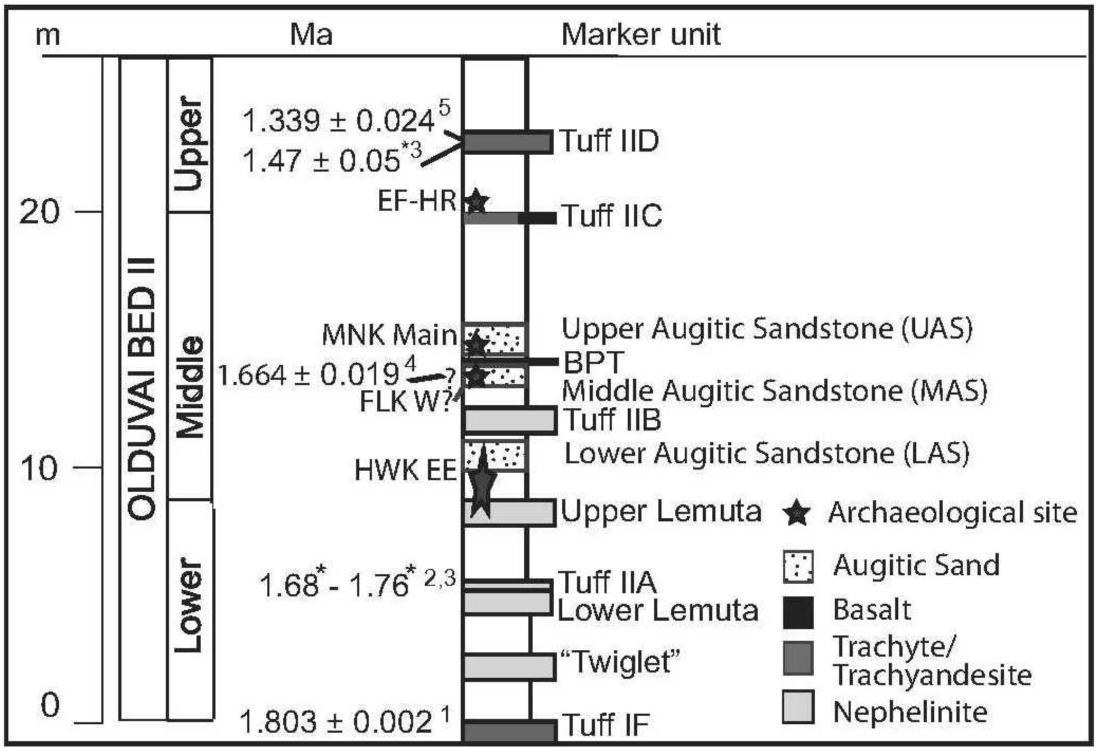

Fig. 7.24 Olduvai Gorge, Bed II Stratigraphy
McHenry and Stanistreet 2018:9, Fig. 2 [1]Deino 2012; [2]Curtis and Hay 1972; [3]Menega 1993*; [4]Diez-Martín et al. 2015; and [5]Domínquez-Rodrigo et al. 2013.* The symbol * denotes dates that have been adjusted for new Ar decay constants as per McHenry and Stanistreet (2018:9).*

OH 16 – *H. habilis* 1.8 mya

Pieces of a cranial vault and most of the teeth, representing a young adult specimen (OH16), were recovered from the Bed II, FLK II (Maiko Gulley) site in November 1963 by M. Mutumbo, part of the Leakey team (L. Leakey and M. Leakey 1964; M. Leakey 1971). Unfortunately, the OH16 specimen had not only been trampled into fragments by Masai cattle, but a large number of these fragments stuck to the mud and clay on the cattle's hooves and were thus transported away from their original location, believed to be approximately one metre above Tuff IF, the uppermost limit of Bed I (L. Leakey and M. Leakey 1964; M. Leakey 1971; Tobias 1991). The OH16 dentition was very similar to that of OH7, and based on this

Fig. 7.25 OH16 cranium
Photo by Suzi Wilson

similarity, it was classified as *H. habilis* (L. Leakey and M. Leakey 1964).

Although there were over a hundred cranial fragments, Tobias and Clark attempted to manually reconstruct the cranium in order to make an estimate of endocranial volume and observe the shape of the endocast (L. Leakey and M. Leakey 1964; Holloway *et al.* 2004; Tobias 1991). The volume was estimated by Tobias as between 622 and 625 using the partial endocast technique, which was adjusted to 638 as an adult (Tobias 1991:446). Tobias additionally noted how the width of the frontal lobes had expanded (Ibid), which Holloway had likewise observed, but Holloway *et al.* also caution how any observations of skull shape for OH16 are tenuous at best, considering the high fragmentation of the skull, pieced together by a large amount of plaster (2004), as seen in Figure 7.25. As a result, any pertinent convolutional details on the endocast were lost.

OH13 – *H. habilis* 1.67 to 1.65 mya

The interval between Tuff IF (the boundary between Bed I and Bed II) through Tuff IIB is well-exposed along a cliff face to the west of Locality 88 of the MNK Skull site, and the horizon where the hominin fossils and stone tools were recovered lies in between the chert-bearing unit above Tuff IIA and the orange tuffaceous siltstone of Tuff IIB (de la Torre *et al.* 2021). In October of 1963, OH13, OH14 and OH15 were recovered by N. Mbuika with the Leakey team and assigned to *H. habilis* (L. Leakey and M. Leakey 1964; M. Leakey 1971; Tobias 1991). Specimen OH15 consists of only three teeth whilst OH14 represents a few cranial fragments of the very thin calvaria of a child (M. Leakey 1971).

Specimen OH13, however, is represented by most of the mandible and maxillae, all of the mandibular teeth with some of the maxillary teeth, a possible humeral shaft, and the majority of the right parietal bone with a good part of the left, both of which articulate with the central and left portions of the occipital bone (L. Leakey and M. Leakey 1964; L. Leakey *et al.* 1964; M. Leakey 1971; Holloway *et al.* 2004; Tobias 1991; de la Torre *et al.* 2021). The Leakeys believed OH13 (nicknamed 'Cinderella' or 'Cindy') represented a late adolescent whilst Tobias identified the specimen as a 15-year-old female (L. Leakey and M. Leakey 1964; Tobias 1991; de la Torre *et al.* 2021).

The specimen's endocranial volume was estimated by Holloway via the reconstruction of the missing parts followed by water displacement, with an adjustment for age, which produced an estimated adult volume of 650 ml (1975:397), whilst Tobias employed a partial endocast method, also with an adjustment for age, which resulted in an adult volume of 673 ml (1991:717). Although both the superior sagittal sinus and right transverse sinus have left their impressions on the endocast,

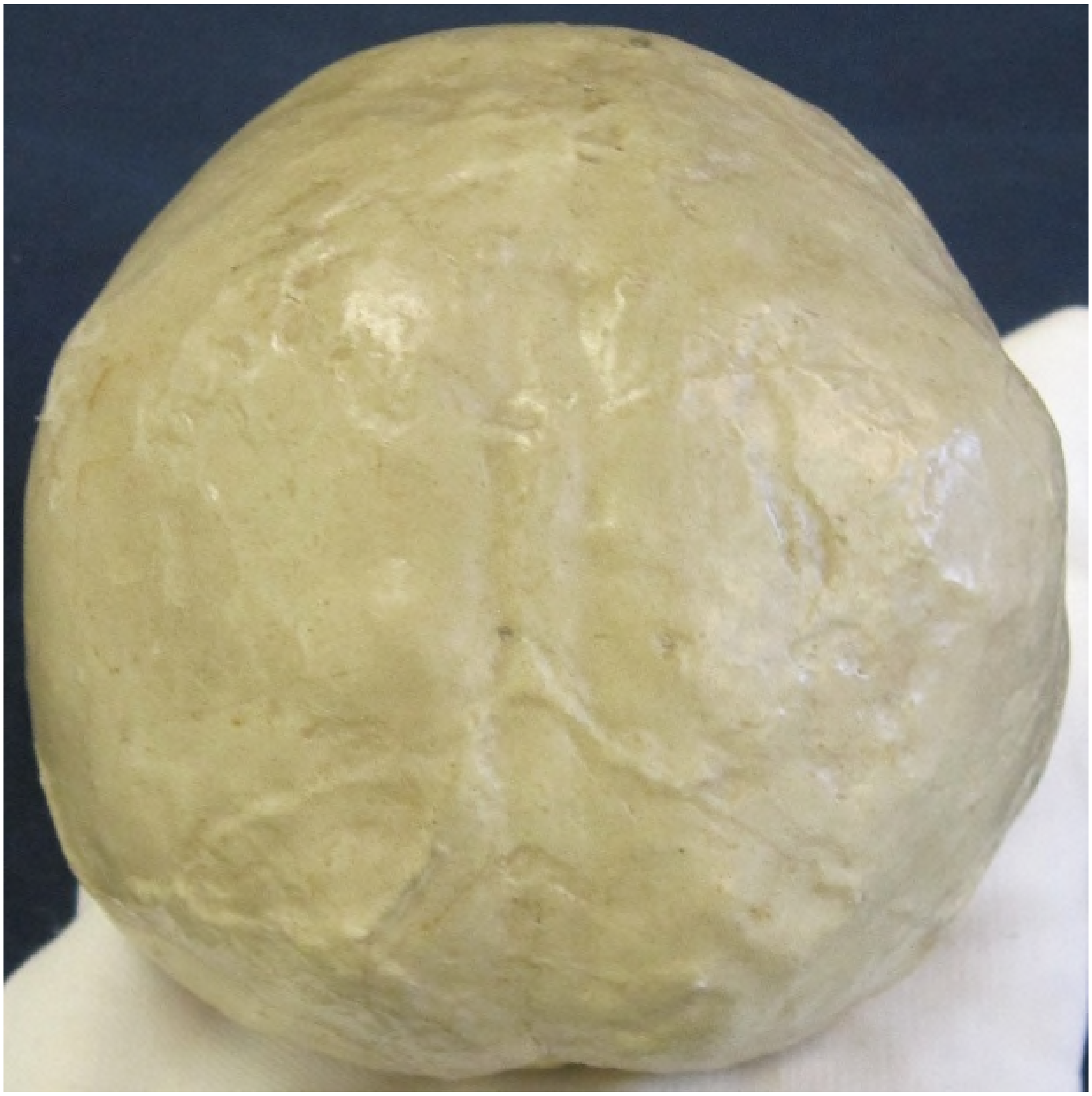

Fig. 7.26 OH13 Endocast mould, posterior view
Photo by Suzi Wilson

any relevant sulci are either not visible or not reliable due to the damage on the internal table of bone. The parietal lobes, however, present some interesting information due to their enlarged or 'swollen' (*i.e.,* 'bossing') appearance, likely indicating some expansion in the superior parietal lobules, which Holloway *et al.* and Tobias believe might indicate some form of brain re-organisation (Holloway *et al.* 2004; Tobias 1991). As previously mentioned, both of these regions are important for visuo-spatial skills and process sensory (tactile) information to guide hand/arm movements toward objects within peri-personal space, in order for the hand to grasp and/or manipulate.

Tobias also observed a right occipital petalia (1991), but Holloway *et al.* argued for a left occipital petalia (2004). There is a case for either depending on how the endocast is oriented and viewed. Furthermore, the regions where corresponding frontal petalias (if present) would be found were missing, making it even more difficult to determine. As we see increasingly more petalias in the fossil record coupled with the cultural evidence of freehand knapping, it is likely that handedness in these hominins was becoming more common, although it will not be apparent in all the crania examined, just as it was not always apparent in the modern human studies, previously discussed.

Although most of the OH13 fossils were recovered from the surface, the two parietal pieces (which articulate with the occipitals) were found approximately 24 feet (~7.3 metres) above the base of Bed II, from which M. Leakey believed OH 13 derived (M. Leakey 1971). She also observed lime concretions encrusted on most of the OH13 bones, further supporting this point of origination and thus dating them to between 1.67 and 1.65 mya (M. Leakey 1971; de la Torre *et al.* 2021). The *in situ* OH13 remains were found in association with some mammal bones and an assemblage of tools made predominantly from chert, which is expected given that the MNK Skull site sits on a bed of chert (M. Leakey 1975; de la Torre *et al.* 2021).

Both freehand knapping and on-anvil flaking were found in the assemblage, although on-anvil knapping represented less than 20% of core reduction, based on the number of bipolar cores, pitted stones and possible split cobbles present (de la Torre *et al.* 2021). The plurality (40%) of the tools produced by freehand knapping were bifacial, followed by unifacial flaking at 31.1% and roughly 10% consisting of multi-facial reduction (de la Torre *et al.* 2021). In general, the reduction sequences at MNK were typical of the Oldowan at Olduvai Gorge, although there were higher proportions of bipolar flaking and retouched tools (versus the assemblages recovered below the Lemuta Tuff), and the tools appear to be more extensively shaped (de la Torre *et al.* 2021). Considering the stratigraphic position of this assemblage, which is slightly higher than HWK EE (and where other toolkits have been recovered, including Acheulean assemblages), the MNK Skull site is the youngest 'handaxe-free' site and thus the last Oldowan assemblage at Olduvai Gorge (M. Leakey 1975; de la Torre *et al.* 2021). With a late age of roughly 1.65 to 1.67 mya, the OH13 specimens may also represent the youngest *H. habilis* fossil remains in Eastern Africa (Spoor 2007, 2015; de la Torre *et al.* 2021).

The South Africa Oldowan

From Dart's first discovery of the Taung child cranium in 1924 to the 1950s, excavations in South Africa focused on the recovery of hominin fossil specimens, and stone tools were not known, or particularly even considered, during this time frame. Then in 1954, C.K. Brain recovered 129 dolomite artefacts from the Makapansgat cave site (north of Pretoria) within close proximity to a hominin fossil assemblage later recovered by Dart, and the possibility that these early hominins made stone tools[1] was realised (Brain *et al.* 1955; Brain 2007). A few years later in 1956, Brain would also find toolkits at Sterkfontein (2007), and the search for South African artefacts continued. Although stone tools have also been recovered from Drimolen, Kromdraai, Gladysvale, and Coopers, they are small in number. However, nearly 4,000 artefacts (Oldowan and Acheulean) have been recovered from two members at Sterkfontein, and nearly 1,000 artefacts have been found at Swartkrans from three members (Kuman 2003).

Hominin remains from both *P. robustus* and early *Homo* have also been found at these two sites, as well as Kromdraai, and all three sites are located within close proximity to one another, about 30 km north of Johannesburg. Swartkrans, located

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[1] *Mason argued that the objects recovered at Makapansgat were produced by natural fracture (1965:13), and their authenticity has not been fully resolved (Kuman 2003:253).*

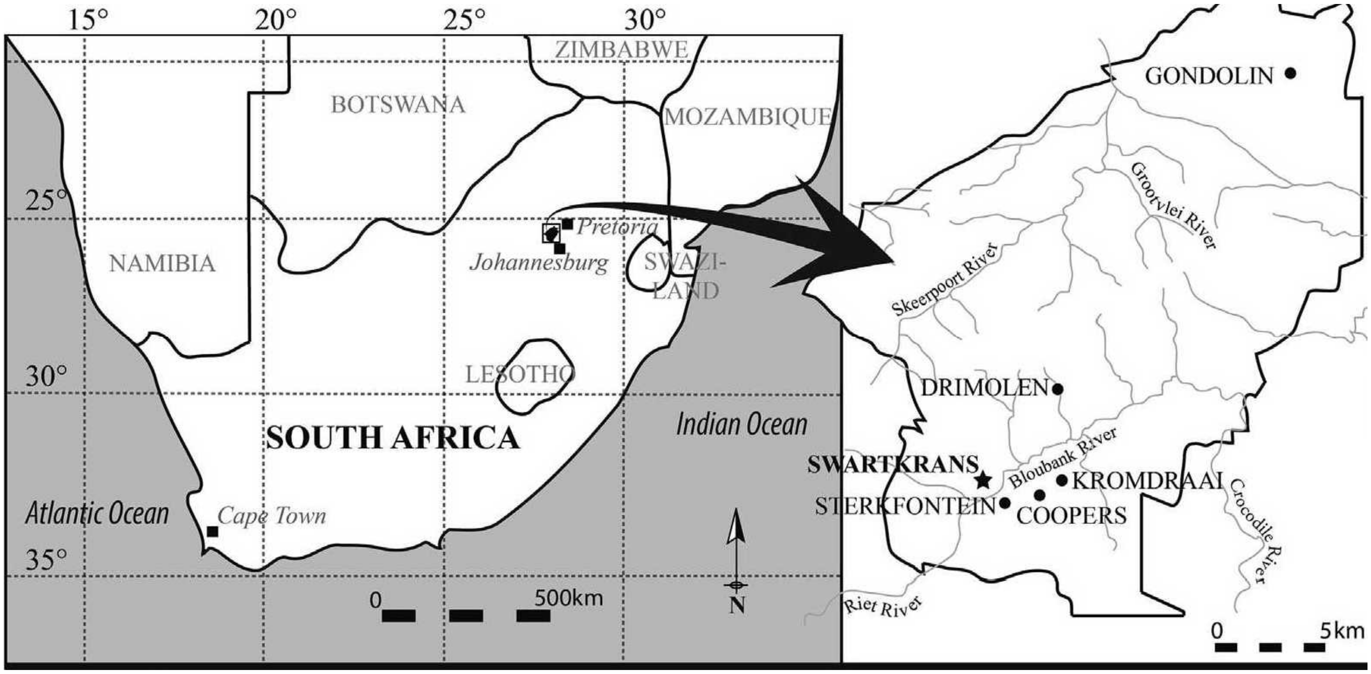

Fig. 7.27 South African sites
Gibbon et al. 2014:11

on the Blaauwbank River, was initially excavated (via the lime-mining refuse dumps) by Broom and Robinson for hominins in the late 1940s and early 1950s (Broom and Robinson 1952; Kuman 2018), and later, by Brain for artefacts starting in the 1960s when he recovered about 30 stone tools from the dumps (Kuman *et al.* 2018). At Brain's invitation, Mary Leakey visited the site to examine the artefacts, which she believed resembled the Developed Oldowan found in Bed II at Olduvai Gorge (M. Leakey 1970). She additionally compared them with the contemporaneous and greater assemblage (in number) recovered by Robinson at Sterkfontein, and although she observed how the tools from Swartkrans and Sterkfontein were much larger in size, she felt they should all be classified as Developed Oldowan (1970).

