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**Born to throw, climb, squat AND run. Biomechanical evolution within the human lineage and its inference for health and fitness**

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**Born to throw, climb, squat AND run. Biomechanical evolution within the human lineage and its inference for health and fitness**

**Masters by research thesis- Bangor University**

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**Author's declaration**

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

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## **Abstract**

This thesis explores four physical behaviours thought to be important in the evolution of hominids, namely climbing, squatting, running and throwing. It aims to comprehensively explore the evolutionary background and anatomical adaptations involved in each behaviour, and to holistically explore the concept of evolutionary mismatch in modern humans. My approach employed a series of systematic reviews, with each behaviour being considered independently. Search terms specific to each behaviour were used in three different literature search engines to identify relevant articles by title and abstract, before a full read through applying additional criteria determined their eligibility. Articles meeting all the relevant criteria, such as containing specific reference to the behaviour in question within an evolutionary context, made up the literature base for each review.

Climbing is hominids' most ancient locomotory mode, with evidence for its utilisation stretching back at least 20 million years ago (mya) to some of the earliest hominid fossils currently known. Its use greatly diminished with the adoption of habitual bipedalism, particularly within the genus *Homo*, although it retained usefulness for certain foraging behaviours such as the acquisition of honey. Anatomical adaptation for climbing is mostly seen in the shoulder and hands as the major weight-bearers. Prolonged deep squatting is a posture that equals climbing in terms of time-depth, and was used by our ancestors as a means of simple resting or for key behaviours such as defaecation and childbirth. Its significance has received little attention. Evidence for squatting is found in the ankle with 'squatting facets' present upon the talus in archaeological samples. Ankle dorsiflexion seems to be the key limiting factor of this posture. Endurance running is a behaviour adopted by hominins as they became terrestrial hunter-gatherers, likely as a means of moving swiftly to pursue hunts or scavenging opportunities. Major adaptations for running are found throughout the modern human body, including spring-like tendons in the legs, large articular surfaces on weight-bearing joints, stabilising upper-body mechanics and several specialist thermoregulatory features. Finally, projectile throwing in combination with more sophisticated hafting of weaponry vastly improved the hunting success of later hominins- certainly *Homo sapiens* but also, most likely, *Homo neanderthalensis*. Adaptation for throwing in modern humans can be seen notably in the shoulder, wrist and hands. Modern humans in today's society behave very differently. Behaviours such as climbing and running, which were once so important to our hominin ancestors, now have little bearing on our survival. This is partly due to technological innovation and our emerging division of labour. One health concern of such a shift is the risk of evolutionary mismatch, with barefoot running being the most well-known case: several authors have suggested that a lack of running is a source of health concern for our running-adapted species. The information reviewed herein suggests further possible mismatches, such as the lack of squatting and abundance of chairs in modern society, a lack of general daily strenuous activity, and perhaps interaction between behaviours that require similar anatomical adaptations. Although further work is needed on the specific topics covered, this thesis concludes that the modern human form is adapted to regularly perform a range of physical activities, and that cross-training might be a key way of improving health and fitness today.

### Footnote to abstract

It should be noted that this thesis uses the modern Wood and Lonergan (2008) use of Hominini- the taxonomic tribe attributed to the human lineage after the split from *Pan*. Hominidae is therefore the overarching family which includes all of the great apes including humans, and all of their relatives.

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## **Introduction**

Evolution via natural selection is the driving force that adapts organisms to their environments. This stalwart theory of modern biology was first conceptualised in the mid-1800s by Alfred Wallace and Charles Darwin, who while working independently came to very similar conclusions, co-publishing their first seminal work on the topic in 1858 titled '*On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection*' (Darwin and Wallace 1858). This was followed by Darwin publishing the first edition of his famous book '*On the origin of species*' the following year, which today is seen as the classic text on the subject (Darwin 1859).

Under both background and novel environmental conditions there is a positive selection for traits within a population that promote maxima reproductive fitness. This is because those individuals that possess the most favourable traits are most likely to survive, and thus live long enough to reproduce and further their genetic material (Darwin 1859). By this mechanism the most well suited suite of adaptations for a particular environment becomes most common within a population. Darwin's finches might be the most classic example of natural selection, indeed these species were the subjects of some of the very earliest theories of evolution, as a younger Darwin explored the Galapagos Islands upon HMS Beagle in the 1830s (Darwin 1859). Geographical isolation on the volcanic islands of Galapagos has caused adaptive radiation of the finch species present there, each being defined by the dietary niche that they utilise (Lawson and Petren 2017; Carvajal-Endara et al. 2020).

Morphological variation is especially visible in their beaks- some of which are large and robust for cracking into stubborn nuts, while others are long and pointed for insectivory (Sulloway 1982; Lawson and Petren 2017; Carvajal-Endara et al. 2020). Natural selection for beak variation has adapted each finch species to its specific dietary requirements, allowing them to feed most efficiently thus improving their reproductive fitness.

The finding of ancient fossils is a key way in which we are able to reconstruct the plant and animal assemblages of the past. Thanks to our knowledge of natural selection we can predict the kinds of environmental pressures that fossil organisms were facing and the behaviours they adopted, based on the adaptations that their morphology alludes to. As an example of the basic reasoning involved and to return to the previous finch example, we know that beak morphology is a useful proxy for diet in extant finches, therefore we can fairly safely assume the same for extinct finches in the fossil record, allowing us to predict their feeding behaviours. Such inferences can even be made between totally unrelated species thanks to homoplasies- convergent features of organisms that have come about through occupying a similar niche or reacting to the same selective pressures (Gordon and Notar 2015). An example of such homoplasy in the natural world is lekking behaviour- small territories that males occupy, compete for and display within to attract females- that is practiced by perhaps 35 phylogenetically diverse bird species, as well as seven species of mammal, without any genetic component linking species (Wiley 1991; Gordon and Notar 2015). Another is that of winged-flying species both extant and extinct such as arthropod insects, the pterosaurs, dinosaurian birds and mammalian bats all sharing many features in order to conquer extended flight, notably that of possessing very similar aerodynamics in order to become airborne and maintain elevation (Gordon

and Notar 2015). Using analogies like this is a key tool in reconstructing biological lineages, just as Jolly (2001) did in their classic work, utilising analogies from extant primate species such as baboons and mandrills to provide insight into the genetic outcome of early-modern human and neanderthal hybridisation in Europe.

In addition to morphological variation brought about by natural selection, habitual movement patterns and postures carried out throughout the lifetime of an organism leads to flattening and sometimes ridging upon articular surfaces of bones, caused by long term and consistent contact along a particular plane of movement (Bandovic and Futterman 2019). These musculoskeletal stress markers are often given several names, such as enthesopathies, bone imprints or simply facets, and can be very different in form and location particularly upon highly weight-bearing structures, even between individuals of the same species, helping us predict the biomechanical behaviour of the specific fossil in question (Bouille 2001; Villotte et al. 2010; Narayanan et al. 2018). For instance, the facets present on the tarsal bones of hominins are useful in predicting the extent of bipedalism within the fossil sample, as well as prevalence of deep-squatting (Dlamini and Morris 2005; Gebo and Schwartz 2006; Narayanan et al. 2018). This sort of variation between individuals without any genetic component is known as phenotypic plasticity, and was first coined in the study of plants by Bradshaw (1965).

Taking both our knowledge of natural selection and phenotypic plasticity together one can start to interpret bony anatomy to build a picture of the kinds of behaviours performed by extinct species within the fossil record. In the study of human evolution for which this thesis is based there have been many notable discoveries that have revolutionised our understanding of our past. For example the famous fossil discovery known as 'Lucy' (or more specifically A.L. 288-1), as well as a range of other specimens uncovered in Ethiopia and Tanzania in the 1970s, vastly widened our understanding of the hominin species *Australopithecus afarensis* (Kimbel and Delezenne 2009). This was a pivotal species in the transition of hominins towards more terrestrial activity and habitual bipedalism, and is a species referred to extensively throughout this thesis. By piecing together such finds anatomy, ecology and behaviour researchers have been able to begin to reconstruct modern humans' hominid ancestry, as well as allude to their behavioural shifts over time, which is the main subject herein.

### **Major transitions in human evolution**

The taxonomic tribe Hominini (referred to here-after as the 'hominins') includes all species more closely related to *Homo sapiens* than to other living great apes (Wood and Lonergan 2008). An important distinction should be made here between the use of the terms hominins and hominids, the latter describing the overarching taxonomic family Hominidae, which while including all hominins also includes other great ape groups such as orang-utans and gorillas, and therefore has a far older taxonomic origin, exceeding 20mya (millions of years ago) (Crompton et al. 2008; Langergraber et al. 2012).

The evolution of the anatomically modern human (*Homo sapiens*) has seen key shifts as a result of changing locomotary styles. Within the extant animal kingdom humans are most closely related to the other great-apes, indeed hominins and chimpanzees split from a fairly generalised arboreal ape somewhere between 7 and 8mya (Crompton et al. 2008; Langergraber et al. 2012). Combined with

the knowledge that extant great-apes such as chimpanzees, orang-utans and gorillas (as well as the majority of other primate species) are highly capable within the arboreal environment, we can confidently say that our earliest ancestors were climbers. However after this split this began to change, with subsequent species within the human lineage such as *Ardipithecus* (~4.4mya) and the Australopithecines (~4-1.5mya) starting to climb less and spending more time terrestrially, while slowly adopting a more habitual bipedal posture (MacLatchy 1996; Stern 2000; Sarmiento and Meldrum 2011). Selection for more efficient terrestrial bipedalism followed, gradually improving with the inception of the genus *Homo* and subsequent species, culminating in later individuals of *Homo erectus* (1.9mya) who by this point were obligate bipeds likely of equal efficiency to that of modern humans (Lieberman 2007; Hatala et al. 2016).

Endurance running was one form of terrestrial travel likely first performed by *Homo erectus*, enabling swift and fluid travel over larger distances, and perhaps improving their hunting potential (Bramble and Lieberman 2004; Liebenberg 2008; Pontzer 2017). As bipedal hunters within a semi-open forest habitat *Homo erectus* became the first hunter-gatherers, an energetic omnivorous lifestyle relying on consistent foraging of wild plants combined with regular hunting of potentially large mammalian game in order to meet calorific requirements, while also expending energy on raising young, fashioning tools and clothes and a plethora of social interactions (O'Dea et al. 1991; O'Keefe et al. 2011). This physically testing lifestyle further developed the species' physical capabilities, particularly those involving endurance, as individuals had need for consistent high levels of exertion. Hunting ability (as well as defence and warfare) was enhanced with the adoption of projectile throwing around the inception of *Homo sapiens* ~300ka (thousands of years ago), allowing striking at distance of a prey item or foe, reducing the risk of harmful retaliation (Lombardo and Deaner 2018). This energetic hunter-gatherer lifestyle was practiced by humans up until around 10,000 years ago; if a *Homo sapiens* origin of 300ka is assumed, then hunter-gathering has been practiced by our species for over 95% of our existence (Marlowe 2005; Stringer 2016).

### **The rise of agriculture and industrialisation**

Agriculture was invented around 10,000 years ago at independent sites across the globe, including in Asia, North America and Europe, perhaps linked with an extended period of climatic stability at the time (Feynman and Ruzmaikin 2019). No longer were humans roaming large distances hunting and gathering, but settling in a single place and cultivating the land around them. Although early farming without the help of machinery or efficient tooling must have been an arduous lifestyle, this transition towards agriculture incurred an overall reduction in the average individuals total physical labours, which can be seen in femoral thickness and rigidity from fossils at this time period (May and Ruff 2016). While not all adopted farming- as is demonstrated by the persistence (although rare) of hunter-gathering societies today- this way of life became obsolete for the early agriculturalists, with little need for physical activities such as climbing, running and throwing which had previously been the objects of strong natural selection over millions of years. The agricultural transition also appeared relatively quickly, as while the yearly speed of the spread of agriculture seems slow (0.6-1.3km/yr speed of spread through Europe) it reached the furthest extent of North-Western Europe from an origin in the



Middle East within 3000 years, which from an evolutionary timeline perspective is very fast (Pinhasi et al. 2005).

Far more recently within the last 400 years the more developed and wealthiest nations transitioned through industrial revolution, where we began harnessing energy-rich fossil fuels such as coal and oil, enabling mass automation of the production of goods and making transportation significantly faster and more convenient (Mokyr and Nye 2007). Industrialisation vastly widened the variety of ways in which people spent their days, in both how they made a living and how they provided food and shelter for themselves and their families. Generally physical activity levels among the majority of people further declined, and once again within an incredibly short period of time, perhaps 8 generations for industrialisation compared to 350 for agriculture, both of which lengths of time wane in comparison to the 84,000 generations we spent as hunter-gatherers (O'Keefe et al. 2011).

### **Evolutionary mismatch**

The relative speed with which humans have changed their environments, behaviours and thus physical workloads has led to what is known as evolutionary mismatches, which occur when an organisms current behaviour or environment is out of sync with its evolutionary past (Riggs 1993; Li et al. 2018). The result is physiological stress which the organism is not well adapted for, potentially leading to illness and/or injury. Evolutionary mismatches are the product of the pace of natural selection generally being slower than other forms of environmental change, such as the rapid shift towards industrialisation. For humans they have been caused by the differential speed of cultural evolution verses biological evolution. The later is the Darwinian theory of evolution via natural selection (discussed previously), and occurs over multiple generations. Cultural evolution in contrast is the within and between generation sharing of knowledge via highly social environments, essentially inheriting not only the genes from your parents but also learning throughout your life from others about skills, customs, beliefs and much more (Ehrlich 2002; Henrich and McElreath 2003). This form of cultural transmission involves individuals learning far more and far quicker than they would be able to do by themselves via trial and error, and although originally it was thought to be uniquely human, some songbirds and chimpanzees also exhibit such behaviour (Boyd and Richerson 1995; Whiten et al. 1999). Essentially, 10,000 years (or ~400 years since big changes in the industrial revolution) has simply not been enough time for natural selection to keep up and adapt humans to their established rapid rate of cultural evolution and the magnitude of different ways that we have changed our environments (Li et al. 2018).

Today humans have modified over 75% of the global landmass, with 54% of us living in urban areas (2014) and projections for this to rise to 75% by 2050 (Ellis et al. 2010; Zhang 2016). Our nomadic hunter-gatherer adaptations are being used in radically novel ways, leading to a plethora of health issues. For example type 2 diabetes and coronary heart disease are both conditions of excessive sugary and/or fatty foods, combined with poor levels of physical exercise. These diseases have exploded in prevalence since the advent of fast food, and are more or less non-existent in primitive societies today- demonstrating their mismatch status (O'Dea et al. 1991; O'Keefe and Cordain 2004;

O'Keefe et al. 2011). Evolutionary mismatches can thus have significant impacts on our lives and health, and deserve more attention from the human sciences.

### **This thesis**

This thesis will explore the biomechanical aspects of evolutionary mismatch among modern humans, specifically the ways in which modern humans move today- plus the tools and technology we use to help us move- and whether and how this is out of sync with the physical behaviours that humans and their ancestors have performed for the majority of their evolution. Four major themes within hominid evolutionary biomechanics can be identified, the first three have been described previously- climbing, running and throwing- which were important biomechanical shifts in order to adapt to the demands of a changing environment, among other novel selection pressures. Prolonged deep squatting can be added to these three as a passive resting posture, as well as a means of defaecation and childbirth, that has been practiced by humans as well as the majority of other primates for millions of years (Rosenberg and Trevathan 2002; Ingold 2004; Zhang et al. 2004; Sakakibara et al. 2010). Although other important behaviours exist such as load carrying, taken together these four represent the major biomechanical forces guiding biomechanical selection in hominids, certainly over the last 10million years.

In the modern day, particularly within the more developed world, all four of these behaviours are neglected by the majority of people, resulting in possible evolutionary mismatch. In running, especially in terms of how we run and the shoes we put on our feet, this has been explored quite extensively. By wearing running shoes (a very recent invention) modern humans are hypothesised to be altering their running kinematics significantly enough to cause injury, a topic that has attracted considerable research interest over the last 15 years (Jenkins and Cauthon 2011; Altman and Davis 2012; Lieberman 2012; Murphy et al. 2013; Perkins et al. 2014; Tam et al. 2014). Current research into evolutionary mismatch among humans is heavily biased towards running, despite it being but one of several key physical behaviours performed by hominids during their evolution.

The aim of this thesis is to provide a comprehensive review of the four behaviours previously described- climbing, squatting, running and throwing- especially in terms of the ideal physiology and anatomy required to perform them. These independent reviews will provide an up-to-date summary of our current understanding of each behaviours biomechanics, something that has never really been done for ancient activities such as climbing and squatting, or is somewhat out of date (see Watanabe (1971) for a classic example of locomotary review).

With the insight gained from this I will then collate the information on all four behaviours, providing a discussion on how the anatomy and physiology of hominids has changed throughout their evolution in response to the biomechanical demands their lifestyle exert. This will create an understanding of which regions of the body have seen the most modification through the human lineage, which similarities and differences exist between them, and what physical activities humans are adapted for today. Finally, by comparing our ancestral behaviours with the common movement patterns of the 21<sup>st</sup> century, new evolutionary mismatches will be explored. Only by considering different physical

behaviours together and the adaptations they have driven across the human body can we truly understand the extent and impacts of evolutionary mismatch among humans.

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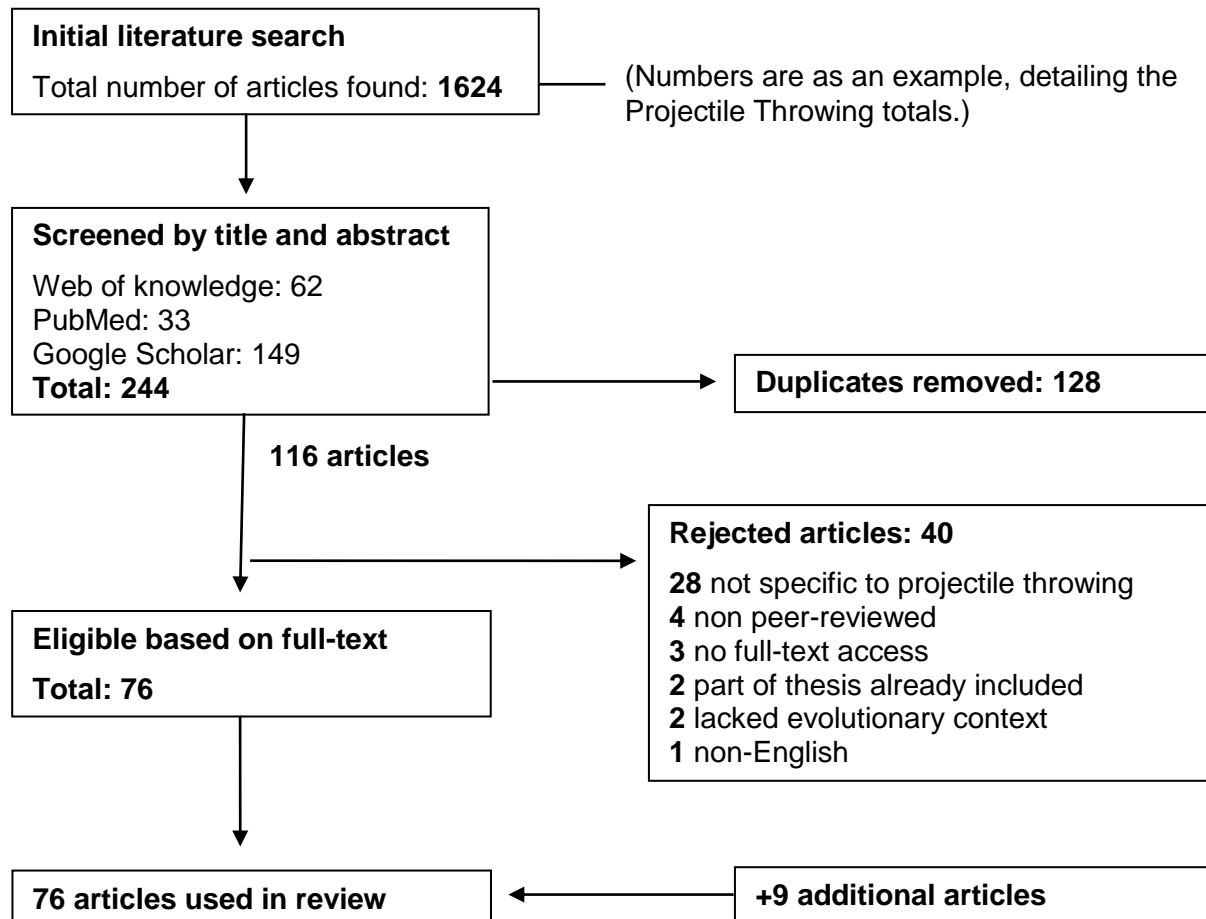
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## **Methods**

Four independent systematic literature reviews were carried out as the basis of this thesis, covering each of the four behaviours previously described- climbing, running, throwing and squatting. A systematic approach was taken to identify the relevant articles in each case as illustrated by figure 1 below and described thereafter, utilising several searching and screening steps in order to gain adequate coverage of current published literature.