Following new excavations in 2005 by the Swartkrans Palaeoanthropology Research Project under the direction of T.R. Pickering, additional artefacts were recovered and similarly analysed in comparison with those of Sterkfontein (Kuman *et al.* 2018). In general, there were no significant differences between the technologies, although Kuman *et al.* noted that flaking was much exhaustive at Sterkfontein, with an emphasis on sharp-edged flakes for cutting made from quartz (2018). Bipolar and freehand knapping were evident at both sites (Ibid), and it is not surprising that Acheulean artefacts would later be found at these sites.

The Acheulean Industry

John Frere was the first (known) to recognise the significance of Acheulean handaxes in 1797, when he recovered several examples from prehistoric lake deposits in association with animal bones at Hoxne (Suffolk). He forwarded the artefacts to the Royal Academy, believing them to be very ancient and made by early humans who did not have access to metal. Although he was correct, he was ignored by his pre-Darwinian contemporaries as was Jacques Boucher de Crèvecoeur de Perthes, who also found handaxes with animal bones in the gravel river terraces near Abbeville in northern France between 1836 and 1846. It was not until after Dr. Marcel Jérôme Rigollot, a rival of Perthes, also found handaxes near Saint Acheul in northern France in 1858, that Frere's beliefs regarding prehistoric people and tools would begin to be considered. Less than a year later in April of 1859 (just seven months prior to the release of Darwin's *On the Origin of Species*), British geologists/ archaeologists Evans and Prestwich discovered a handaxe in the gravel pit near the Seminary of St. Acheul, whereby they also established means and protocols for authenticating archaeological observations in the field (Gamble and Kruszynski 2009:463).

The handaxes were described and typified (as specimen artefacts) in 1872 by Louie Laurent Gabriel de Mortillet (1873:436) and characterised as *L'Epoque de St. Acheul*, the type site, with the industry renamed simply 'the Acheulean' in 1925. In its simplest definition, the Acheulean handaxe is a teardrop-shaped, un-hafted bifacially worked large cutting tool[1] (LCT), thicker towards the base (glob-butt) and thinning

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[1] *However, LCTs are not necessarily Acheulean (de la Torre 2016:42).*

out toward the tip and cutting edges, which are refined through bifacial trimming (Wynn and Gowlett). The earliest Acheulean, however, were often only unifacial and not particularly symmetrical, with thick pointed tips and long, durable cutting edges (Beyene *et al.* 2013; de la Torre 2016).

Semaw *et al.* stress how the Acheulean was a significant technical advancement over the Oldowan, which signalled not only postcranial adaptations in terms of strength and motor skills but also adaptations with respect to cognitive abilities (2009). The early Acheulean toolmakers specifically sought out sizable cores for the removal of large flake blanks (10 cm or greater), suggesting different objectives from those of the Oldowan toolmakers as well as different requirements for both the raw materials procured and the physical means in terms of force to accurately manipulate these larger resources (Semaw *et al.* 2009). Evidence from East Africa and Iberia suggest a modern hand morphology was in place by the time of the early Acheulean (Ward *et al.* 2014; Lorenzo *et al.* 2015; Shipton 2018). Beyene *et al.* believe that the Acheulean LCTs and picks were created to either provide a more efficient exploitation of existing activities or as a means to accomplish new objectives (Beyene *et al.* 2013). Over time, the Acheulean became more symmetrical and complex, with additional shaping of the tool, which may have reflected an aesthetic component beyond the functional construction of the handaxe – one that draws from both the culture of the hominin community, as well as the culture (if not also the personal 'branding') of the individual toolmaker.

When bifacial tools were first recovered by the Leakey team in 1963 at the EF-HR site in Olduvai Bed II, which were believed by M. Leakey to be about 1.4 mya[1] (as did Glynn Isaac), they were assumed to represent the earliest occurrences of the Acheulean Industry (M. Leakey 1971; M. Leakey 1975; de la Torre *et al.* 2018; Stanistreet *et al.* 2018). It was not until 1991 that a much older Acheulean assemblage would be found, recovered from site KGA6-A1 in Konso-Gardula, located at the southwestern end of the Main Ethiopian Rift (Beyene *et al.* 2013; WoldeGabriel *et al.* 2005; Suwa *et al.* 2007). The toolkit was initially dated to between 1.74 and 1.66 mya, with a most likely date of 1.74 ± 0.03 mya based on correlation studies between the Konso Turoha Tuff (TRT) and the KBS and Chari tephra of the Turkana Basin, which included the ^{40}Ar/^{39} Ar dating of glass shards and crystals within these tephra (WoldeGabriel *et al.* 2005; Beyene *et al.* 2013).

A few years later between 1997 and 2001, the Kokiselei Complex of the Kaitio Member of the Nachukui Formation (Kenya) was excavated, yielding another Acheulean assemblage at site KS4. The site is located slightly above the Olduvai Subchron and dated to 1.76 mya, based on regional correlation and sedimentation rates (Roche *et al.* 2003; Lepre *et al.* 2011; Beyene *et al.* 2013), although Diez-Martin *et al.* suggest 1.7 mya as the most likely age (2015).

Finally, yet another early Acheulean assemblage[2] was found at the FLK West site, just west of the FLK site at the base of Bed II in Olduvai Gorge (Yravedra *et al.* 2017). The FLKW site was discovered by the Olduvai Palaeoecology and Paleoanthropology Project in 2013, and is located in the lowermost Bed II, directly above Tuff IIA, and initially dated to between 1.7 mya based on ^{40}Ar/^{39}Ar dating of sanidine single crystals (Diez-Martin *et al.* 2015; Yravedra *et al.* 2017), although later revised to approximately 1.65 mya after further investigations into the temporal migrations of the stratigraphy in Bed II (Stanistreet *et al.* 2018). As a result of these temporal migrations, Tuffs IIA and IF[3] were no longer deemed proper chrono-

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[1] *Hay had originally dated the Acheulean sites in Bed II as between 1.2 and 1.3, but M. Leakey (and G. Isaac) believed them to be older, around 1.4 mya. They were later proven correct based on the core drilling studies by the OCAP (M. Leakey 1975:486; de la Torre et al. 2018:3).*

[2] *It is possible that artefacts dating to 1.8 mya at Karakhack may represent the earliest Acheulean, but they are not convincing and more likely transitional (Trivonov et al. 2016; Shipton 2020:19).*

[3] *Although not considered a proper chronostratigraphic marker by the geologists, Tuff IF is frequently referred to as the boundary between Bed I and Bed II in the archaeological literature.*

stratigraphic markers (Stanistreet *et al.* 2018).

In 2012, Stanistreet introduced a new approach to the stratigraphy at Olduvai based on what he referred to as 'lake-parasequences' which marked the major withdrawal and advances of the lake system and correlated with the incised surfaces, established by Hay in the 1970s (2012). Accordingly, the new boundary between Lower and Middle Bed II is now the top of the Lemuta Member sandstones, thus placing the FLKW Acheulean levels within the 'Middle Augitic Sandstone' and providing a boundary between the Oldowan and Acheulean technologies in the earliest Middle Augitic Sandstone (Ibid). Although the earliest FLKW Acheulean assemblage is located at the base of the Augitic Sandstone sequence, there is a disconformity in the stratigraphy that cuts deeply into Bed II, and sequences 1 and 2 have been largely eliminated below the disconformity making the site difficult to properly date (Ibid). However, Diez-Martin *et al.* observed a clay tuff ('FLKWb') dated to 1.664 ± 0.019 mya that lies just above the disconformity (2015). Thus, Stanistreet *et al.* believe it is more appropriate to date the FLKW Acheulean assemblage based on the clay tuff and thus propose an approximate date of ~1.65 versus the ~1.7 proposed by Diez-Martin *et al.* (Stanistreet *et al.* 2018).

The most notable difference between these three early Acheulean assemblages and M. Leakey's Developed Oldowan are the very big cores, which produced large flakes and cutting tools (LCTs) such as picks, handaxes, and cleavers. Not only did these hefty cores need to be properly supported and positioned prior to striking, but they also required strong upper bodies with deft hands which could produce sufficient percussive blows, which likewise required enhanced motor skills in order to deliver great force with precision. Although the Acheulean Industry is known for bifacial reduction, the earliest Acheulean toolkits were often only unifacially worked (Beyene *et al.* 2013).

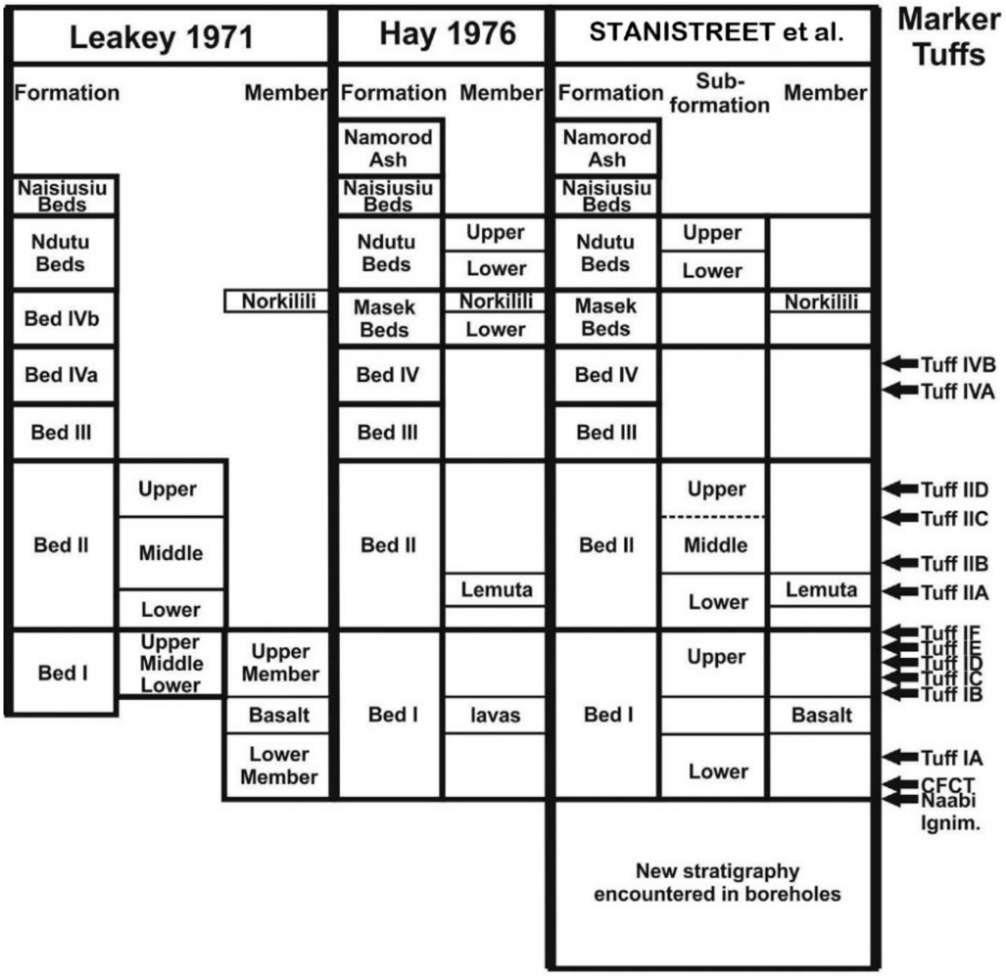

Fig. 7.28 Revised Boundaries – Bed II
Stanistreet et al. 2018:21

The FLKW toolmakers appeared to prefer quartz, as the majority of the FLKW artefacts (73.67%) were made from the Naibor Soit quartz with the remainder made from either basalt (18.2%) or chert (7.07%) even though the bed load at FLKW consisted primarily of basalt (Diez-Martin *et al.* 2015). At Konso the raw materials used were almost exclusively the readily available basalt (Beyene *et al.*2013), whilst at Kokiselei, the predominant resource was the local phonolite (Roche *et al.* 2003; de la Torre 2016).

The assemblage recovered from the KGA6 site at Konso consisted mostly of large crude picks and LCTs, some of which had been worked bifacially with thick pointed tips and long cutting edges (Beyene 2013). The longest pick (fourth from left

Fig. 7.29 Konso flakes/picks – dorsal/ventral
Beyene et al. 2013:1586

in Figure 7.29) is roughly 23 cm long with a trihedral section of 9 cm thick (Ibid).

The artefacts from the KS4 site at Kokiselei likewise consisted of large picks (trihedral and quadrangular) with some over 15 cm long as well as other LCTs, including some cleavers (de la Torre 2016). Kokiselei handaxe lengths ranged between 13 and 25 cm in length, often with less than 50% of the surface shaped and the ventral side unmodified (Ibid).

The slightly later Acheulean assemblage (1.65 to 1.7 mya) from FLK West at Olduvai Gorge totals 2,120 artefacts, again consisting mostly of large LCTs but with a wide range of other forms as well, including medium-sized flakes (Diez-Martin *et al.* 2015). Cores were worked using a variety of unifacial, bifacial and multi-facial reduction strategies, and there is even some evidence of some bipolar on anvil reduction (Ibid). Some of the handaxes demonstrate advanced knapping on a level not previously seen at either Konso or Kokiselei, such as the symmetry in the bifacially flaked handaxe made from the Olduvai basalt in Figure 7.30.

Fig. 7.30 Bifacially flaked handaxe
Made from basalt at FLK West
Diez-Martin et al. 2015:6

This advanced knapping at no younger than 1.65 mya establishes that the upper body strength and dexterity as well as the neural correlates of the toolmaker were already in place at this time. Thus, the variation in the assemblages found at FLKW suggests that some of the seemingly less impressive tools produced were perhaps: (i) made for different needs/tasks, which did not require a well-shaped symmetrical handaxe; (ii) the result of other behaviour not necessarily related to cognitive abilities, such as tools made by children learning the trade; or (iii) produced by different species, likely based on different needs, such as diet, but also possibly due to diverse abilities between/among hominin species.

Lepre *et al.* believe that different hominin groups with different skill sets made different tools (2011), whilst Beyene *et al.* argue that the "obvious alternative" was that the Acheulean LCTs were made for either new activities or new/better solutions to existing activities, and Lepre *et al.* do acknowledge the possibility of a "within-species cultural disparity" (Lepre *et al.* 2011:85; Beyene *et al.* 2013:1588). Semaw *et al.* additionally note that the co-existence of the Oldowan alongside the Acheulean may be related to the need for "expedient tools," which could be made quickly for an immediate need/task (2018:124). If so, 'temporary need' tools were likely made from the most easily sourced raw materials, which would explain some of the resource choices.

The argument for needing expedient tools for different tasks is certainly plausible, if not compelling, especially considering that however crude the Oldowan may have been, Schick and Toth effectively demonstrated that Oldowan tools were, nevertheless, capable of slicing through the thick hides of large animals when they enlisted their students and together, butchered an elephant[1] using only replicated Oldowan tools (Schick and Toth 1993). Indeed, as modern human analysts, we tend to measure and judge the merits of Palaeolithic toolkits based on design and execution versus function and utility (Isaac 1989:162). Although true, we still have to consider the possibilities as to why so many of the Oldowan artefacts were poorly made (*e.g.*, Lokalalei 1A, Olduvai Bed I), yet other Oldowan assemblages were exceptionally crafted (*e.g.*, Kada Gona EG10/EG12, Ounda Gona OGD-7, Lokalalei 2C). Thus, it is possible that both hypotheses can explain the variation between and among the assemblages.

Often, the Oldowan is associated with *H. habilis* whilst the Acheulean is presumed to be the product of *H. erectus*. However, there is no evidence that *H. habilis* was not capable of making the early Acheulean, and Oldowan-type artefacts remained ubiquitous throughout the Palaeolithic (Semaw *et al.* 2018), long after all but *H. erectus* had gone extinct.

Homo erectus

Homo erectus originated in Africa likely around 1.9 mya (Antón 2003; Baab 2021), and possibly as early as 2.04 mya (Herries *et al*. 2020). Their bodies were bigger than the earlier hominins, ranging between 45 and 68 kg (Cartmill and Smith 2009) with an average height of roughly 160 to 180 cm (McHenry and Coffing 2000; Stanford *et al.* 2017), and it was previously believed that they had begun to develop a proto-modern human skeleton with a less funnel-shaped thorax among other derived

[1] *The elephant died of natural causes and was donated by a zoo.*

morphology (Stanford *et al.* 2017). The hip bones from erectine specimens KNM-ER 3228, OH 28, and KNM-WT 15000 are very similar to those of modern humans in a number of ways, such as in the size of the acetabulum and length of the ischial body (Rose 1984; Cartmill and Smith 2009). This more derived pelvis coupled with their longer legs would have provided greater speed and efficiencies for bipedal locomotion. Bramble and Liebermann argue that this adaptation may have enabled endurance running (2004), which would have likely played an important role in their survival. However, Simpson *et al.* disagree and argue instead that the adaptation observed in the pelvis of female *H. erectus* specimen BSN49/P27, most likely accommodated the birthing of larger brained babies (Simpson *et al.* 2008).

Their crania were typically longer than wide and appeared low and angular in a profile view. Their skulls looked somewhat 'pentagonal' from a posterior view. In general, the *Homo erectus* braincase was quite thick and robust, although the Asian crania were even thicker than the African specimens (Stanford *et al.* 2017). Their faces were considerably less prognathic than the earlier species and their teeth were much smaller in size, likely indicating an adaption to accommodate a change in diet. They are known for their 'shovel-shaped' incisors, which are concave on the lingual side with ridges, possibly to prevent damage. Additionally, there are a number of bone 'thickenings' on the crania in the forms of tori and/or keels. Unlike the paranthropines who often had big crests to support chewing muscles, these tori and/or keels did not serve as anchors for muscle attachment.

Although there is regional variation in the species, both the very thick and prognathic supraorbital torus and occipital torus (horizontal ridge across the occipital) were fairly common. However, the angular torus (back of parietal bone), sagittal torus/keel (lower and more rounded than a sagittal crest) and the metopic keel (front midline/above brow) are more common in the Asian erectines. Sometimes, the sagittal and metopic keels can still be seen in modern humans. Also

Turkana Boy
African erectus

Fig. 7.31 Absence of sagittal keel
Photo by Suzi Wilson

Peking Man
Asian erectus

Fig. 7.32 Sagittal keel
Stones and Bones Superstore[1]

Sir Patrick Stewart
Modern Human

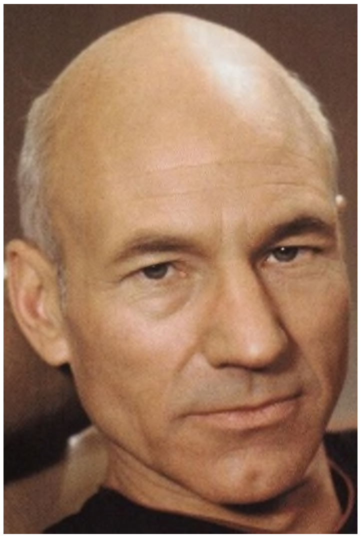

Fig. 7.33 Slight keel
German Fans Share[2]

interesting among these three photos is the percentage of 'face' versus the portion occupied by 'brain' in erectines versus the modern human.