**Figure 1:** Flow diagram illustrating the steps undertaken to acquire the literature base for the main reviews of this thesis. This entire process was undertaken four times for the four physical behaviours considered herein: climbing, squatting, running and throwing. The figures displayed above provide an example, detailing the throwing totals. Eligibility of articles following a full-text read through was based on criteria specific to each behaviour. Additional articles were sourced from Web of knowledge, PubMed or Google Scholar where gaps in the research base were revealed.

### **General search criteria**

This section describes the individual steps taken to identify the relevant literature for each review. Although specific criteria were applied to each biomechanical theme (described later), some general rules applied to all stages. Firstly eligible literature could include both primary research and/or secondary review articles (with the exception of the running theme, as explained later), although only if they were from peer-reviewed sources (submitted PhD and masters theses were included in this).

Secondly the available full-text version of the articles had to be written in English, unless a translation already existed and was easily available. Thirdly articles could concern solely humans or any other primate species as well, so long as they had significant reference to the biomechanical theme within an evolutionary setting. Under each behaviour, literature was sourced from three databases independently before they were collated and any duplicates removed. The steps involved were as follows, as also outlined by figure 1 above:

1. An initial screening of the literature was conducted on search terms specific to each biomechanical theme. Each papers inclusion at this stage was based on a subjective consideration as to the relevance of the title and abstract content only.
2. Articles passing the initial screening were read in full. Where access to the full text was not available the article was removed from the sample. Inclusion at this stage was based on specific criteria for each behaviour, as described below.
3. Successful articles that met both the specific theme search criteria and the general rules outlined earlier made up the literature base for each behavioural review.

In addition to the literature identified by this screening process, a small number of extra articles were added. This was carried out towards the end of the reviewing process, with quite specific targeted searches of Web of Knowledge, PubMed and/ or Google Scholar in order to fill certain gaps or further particular points that were lacking in evidence within the original systematically searched body of literature. Articles were added on an ad-hoc basis and the numbers were minimal in nature- the totals are stated at the beginning of each review along with a brief description of their content. At the same time, where needed, literature was sometimes shared between behavioural themes, i.e. an article identified during the projectile throwing screening might also have relevance for and shared with the climbing review. This was normally because of an ideal or particularly concise description of a piece of anatomy relevant to both behaviours within an article.

### **Search terms**

Web of Knowledge (all fields including Medline), PubMed and Google Scholar were searched from their inception up until the time of this study (March 2019). Endurance running literature was obtained the week of 02/11/2018, climbing literature 12/12/2018, projectile throwing literature 01/1/2019 and finally squatting literature 07/3/2019.

Although potentially contentious in a systematic setting due to its somewhat variable search output between users and sometimes unknown accuracy of results, Google Scholar was included due to the vast range of literature sources that it covers, and thus its ability to find anything that the other two databases missed (Crowther et al. 2010). Due to the volume of results that Google Scholar provides, the search was limited to the first 200 results, which seemed to be the point at which search relevance and/ or quality significantly diminished. Individual searches within Google Scholar were undertaken once and carried out fully within a single day, in order to minimise the variability in results that can occur with this database.

Identification of the most effective search terms was done via trial and error previous to carrying out the searching process, utilising previous knowledge of the literature and the keywords from articles found in an initial non-systematic survey to shape the terminology of further searches.

For the endurance running search, 'running', 'endurance running', 'persistence hunting', 'review' and 'human evolution' were used in various combinations.

For the climbing search, 'climbing', 'clambering', 'honey', 'tree foraging', 'arboreal foraging' and 'human evolution' were used in various combinations.

For the throwing search, 'projectile throwing', 'spear throwing', 'throwing', 'hunting technology', 'overarm throwing', 'overhead throwing' and 'human evolution' were used in various combinations.

Finally for the squatting search, 'squatting', 'hunter gatherer', 'squatting facet', 'sitting', 'floor sitting', 'back pain', 'defaecation', 'childbirth' and 'human evolution' were used in various combinations.

### **Specific theme search criteria**

Although the initial screening by title and abstract provided a solid base of literature, extra criteria were required to ensure that the articles retained in this project were behaviour relevant and useful within the evolutionary context of this thesis. These second-stage specific theme criteria were therefore applied to the full-text articles, as a second stage of screening. Those deemed unsuitable were again subsequently rejected from the sample.

#### Endurance running

As previously mentioned, due to the well researched nature of this theme there was little reason to explore the primary evidence concerning the pros/cons of endurance running, as plenty of excellent reviews already existed. Indeed a key aim of this project was to reduce the bias that running seems to have attracted in the human-biomechanical literature. Therefore only review articles were targeted in an attempt to provide a 'review of the reviews', summarising the information they contain between them.

- Articles were therefore required to be specifically **review** documents bringing together primary evidence from a range of sources, where the main research interest concerns the evolutionary significance of endurance running.
- These could include papers on specific applications for running such as persistence hunting.

#### Projectile throwing

- Articles were required to concern the evolutionary significance of throwing performance and/or biomechanical adaptation to throwing.
- Articles concerning spear-point technology from archaeological findings were included as long as they alluded to the projectile capabilities of the weapon, and thus the hunting behaviour of the hominin.

#### Squatting

- Articles must have discussed the evolutionary and/or modern day significance of a deep squatted position at rest.
- They were also included if they concerned archaeological findings and/or observational studies relating to habitual squatting, such as work on articular facets on bone remains.
- Other types of 'floor sitting' such as those practiced by Asian cultures were included if they concerned the biomechanical effects of the posture specifically.
- Literature regarding other uses of a deep squatted position- such as defecation or childbirth- were included so long as the effect of the posture was the primary focus. This also applied to articles reporting technology to assist in holding a squatting posture.
- Some of the themes within squatting have a very long academic history, therefore literature published before 1960 was excluded to limit the number of results.

### Climbing

- Articles must have concerned the evolutionary significance of climbing/ arboreal activity and/or biomechanical adaptations to climbing.
- This could include description of fossil hominid characteristics or non-human primates as long as climbing ability was a major aspect of the article, and the implications for hominid evolution was discussed.
- Included articles could also include major application for climbing such as the acquisition of honey, so long as climbing technique and or ability was a specific discussion within.

## References

Crowther, M. et al. 2010. Systematic review and meta-analysis methodology. *Blood* 116(17), pp. 3140–3146. doi: 10.1182/blood-2010-05-280883.