Brain volume for the earlier African erectines ranged from roughly 600 to 900 ml between 1.7 and 1.4 mya, which is not a substantial increase over *H. habilis* whose brains ranged from 590 to 850 ml. Although endocranial volume would increase for the African erectines over the next 200k years, with a large endocranial volume of 1,067 ml for OH 9 (from Olduvai) at 1.2 mya, there were also specimens with smaller volumes such as DAN 5 from Gona, with

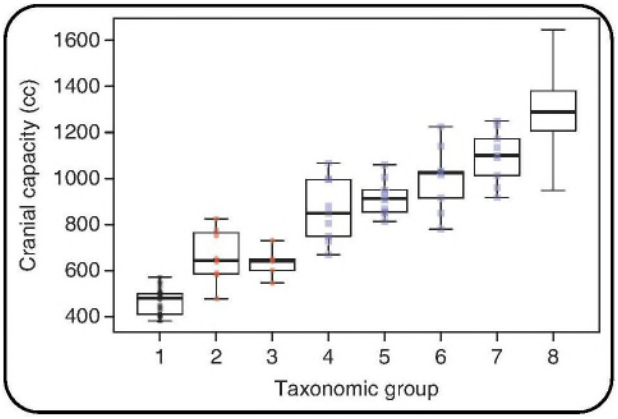

Fig. 7.34 Hominin Brain Size, Cofran 2017:2
1 – Australopithecus
2 – Early African Homo
3 – Dmanisi H. erectus
4 – African H. erectus
5 – Early Indonesia H. erectus
6 – Chinese H. erectus
7 – Late Indonesia H. erectus
8 – Modern Humans

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[1] *www.skeletonsandskullssuperstore.com/product/peking-man-skull-replica/*
[2] *german.fansshare.com/gallery/photos/18665660/hulu-et-intv-patrickstewart-patrick-stewart/*

a volume of approximately 598 ml, at 1.5 mya. The wide range of variation, which *H. erectus* is known for, is illustrated with respect to endocranial volumes represented in the boxplots numbered 3 through 7 in Figure 7.34. However, their bodies were likewise getting bigger, which presents the issue of determining how much brain growth was above and beyond the expected growth, allometrically.

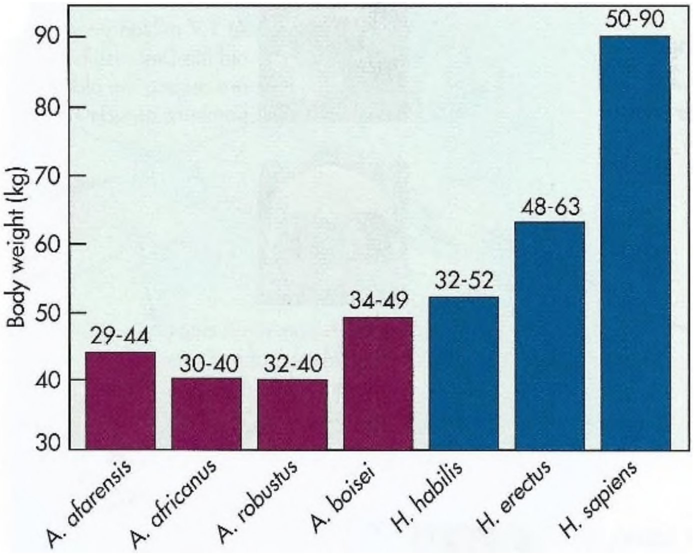

Fig. 7.35 Hominin Body Weight
Stanford et al. 2017:347

Figure 7.35 shows a bar chart from Stanford *et al.* illustrating the increase in body weight[1] from *A. afarensis* to *H. sapiens* with the 'bars' corresponding to the maximum weight for each species (versus the species average) within each estimated range. It seems that increases in brain volume against body weight were either fairly allometric or slightly underperforming until *H. erectus*, but even then - the increase in erectine brain volume is only slightly disproportionate over allometry, as the major increases in brain size do not become markedly disproportionate above expected allometry until speciation approaches *Homo sapiens*. Furthermore, *H. erectus* may have been a bit stouter than was previously thought.

In spite of having the benefit of a nearly complete skeleton specimen in KNM-WT 15000 (Turkana Boy), the 'long and lanky' body of *Homo erectus* has been challenged as of late based largely over the ontogenetic development of Turkana Boy as well as a recent comparison of the thorax of *H. erectus* with both modern humans and Neanderthals (Antón *et al.* 2014, Ruff and Burgess 2015, Bastir *et al.* 2020).

[1] *There are currently no postcranial fossils to predict weight in P. aethiopicus and only one or two fossils for A. garhi and H. rudolfensis, which cannot conclusively be associated the respective species.*

Bastir *et al.* performed a principal component analysis (PCA) and digitally measured and compared the Turkana Boy's rib cage with that of modern humans and the Kebara 2 Neanderthal. Their analysis suggests that the rib cage of *H.erectus* was wider, shorter and deeper than modern humans and more similar to the Kebara 2 Neanderthal (Bastir *et al.* 2020:1182), which implies a more recent origin for the *Homo sapiens* slim torso. If true, perhaps the increase in endocranial volume in *H. erectus* was more allometric than previously thought.

Additionally, the briefly mentioned nearly complete adult female *H. erectus* pelvis (specimen BSN49/P27) recovered from the Busidima Formation at Gona indicates that although the individual was likely short-statured, the inlet circumference is within modern female ranges, whist the pelvic midplane (bispinous) and pelvic outlet (bitubercular) transverse widths are greater than most modern human females (Simpson *et al.* 2008:1089-1090). This evidence further supports the notion that bigger brains were likely not significantly outpacing allometric expectations for the postcranial body, as previously presumed.

The *H. erectus* crania and/or endocasts for the period between 2.0 and 1.4 mya will be examined below. The chart includes two of the surviving paranthropines for comparative purposes, but only the *H. erectus* specimens will be discussed:

Specimen	**Location**	**MYA**	**Age/Sex**	**Brain Volume**	**Description**
H. erectus DNH 134	Drimolen So. Africa	2.04 to 1.93	2 to 3 years	538 child/ 551 to 661 Est. Adult	Partial cranium
H. erectus KNM-ER 2598	Koobi Fora	1.9 to 1.88	N/A	N/A	Occiput only
H. erectus KNM-ER 3733	Koobi Fora	1.63	Adult Female	848	Mostly complete

H. erectus KNM-ER 3883	Koobi Fora	1.63	Adult Male	804	Partial cranium
H. erectus DAN5/P1	Gona (Afar)	1.6 to 1.5	Adult	598	Mostly complete
Homo erectus KNM-ER 42700	Ileret Kenya	1.55	Young or Sub-Adult	732	Calvaria
P. Robustus SK1585	Swartkrans	1.53	Adult	530	Mostly right side
H. erectus KNM-WT-15000	West Turkana	1.53	Young or Sub-Adult	880 (with 908 as adult)	Mostly complete
H. erectus KGA 10-620	Konso	1.42		N/A	Right parietal frag
H. erectus KGA 10-656	Konso	1.42		N/A	Right parietal & frontal frag
P. boisei KGA-10-525	Konso	1.4	Male Adult	545	Mostly complete Braincase
H. erectus KGA 7-395	Konso	1.3		N/A	Right occipital frag

DNH 134 – *H. erectus* 1.93 to 2.04 mya (Drimolen)

The DNH 134 partial cranium of an infant from the Drimolen Quarry in South Africa was recovered from a deposit with reversed palaeomagnetic polarity (the C2r.1r reversed Subchron), associated with the 1.934 to 2.120 mya time interval (Hammond *et al.* 2021). Additionally, the flowstones underlying the deposit were dated using uranium-lead (U-Pb) geochronology, coupled with uranium-series electron spin resonance (ESR), dating the fossil specimen to between ~2.04 and 1.95

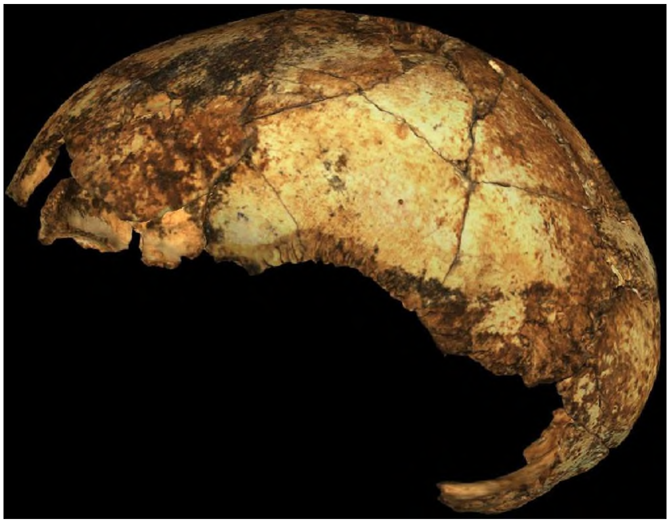

Fig. 7.36 Drimolen DNH 134 partial cranium Herries et al 2020:3

mya, thus marking the earliest appearance of *Homo erectus* (Herries *et al.* 2020:1-2). Unlike Sterkfontein, Swartkrans and other cave sites, the Drimolen palaeo-cave complex does not have multi-generational phases of karstification and infill, and has a fairly simple depositional history. It has yielded over 150 hominin specimens, a large fauna collection, and one small stone tool assemblage (Ibid).

The partial cranial specimen is comprised of most of the parietal bones and frontal squama, as well as a good portion of the occipital squama. There are no anterior and posterior fontanelles, and the cranial sutures are at an early stage of fusion, whilst the metopic suture was fused externally, suggesting an age at death of between 12 and 36 months. An endocranial volume of 538 ml was estimated based on linear regression using the partial endocast method, with a wide range for adult volume between 551 and 661 ml (Ibid:3). The cranium presents features indicating it is most likely *H. erectus*, such as a long and low cranial vault, a somewhat pentagonal shape posteriorly, and occipital curvature with some lambdoid flattening. Additionally, it presents some sagittal keeling on the frontal and parietal bones, which is more common in Asian *H. erectus* but not so unusual for African *H. erectus*. At present, no endocast study has been published nor have the authors made a digital scan of the interior table of bone available for other scholars to examine.

Although the various theories regarding dispersals from Africa are not germane to the focus of this thesis, it is nevertheless significant to note that the presence of a 2.1 to 1.9-million-year-old *Homo erectus* in South Africa would lend support to the theory that *Homo erectus* evolved in Africa, versus the notion that *Homo erectus* derived from an earlier *Homo* in Eurasia, then returned to Africa.

KNM-ER 2598 – *H. erectus* 1.9 to 1.88 mya (Koobi Fora)

Based on recent geological investigations, the provenance of the KNM-ER 2598 occiput has been stratigraphically redefined to four metres below the KBS Tuff in collection Area 13 of the Upper Burgi formation (versus Area 15 as initially reported), thus indicating an age of between 1.9 and 1.88 mya (Hammond *et al.* 2021:2). Also collected from the upper Burgi Member of Area 13 were cranial vault fragments, a partial ilium and a proximal third metatarsal, which unfortunately, cannot be positively associated with the KNM-ER 2598 occiput.

The thick occipital fragment, described by Kimbel and Villmoare as "unmistakably *H. erectus*-like in its greatly thickened, strongly flexed squama surmounted by a prominent occipital torus" (2016:5) consists of most of the central occipital bone. At this stage, there has been no endocast for the occipital lobe, digital or otherwise, nor an estimate of endocranial volume for this early *Homo*

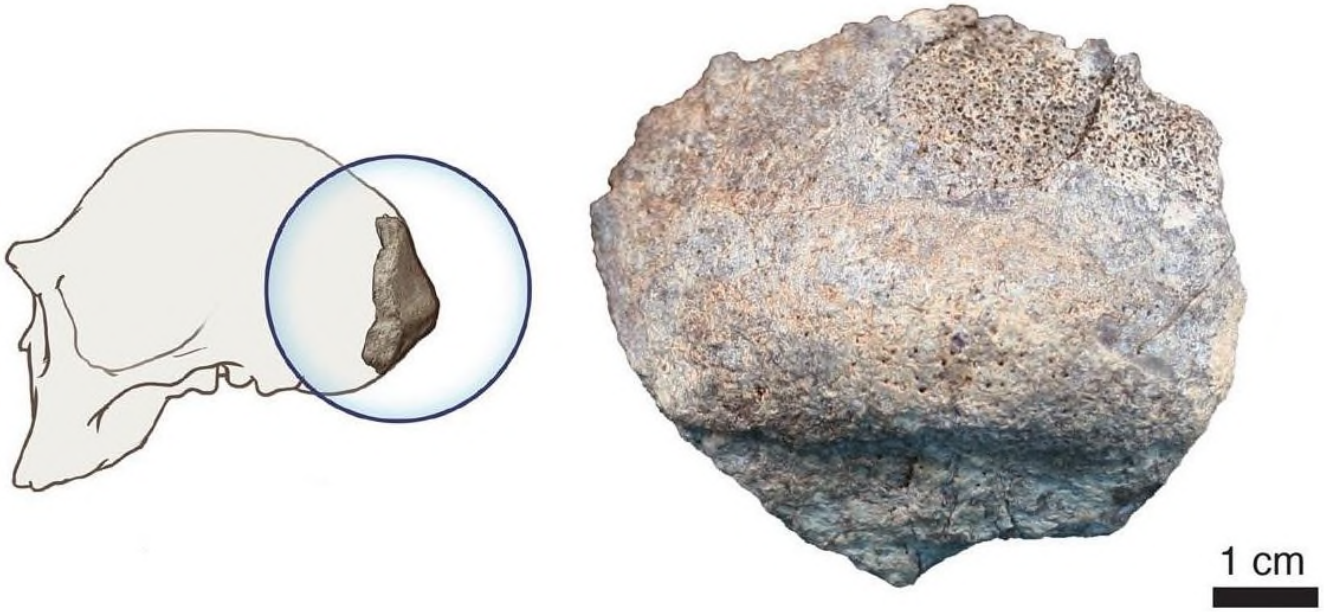

Fig. 7.37 KNM-ER 2598 Occiput
Hammond et al. 2021:2

erectus. Unfortunately, no *H. erectus* crania have yet been recovered representing the 250,000-year-period in Africa between 1.88 and 1.63 mya.

KNM-ER 3733 – *H. erectus* 1.63 mya (Koobi Fora)

In 2015, Lepre and Kent re-dated KNM-ER 3733 to 1.63 mya, based on their magneto-stratigraphy work from 2010 as well as: (i) the work by Brown *et al.* (2006) in reinterpreting the upper position of the Olduvai Subchron above the KBS Tuff; (ii) the interpolated age of the White Tuff, which is the nearest stratigraphic marker to Area 104, by Gathogo and Brown (2006a); and (iii) the geochronological work by McDougall *et al.* (2012) with respect to interpolating a date for the Morte Tuff (above the White Tuff). The Morte Tuff was correlated with the dating for the White Tuff as well as Tuff T9b. The excavation site for KNM-ER 3733 was approximately 1.5 metres below the White Tuff, thus leading to a suggested age of 1.65 mya for the

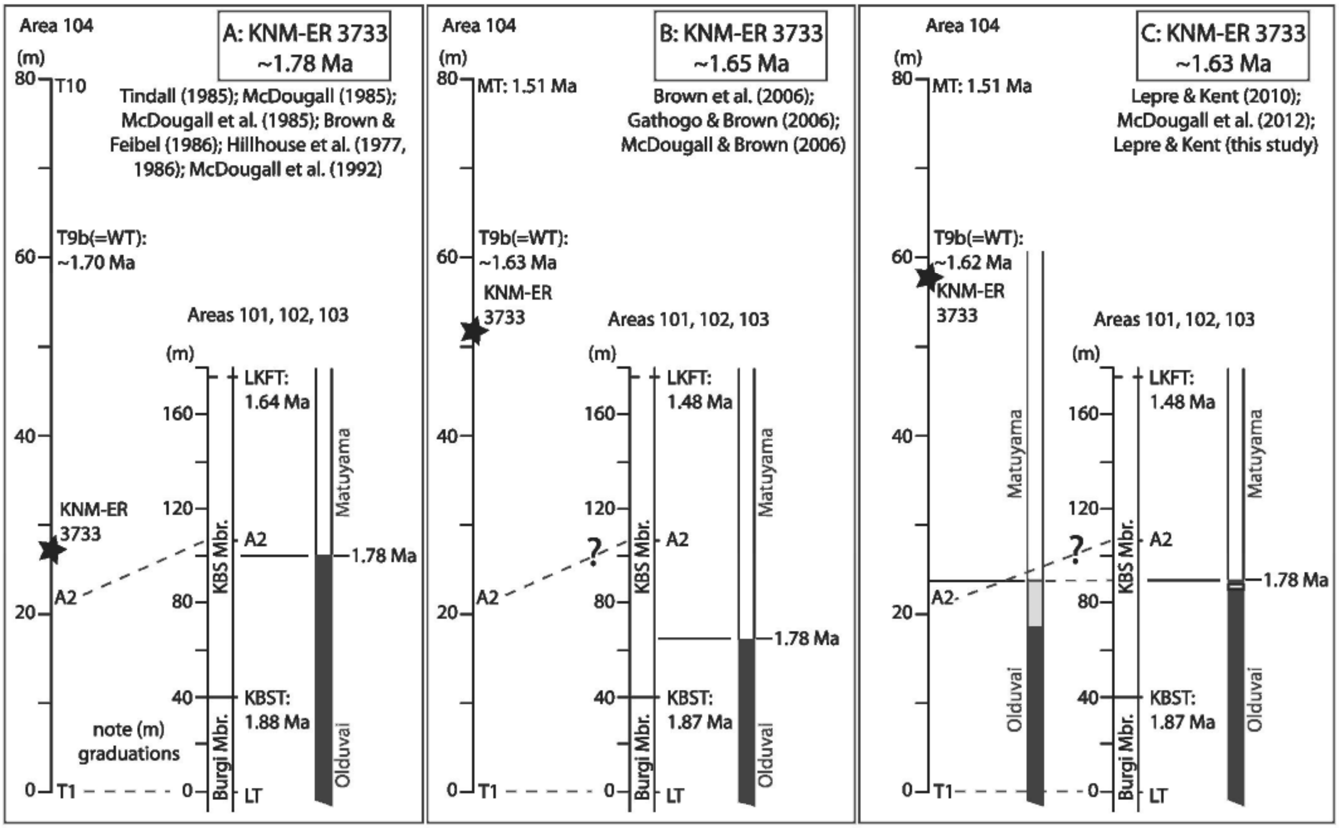

Fig. 7.38 Koobi Fora scientifically revised stratigraphic interpretations over the past few decades Lepre and Kent (2015:102)

KMN-ER 3733 specimen (Brown *et al.* 2006; Gathogo and Brown 2006a; McDougall *et al.* 2012; Lepre and Kent 2010). Based on the work of these authors, Lepre and Kent then performed a magneto-stratigraphy study for Area 104, specifically regarding the boundary between the normal Olduvai Subchron and arrived at an estimated date of 1.63 mya for specimen KNM-ER 3733 (2015:105).