## **Section 1- Climbing**

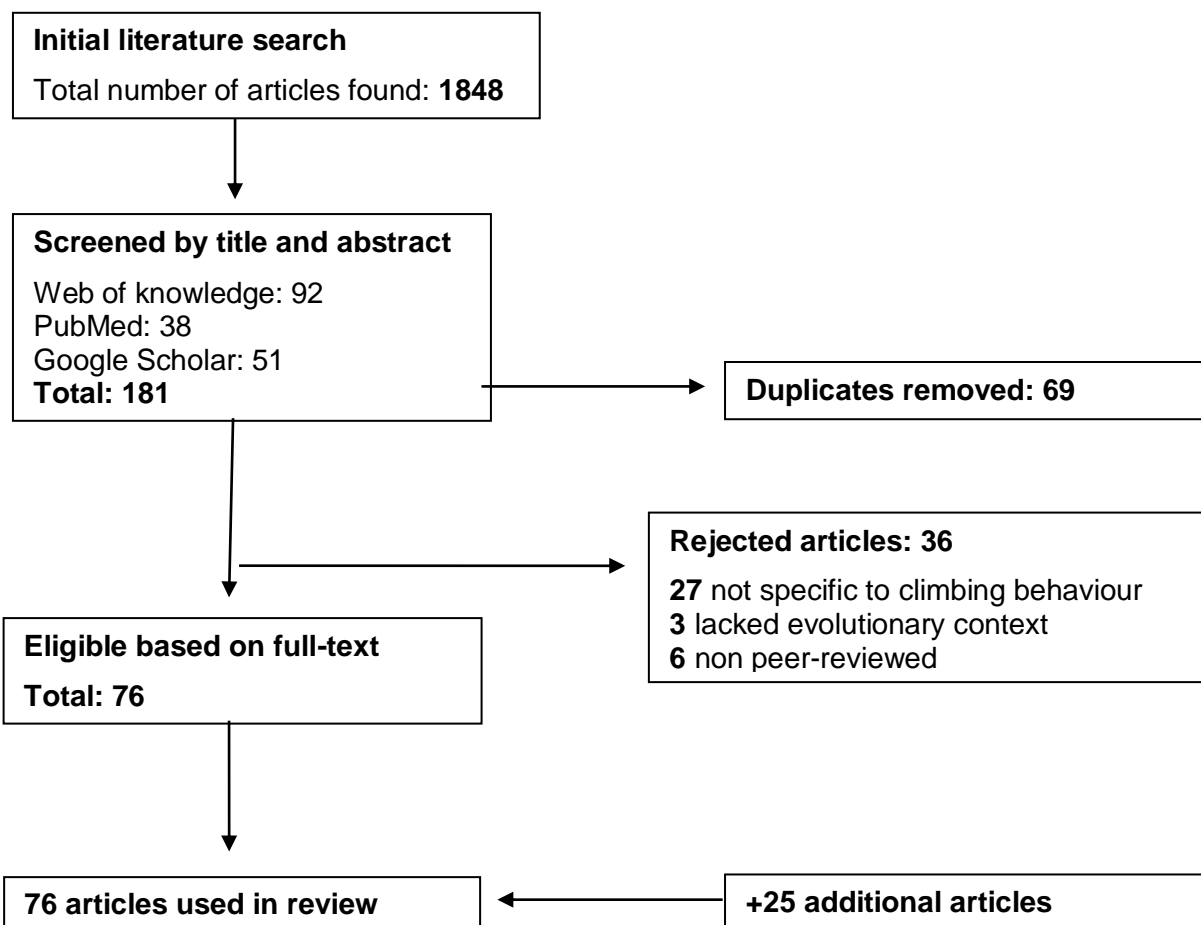
### **Overview**

Climbing is the first behaviour reviewed in this thesis, mainly as it predates the others considered herein (except perhaps squatting). This means that the literature on climbing concerns many ancient fossil hominids, making it an ideal place to introduce the basal species involved within the evolution of humans and their biomechanics. The first few sections of this chapter concern humans' most recent ancestors before the adoption of bipedalism, and then the gradual transition away from the trees towards more terrestrial behaviour. Climbing ability, need and psychology within modern humans today are then considered, before ideal climbing anatomy and biomechanics are explored in depth towards the end of the review. The overall aim herein is to provide a detailed understanding of the origin and utilisation of climbing within human ancestry, and to review the key anatomy that enables this behaviour.

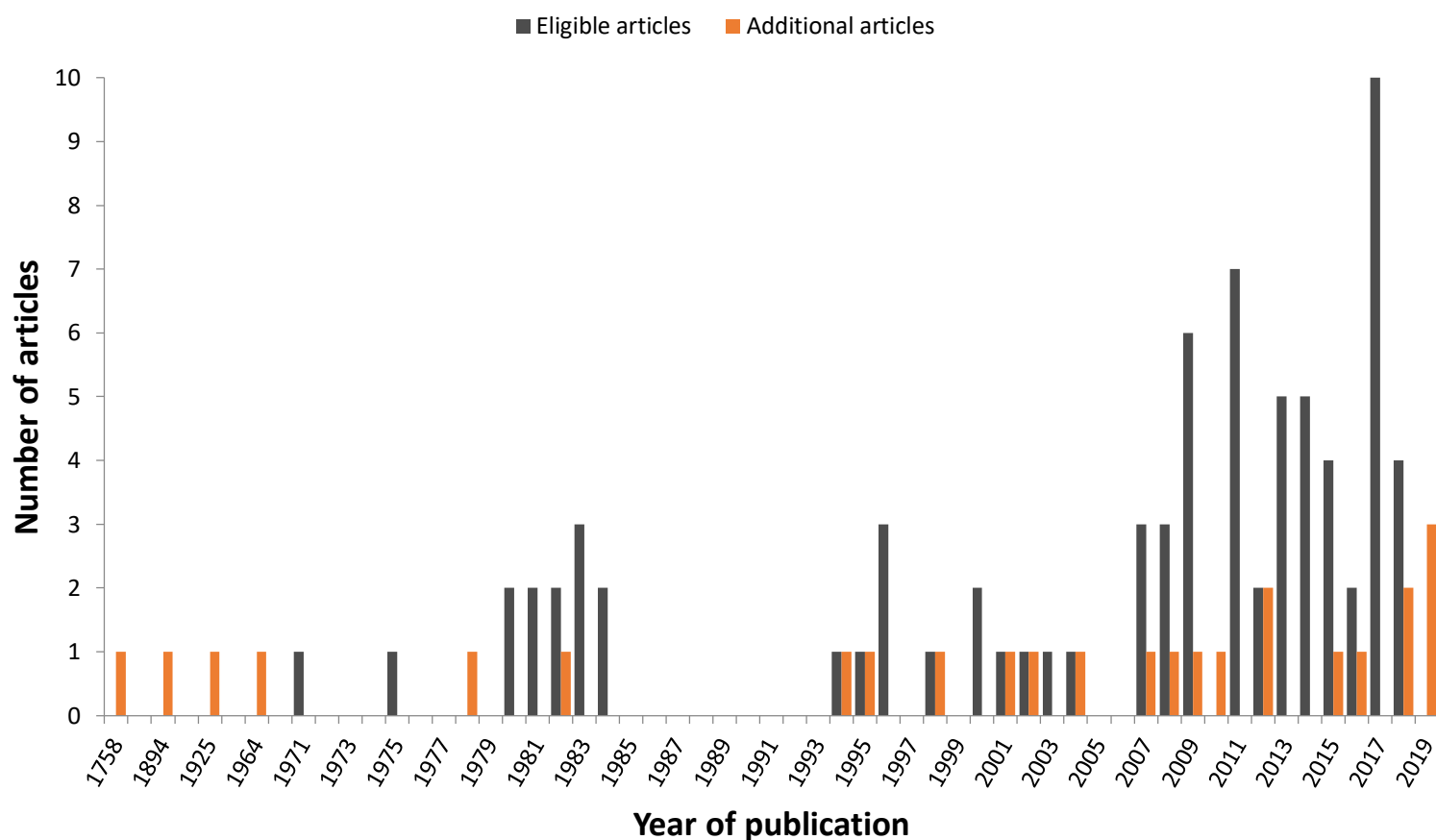
Figure 2 below summarises the steps undertaken to acquire the literature base for this section. The initial search of the climbing related literature identified 1848 articles, of which 181 were screened by title and abstract. Once duplicates were removed (69) this left 112 articles to check for eligibility. A total of 36 articles were rejected after checking of their full text: 27 lacked any significant reference to climbing and focussed instead too specifically on topics such as bipedalism, 3 articles lacked evolutionary context, while the remaining 6 were not peer-reviewed literature. This left 76 full text articles that are used in this review.

In addition to these, 25 extra papers were added at the end of the writing process to provide further evidence within specific topics that was seemingly lacking from the systematic search. One was taken from the projectile throwing literature search, to help explain the concept of humeral torsion. The rest were sourced via targeted searching of Web of knowledge, PubMed and/or Google Scholar. As this section introduces for the first time a number of hominids, a large number of these additional articles (15) comprised of the first published papers describing the species' or the particular archaeological finding. This is a common academic practice, giving credit to the initial discovery. Further articles concerned details on paleoenvironments and climate change (2), the chimpanzee- hominin split (2), early *Homo* locomotary behaviour (2), detail into primate foot anatomy (1), exaptation (1) and finally taxonomic clarification of the hominin fossil record (1).

As demonstrated by figure 3 below, the majority of the included literature was published between 1971 and 2019, with the exception of a few rather old additional papers describing a particular discovery at the time. Despite a fair number of articles published between 1980 and 1984, the largest bulk of articles were written within the last 15 years, between 2007 and 2019.



**Figure 2:** Flow diagram illustrating the steps undertaken to acquire the literature base for the climbing section of this thesis. Eligibility of articles following a full-text read through was based on specific criteria stated within the methods section previously in this thesis. Additional articles were sourced from Web of knowledge, PubMed or Google Scholar where gaps in the research base were revealed, as outlined in the introductory text above.



**Figure 3:** Graph showing the range of literature by year of publication that was sourced for the climbing section of this thesis. Literature was sourced in accordance to the methods section previously, as diagrammed by figure 2 above. Eligible articles are shown in grey, representing the core relevant literature sourced by the systematic searching process. Additional articles are shown in orange, representing the further literature sourced to provide extra detail or reference at the end of the writing process. The year of publication of the four earliest articles- 1758, 1894, 1924 and 1964- considerably predate the others, and as such have been placed on the far left of the scale, with non-linear distances between them. The remaining articles range along a linear scale from 1971 to 2019.



## Hominid climbing ancestry

To find the origin of climbing in hominins one must go back to the very origin of this group, as this is undoubtedly an activity with an ancient history. As previously noted, the taxonomic tribe Hominini (hominins) split from chimpanzees between 7 and 8mya (Langergraber et al. 2012). The hominids previous to this split were generalised ape-like climbers, much like some of the great ape species extant today. *Morotopithecus bishopi* is potentially the oldest hominid we know of at ~20.6mya (MaClatchy et al. 2000; Crompton et al. 2008). The few femoral, scapula and vertebral fragments of this species found in Uganda point towards a large bodied orthograde climber with significant upper-body mobility, much like a modern day orang-utan (MaClatchy et al. 2000). *Nacholapithecus kerioi* of the middle Miocene (~15-11mya) was a smaller ape, certainly with suspensory specialisations, although perhaps with a lesser habit of orthograde clambering than previous species (Nakatsukasa et al. 2003; Crompton et al. 2008). *Hispanopithecus laietanus* was a later hominid (9.5mya) of similar orang-utan like character, possessing a notable double-locking mechanism of the palm improving the security of their grasp during arm-swinging, as well as a host of other features making them excellent climbers (Almecija et al. 2007; Crompton et al. 2008; Susanna et al. 2014). These examples demonstrates the climbing lifestyle of but a few of the early hominids, although there were certainly many more, as best reviewed by Crompton, Vereecke and Thorpe (2008), and with new discoveries being described very recently (e.g. Böhme et al. 2019; Ward et al. 2019)

## The first hominins

The genera *Sahelanthropus* (~6.5mya, Brunet et al. 2002) and *Orrorin* (~6mya, Pickford and Senut 2001) represent possibly the earliest hominins, described as such from their likely bipedalism when on the ground and small rounded canines (Crompton et al. 2008). *Ardipithecus ramidus* (~4.4mya, White et al. 1994) was a species more confidently placed within the tribe Hominini, known from fossils found in Ethiopia. It displays highly generalised proportions with both 'ape like' and 'human like' features, most closely resembling the proportions of an extant ape like the gorilla, who while possessing climbing ability is mostly terrestrial (Sarmiento and Meldrum 2011). Unlike the highly flexible grasping foot of extant great apes, this species had a far more rigid foot, known from the presence of a small bone called the os peroneum (Lovejoy et al. 2009b). This bone is found in extant monkeys, generating a firm rigid base to the foot for them to leap from which is key aspect of their behaviour (Lovejoy et al. 2009b; McNutt et al. 2018). In *Ar. ramidus* it's thought that instead their rigid foot would have substantially improved the efficiency of their upright walking, while allowing them to retain an opposable big toe for grasping tree limbs (Lovejoy et al. 2009b).