This specimen is a mostly complete and undistorted adult cranium, consisting of a complete calvaria with most of the facial bones and a good portion of the teeth. It has a large prognathic supraorbital torus, as expected for *H. erectus*, and has reduced

Fig. 7.39 KNM-ER 3733 Cranium
Photo by Suzi Wilson

postorbital constriction which typically indicates a larger brain, as previously mentioned. It was found *in situ* by B. Ngeneo (with KFRP team) in Area 104 within the upper portion of the KBS Member in the Koobi Fora formation (R. Leakey and Walker 1976).

Endocranial volume was measured as 848 ml via the water displacement method (Holloway *et al.* 2004:127). Although the cranium is mostly complete and undistorted, there has been much erosion on the internal table of bone, creating a very lumpy and gnarled endocast surface. As a result, what might appear to be convolutional detail is difficult to see and unreliable. There is a prominent left

Fig. 7.40 KNM-ER 3733 Endocast mould posterior view
Photo by Suzi Wilson

occipital petalia (see Figure 7.40), although the right and left frontal bones appear symmetrical. Unfortunately, one of the few missing pieces is part of the left Broca's cap region, although the area on the left side where it would be found is somewhat more projected laterally than on the right side. Some remnants of meningeal vessels and sinuses are visible, but no definitive gyri or sulci.

However, a Sylvian notch, can be seen from the basal view (bottom of the frontal lobe looking upward) in Figure 7.41, demonstrating further operculation of the insula, which indicates a more derived condition (See the Evolution of the OFC in Chapter 2). Its presence can also be detected from a lateral view, but the detail is lost due to the gnarled surface of the endocast.

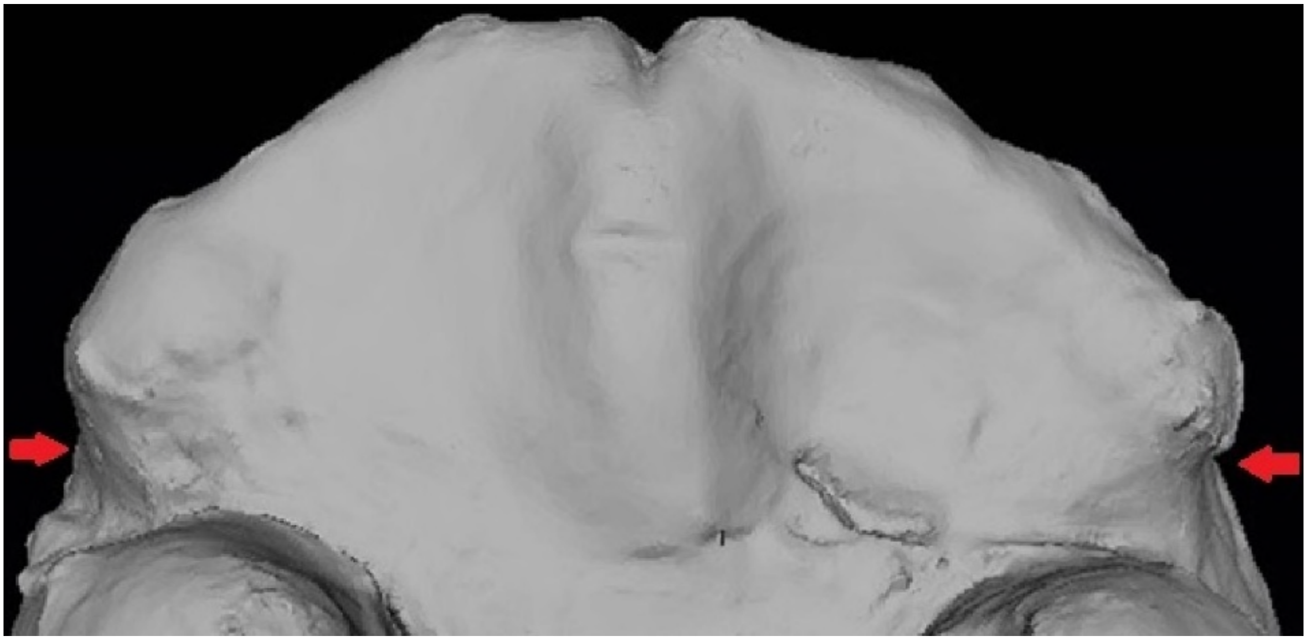

Fig. 7.41 KNM-ER 3733 Basal view looking upward at frontal lobe with Sylvian notch indicated by red arrows. Scan of endocast mould provided by Holloway. Modifications by Hurst 2017:128

KNM-ER 3883 – *H. erectus* 1.63 mya (Koobi Fora)

This partial cranial specimen was recovered from Area 3 of the Ileret beds at Koobi Fora at approximately the same horizon as KNM-ER 3733 (Walker and R. Leakey 1978). It is similar to KNM-ER 3733 in terms of shape and size, but with features a bit more robust such as a large protruding supraorbital ridge and very big mastoid processes, suggesting it is likely male. Also similar to KNM- ER 3733 is the erosion damage to the internal table of bone, making it difficult, if not impossible, to discern gyri and sulci or even elements of the sinus system or meningeal patterns, except for a bit of the left sigmoid sinus. However, it also has a definitive left occipital/right frontal petalia both posteriorly and laterally, likely indicating right-handedness.

Fig. 7.42 KNM-ER 3883 Face
Photo by Suzi Wilson

Fig. 7.43 Endocast mould, aerial-posterior view
Photo by Suzi Wilson

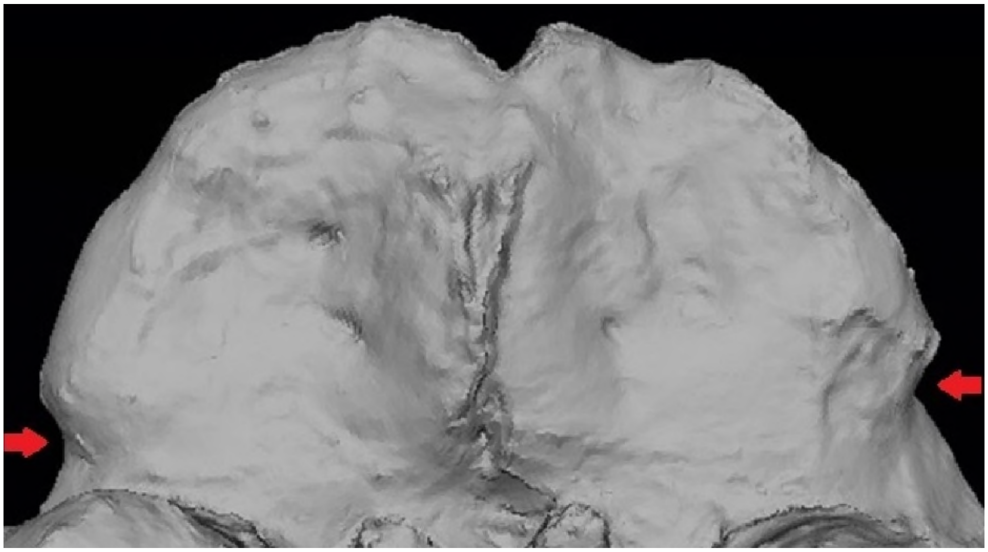

Fig. 7.44 KNM-ER 3883 Basal view looking upward toward frontal lobes, with Sylvian notch indicated by red arrows. Scan of endocast mould provided by Holloway. Modifications by Hurst 2017:128

The left Broca region is too damaged to observe any convolutional detail, although it does seem to project more laterally on the left side than the right, and a Sylvian notch can be seen in Figure 7.44. Albeit not particularly relevant to the aims of this thesis, Holloway believes that some of the posteriorly located cranial nerves can be seen such as the hypoglossal nerve, but I am not convinced due to the amount of erosion/damage.

DAN 5/P1 – *H. erectus* 1.6 to 1.5 mya (Gona)

Cranial fossils were found at the Dana Aoule North (DAN) 5 site at Gona in direct association with both Oldowan and Acheulean tools. Much of the cranium was found on the surface, but the occipital and left maxilla were recovered *in situ*, along with six manuports and one Oldowan core (Semaw *et al.* 2020). Other Oldowan tools as well as an Acheulean assemblage were also found at the hominin site (although not in direct association with hominin remains), along with fauna fossils bearing cutmarks.

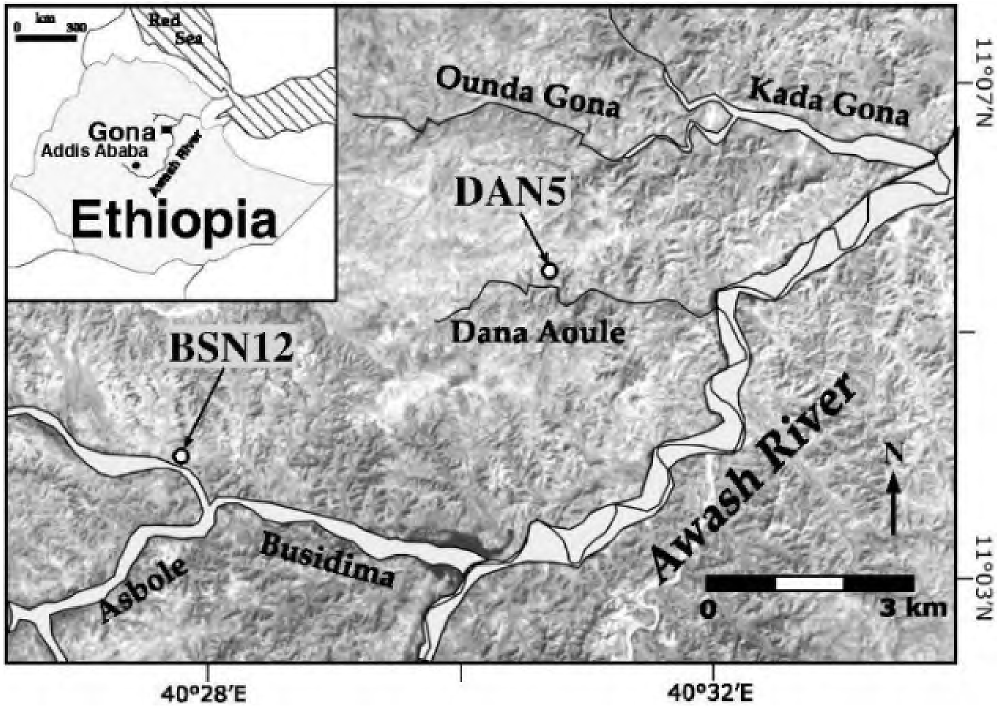

Fig. 7.45 Dana Aoule North site
Semaw et al. 2020:1

Assemblages of both technologies were also recovered from DAN5-South (approximately 140 metres to the south/southwest) and DAN5-West (approximately 50 metres to the west/northwest). All three of these sites are within the same stratigraphic context, bounded temporally by the base of the Jaramillo Subchron above (dated to 1.07 mya) and the top of the Olduvai Subchron below (dated to 1.78 mya) (Ibid). Using average local sedimentation rates, Semaw *et al.* interpolated the age of the DAN 5 cranium to between 1.6 and 1.5 mya (Ibid).

Fig. 7.46 DAN5 Cranium
Semaw et al. 2020:3

The cranial vault is globular in shape, with an arching supraorbital torus and an angular torus at the back of the parietal. There are also thickenings at the asterion and lambda. There is no sagittal keel. In general, the cranium is characteristic of a typical early African *Homo erectus* except that its endocranial volume is only ~598 ml, making it the smallest of the adult African erectines.

In 2022, Baab *et al.* published a detailed digital analysis on *H. erectus* variation and likely sexual dimorphism whereby the shape and other cranial characteristics of DAN5/P1 were compared to a younger *H. erectus* cranium: specimen BSN12/P1, dating to 1.26 mya, also from Gona but with a greater endocranial volume of 882 to 910 ml (2022:1). Although the authors were unable to identify consistent differences between male and female erectines with regard to endocranial volume or cranial shape, they did find many similarities between the DAN5/P1 cranium and the five crania from Dmanisi in Georgia, which range in volume between 546 and 730 ml (Lordkipanidze *et al.* 2013:327).

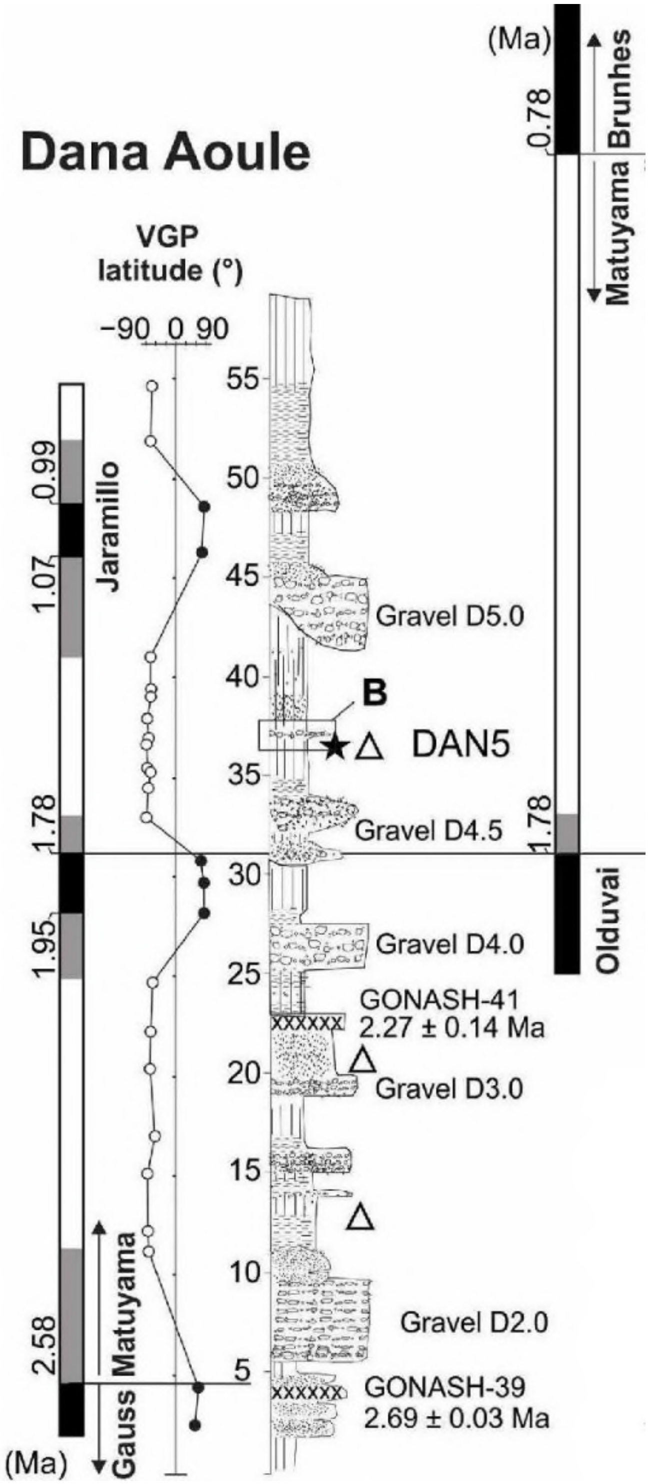

Fig. 7.47 Gona Stratigraphy
Semaw et al. 2020:2

The Dmanisi crania are non-African erectines and thus, outside the scope of this thesis, but it is nevertheless relevant to note how they compare in endocranial volume considering their proximity to Africa and as a means to further examine the extensive variation seen during the period between 2.0/1.9 and 1.4 mya, which is apparent in most of the early *H. erectus* specimens.

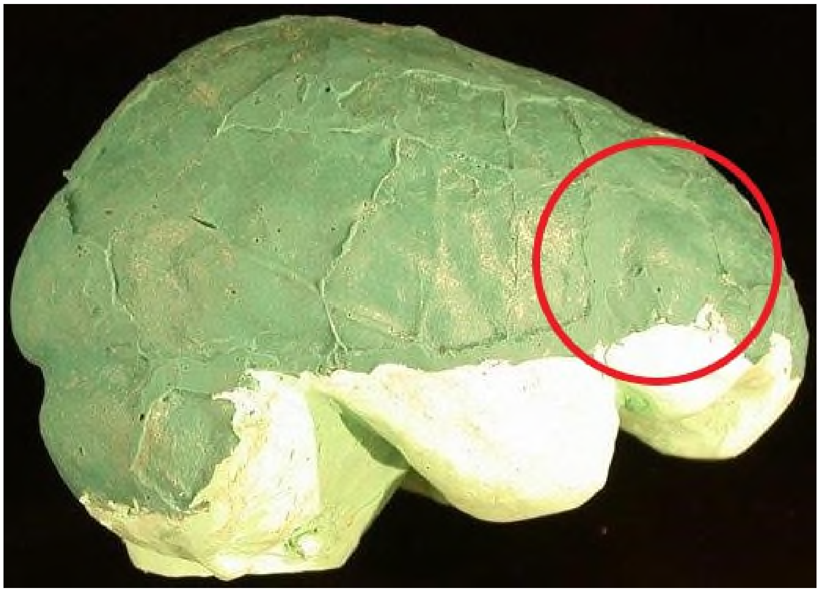

Fig. 7.48 DAN5 Endocast mould, right lateral view of Broca's area
Photo by Sileshi Semaw, courtesy of Ralph Holloway

The Dan 5 endocast is mostly complete but missing the temporal lobes, a basal portion, and a small bit of the inferior right cerebellar lobe. These areas were reconstructed by Holloway, based on the curvature of the frontal, parietal, and cerebellar lobes in order to measure the endocranial volume via water displacement. Five measurements were taken, ranging between 594 and 602 ml, producing an average volume of 598 ml (personal conversation 18-Feb-22). Some convolutional details are visible in the frontal lobe, where the superior, medial, and inferior frontal gyri can be identified. The right Broca's area (BA 44 and 45) is quite developed and more pronounced than the left, which is unusual, as discussed in Chapter 3. Although there is some patterning in this region, it is too difficult to delineate the Brodmann areas, although Holloway believes that the *shape* of Broca's area in DAN5, is more similar to that in modern humans, albeit smaller (Ibid).

The occipital poles are well developed and protrude posteriorly, and there is a small sulcus several millimetres posterior to the lambdoid suture on the left side, which Holloway believes might be a lunate sulcus, indicating parietal expansion (personal conversation 18-Feb-22). However, the variation in the occipital sulci of modern humans is considerable, as mentioned, making them difficult to positively identify without supporting occipital landmarks. I agree it is *possible* this sulcus could be a lunate sulcus in a more posterior position, but other than the occipital pole – there are no other occipital features to support this notion.

Unfortunately, I was unable to properly capture the suggested lunate sulcus in any of my photos, nor can it be seen in the photos provided by Semaw. Finally, there also seems to be a slight left occipital/right frontal petalia, indicating the individual was likely right-handed.

Fig. 7.49 DAN5 Endocast mound, posterior view
Photo by Suzi Wilson

KNM-ER 42700 – *H. erectus* 1.55 mya (Ileret)

The partial cranium was recovered *in situ*, embedded in a matrix of coarse sandstone and carbonates from the Ileret outcrop (part of the Koobi Fora formation) and dated to approximately 1.55 mya (Spoor *et al.* 2007). The spheno-occipital synchondrosis was approximately two-thirds fused at time of death, suggesting the

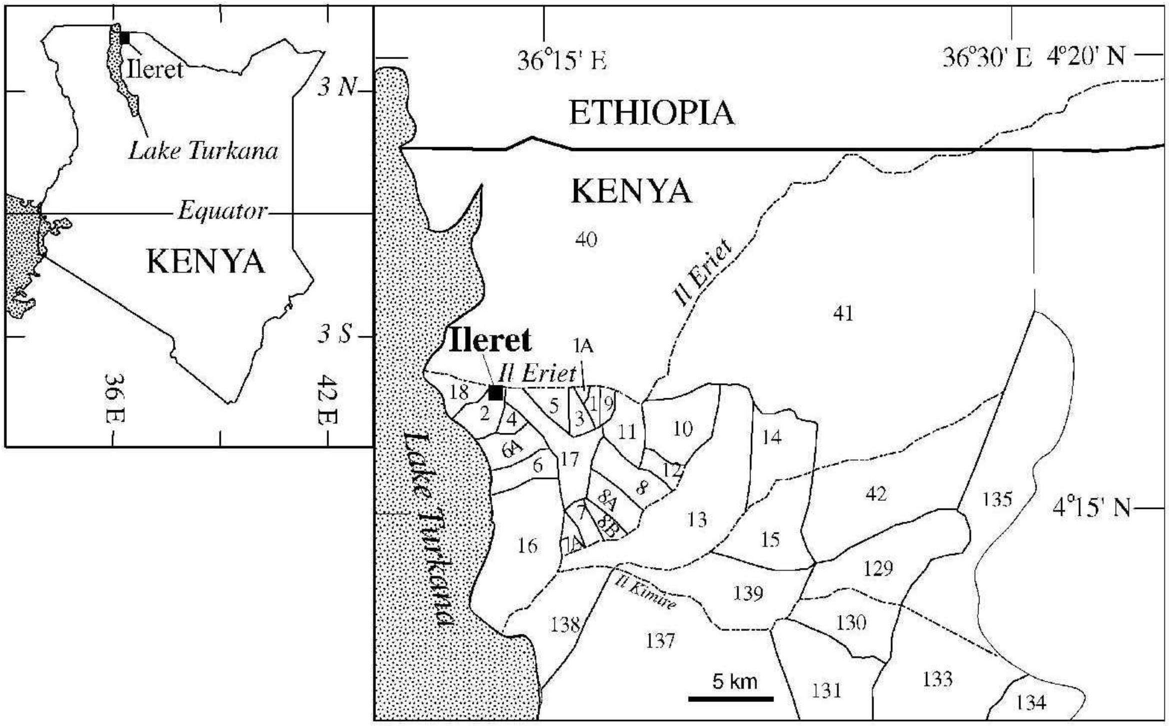

Fig. 7.50 Ileret, Kenya site
Gathogo and Brown 2006b:370

Fig. 7.51 KNM-ER 42700 Face
Spoor et al. 2007:689

Fig. 7.52 KNM-ER 42700 Posterior View
Spoor et al. 2007:689

individual was either a young adult or late adolescent (Ibid). The specimen is a relatively well-preserved calvaria, largely intact but with some damage and deformation primarily on the right side - particularly the frontal squama and right parietal (Spoor *et al.* 2007; Neubauer *et al.* 2018).

Posteriorly, the calvaria has that pentagonal shape associated with *H. erectus*, and there is also frontal and parietal keeling, yet the occipital bone lacks an occipital torus. Furthermore, the supraorbital torus is somewhat thin (compared to most erectines) and does not project anteriorly. Spoor *et al.* believe that the vault shape and size had fully matured, but suggest that supraorbital, mastoid and nuchal regions had not (Spoor *et al.* 2007). CT scans were made to measure endocranial volume and to correct for deformation. Based on these scans, brain volume was estimated as 691 ml (Ibid), which is, again, relatively small for a *Homo erectus* at 1.55 mya. Spoor *et al.* acknowledge that the size of KNM-ER 42700 is closer to *H. habilis*, but a multivariate analysis of “calvarial dimension” was performed by the authors, who argue it has six clear cranial features associated with *H. erectus* and should be classified accordingly (Ibid:688). Baab, however, was not convinced and performed her own geometric morphometric PCA of external neurocranial shape by comparing 36 three-dimensional cranial landmarks of the 42700 cranium specimen with other erectines, as well as other *Homo* species (Baab 2008:741).

In the analysis of the first landmark set, the KNM-ER 42700 calvaria plotted closest to the Daka[1] and Dmanisi[2] D3444 crania, whilst in another analysis that focused on shape, KNM-ER 42700 appeared closer to modern humans than any *H. erectus.* Overall, Baab argued that 42700 is unique and apart from the other *H. erectus* specimens, and its “wider and more posteriorly expanded vault, decreased constriction across fronto-temporale, and steeper frontal squama with thinner

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[1] *Daka is a 0.8 to 1.0 myo cranium with an endocranial volume of 995 ml (Baab 2016:1,18).*
[2] *Dmanisi D3444 is an estimated 1.77 myo cranium with an endocranial volume of 641 ml (Rightmire et al. 2019:481, 483).*

supraorbital elements . . . is well outside the documented range of variation for the [*H. erectus*] species" (Ibid:744).

In response to Baab, Spoor *et al.* replied that neither the distortion nor the late juvenile age of the specimen had been accounted for in her study, both of which could affect the results of the shape analyses and suggested a full virtual 3D reconstruction would be required to resolve some of these issues (2008). Neubauer *et al.* performed such a digital reconstruction, similar to their reconstruction of *A. africanus* specimen MLD 37/38, described in Chapter 5. The remaining matrix was removed digitally (via segmentation), the damage and distortion were corrected, and 935 endocranial landmarks and semi-landmarks were measured on curves and surfaces (Neubauer *et al.* 2018). Neubauer *et al.* also produced six reconstructed versions of KNM-ER 42700 with endocranial volumes ranging between 721 to 744 ml (732 average), still a bit on the small side, which may be related to age (Ibid:32).

These six reconstructions were then compared with the data from *H. erectus* specimens (four African and five Asian), *H. rudolfensis* (KNM-ER 1470), *H. habilis* (KNM-ER 1813) and modern humans (80 adult and 40 juveniles). Although the KNM-ER 42700 reconstructions naturally clustered with one another, they did not cluster with any of the four other morphotypes. However, they appeared close to the *H. erectus* samples, KNM-ER 1470, and the *H. sapiens* samples, yet were furthest from KNM-ER 1813 (*H. habilis*) (Neubauer *et al.* 2018:33). In summary, Neubauer *et al.* compiled five plausible hypotheses for explaining the morphology of specimen KNM-ER 42700. They favour the thesis that KNM-ER 42700 is *H. erectus*, but a younger individual than previously assumed, thus explaining why the shape of the cranium does not conform to the range of shape variation for adult *H. erectus*. They acknowledge that accepting this hypothesis requires the assumption that an early closure of the spheno-occipital synchondrosis had occurred, which would not have affected the ontogenetic shape of the cranium, up to that point of development

(2018:38). They also present photos of the digital endocasts, but do not comment whether or not any relevant sulci or gyri were viable.

KNM-WT 15000 – *H. erectus* 1.53 mya (Turkana Boy/Nariokotome)

The explorations which began on the west side of Lake Turkana were a "natural offshoot" of the Koobi Fora Research Project, originally established in 1968 (Walker and R. Leakey 1993:2). In 1984, a small portion of a hominin frontal bone was found by Kamoya Kimeu on the south bank of the Nariokotome River in Kenya, just west of

Fig. 7.53 Turkana Boy cranium, Aerial/Lateral View
Photo by Suzi Wilson

Lake Turkana (Brown *et al.* 1985), which ultimately led to the recovery of the most complete *H. erectus* skeleton of an individual, dated to approximately 1.53 mya (Brown and McDougall (1993).

The height and weight of the KNM-WT 15000 adolescent/sub-adult (aka 'Turkana Boy') at death was initially estimated as 160 cm and 48 kg, respectively (Ruff and Walker 1993). However, his height and weight as an adult has been largely debated over the past decade, primarily regarding whether or not *Homo erectus* experienced the same kind of 'growth spurt' that modern human adolescents experience, as well as his age at time of death (Cunningham *et al.* 2018). Initially, the age for the Turkana Boy was estimated between 11 and 12, with an upper limit of 14 based on the lack of epiphyses in the long bones with shafts (Ruff and Walker 1993). Yet some suggest the individual may have been as young as between 7.6 and 8.8 years, based on dental microstructure (Dean and Smith 2009) whilst others argue the appropriate age range should be between 14 and 16 years, based on the physiological

Fig. 7.54 Turkana Boy endocast mould, left lateral View
Photo by Suzi Wilson

Fig. 7.55 Turkana Boy endocast mould (II), aerial view
Photo by Suzi Wilson

stage of the distal humerus (Cunningham *et al.* 2018). Determining the likely age at death is crucial for properly gauging future ontogenetic development into adulthood, which would also impact estimates for height, weight, and endocranial volume.

The cranium was thick and robust (Ruff and Walker 1993), characteristic of *H. erectus*, and was recovered in many pieces with only the facial bones found *in situ* (Begun and Walker 1993). The cranium was reconstructed, and an endocast was made, which is mostly complete and undistorted. Begun and Walker estimated an endocranial volume of 880 ml for the original endocast based on water displacement (1993:346). Holloway also made an endocast and agrees with the endocranial volume, adding that it would have likely grown to 908 as an adult, notwithstanding the current ontogenetic debate discussed above (Holloway *et al.* 2004:139). There is a very pronounced left occipital/right frontal petalia, suggesting that the individual was likely right-handed. Similarly, the Broca region is more developed on the left than the right, which was also noted by Begun and Walker on the original endocast (Begun and Walker 1993). Some of the sinuses are evident, such as the sigmoid and both transverse, as well as some meningeal patterns, but otherwise – there is no convolutional detail to be seen.

KGA 10-656, 10-620, & 7-395 *H. erectus* cranial fragments (Konso)

Unfortunately, none of these cranial fragments from Konso provide any useful cognitive information, yet they represent the only fossil cranial evidence (to date) between 1.53 and 1.2 mya. Between 1991 and 2000, eight cranio-dental specimens attributed to *Homo erectus* were recovered from the Konso Formation, three of which are cranial fragments (Suwa *et al.* 2007). KGA 10-620 is a right parietal fragment, whilst KGA 10-656 is a combined right parietal/right frontal fragment. Both fossils were found in 1994 at or just above the Lehayte Tuff (LHT) in the Kayle Member, and thus dated to 1.42 mya. The third specimen is a right occipital fragment found in 1997 just below the Boleshe Tuff (BOT) and dated to approximately 1.3 mya. Although a modest assemblage, these specimens are currently the only cranial fossil evidence of the East African *H. erectus* lineage during this gap, serving as a link between the earlier and later African species and possibly providing some insight into Eurasian *H. erectus*.

KGA10-656 consists of a large portion of the anterior parietal bone, attached to a small fragment of the frontal bone at the coronal suture. The thin bone and open sutures suggest this is a young individual (Suwa *et al.* 2007). The external bone surface has been modified with fine, shallow parallel grooves that appear in sets mostly in the lower half of the parietal squama (Ibid). The cranial impressions of the meningeal vessels are easily visible as well as some of the sinuses, but no relevant sulci or gyri.

KGA10-620 is a small fragment of the posterior-inferior portion of the right parietal, with small sections of the lambdoidal and parieto-mastoid sutures near the asterion. Although these sutures have not closed, Suwa *et al.* believe that the individual may represent an adult (or sub-adult) based on the overall thick bone (2007). There is also a slightly developed angular torus.

Finally, KGA7-395 is a portion of the right occipital from near the midline laterally to the asterionic region, preserving portions of both the right lambdoidal suture and the occipito-mastoid suture. Neither of these sutures had closed, but again Suwa *et al.* believe the individual is an adult or near-adult based on the thickness of the bone (Ibid). There also appears to be a weakly expressed occipital torus. On the interior table of bone, the right transverse sulcus is visible along with a small portion of the sagittal sulcus, but again – no relevant sulci/gyri observed.

Although only a few of the erectine crania presented herein tell us anything about hominin brains between 2.0 and 1.3 mya, they do offer information on the *H. erectus* species itself – especially with respect to the wide range of variation, and endocranial volume during this period. Thus, any insight regarding *H. erectus* cognition will likely be better observed through the neural correlates of their tool-making culture.

The Neural Correlates with Acheulean Tool-making

The previously discussed study by Stout *et al.* (2008), whereby three expert toolmakers made both Oldowan and Acheulean tools, offers some interesting insight on the differences in the brain regions that were activated during expert Oldowan toolmaking compared to those activated for expert Acheulean toolmaking. The subjects were instructed to make *Late* Acheulean handaxes from large Obsidian blanks, provided on a cart. Although the Late Acheulean is beyond the scope of this thesis, the identification of the neural areas activated are nevertheless useful in that they demonstrate the cognitive trajectory between Oldowan toolmaking and Late Acheulean toolmaking.

It is not particularly surprising that the ventral premotor (PM_v)cortex, part of BA 6, is more highly activated during expert Acheulean toolmaking, considering how the PM_v is responsible for choosing the grasp to be employed by the hand from the available options (affordances), presented by the anterior intraparietal sulcus (AIP). The most notable difference between the expert Oldowan scans and the expert Acheulean scans is the marked increase in right hemisphere activity, such as the right supramarginal gyrus and additional clusters in the right PM_v cortex (Stout *et al.* 2008). Although this is somewhat surprising, it is likely due to the increased responsibilities of the left hand for working in tandem with the right hand as a single system, not only in stabilizing a much larger core but because a strong, precise grip was critical whilst the handaxe was being thinned in order to absorb shock and avoid breakage. This was not so important for the thicker handaxes of the early Acheulean but became increasingly crucial as handaxes became thinner.

The increased activation of the right supramarginal gyrus (Brodmann 40) is somewhat puzzling, but Stout *et al*. believe it reflects further increases in visuo-spatial skills relating to the overall tool + body system (2008). As noted earlier, the right supramarginal gyrus also plays a major role in extending empathy to others as well as egocentrism, which may have begun to be increasingly more important considering how toolmaking was likely a social activity and egocentrism may have led to the individualism of the toolmaker (to be further discussed). It is also a part of the mirror neuron system and identifies the postures and gestures of others, useful for young knappers, learning to flake by observing the experienced knappers.

Most intriguing is the activation of BA 45 (part of Broca) in the right hemisphere. Whilst BA 44 of Broca's area is more involved with phonological processing and the production of speech, BA 45 predominantly serves semantic processes and motor sequencing, including the ability to manually combine objects (Greenfield 1991; Friederici 2017). Stout *et al.* note that the prefrontal cortex (PFC) plays an important role in the coordination of goal-directed behaviour, and they also suggest that PFC activation might indicate higher demands for the organisation of the complex actions within the toolmaking task (2008). These areas of the frontal cortex also play an important role in abstract representation (Price 2000; Kandel and Hudspeth 2013).

However, the activation of the dorsolateral prefrontal cortex (dlPFC) was, once again, not observed, and yet the right ventrolateral prefrontal cortex (vlPFC) was highly activated. Stout *et al.* seemed surprised at this result considering how the dlPFC taps into working memory and is typically involved in the perception of space and the strategic planning of complex cognitive acts following by execution. Stout *et al.* suggest that the activation of the vlPFC versus the dlPFC indicates that expert Acheulean toolmaking required the cognitive coordination of ongoing complex actions, in lieu of an internal review and evaluation for action planning (Ibid). It makes sense that the right vlPFC would be involved (versus the dlPFC) when considering how the right and left hands were performing complex separate actions at the same time. This, combined with the activation of the right supramarginal gyrus, supports the suggestion of Stout *et al.* with respect to how toolmaking becomes internalized within the whole body + tool system. Finally, the vlPFC also plays a crucial role in task-set switching, which would have been an ongoing part of late Acheulean toolmaking among flaking, edging and thinning.

Although the early Acheulean tools were not as refined or well-shaped as the Late Acheulean, these neural correlates were likely developing, if not already in place.