*Ar. ramidus*' bipedal ability is further displayed by their pelvis, which while retaining ape-like morphology for the most part, also displayed modern-human-like features such as a characteristic growth on the iliac spine allowing gluteal repositioning, enabling far more efficient upright travel than their ancestral precursors and extant apes (Lovejoy et al. 2009d, also see Kozma *et al.*, 2018 for hip-extensor mechanics discussion). In the trees, *Ar. ramidus*' mode of arboreal travel probably resembled slow climbing and clambering, due to their relatively short forelimbs and phalanges (compared with extant apes), which would have reduced climbing efficiency (Sarmiento and Meldrum

2011). This would have imposed a significant problem when trying to cross gaps in the canopy, suggesting that they were probably more proficient leapers than extant great apes- aided by their rigid feet (Lovejoy et al. 2009b; Sarmiento and Meldrum 2011). *Ar. ramidus*' contrast to extant great apes continues with their hands and wrists, which were far more flexible than those of typical knuckle-walking apes, suggesting they weighted their palms instead (Lovejoy et al. 2009a). Such flexibility enabled *Ar. ramidus* to lean well forwards onto their forelimbs while still grasping the support, improving their careful climbing (Lovejoy et al. 2009a). Taken together this mosaic of climbing and bipedal features seen in *Ar. ramidus* provides insight into the locomotary transition of hominids out of the arboreal environment (Lovejoy et al. 2009c).

### **The beginnings of bipedalism**

The earliest group members with the ability to walk upright upon two legs were likely typical arboreal quadrupedal climbers, with later species transitioning towards forelimb suspension and upright brachiating (much like an orang-utan) before certain lineages moved onto terrestrial quadrupedalism and bipedalism (Gebo 1996). Bipedalism may well have first arisen within the trees, as Thorpe et al. (2007) have hypothesised by observing orang-utans, who often utilise an upright posture to move along far more slender branches than they would otherwise be able to. They achieve this because bipedalism enables their free forelimbs to grasp other tree limbs above their heads as they move, providing security in case of a slip, some weight-bearing and improved balance (Thorpe et al. 2007). This is particularly useful for moving between different trees safely, as their outermost branches are nearly always thinnest and most fragile (Thorpe et al. 2007). The postural feeding hypothesis is an alternative if not similar idea of the origins of bipedalism, centring around a key mode of arboreal feeding, where by an individual stands upright upon its hind legs on a branch, supporting itself with one of its forelimbs on a higher branch, while the other forages food at or above the head (Hunt 1996). Such postural behaviour mimics upright bipedalism, and is often utilised by extant great ape species such as chimpanzees and orang-utans (Hunt 1996). Its benefits are fairly plain to see, as it enables a comfortable and safe feeding position with far greater reach (and thus more available forage) from a fixed position than could be gained from a quadrupedal stance. In essence the above hypothesis' are extensions of the older 'hylobatian model' for the origins of hominin bipedalism, where by a small bodied brachiating gibbon-like primate, ancestral to all later hominins, is hypothesised to have utilised bipedalism for foraging during short sprints to catch insects, and potentially also as means of display (Crompton et al. 2008).

In terms of evidence, an arboreal stage of hominin bipedalism like those theorised above is supported by several archaeological findings, such as that of the Sterkfontein Little-foot skeleton (Clarke 1998) and the Woranso-Mille skeleton (Haile-Selassie et al. 2010). Both are of the genus *Australopithecus* (described in next section), and feature many bipedal-enabling anatomical features of the hind-limbs, in species' that were likely still spending a considerable time in the trees (Clarke 1998; Haile-Selassie et al. 2010). Furthermore, a recent description of an 11.6 million years old Miocene ape *Danuvius guggenmosi* (Böhme et al. 2019) has shed further light on a hand-assisted arboreal stage of bipedalism, deep in hominid history. This find displays features that suggest 'extended limb

clambering'- described as such from the postural extension of the hips and knees over a stable ankle, combined with a highly mobile elbow joint and strong hands (Böhme et al. 2019). This method of locomotion seems to reflect a primitive form of assisted bipedalism within an arboreal setting, just as Thorpe et al. (2007) and Hunt (1996) have hypothesised.

Under these ideas, the habitual adoption of supported upright walking and foraging in the trees later provided an exaptation (characters evolved for a particular function now used in a different novel way) in these species for terrestrial bipedalism, where bipedalism would have maintained its usefulness for foraging higher above the head, while also providing biomechanical benefits in efficiency for long distance travel (Gould and Vrba 1982; Hunt 1996; Thorpe et al. 2007).

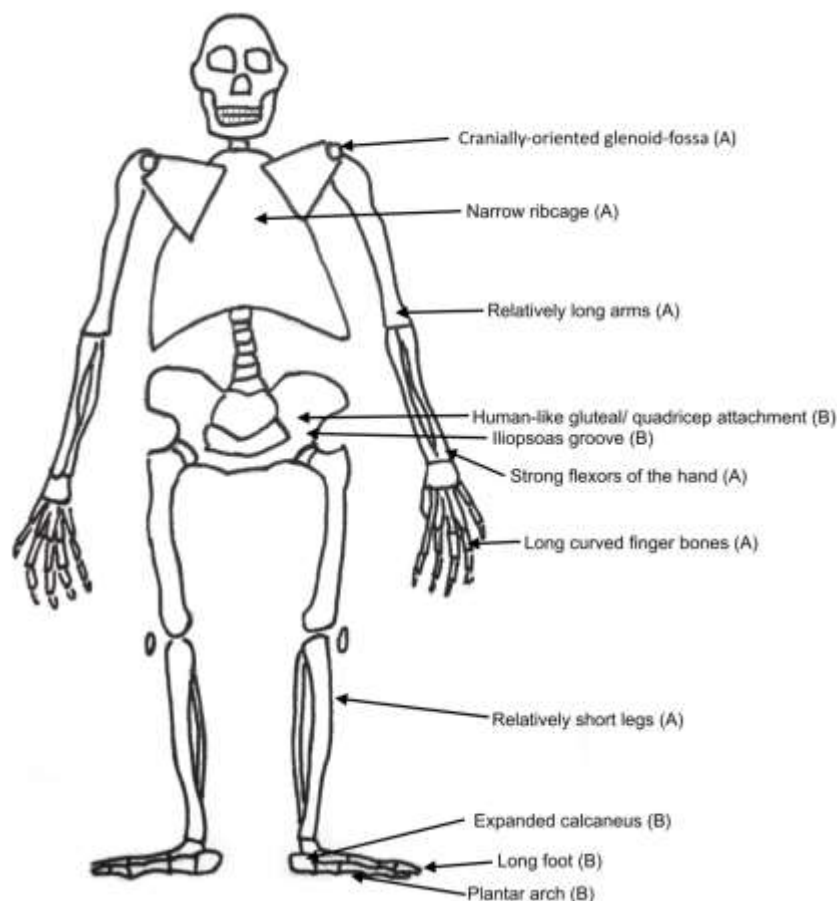
However, a hand-assisted origin for hominin bipedalism is just one hypothesis, and many other theories have been proposed in the past with varying degrees of support. For instance, the knuckle-walking hypothesis places greater emphasis on a distinct terrestrial quadrupedal stage prior to the adoption of bipedalism (Crompton et al. 2008). Alternatively the vertical climbing hypothesis suggests that the biomechanics of ascending a vertical support are very similar to that of walking bipedally, and thus would have pre-adapted (or more correctly provided exaptation) the musculature of our hominid ancestors for a later adoption of habitual bipedalism (Fleagle et al. 1981; Gould and Vrba 1982; Crompton et al. 2008). For a comprehensive discussion of hominin bipedal origins with reference to extant great apes see Crompton (2016).

Whatever its exact origin, bipedalism ultimately became the dominant mode of locomotion among hominins. Beginning towards the end of the Miocene (~5mya) climatic change upon the continent of Africa meant cooler and drier conditions and thus a general reduction in forest cover, creating ever larger gaps in many areas that hominins must have crossed terrestrially (Susman et al. 1984; deMenocal 2004; Senut et al. 2018). Originally termed the 'savannah hypothesis' this reduction in tree cover was once believed to be the primary reason for hominins' adoption of bipedalism, although since then a far earlier origin of an upright stature has been found (deMenocal 2004). Nonetheless, bipedalism would have provided a solution to increasing reliance on terrestrial travel, explaining why it maintained its selective advantages, and thus brought about the emergence of a habitual upright posture in all subsequent hominins.

### **Australopithecus**

The Australopithecines were a large group of Archaic hominins, not generally included within the later *Homo* and *Paranthropus* genera, consisting of seven or possibly more species living from ~4 to ~1.5mya, including most notably *Australopithecus anamensis* (Leakey et al. 1995), *A. afarensis* (Johanson et al. 1978) and *A. africanus* (Dart 1925) (also with reference from: Stern 2000; Wood and Lonergan 2008). These were proficient at slow cautious climbing, as is evident mainly from their scapula and forelimb morphology which closely resembles extant primate species such as *Alouatta* (howler monkeys) which are known to practice this form of locomotion (Rein et al. 2017; Selby and Lovejoy 2017). However they were also very likely to have been bipedal while on the ground, evident in part from their hip morphology, which demonstrates that this group was still further along in the ongoing transition from more 'ape-like' to more 'human-like' hominins, with a mosaic of anatomical

features (Oxnard 1975; Stern and Susman 1983; Susman et al. 1984; MacLatchy 1996; Meyer et al. 2017). Stern (2000) has compiled a significant amount of literature on the climbing vs walking adaptations seen in the Australopithecines, for which figure 4 below summarises showing some of the key features. It demonstrates that while the upper body of *Australopithecus afarensis* displayed relatively primitive ape-like morphology such as a cranially-oriented glenoid fossa, long arms and curved phalanges, areas of the body most utilised during bipedal biomechanics such as the hips and feet had begun to resemble human-like morphology, gluteal attachment and a plantar arch being examples.



**Figure 4:** Illustration of the fossil hominin species *Australopithecus afarensis*, detailing key features of their structural anatomy which indicate their locomotory repertoire, as labelled. Of the labels, those thought to be related mainly to arboreal activity are marked with the letter 'A', where as those relating to primitive forms of bipedalism are marked with the letter 'B'. This figure demonstrates the mosaic of anatomical features displayed by this species, both relating to their primitive 'ape-like' climbing ancestry, and future bipedalism. It has been produced using anatomical information from Stern (2000) along with graphical reference from Bramble and Lieberman (2004).

Pontzer and Wrangham (2004) studied the energetic cost of locomotion among chimpanzees, concluding that while chimpanzees have many arboreally focussed adaptations they spend a relative minority of their time climbing vertically, and that adaptations aiding in not falling from the canopy are

probably more selectively advantageous than those for pure climbing efficiency. A parallel is drawn here with the Australopithecines who were likely walking even more due to the increasingly open nature of their habitat, with selection likely favouring terrestrial efficiency and arboreal stability when feeding or seeking refuge in the canopy, not swift vertical climbing (Pontzer and Wrangham 2004). In the trees these species would have been slow and cautious so as not to risk injury.

### **The genus *Homo***

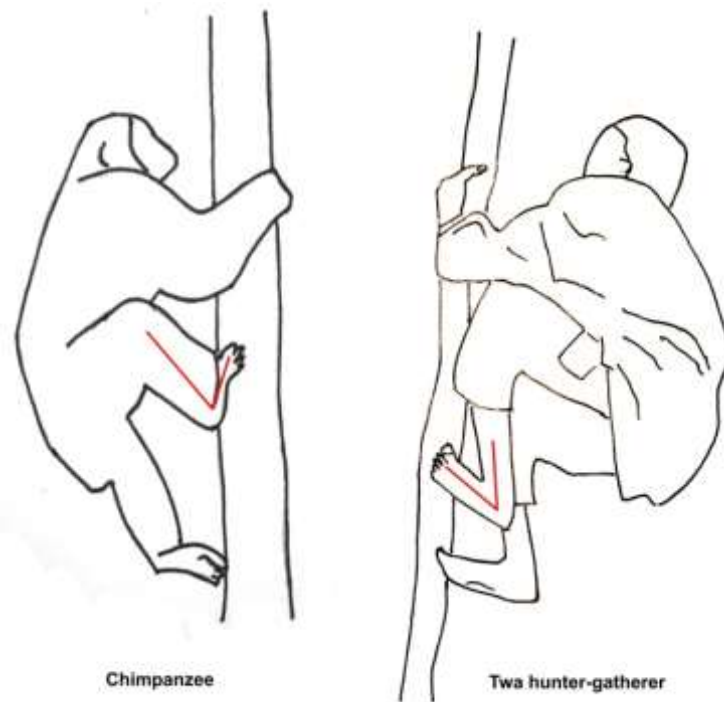
By around 2mya, the first hominin species of the genus *Homo* appeared. *Homo habilis* (Leakey et al. 1964) was certainly a habitual biped, possessing features of the leg bones and joint surfaces that could easily be found in a moderate modern human sample, although also retaining certain features of the hand and upper body that would have functioned for arboreal grasping and loading (Susman and Stern 1982; Ruff 2009). Climbing trees likely maintained its usefulness for escaping predation and foraging as it does in extant primates, explaining its retention (Susman and Stern 1982; Ruff 2009). By the time of *Homo erectus* (~1.9mya, Dubois 1894) bipedal efficiency was very similar to that of modern humans, evident in part from the ~1.5mya Ileret footprints from Kenya, many of which are indistinguishable from the prints made by habitually unshod people today (Hatala et al. 2016). In fact, although variable especially in early samples, *Homo erectus* had a body very similar to modern humans, which would be most recognisable from the head due to the lack of snout and general flatness of the face, as well as smaller teeth and large braincase (Lieberman 2007).

Although arboreal activity significantly diminished within the genus *Homo*, it seems that the transition was not uniform among all. *Homo naledi* (Berger et al. 2015) is a fairly recent discovery of hominin that lived around 300ka. Although a capable bipedal walker, this species had a fairly primitive upper body with many ape-like characteristics, such as a cranially-oriented glenoid fossa and narrow thorax (Feuerriegel et al. 2017; Williams et al. 2017). This suggests that climbing ability still harboured selective benefits fairly recently in hominin evolution, at least within certain species and/or geographical regions. It also furthers the concept that the upper and lower body have not universally evolved in tandem- the upper lagging behind in certain situations such as that of *Homo naledi* (Feuerriegel et al. 2017).

By the emergence of our own species *Homo sapiens* (~300ka, Linnaeus 1758) we were well and truly efficient bipedal walkers, and as such climbing became rare due to a lack of real requirement for it. Modern humans today no longer retain the majority of the climbing-focussed adaptations of our ancestors (as explored in climbing anatomy section below), and as such we likely perform far inferiorly to those early hominins, with our energy expenditure climbing approximately seven times more than when we are walking (Hurov 1982; Elton et al. 1998). Our lack of climbing also suggests that we generally underutilise our joint movement ranges compared with our closest extant relative the chimpanzee (Alexander 1994). However due to our deep climbing ancestry our connection with the forest remains very strong, both from a sense of innate safety that we feel when within a tree (high-up away from the ‘dangers’ of the ground), and the aesthetic connection- how the majority of people find trees in most environments (both natural and urban) pleasing to the eye, and how architects have emulated forests in the structures of our cities (Townsend and Barton 2018). Through

this connection we retain some innate behaviour, such as Palmers grasp reflex in babies originally required for grasping tightly onto your mothers fur so as to not fall during arboreal activity (ibid.). Plus the seemingly universal love for climbing anything and everything seen in children, best observed by the monkey bars in a playground (Townsend and Barton 2018). Therefore although modern humans may no longer be biomechanically optimised for climbing, we have certainly been shaped by it, with several profound mental capabilities such as that of self- conception potentially owing their roots to negotiating complex arboreal environments (Povinelli and Cant 1995). In addition, climbing has gained popularity recreationally for sports such as rock climbing and parkour, for which with adequate long-term practice and training individuals can become highly skilled, scaling vertical faces with little more than half-finger-pad edges (Halsey et al. 2017).

A number of hunter-gatherer groups still habitually climb trees, both as a means to forage valuable resources such as honey, fruits and seeds, and to provide a vantage point from which to hunt- most often utilising projectiles such as a blowgun (Watanabe 1971; Kraft et al. 2014; Marlowe et al. 2014). Indeed a resource such as honey is so rich in calories (>3000kcal per kg) that hunter-gatherers such as the Hadza of Tanzania or Vedda of Sri-Lanka routinely take great risks in order to acquire it, ascending or descending long vines or bamboo stalks up cliff-faces to a height where a fall would undoubtedly be fatal (Marlowe et al. 2014). Climbing has therefore remained an important activity for such groups, and as such they are more than adept at it. Two major methods of unassisted climbing are often utilised, the first 'changwod' style involves climbing much like a chimpanzee, placing the soles of the feet against the support and 'walking' up the tree with hands and feet alternatively using counter pressure, as depicted by figure 5 below (Kraft et al. 2014). The second 'chinbodn' style sees the climber hug the tree (normally of larger diameter) with their inverted feet in contact with the trunk, and slowly pulse up the support with controlled movements (Kraft et al. 2014). These techniques rely greatly upon ankle flexibility, for which certain groups such as the Twa of Uganda have developed incredible levels of plasticity, able to comfortably dorsiflex (foot towards shin) their ankles to an extreme 40° (Venkataraman et al. 2013a; Venkataraman et al. 2013b, figure 5). This is achieved via elongated gastrocnemius (calf) muscle fibres, which are the significant constraint on other groups' dorsiflexion ability (Venkataraman et al. 2013a). Such findings potentially have implications for determining the climbing behaviour of fossil hominins such as *Au. afarensis*, as the seemingly 'walking adapted' foot form of later hominins can clearly still be functional in an arboreal environment, therefore basing behavioural interpretations on foot morphology might be prone to misinterpretation (Venkataraman et al. 2013b).



**Figure 5:** Illustration depicting a chimpanzee and human Twa hunter-gatherer climbing a vertical support. Both have adopted the same 'changwod' style of climbing, placing their feet against the support and essentially walking up by creating counter-pressure with their arms, which wrap around the other side of the support. In red at their feet is highlighted their degree of ankle dorsiflexion (foot towards shin), which is a key element producing improved security while climbing like this, as greater dorsiflexion enables more of the sole of the foot to be contact with the support, thus producing greater friction. Both chimpanzees and some hunter-gatherer groups such as the Twa of Uganda display extensive ankle dorsiflexion throughout their habitual climbing. Both climb routinely to acquire forest resources such as fruits and honey. Figure produced utilising graphical reference from Venkataraman et al. (2013a, 2013b).