The Acheulean between 1.65 and 1.2 mya

The early Acheulean was found in other sites across Africa, aside from the three already discussed, including the Rietputs Formation of the Lower Vaal River, southwest of Johannesburg, which dates to approximately 1.6 mya via cosmogenic burial dating (Gibbon *et al.* 2009); Garba IVD of the Melka Kunture Formation in Ethiopia, also dated to 1.6 mya (Gallotti and Mussi 2018); and the OGS-12 site at Gona dated to between 1.6 and 1.2 mya (Semaw et al. 2018). At approximately 1.5 mya, Acheulean forms continued to focus on thick pointed tips and long cutting edges, yet some evidence of refinement in handaxe shape had begun to emerge (Beyene *et al.* 2013), as well as a growing proportion of handaxes which had been bifacially flaked. Although these early handaxes remained crudely worked, Beyene *et al.* note how they gradually acquired façonnage over time, including some standardisation with respect to edge and tip shape (Ibid).

Whilst there was a modicum of design in the earliest artefacts, it became increasingly common after 1.5 mya (Isaac 1989; White and Foulds 2018; Shipton *et al.* 2018), and at the same time – more complex. Isaac notes how this increased complexity did not necessarily equate to "better," and it was not entirely due to the imposition of form in terms of "arbitrary, preconceived design norms," but also because an extra step had been added to the process by the deliberate striking of a large flake to serve as the blank from which the bifaces would be made (Isaac 1989:371). Isaac stresses that typically, we would assume an adaptive functional significance was driving these innovations, yet we have been unable to identify what that functional significance might have been (Ibid).

The Significance of Insignificance

According to Holloway, 'arbitrary form' and 'imposition' are two attributes used by man to organise his existence, and he further asserts that "imposition of arbitrary form on the environment" is a part of culture which can be identified in stone tools (1969:47). Although Binford argued that the environment dictates the shape of stone tools according to function, Bordes contended that the artefacts were shaped by cultural tradition (Binford 1983; Mellars 1996), which Porr stresses were the mental images or concepts stored in the minds of the hominin toolmakers who transmitted the construction of their imagery from generation to generation (Porr 2005:69). For example, symmetry is not an essential property for an effective handaxe, and although symmetry in handaxes is not universal – it became increasingly common after 1.5 mya. Although the topic of whether or not symmetry serves a useful function has been debated, a butchery experiment revealed that symmetry only slightly increased efficacy (Machin *et al.* 2007; Shipton *et al.* 2018).

There has additionally been argument over whether or not symmetry was deliberately imposed versus created due to unintended epiphenomenon resulting from either perceptual bias or as an accidental by-product of bifacial flaking. To test these possibilities, Shipton *et al.* performed a number of experimental studies[1], which provided compelling results indicating that symmetry was most likely an arbitrary and "intentionally created" imposition of form (2018:75). Furthermore, Wynn has argued that symmetry was intentionally imposed because it was typically achieved via the least number of removals to mirror the opposite edge (Wynn 1995, 2002).

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[1] *Involving modern humans as subjects*

Why, then, would these hominins further complicate the toolmaking process?

White and Foulds suggest that creating symmetry in tool-making provided an aesthetic self-gratification to the individual (2018), whilst Hodgson proposes it could have been an early appreciation for visual culture, possibly as art (Hodgson 2011). There is also the highly speculative, (and somewhat misogynistic) 'mate suitability' hypothesis, loosely based on Darwin's sexual selection hypothesis (but more likely influenced by mid-20th century social norms), which suggests that symmetry was imposed to demonstrate suitability as a mate and thus, attract females (Kohn and Mithen 1999). In turn, this theory sparked debate as to whether or not handaxe symmetry is sexually appealing (Burris 2009; Hodgson 2009; Machin 2008; Mithen 2008; Nowell and Change 2009). Perhaps Kohn and Mithen believe that showing a potential female mate a perfectly symmetrical handaxe was the equivalent of a mid-20th century man showing a woman his sports car, large gun, or some other surrogate phallic symbol, as a means to compensate for a sexual inadequacy. Furthermore, why are these white male scholars so certain that women did not make the symmetrical handaxes?

Additionally, Spikins has suggested the 'trustworthy handaxe theory,' which argues that this imposed form signalled trustworthiness and empathetic concern with altruistic intent (2012). Although also highly speculative, there is some supporting scientific evidence based on the activation of right supramarginal gyrus (from the Stout *et al.* 2008 study), which plays a crucial role in extending empathy to others (Stoeckel *et al.* 2009; Silani *et al*. 2013; Preckel *et al.* 2018). McNabb proposes that the makers of the symmetrical and well-shaped handaxes did so to demonstrate their expertise as a means to escalate their social status within the group, as part of his Visual Display Hypothesis (2012), whilst Gamble suggests that artefacts were a source of social power and performance in group social settings (1999).

Most of these theories have merit, and although the purely speculative mate suitability hypothesis leans toward the absurd (which Nowell & Chang (2009) made abundantly clear), it could simply be that symmetry was, indeed, its own reward as White and Foulds advocate, and/or perhaps an early art form as Hodgson proposes, or both. It is also possible that whilst these highly symmetrical handaxes provided their makers with sentiments of gratification and pride (and the associated endorphins), it also gave them a sense of identity – one which could be inscribed in their handaxes.

Art, Agency, and Handaxes

The ancestors of the hominin lineage started living together in social groups, approximately 52 mya, and our socialisation was greatly enhanced by bipedalism, as discussed (Swaab 2014; Barrett 2013). Tool-making was likely a social activity where hominins could help one another and pass on this culture to the younger generation,[1] by teaching them how to knap. In this setting, the Acheulean culture was socially transmitted (as were the earlier technologies) from generation to generation, and shared among the community at large (Shipton 2020). Although a social activity, it was also an arena for an individual to 'show off' his/her craftmanship and expertise in knapping, as Gamble suggests, and perhaps symmetry and shape were the artists' signatures[2] on their creations, a sort of 'branding' in the way the tools distinguished the toolmaker.

[1] *When crudely worked tools are found alongside well-made tools, especially during the Late Acheulean, the parsimonious explanation may simply be that they were produced by tool-making students, considering how a big part of the 'learning-to-knap' process was attempting to make tools of their own whilst observing/imitating the experts in the social setting.*

[2] *This sense of signature or 'branding' by the individual is also seen in the Etruscan potters who would leave their thumbprints at the base of the handles on vases (personal experience, Italian excavations 2012, 2013 & 2014).*

At the same time, these symmetrical and shaping features were (and still are) aesthetically pleasing to the eye, possibly as objects d'art. Thus, on one hand, there is the mental template of the handaxe, with some level of standardisation for all to follow, which had an influence on the community at large, perhaps as a sort of societal 'glue' in the Durkheim (1912) sense that served to bind the group together. (I am not suggesting that the handaxe was the first totem, but it is not inconceivable.) On the other hand, there is an opportunity within the range of acceptable variation for handaxes to deviate and for the individual to impose his/her own arbitrary form, possibly as an art form or as a means to imbue it with agency as representative of the toolmaker, or perhaps both.

Sally Price (1989) discusses the difficulty in interpreting "Primitive Art" as perceived through a Western [and modern] lens (1989:92-3; Gell 1998:2). First, we should accept and be aware of our Western bias as well as recognise that early hominin tool-makers/artists likewise had their own bias, as well as their own discriminating eye for aesthetics, both of which we will never know/understand. Alfred Gell further suggests that there is an "obvious analogy between 'culture-specific aesthetics' and 'period-specific aesthetics'" in Western culture, which impacts how art is perceived over the longue durée because 'ways of seeing' change over time (Gell 1998:2). Although we may not know what the Early Palaeolithic 'way of seeing' aesthetics may have been, from culture to culture, we can consider whether or not they existed and what possibilities they may have presented. For Gell, however, aesthetics alone were insufficient.

Gell rejected most definitions of 'art' including Morphy's definition of art objects as "having semantic and/or aesthetic properties that are used for presentational or representational purposes" (Morphy 1994:655). Gell stressed how emotional/social responses to artefacts "in the unfolding patterns of social life cannot be encompassed or reduced to aesthetic feelings" (Gell 1998:6). Indeed, the individual Western perception to an art object might be terror or fascination versus beauty. Many were horrified by the *Flaying of Marsyas* in the late 1500s and considered it the most repulsive of Titian's works, but this popular opinion did not render Titian's masterpiece any less of a work of art. Gell explores the ways in which 'things' or 'objects' merge with 'people' through social relations, and he focuses on social relations *via* things (Gell's emphasis) (Ibid:12), which might be applicable in the making of stone tools among hominins. There is not only the social aspect of performing a task together and helping one another, but also the tool + body system that Stout *et al.* refer to, whereby the right and left hands are working together in tandem and performing portions of the tasks at hand via muscle memory without really having to think about it. In this way, they would essentially become 'one with the tool,' not anthropomorphically but within their minds.

Gell argues that an art object should not be relegated to exclusively 'art' (as its only function), and he refutes the linking of 'art' with symbolism by instead referring to the representational aspect of art objects as 'indexical' in the Peircean sense, which Gell describes as meaning 'natural sign' (1998:7,12). This somewhat conflicts with Gell's distaste for Morphy's definition of art as having representational purposes, and Pierce's discourse on indices is more complicated than a simple definition. It is likely that Gell is referring to Peirce's reference regarding how an index (Peirce's 'secondness') does not necessarily need to resemble the object it represents, as an icon does (Peirce's 'thirdness') (James Hoopes 1991). In other words, Gell does not want to address the possible symbolism in art objects but rather to focus on the *indexical* nature of the art object in terms of what it might imply. Simple indices include smoke in the sky suggesting a nearby fire, or the sound of a train whistle, informing those waiting on the platform that a train will soon be pulling into the station. However, whilst smoke might infer a fire, the smoke could also be the result of something else altogether, such as a car's malfunctioning engine or exhaust.

Our internal interpretation of indices is based on patterns observed through experience, and although we may not consciously 'list' all the times we've noticed an index which resulted in a likely outcome, our subconscious does. Accordingly, we have an inner sense regarding the likelihood of a particular result that corresponds with an (subconsciously) observed index, based on how often we have seen it come to pass. We often refer to this sense as a 'hunch' when it is actually drawn from the memories of previous experiences within our subconscious, relating to these observed patterns. Gell employs the term 'abduction' as a form of logical deduction or cognitive interpretation applied to the index in order to properly determine (or 'best guess') the most likely outcome, correlation, meaning or object, inferred by the index (Ibid:15).

For example, we use abduction when encountering an index in a social setting, in order to gauge the dispositions and intentions of 'social others' based on the likely outcomes we infer from indices, which (according to Gell) are neither 'semiotic conventions' nor 'laws of nature' but rather something in between (Ibid). This is akin to feeling a 'bad vibe' about a person you've just met. You may not be able to identify the index that is giving you the bad vibe about this person, but your subconscious has accessed your memory banks and observed behavioural patterns that correlate with negative outcomes, based on your prior involvements with others who likewise displayed whatever that subconsciously unrecognized index is. This is what Gell refers to as a 'social index,' and according to Gell, the indices employed in his discourse regarding art and agency are thus restricted to only include those which permit the "abduction of . . . social agency" (Ibid).

Gell is not interested in 'natural' signs, such as how a lightning strike might cause the fire that produced the index smoke (a natural sign). However, when the origination is unclear, agency may still apply:

> “. . . suppose that, strolling along the beach, we encounter a stone which is chipped in a rather suggestive way. Is it perhaps a prehistoric handaxe? It has become an ‘artefact’ and hence qualifies for consideration. It is a tool, hence an ..index of agency; both the agency of its maker and of the man who used it. It may not be very ‘interesting’ as a candidate object for theoretical consideration in the ‘anthropology of art’ context, but it certainly may be said to possess the minimum qualifications, since we have no a priori means of distinguishing ‘artefacts’ from ‘works of art’ (Gell 1996). This would be true even if I concluded that the chipped stone was not actually made by a prehistoric artisan, but, having taken it home anyway, I decide to use it as an ornament for my mantelpiece. Then it has become an index of my agency, and qualifies yet again (besides which it is now obviously a ‘work of art’ i.e., a ‘found object’)” (Gell1998:16).

Thus, a handaxe can act as an agent as well as an index. According to Gell, any artefact (as a manufactured thing) can indicate the identity of the agent who made or originated it, because its existence was ‘caused’ by their makers, just as smoke is cause by fire (Ibid:23). When examining an Acheulean assemblage, it is sometimes possible to identify the tools knapped by the same individual (Hopkinson and White 2005).

However, the tool-making needs of the individual had to be balanced with the needs of the group. Gamble believes that although the chaîne opératoire, in a technical sense, is considered by most scholars to equate with the lithic reduction sequence (Hodder 1990), the concept is much broader, incorporating also the social aspects of a tool-making gathering (Gamble 1999). Gamble refers to Schlanger’s description of the chaîne opératoire as an “interplay between fixed and flexible” (Schlanger 1994), and he explains how raw materials have physical properties which make them somewhat ‘fixed,’ whilst the choices regarding the actions taken upon the raw materials are flexible (Gamble 1999). These choices are embedded in the culture and thus, tool-making gatherings become a form of societal performance whereby the mental template expresses the social identity but at the same time, allows flexibility for the individual to also inscribe his/her identity in the process. In this sense, the social influence was necessary to ensure the template tradition of the societal representation.

Gamble's work is based largely on that of Leroi-Gourhan (1993), who did not fully integrate the social aspect, as Leroi-Gourhan viewed society as a collective (like Durkheim 1912), but also believed that individuals could accomplish a "cartesian separation" between their internal and external environments (Leroi-Gourhan 1993:235; Gamble 1999:83). However, Leroi-Gourhan also believed that over time, the individual gradually disappears into the collective with each technical advance that affords external memory storage, outside of the body (Leroi-Gourhan 1993). This might be true in some respects, but there were also aspects of individualism within the Acheulean handaxe, which managed to resist fading entirely into the collective. Thus, the manufacture of handaxes allowed the individuals to participate in a tool-making social gathering and transmit the society's mental template to the next generation, whilst at the same time, allowed for the inscription of the individual's agency onto the handaxe with his/her symmetrical and shaped 'signature,' similar to the way in which the Etruscan potters 'signed' their vases with their thumbprints.

Broca's area and regions in the prefrontal cortex play important roles in abstract representation (Price 2000; Kandel and Hudspeth 2013), and were activated during the Acheulean tool-making study by Stout *et al.* (2008). However, the prefrontal cortex may have been activated because of how it coordinates goal-directed behaviour or the higher demands for the organisation of the complex actions within the toolmaking task, whilst the activation of Broca's area may have correlated with motor sequencing and the ability to manually combine objects. Furthermore, the angular gyrus (BA 39), which is heavily involved in agency (Ingelström and Graziano 2017), social cognition (Seghier 2013; Price *et al.* 2015; Ingelström and Graziano 2017) and self-consciousness/self-awareness (Swaab 2014) was not engaged in the 2008 study. However, these results could be explained as a limitation of the 2008 study presented by the modern human participants. Although the modern humans may have experienced a feeling of pride in making a beautiful Acheulean handaxe, it unlikely that they would have been mentally engaged in thoughts related to social cognition, individualism or agency during the experiment.

Some Acheulean toolmakers intentionally made handaxes increasingly thin, symmetrical and shaped over time, and whilst the parsimonious explanation is likely that creating a thing of beauty, a work of art, was done for their own reward, as White and Founds suggest, it is also possible that additionally, these handaxes were representative of, if not an extension of, their makers. After the toolmaker was gone, his/her handaxe remained as a reminder of this person's presence and influence (or even just their likeability) within the community. Although these representational handaxes may have been created as extensions of themselves, the artefacts, imbued with their own agency, can act indexically in both their representation of the toolmaker as well as with other representations/meanings that we will likely never know/understand.

What we do know is that prior to the emergence of these more complex handaxes, we did not see stone tools with features that could not be explained because they seemed to serve no functional purpose. Furthermore, even though handaxe complexity additionally increased further after 1.2 mya with symmetry and façonnage becoming more common, these aspects were not an "invariable" part of the process (Isaac 1989). Whether these qualities of thinness, symmetry, and shaping were actively representational or passively features of beauty to behold, they demonstrate not only a more advanced skill set, technically, but also an emerging aspect of cognition not previously seen in the behavioural evidence.

Summary/Conclusion

The severe cyclical glaciation beginning around 3.0 mya, and oscillating climate between moisture and aridity, created a highly variable and changing landscape for both fauna and flora, ultimately resulting in extensive variation, speciation and extinction among all the mammalian species (Vrba 1993; Antón *et al.* 2014; Stanford 2017). As hominins struggled to find sustenance and survive, they had to adapt in order to live in a much wider range of environments. The earliest Oldowan, dated to 2.6 mya, emerged at Gona and evidence of cognitive adaptations can now be seen in the fossil record.

The 2.03 mya endocast of the *H. rudolfensis* 1470 specimen revealed several derived features. The anterior ascending ramus of the lateral fissure (aalf) and the horizontal ascending ramus of the lateral fissure (half) seem to be forming the boundaries of an early pars triangularis, or BA 45, of Broca's area. The configuration is a bit more narrow than the pattern in modern humans, but this is the first known evidence of significant sulcal indication representing Broca's area in the hominin fossil record. Although BA 45 is known to be highly correlated with semantic processes in speech, it also plays a major role in motor sequencing and the ability to manually combine objects, crucial for making stone tools (Greenfield 1991; Friederici 2017). It is also possible that the pars opercularis (BA 44) of Broca's area is present, based on the increased coverage of the operculum, as evidenced by the presence of the Sylvian notch, another derived condition (in Figure 7.10). Additionally, the pronounced left occipital / right frontal petalia suggests that KNM-ER 1470 was likely right-handed. Sulci patterning in the Broca region can also be observed in another *H. rudolfensis* specimen, KNM-ER 3732, who also exhibits a Sylvian notch, whilst *H. habilis* specimen KNM-ER 1805 likewise seems to display some sulci patterning in the Broca region, as well as a possible Sylvian notch, but the features are more difficult to discern on KNM-ER 1805. Although sulci are harder to see on the larger crania of *H.*

erectus, the Broca sulci patterning can be observed on specimen DAN 5 (a smaller *H. erectus* cranium), whilst a Sylvian notch is evident on specimen KNM-ER 3733.

In addition to the severe and fluctuating climate causing disappearing food sources, there were at least five sympatric hominin species *P. boisei*, *P. robustus*, *H. habilis*, *H. rudolfensis*, and *H. erectus* living contemporaneously between 1.88 and 1.5 mya in Africa, creating intense competition for resources and sustenance. However, between 1.5 and 1.4 mya, they all went extinct except for *H. erectus* (Toth and Schick 2018:9), who had a (literal) 'leg up' on the competition. *H. erectus* had not only mastered bipedalism with a gliding, striding gait, but it is highly likely they could also run (Bramble and Liebermann 2004). Additionally, they had acquired the ability to live in extremely arid and open landscapes (Reed 1997; Antón *et al.* 2014), and they improved their technology with a new state-of-the-art tool for the Pleistocene: the Acheulean handaxe.