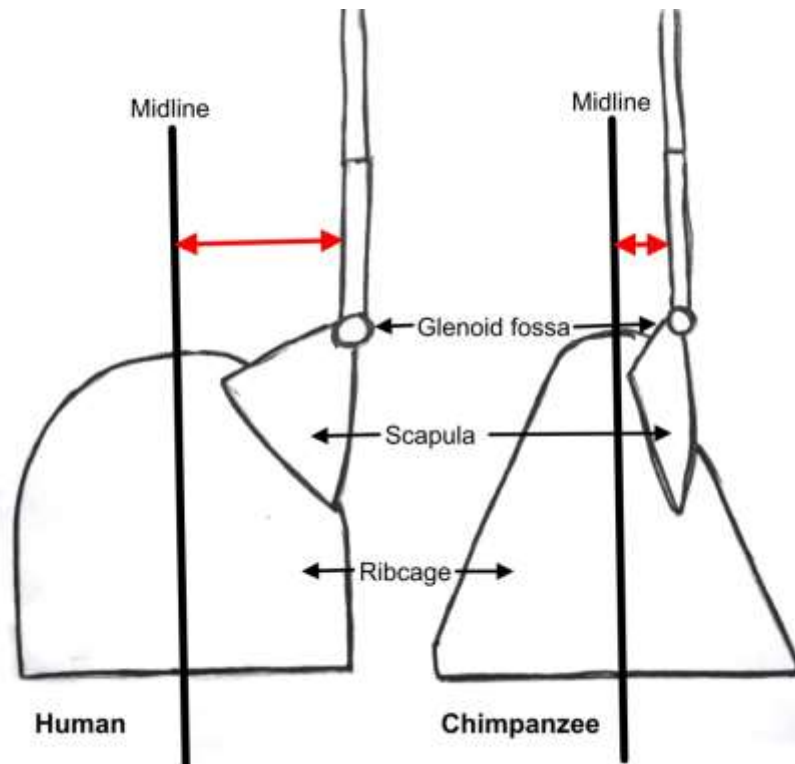
### Climbing anatomy and biomechanics in hominids

Climbing is a strenuous activity which requires good muscular strength as well as limb mobility in order to be efficient. As such the mechanics of climbing vary among primates depending on the extent of their habitual use of this activity (Hanna and Schmitt 2011b). This section will describe the major adaptations for suspensory activity seen in primates.

#### The shoulder

The mobility and strength of the shoulder are crucial for climbing ability and efficiency, as they bear considerable strain during climbing activities (Chan 2008). The glenoid fossa is the site of articulation between the humerus of the upper arm and the scapula, and varies in shape and orientation among hominids depending largely upon their level of arboreality (ibid.). A more cranial orientation of this joint (closer to the head and midline of the body) provides the best mechanical advantage during intense arboreal activity such as hanging from a single arm, as the ligaments surrounding the joint are stretched (and thus utilised) evenly (Hunt 1996; Green and Alemseged 2012). The further the glenoid fossa orients from the body's midline the greater reliance is imposed upon the ligaments of the lower

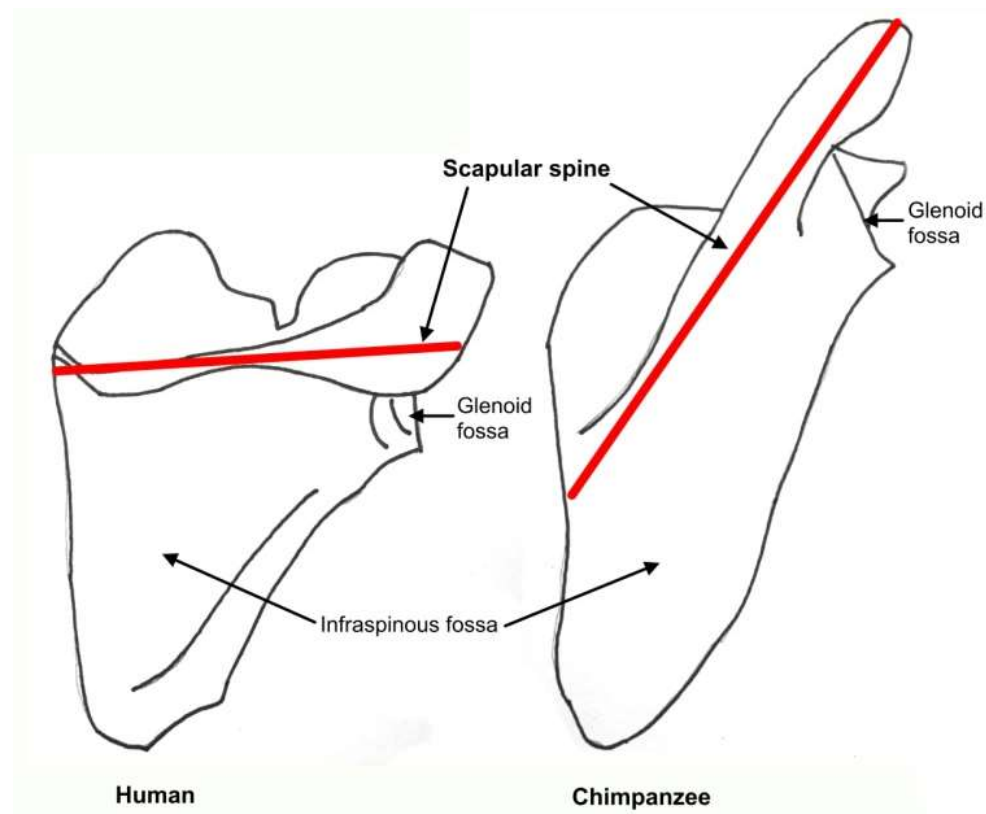
portion of the capsule to bear weight, which is both less efficient and thus more likely more prone to injury (Hunt 1996- figure 6).



**Figure 6:** Illustration depicting a simplified model of the ribcage and arm of a modern human vs chimpanzee. Modern humans display a wider more laterally oriented glenoid fossa- the attachment site between the scapula of the shoulder and the humerus of the arm. Narrow more cranial orientation as seen in extant chimpanzees is advantageous for arboreal behaviour as the arm is closer to the midline of the body (marked in red) when hanging, stretching the ligaments of the shoulder more evenly than with the human condition. Cranial orientation of the glenoid fossa is aided by a narrow ribcage- which resembles that of a teardrop in chimpanzees, enabling the scapula to sit closer to the bodies' midline. Figure produced using graphical reference from Hunt (1996).



Coupled with a high glenoid fossa in highly arboreal hominids is a more obliquely positioned spine of the scapula (also pointing upwards) (Green and Alemseged 2012; Larson 2012). This varies together with the shape and relative proportions of the muscles of the shoulder blade as it is a major attachment site, particularly for the infraspinatus muscle which is a key stabiliser of the shoulder during climbing (Green and Alemseged 2012). A more oblique scapula spine orientation indicates a narrow infraspinatus muscle, thought to be better suited mechanically to overhead weight-bearing compared with the broad form of this muscle seen in species with more horizontal scapula spines (Green and Alemseged 2012- figure 7). Green (2013) found that infraspinous fossa shape (the site of the infraspinatus muscle attachment on the scapula) sorted suspensory from non-suspensory great-apes fairly well, with a general broadening of this fossa as individuals got older and climbed less, favouring instead terrestrial knuckle-walking. However when compared with wider primate groups there appears to be little relationship between infraspinatus muscle size and locomotion behaviour, therefore perhaps this isn't as important for climbing as previously thought (Selby and Lovejoy 2017).



**Figure 7:** Illustration depicting the scapula of a modern human vs a chimpanzee. Chimpanzees display more cranial orientation of the glenoid fossa, where the scapula articulates with the humerus of the arm, which more evenly stretches the ligaments of the capsule when hanging from the hands (figure 5 previously). This cranial orientation means that the scapula spine- a bony ridge that traverses the length of the scapula, also faces more cranially. The angle of the scapula spine indicates the shape of the attachment for the infraspinatus muscle of the shoulder, where a more narrow form generally indicates more habitual arboreal activity. Figure produced using graphical reference from Larson (2012).

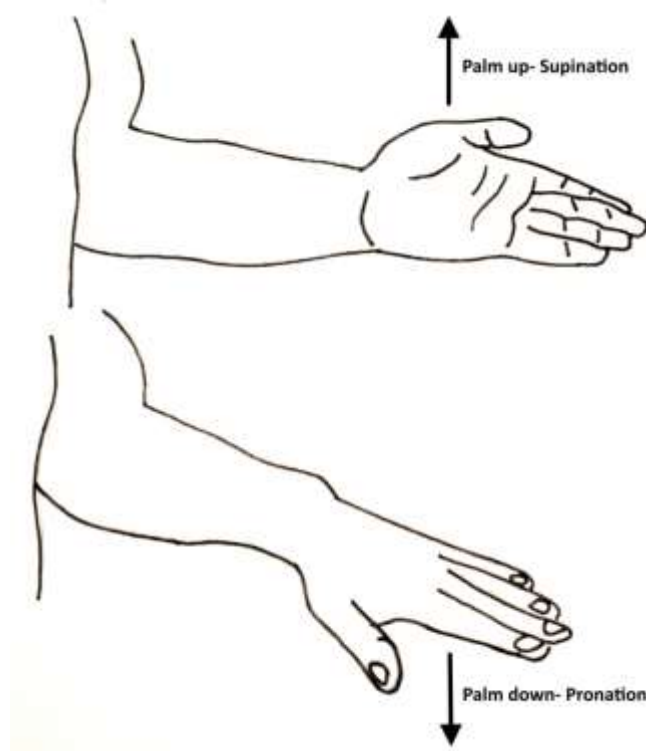
In modern humans the glenoid fossa and scapula spine orient far more laterally (out to the side) and horizontal than both extant great apes and more ancient species such as the Australopithecines (Larson 2012; Green 2013). Transition towards more lateral orientation of the glenoid fossa seems to be a characteristic of the genus *Homo*, reflecting the gradual decrease in climbing in this group, and perhaps selection in the shoulder for a different activity such as running (or throwing later), or at least a relaxation in the selection of the upper body (Bramble and Lieberman 2004). Indeed by *Homo erectus* 1.8mya the shoulder was almost that of modern humans (Larson 2012).