These large cutting tools were sturdy and well-crafted, able to perform various functions, including serving as a weapon if necessary. Certainly, the derived postcranial morphology in the hands, arms and shoulders played important roles, but the cognitive means to create, strategize, and execute a plan to make a handaxe of this design suggest a significant advancement. Furthermore, many of these handaxes were beautifully crafted in ways which added little, if anything, to their overall efficacy. These elements of design such as symmetry and shaping suggest an "imposition of arbitrary form" as an unidentifiable cultural adaptation, which was likely transmitted from generation to generation in a social setting. Most likely, there was a community template for the handaxes within which the makers were allowed to deviate and impose their own sense of identity onto the handaxe, which gave the tool-makers a sense of pride. In turn, their handaxes were extended agency in the process, likely representative of themselves but also possibly agency for the handaxe itself.

Not only did Acheulean handaxes improve the quality of Pleistocene life for procuring, processing, and protecting sustenance, they possibly also played a social role in a combined a sense of community and individualism. If so, this may have marked the beginning of representational thinking.

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Chapter 8: Conclusion

The Initial Catalyst

The cognitive evolution of the hominin lineage which ultimately derived into *Homo sapiens* has always been of curious interest in terms of how and why it occurred, as well as how it might be examined in the fossil record. Chimpanzee and bonobo genomes share 98.7% in common with modern humans, yet something set our lineages apart more than five million years ago (Prüfer *et al.* 2012:527). Although the ancestral split with the apes giving rise to the hominin lineage is predominately defined by bipedalism, why hominins adopted this form of locomotion remains a mystery, although there have been multiple hypotheses. Regardless of how and why this change in locomotion occurred, bipedalism enabled the evolution of the brain in several ways.

A more erect posture lifted the cranio-facial morphology, which allowed for brain expansion, and the many postcranial adaptations required for bipedalism would have produced corresponding changes in the brain, likely resulting in an early form of brain re-organisation. Additionally, bipedalism freed the hands for other uses, such as carrying children or sustenance, and over time, the wrists acquired mobility compared to the pre-hominin 'locked-in' stiff wrists needed for quadruped locomotion. Once derived, the enhanced mobility and dexterity of the hands and wrists allowed for a greater exploration of objects, materials, the environment, and even other hominins. However, the ability to regularly stand or sit upright with arms and hands free to either 'help or harm' also would have presented intense social situations for these early hominins, which in turn, prompted expanded social and communicative abilities in order to better read and relay intentions in these new amplified social situations. These deepened social relations likely resulted in further brain development, as suggested by the Social Brain Hypothesis (Maruyama 1963; Holloway 1967; Brothers 1990; Gamble *et al.* 2014).

The trickle-down effects of bipedalism leading to the first forms of cognitive evolution are somewhat obvious, but the benchmarks to follow have been more difficult to identify. Thus, this thesis has taken a comprehensive approach by examining the hominin brain endocasts in concert with the behavioural evidence provided by hominin-produced artefacts (stone tools) to provide a synthesis of the relevant information. From this synthesis, we can hopefully draw better hypotheses regarding the hominin cognitive timelines and thresholds, but the following factors are required and have been presented herein:

(i) a basic understanding of the neural functions of the various regions of the cerebral cortex, and a more detailed understanding specifically related to the functions of the relevant Brodmann areas;

(ii) an awareness as to how postcranial morphology adapted and changed over the course of hominin evolution, both in terms of how these physical adaptations would have caused corresponding effects in the brain, as well as providing the means to gauge the difference between perhaps 'not enough power/dexterity' in the hands/arm versus 'not enough brain' when examining the behavioural evidence;

(iii) the consideration of the many ways in which the transition from quadruped to biped might have affected social life for hominins, now that the arms and hands were available for actions other than locomotion; and

(iv) a knowledge of the underlying climate/environmental conditions at the end of the Pliocene/beginning of the Pleistocene, in order to better understand how these pressures may have forced neural and physiological adaptations in hominins for their survival.

Today's Neural Science

The technological innovations for neural imaging, especially during the late 20th century, provided (and continue to provide) great insight into the functions of the various regions and subregions of the human cerebral cortex. As a result, brain activity been linked not only to the specific Brodmann areas of the brain but also to the tiniest segments of gyri and sulci (e.g., the anterior interparietal sulcus). Additionally, today's neural science is also capable of recording brain activity simultaneously from several different neural regions, which together, often compose an association area of the brain, thus demonstrating how cognition is processed from cerebral *systems*. Furthermore, brain imaging has also allowed us to observe the regions and/or subregions of the brain which are actively engaged during various tasks, such as toolmaking. As a result, we now have access to a fairly constant stream of updated neural knowledge based on science versus outdated psychological theories, from which we can rely on, moving forward.

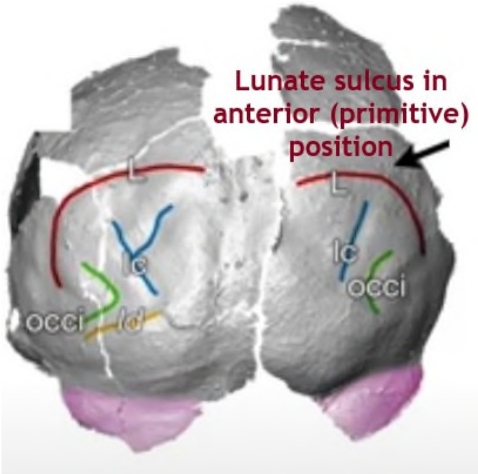
Whilst these technical innovations continue to improve our knowledge on modern neural science, new scanning and imaging technology has also improved our means for examining the brain endocasts of hominins. Although the endocast moulds created by Holloway and others introduced the only *direct* scientific evidence that could provide some insight with respect to the brain configuration of early hominins, it has often proven difficult to discern the sulci, gyri and other neuroanatomical landmarks on these moulds with the naked eye. Furthermore, the making of the rubber latex moulds always causes the cranial imprints to lose at least some level of definition on the internal table of bone, and additionally presents potential damage to the cranium itself – especially when the mould is pulled through the foramen magnum.

Digital scanning, however, poses no threat of damage to the crania, and the various software packages available can now remove matrix and other debris from a scanned crania via a segmentation program, also without causing damage (versus the use of knitting needles, as Dart used on Taung). These digital endocasts provide much greater detail, and the resulting .ply files can be easily shared with other palaeoneurologists. Although those in possession of the scans have been reluctant to share them with the public, most have been willing to at least share 2-D photographic imagery of the scans, which has been helpful.

Summary/Conclusion

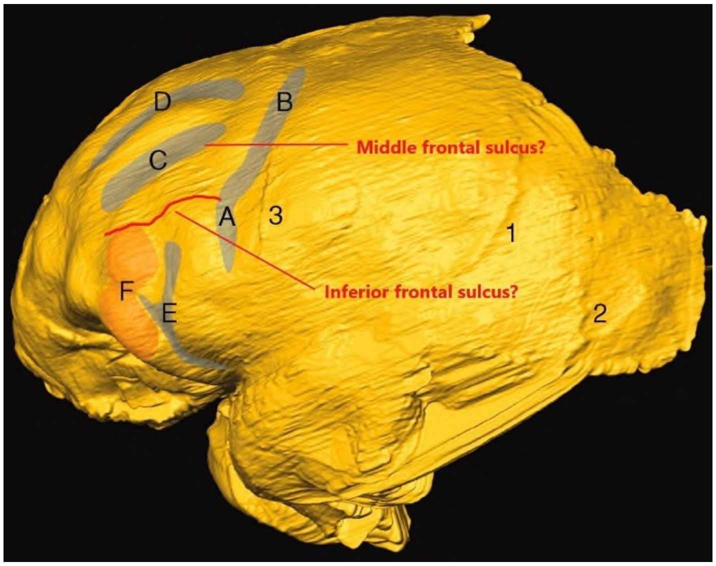
Although the australopithecine brain endocasts observed in this thesis did not particularly contribute much evidence in terms of brain re-organisation (other than a few instances of developed Broca areas and/or other brain lateralisation), the transitional evidence in *A. sediba* at nearly 2.0 mya, regarding the expansion of the orbital frontal cortex, suggests that brain reorganisation must have commenced much earlier. It is thus possible that some reorganisation or advancement developed as early as 3.3 mya, when it occurred to an early hominin living in what is now Kenya that instead of scavenging for a sharp stick or stone to use as tool, perhaps they could make their own. They somehow came up with a plan with their small brains, and managed to bang out a few stone tools from large 15 kg cores with their somewhat clumsy postcranial morphology.

Following the advent of extreme climate change (resulting in highly variable environments and food sources), *Paranthropus* attempted to 'eat their way out' of a tough situation with their small brains and big teeth/jaws, yet at the same time, cannot be ruled out as either an Oldowan or even Acheulean toolmaker. Considering how *P. boisei* found a way to survive until at least 1.4 mya, later than any hominin other than *H. erectus*, they must have had something else going for them, in addition to their megadont masticatory system. *H. habilis* had bigger brains than the australopithecines but their bodies were also larger, thus some of this increase in endocranial volume is attributed to allometry. Their hands, however, were more derived in a number of ways, especially their near-human thumb with a full range of motion in full opposition to the fingers which could flex firmly at the tip. Although the Oldowan were simple tools, likely made by more than one species, the range of variation was considerable. Whilst the assemblages recovered from Lokalalei LA1 were only marginally better than the Lomekwi tools from 3.3 mya, the toolkits from Gona and Lokalalei 2C evinced conscious planning, an advanced knowledge of fracture mechanics, greater accuracy in knapping, and more intense and uniform reduction sequences. Although it is possible that the making of better tools relied more heavily on better hands than better brains, Napier argued that it is the brain that mattered, suggesting that a sufficient brain would be able to overcome any insufficient postcranial morphology (1956:913); however, at the time he made this statement – the impressive Oldowan toolkits from Gona and Lokalalei 2C had not yet been discovered. Several of the *Homo* endocasts revealed how brain lateralisation had become more common among their genus, and a few of the endocasts (particularly *H. rudolfensis*) demonstrate evidence of brain re-organisation, including the continued expansion of the orbital-frontal cortex and increased development in Broca's area, with sulci patterns more closely resembling those of modern humans.

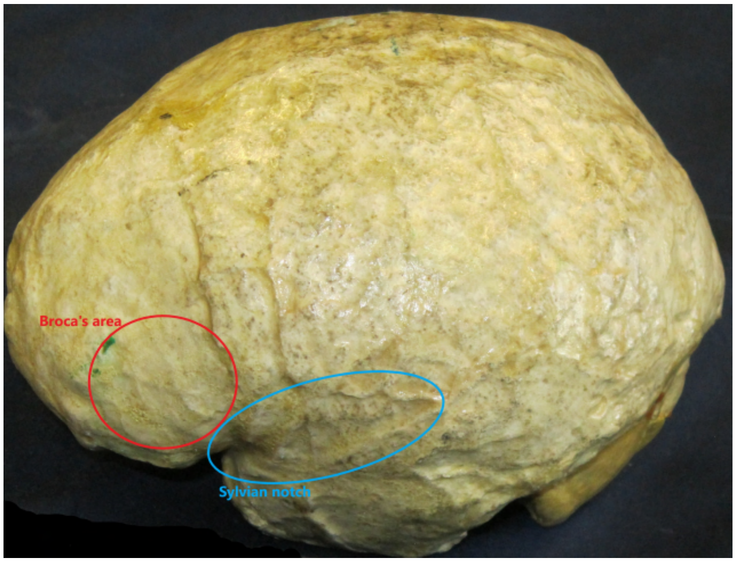


AL 162-28 No evidence of reorganisation
From Fig. 5.22 on pg. 181
Gunz 2020: www.youtube.com/
Watch?v=FAIoK4mtkzM

The evidence for reorganisation during the hominin lineage has been presented herein from *A. afarensis* (early australopith) with little to no evidence, to *A. sediba* (late australopith), where the MH1 endocast shows some expansion in the OFC as well as how the operculum has begun to form over the insula. Although we can still see the fronto-orbital (fo) sulcus, it had begun to transition (see page 240). By the time of early *Homo*, *H. rudolfensis* (early *Homo*) specimen 1470 exhibits not only a more fully formed operculum where the fo sulcus can no longer be detected, but also a Sylvian notch (demonstrating expanded coverage of the operculum) and a more developed Broca's area where the patterning is very similar to that of modern humans (see page 369).



From Fig. 5.63 on page 240
Virtual endocast of MH1 (left lateral)
Carlson et al. 2011:1403
Modifications by Suzi Wilson in red



From Fig. 7.10 on page 371
KNM-1470 Endocast mould (left lateral), with closeup of BA 45 (Broca) and Sylvian notch
Photo/modifications by Suzi Wilson

The oldest Acheulean tools date to approximately 1.74 mya, yet Oldowan tools continued to be produced as late as 1.25 mya, when *H.* erectus was the only known surviving hominin. Whomever made the Acheulean assemblage recovered from FLKW at Olduvai (dated to 1.65 mya) demonstrated increased upper body strength, hand agility, and advanced cognition with respect to planning, execution, increased visuo-spatial skills, advanced motor sequencing, and better coordination between the left and right hands, working together as a single system. Although we presume the maker was *H. erectus*, we cannot be certain. The erectines seemed to have everything going for them: gliding bipedal gait – even the ability to run, larger brain size, agile hands, and a near-modern skeleton, albeit perhaps a little stouter than previously thought. Their endocasts revealed very little but their tear-drop shaped, bifacial Acheulean tools spoke volumes, following the extinction of everyone else.

By 1.5 mya, the making of Acheulean handaxes had become more complex and increasingly refined, with a greater percentage of handaxes worked bifacially and acquiring symmetry, shaping and façonnage over time. Although there seemed to be some standardisation in form with respect to edge and tip shape, there were also more instances of handaxes with elements of design, presumably an arbitrary imposition of form by the maker. This imposition of form may indicate elements of deeper cognitive abilities, seemingly representative in many respects and possibly even symbolic, in nature. Although there was likely a 'mental template' for a level of handaxe standardisation, presumably imposed by the community at large, there was also a measure of freedom for the individual maker to inscribe his/her own identify into the handaxe as a means of branding or possibly even as a means for extending agency to the handaxe. Although we have no way of knowing the underlying intentions behind the imposition of form by the maker, it nevertheless marked a significant advancement in cognition, which should be further explored.

Below is a summary matrix which attempts to provide a 'snap shot' overview of the brains, bodies and behaviour examined throughout this thesis. Although we can make a few likely assumptions based on the current knowledge at hand, there remains much information which is not available and thus, we are unable to draw definitive conclusions. For instance, it is not possible to definitively determine which species made which tools, so we should initially assume that it is *possible* that all contemporaneous species in existence at the time the tools were knapped are potential makers. From there, it becomes a spectrum as to who the most likely makers are on one end of the spectrum whilst the least likely are on the other end, which is all very arbitrary. Furthermore, the species determined to be the 'most likely' makers are often biased based on their proximity to the artefacts recovered. Evidence of cognition also plays a role in which a species, such as *H. rudolfensis*, falls on the spectrum. *H. rudolfensis* specimen KNM-1470 not only had a large brain, but also evinced a Sylvian notch on his endocast, indicating the reorganisation of the orbito-frontal cortex as well as demonstrating a greater covering of the operculum, which included the emergence of BA 45, part of Broca's area which plays a role in motor sequencing and the capability to combine objects (as well as speech, of course, as previously discussed). Hence, KNM-1470 would seem to have a cognitive edge, and thus his species was included as a likely maker of the Acheulean, along with *H. erectus*.

On the negative side of this disclosure is the bias against the *Paranthropus* genus. *P. boisei* somehow managed to survive until 1.4 mya, suggesting s/he had something else going on besides their megadontia and massive muscles of mastication. However, *Paranthropus* was not included as a likely maker because their adaptations favoured the muscles of mastication, which caused increased orbital constriction in the cranium. As a result, there was little room available for brain expansion and the constriction may have also hampered gyri convolution. Yet, we cannot unequivocally state that they were incapable of making the Oldowan (or technically, the Acheulean), but rather that it is less likely for this reason.

Nevertheless, this summary matrix attempts to create a ‘big picture’ comparison of the Lomekwian, Oldowan and Acheulean which should be taken with a grain of salt, based on the assumptions disclosed above, whilst also remembering that it only takes one new discovery to change everything we currently believe to be true.

Lomekwian	**Oldowan**	**Acheulean**
		
Fig. 8.01 Lomekwian *Hovers 2015:294*	*Fig. 8.02 Oldowan – Gona* *Toth & Schick 2009:C-1*	*Fig. 8.03 Acheulean – Olduvai* *Diez-Martin et al. 2015:6*
3.3 mya	2.6 to 1.25 mya	1.74 to 1.0 mya
Most Likely Maker	**Most Likely Makers**[1]	**Most Likely Makers**
Unknown australopith	*A. africanus* *A. garhi* *A. sediba* *H. rudolfensis* *H. habilis*	*H. rudolfensis* *H. erectus*
Behaviour	**Behaviour**	**Behaviour**
Crude/simple forms Focus is on the removal of sharp flakes Most flakes are removed via passive hammer	Simple forms with some exceptions (Gona & Lokalalei 2C) Focus is on the removal of sharp flakes	Large and well-crafted tools for cutting pretty much anything. Focus on crafting and shaping the core into a teardrop shaped handaxe.

[1] *Clearly H. erectus also made Oldowan tools, considering their longevity until 1.2 mya. However, it is believed that H. erectus made them as expedient tools for short term/quickly needed tasks.*

Lomekwian	Oldowan	Acheulean
		
Hammer/bipolar knapping from a single striking platform in the same direction. A few cores indicate multi-directional flaking and some worked bifacially.	Produced via hard hammer percussion using bipolar or freehand knapping with evidence of patterned conchoidal fracture	Although not universal, there are often several instances of the imposition of arbitrary form onto the handaxe, such as symmetry, which serves no function.
Upper Body Strength Cores were large (15 kg) thus requiring upper body strength to lift as avg. hominin weight was only 45 kg. It is also likely that knapping involved lifting the hammer over head with both hands then launching	**Upper Body Strength** Freehand knapping would have required greater strength for making successful blows with only the dominant hand. However, some Oldowan tools were made via bipolar knapping.	**Upper Body Strength** Primarily freehand knapping with great strength required for making successful and highly accurate blows for both symmetry and shaping.
Dexterity Wrists were likely still adjusting to bipedalism and thus stiff. Hands were still very ape-like with short thumbs.	**Dexterity** Freehand knapping would have also required a more derived hand, including a thumb with a full range of motion, in full opposition to the fingers for strength, grasping and control. By now, wrists were likely more flexible.	**Dexterity** Freehand knapping now required strength and control in both (near human) hands, working together in tandem whilst performing separate important tasks.

Lomekwian	Oldowan	Acheulean
		
Cognitive Advanced enough to recognise the affordances offered by the ability to make stone tools versus search for items to be used as tools. Cognition for fracture mechanics was likely slightly better than 'ape-grade' which was likely taught via imitation. Possible origin for cultural transmission (although there is presently no evidence in the fossil record to suggest that this early toolmaking culture spread beyond the Lomekwian site.	**Cognitive** Could recognise the affordances offered by making better tools, as well as the affordances of smaller tools which would be easier to transport. Could also likely recognise the affordances of a grip choice or the power to strike a blow to the core. Endocasts are finally starting to show evidence of brain reorganisation in the frontal cortex. Modern human study for expert toolmakers making the Oldowan show areas engaged in: visuo-spatial planned movement, motor sequencing, motor control. and parts of the mirror neuron system.	**Cognitive** Recognised the affordances offered by a large cutting tool, as well as the affordances that the body offered in making such a tool, as well as the arbitrary imposition of form, possibly as an esoteric means of expressing identity or extending agency onto the handaxe. Although we are unable to identify the meaning behind the form, it nevertheless suggests a cognitive advancement for representational thinking. Furthermore, the symmetry and shaping imposed indicates enhanced visuo-spatial skills as well as an understanding of 3D geometric axioms/postulates.

Future Work on the Synthesis

The synthesis of information provided by this thesis could benefit further via a collaboration between those who specialise in stone tools and those who focus on the study of brain endocasts. From my personal observations, the stone tools specialists seem eager to share their work and samples with others, whilst the endocast makers are highly secretive and miserly with their information. For example, there is an endocast (Yan 1) in Holloway's lab which I was allowed to observe but not discuss in this thesis. It was recovered more than ten years ago in East Africa and sent to Holloway for an endocast to be made, but the discoverer of the endocast has repeatedly told Holloway that he is not ready to publish any information regarding it – not even that it exists. In the meantime, there is additional work to pursue in this endeavour.

It does not really need to be said that we need more samples. Almost all Palaeolithic studies state the need for more samples with respect to future work, but truly we require more crania – especially for the australopithecines. That being said, it would also be very helpful to create high-resolution scans of the existing crania for which we currently only have endocast moulds (or no endocast at all). The difference in the information revealed by the high-resolution scans and what can be seen on an endocast mould is substantial. Furthermore, the relatively thick meningeal vessels between the brains and internal table of bone often mask sulci detail on the endocast moulds (Holloway 1974; Falk 1980), making the availability of digital scans even more crucial.

Although access to the endocast moulds is also limited, Holloway is in the process of scanning all of his endocast moulds and providing copies for me and others, which I intend to share. However, The Max Planck Institute in Leipzig has one of the best scanners in the world, with a resolution so high it is unsafe for living human beings (according to legend). The information acquired by directly scanning

Palaeolithic crania at their facility in Leipzig has been a game changer in terms of the detail that can be detected with their CT high-resolution scanner. Unfortunately, they currently do not share their files – only photographic imagery of the .ply files.

Finally, I would like to continue this study from *H. erectus* to the early *Homo sapiens* and include the Neanderthals as well as *H. naledi*. In addition to stones tools, there would be other behaviour to consider, such as the earliest use of fire and Middle Palaeolithic burial practices.

Future Work: Neurogenomics and Social Plasticity

Neurogenomics combines neuro-biology with the genome sciences. Each cell in the human body contains a genome, which is a complete set of genetic instructions for growing and developing the body. This is accomplished by the unique chemical code in the DNA[1] within the genome, which in turn guides this growth and development (Boguski and Jones 2004:429). By using this genetic and biological information within the body, neurogenomics studies how the genome affects the evolution, development, plasticity, structure, function, and disease of the brain/nervous system. Presently, neurogenomics seems to be primarily focused on neurological diseases such as Alzheimer's and Parkinson's diseases as a means to diagnose and/or prevent their progression (Chiba-Falek 2020), but there are also neurogenomic studies which are investigating the mechanisms of 'social plasticity' (Cardoso *et al.* 2015).

Cardoso *et al.* suggests that social plasticity should be considered an adaptive trait, triggered when the environment is changing faster than the rate of genetic evolutionary change (2015:140). Although adaptation by natural selection typically depends on the inherited phenotype produced by genetic variation, Cardoso *et al.* argue that when environmental change is outpacing genetic evolutionary change,

[1] *The human genome is made of 3.2 billion bases of DNA (Chiba-Falek 2020).*

adaptive change *without* genetic mutation emerges (Ibid). Thus, it is possible, if not likely, that this kind of adaptive change (evolution of phenotype plasticity) was driving the hominin range of variation during the Pliocene to Pleistocene transition. Apparently, phenotype plasticity is favoured when changes in the environment trigger the same genotype (in an organism) to produce different phenotypes based on the trigger (Pigliucci 2001; West-Eberhard 2003; Cardoso *et al.* 2015). Furthermore, Pigliucci observes that behavioural traits exhibit faster and stronger plasticity than morphological traits (2001).

Cardoso *et al.* further address how one of the most unpredictable aspects of the environment is the social domain, which would have certainly been the case during and following the transition to bipedalism. It would have been crucial for individuals to "regulate the expression of social behaviour, so as to adapt their behavioural output to specific situations," which would have relied on the evolution of social plasticity (2015:140), and Holloway agrees that the changes in the brain over the course of evolution would have been underscored by accompanying neurogenomic adaptations, most likely from social and environmental pressures; however, the genetic evidence that could provide better insight with respect to these cerebral developments is not (yet) available (Holloway 2015).

Cardoso *et al.* detail their premises regarding genomic mechanisms of social plasticity at both the molecular and neural level, a discussion of which is beyond the scope of this thesis. However, it should be noted that one of the means for achieving social plasticity at the neural level is structural reorganisation (Ibid:142). At the genomic level, long-term irreversible behavioural changes are presumed to rely on epigenetics (Ibid), which is interesting when considering how epigenetic[1] changes

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[1] *Epigenetics is the study of changes in gene expression that cannot be attributed to variation in DNA sequence (Smith and Schroder 2020). Simply put, it studies how behaviours and environment can cause changes that affect the way your genes work.*

are short-term (reversible) and do not change the DNA sequence. Instead, epigenetics can change the way the body reads a DNA sequence.

As mentioned at the beginning of this thesis, today's modern neural science has grown by leaps and bounds since the turn of the 21st century, and continues to advance at an exponential rate. In the early 1980s, DNA was studied in mummies, then in 2010, Svante Pääbo's team was able to sequence the Neanderthal genome from an arm bone (Pääbo 2014). However, Pääbo stresses how crucial it is to access DNA which had been mummified prior to degradation (Ibid:7). Even then, there are other processes that will continue to degrade genetic information, but at a slower rate. Although it is unlikely that we would ever be able to find and procure usable DNA from three-million-year-old hominins, neurogenomics should ultimately be able to provide, at the very least – clues, and hopefully evidence, as to how and when certain aspects of brain evolution occurred (Holloway 2015:827).

Today, however, we are limited to endocasts and stone tools, but we could greatly improve our knowledge base through an interdisciplinary approach between those who study brains and those who study tools, and it would also prove very helpful to include those with postcranial expertise as the nuances in hand bones are sometimes very difficult to identify/decipher. Finally, a greater collaborative spirit among those with access to digital endocasts would be very much appreciated by all.

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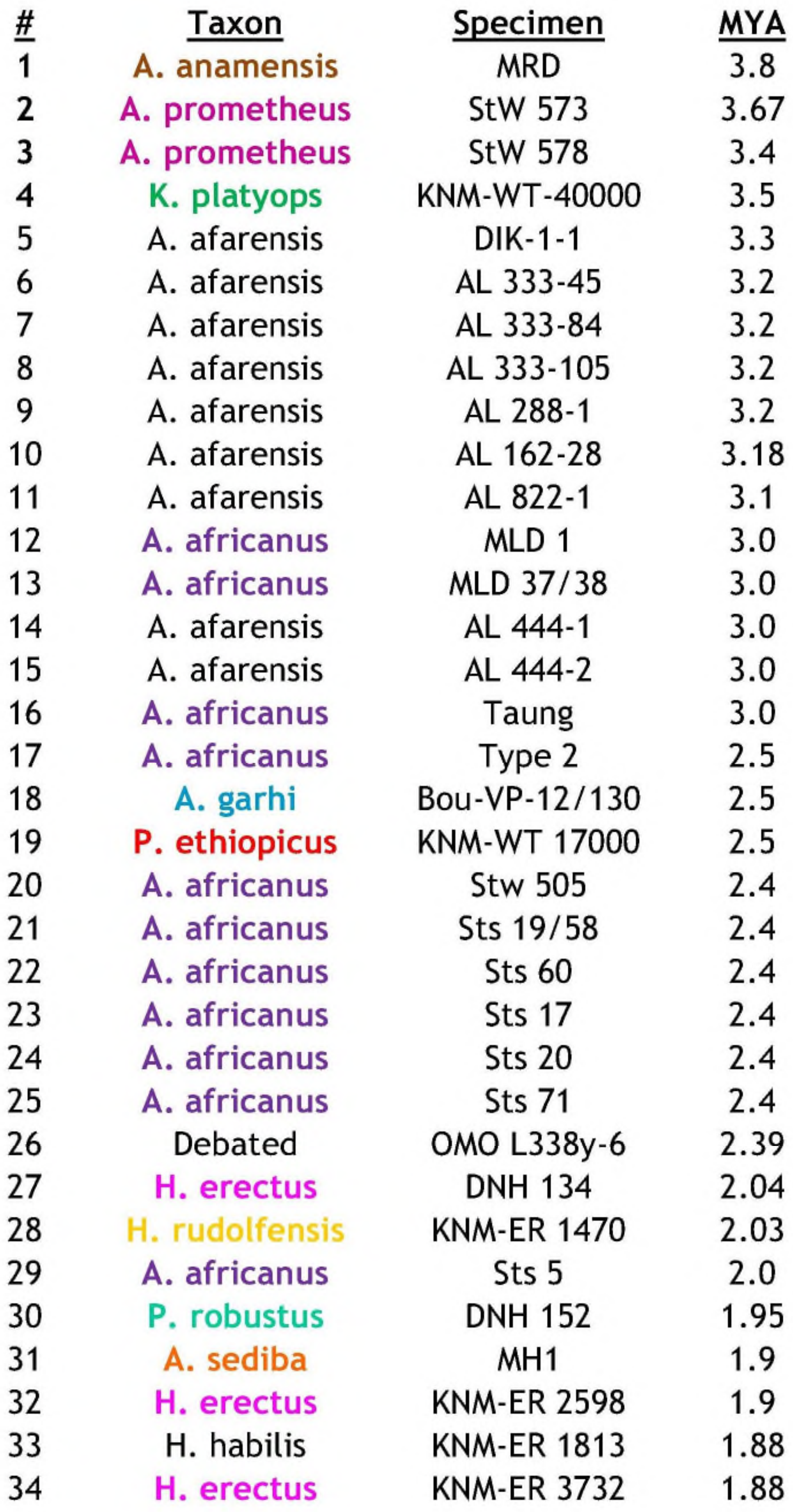
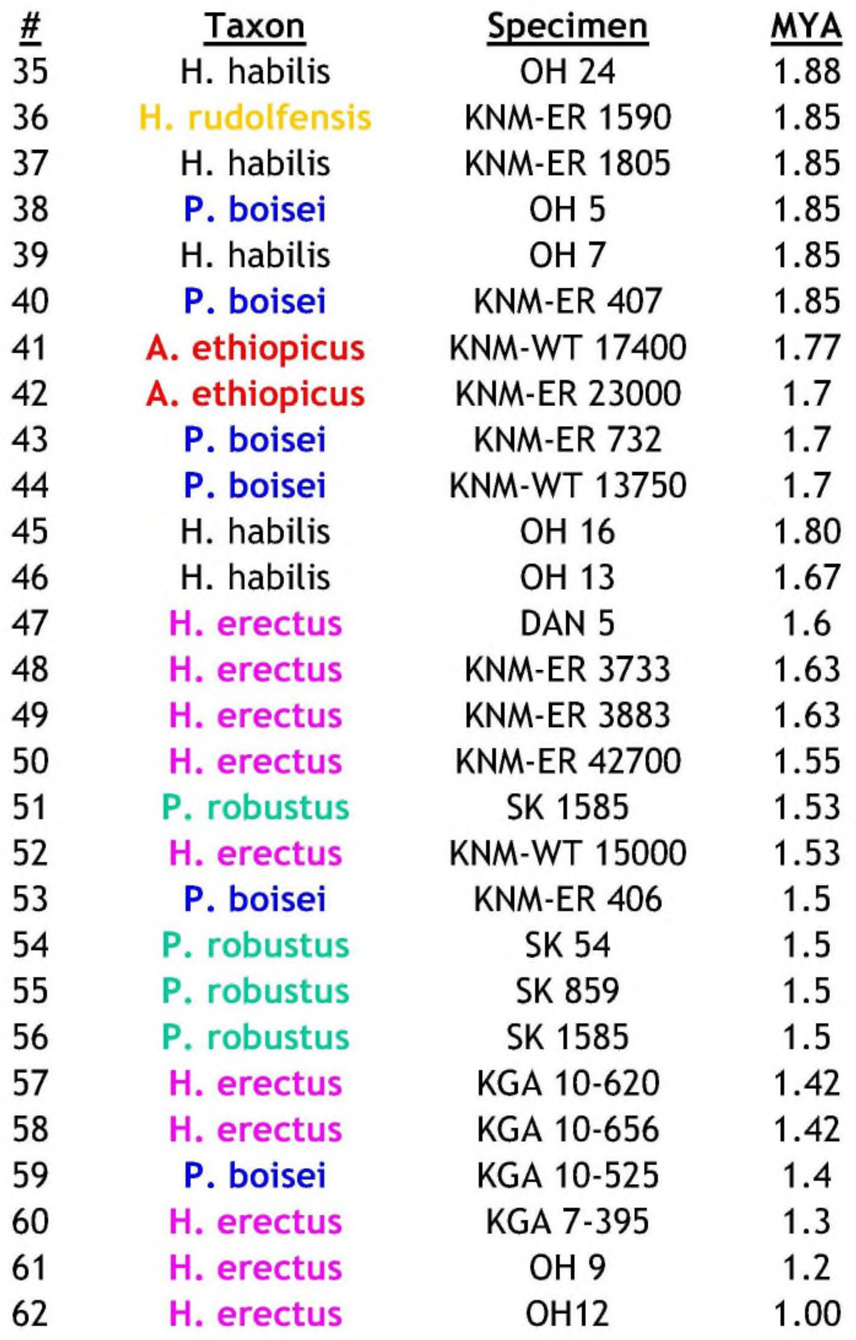
APPENDIX A: ORIGINAL MASTER LIST OF CRANIA*



#	Taxon	Specimen	MYA
1	A. anamensis	MRD	3.8
2	A. prometheus	StW 573	3.67
3	A. prometheus	StW 578	3.4
4	K. platyops	KNM-WT-40000	3.5
5	A. afarensis	DIK-1-1	3.3
6	A. afarensis	AL 333-45	3.2
7	A. afarensis	AL 333-84	3.2
8	A. afarensis	AL 333-105	3.2
9	A. afarensis	AL 288-1	3.2
10	A. afarensis	AL 162-28	3.18
11	A. afarensis	AL 822-1	3.1
12	A. africanus	MLD 1	3.0
13	A. africanus	MLD 37/38	3.0
14	A. afarensis	AL 444-1	3.0
15	A. afarensis	AL 444-2	3.0
16	A. africanus	Taung	3.0
17	A. africanus	Type 2	2.5
18	A. garhi	Bou-VP-12/130	2.5
19	P. ethiopicus	KNM-WT 17000	2.5
20	A. africanus	Stw 505	2.4
21	A. africanus	Sts 19/58	2.4
22	A. africanus	Sts 60	2.4
23	A. africanus	Sts 17	2.4
24	A. africanus	Sts 20	2.4
25	A. africanus	Sts 71	2.4
26	Debated	OMO L338y-6	2.39
27	H. erectus	DNH 134	2.04
28	H. rudolfensis	KNM-ER 1470	2.03
29	A. africanus	Sts 5	2.0
30	P. robustus	DNH 152	1.95
31	A. sediba	MH1	1.9
32	H. erectus	KNM-ER 2598	1.9
33	H. habilis	KNM-ER 1813	1.88
34	H. erectus	KNM-ER 3732	1.88



#	Taxon	Specimen	MYA
35	H. habilis	OH 24	1.88
36	H. rudolfensis	KNM-ER 1590	1.85
37	H. habilis	KNM-ER 1805	1.85
38	P. boisei	OH 5	1.85
39	H. habilis	OH 7	1.85
40	P. boisei	KNM-ER 407	1.85
41	A. ethiopicus	KNM-WT 17400	1.77
42	A. ethiopicus	KNM-ER 23000	1.7
43	P. boisei	KNM-ER 732	1.7
44	P. boisei	KNM-WT 13750	1.7
45	H. habilis	OH 16	1.80
46	H. habilis	OH 13	1.67
47	H. erectus	DAN 5	1.6
48	H. erectus	KNM-ER 3733	1.63
49	H. erectus	KNM-ER 3883	1.63
50	H. erectus	KNM-ER 42700	1.55
51	P. robustus	SK 1585	1.53
52	H. erectus	KNM-WT 15000	1.53
53	P. boisei	KNM-ER 406	1.5
54	P. robustus	SK 54	1.5
55	P. robustus	SK 859	1.5
56	P. robustus	SK 1585	1.5
57	H. erectus	KGA 10-620	1.42
58	H. erectus	KGA 10-656	1.42
59	P. boisei	KGA 10-525	1.4
60	H. erectus	KGA 7-395	1.3
61	H. erectus	OH 9	1.2
62	H. erectus	OH12	1.00

*Represents original crania examined or studied. Several were omitted in the narrative of this thesis due to lack of relevance or lack of an available corresponding endocast.