Chan (2007,2008) has shown glenohumeral (shoulder) mobility to be lower among the majority of hominoids (with the exception of *Hylobates*) compared with other highly arboreal primate groups such as monkeys and lorines, perhaps reflecting how a reduction in habitual climbing affects shoulder biomechanics, or highlighting different style of climbing between species.

It's logical that the upper body muscles of a habitual climber would be more developed, due to their greater utilisation. However this does not seem to be the case. Potau *et al.* (2009) tested five major muscles of the shoulder (including the deltoid and infraspinatus) in humans, chimpanzees and orang-utans, finding that humans and orang-utans have considerable overlap in the proportional mass of their musculature despite obviously contrasting locomotary behaviours. Greater development of some of these muscles in chimpanzees is thought to possibly be an adaptation for knuckle-walking, owing to the contrast with humans and orang-utans (Potau et al. 2009). This needs further study due to small sample sizes, although it implies that although muscle form goes some way to showing locomotary style, it doesn't seem to reliably predict climbing versus non-climbing.

### **The arm**

Long arms relative to legs improve climbing performance by enhancing reach, making gaps more passable in the canopy via bridging moves, while also increasing the distance travelled via the pendulum motion during arm swinging between overhead branches (Preuschoft 2002; Halsey et al. 2017). High degrees of forearm pronation (with forearms stretched forwards, rotating the hands posteriorly) is highly useful for certain climbing behaviours, such as hang-feeding under a single arm, enabling a greater degree of rotation (Stern and Larson 2001- figure 8). The degree of rotation of the forearm is governed by both the muscular power of its supinators and pronators, as well as certain biomechanical features of the elbow and humerus (Stern and Larson 2001; Ibáñez-Gimeno et al. 2014). In extant primates rotational efficiency increases with further flexion at the elbow, which is beneficial considering that flexed elbows are utilised for many different climbing behaviours, both pulling up and stabilisation (Ibáñez-Gimeno et al. 2014). Transitional climbing to walking hominins such as *A. afarensis* have been found to have very similar rotational efficiencies to extant orang-utans (based on the orientation of fossilised forearm remains), demonstrating their probable climbing habit (Ibáñez-Gimeno et al. 2017). Modern humans fall somewhere in-between fully arboreal and fully terrestrial primates in terms of rotational efficiency, which although it might seem initially unlikely due to our lack of climbing behaviour, may instead reflect our complex manipulative ability and precision grip, for which rotation of the forearm is integrally important (Ibáñez-Gimeno et al. 2014).



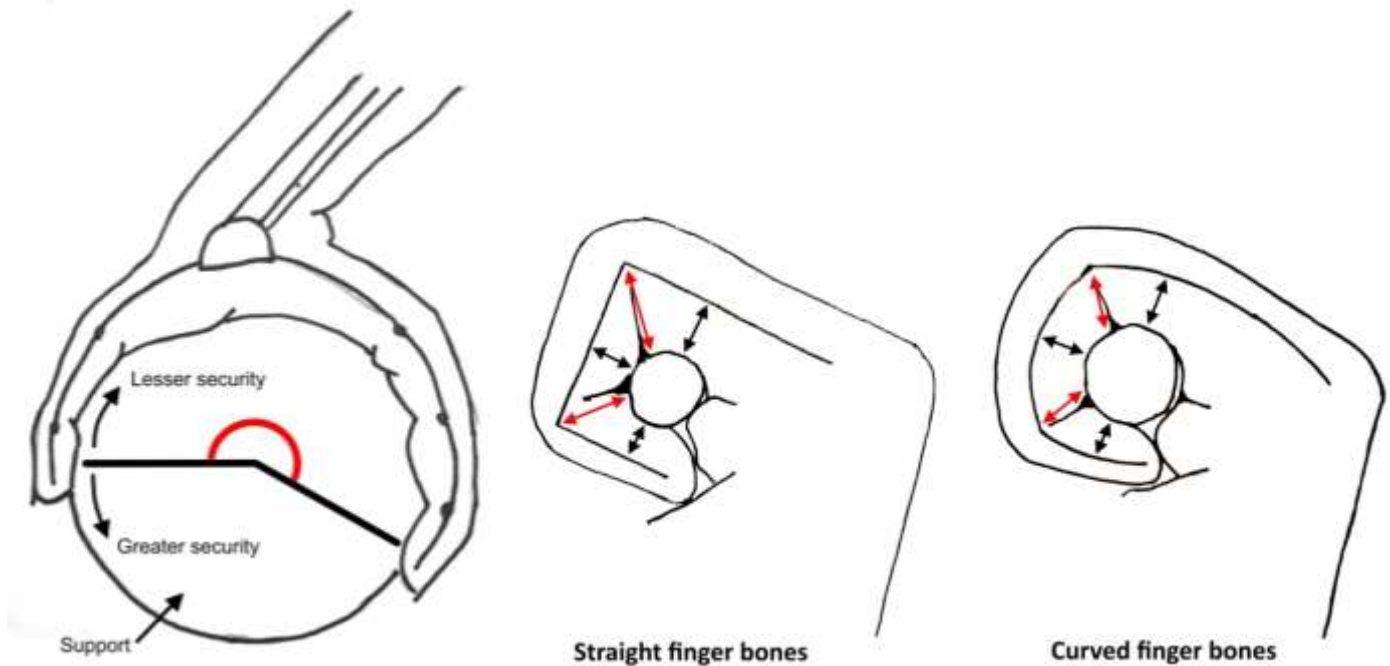
**Figure 8:** Illustration depicting the human forearm and the two forms of mechanical twisting that are possible. Where the neutral position is when the palm is at right angles with the floor, supination is twisting the forearm and palm skyward, while pronation is twisting the forearm and palm towards the floor. This rotational ability is highly useful for arboreal activity such as hang feeding under a single arm, as it enables you to rotate under a fixed point at the wrist, giving access to more forage in three dimensions and allowing movement in more directions.

Humeral torsion describes the orientation of the humeral head and the elbow, essentially the range of external and internal rotation of the forearm with a 90° bend at the elbow (Roach et al. 2012). Rein, Harrison and Zollkofer (2011) found that humeral torsion decreases (giving an improved ability to externally rotate the forearm) with increased levels of quadrupedalism in primates, with more suspensory species having higher levels of torsion. This would make them more able to internally rotate their forearms, perhaps useful in a complex arboreal environment. Humeral torsion is generally considered a projectile throwing adaptation in humans (see throwing section later for greater detail), and its influence on climbing ability in primates seems far lesser researched.

### The Phalanges

Phalanx adaptations for arboreality are most likely to be seen in the third digit, due to its length and position within the hand, while the thumb plays a lesser role, most useful for grasping larger supports (Samuel et al. 2018). Relatively long robust fingers with significant flexor sheaths indicating powerful grasping ability are important adaptations of the hands for climbing, as they enable the hand to wrap around and hold even relatively large branches (Preuschoft 2002; Tocheri et al. 2008; Kivell et al. 2015- figure 9). Phalangeal curvature (towards the palm) is useful for resisting the bending strain on the bones of the hand/foot when grasping small supports (especially the longer the fingers are), as the distance between the support and the bones is uniform within the grip (Susman et al. 1984; Hunt

1996; Rein et al. 2011; Wunderlich and Ischinger 2017- figure 9). With straight bones pressure is highest at the middle of each finger bone where closest to the support, which is potentially more injurious due to higher bending moments of the phalanges (Hunt 1996; Wunderlich and Ischinger 2017). Dorso-plantarly expanded shafts of the phalanges further aids in reducing bending (Wunderlich and Ischinger 2017). Modification of the bones of the wrist and distal end of the ulna can also be useful for climbing, such as wider curvature of the radioulnar joint aiding in stability of the wrist through extreme pronation/ supination (Tallman 2015).



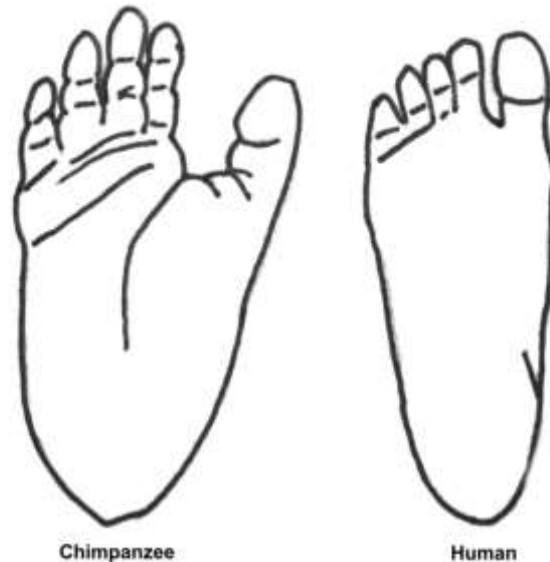
**Figure 9:** Illustrations depicting the hominid hand wrapped around a support. The left image demonstrates how increased length of the phalanges aides in gripping supports. The greater the angle between the distal pads (marked in red) the greater the grip security, as the hand encompasses more of the support thus generating more friction through increased surface area contact. The two right images compare straight finger bones as displayed by modern humans, with curved finger bones of arboreal primates such as chimpanzees. Curved phalanges are advantageous for climbing as the bones are placed a uniform distance from the support within the entire grip, distributing pressure evenly. With straight phalanges the bones are closest to the support at the middle of their shafts (marked in black) and furthest away at the joints (marked in red). This creates potentially injurious bending moments at the centre of each finger bone. Figure produced using graphical information from Hunt (1996) and Preuschoft (2002).

Long robust curved finger bones defined the hand form of early hominin species such as *Ardipithecus* and *Orrorin*, and only began to change later in the Australopithecines with reduced finger length and increased robusticity of the thumb, although maintaining curvature and proportionally large flexor sheaths (Tocheri et al. 2008; Kivell et al. 2011). With the arrival of the genus *Homo*, curvature lessened and finger length further decreased, with robusticity fully shifting towards the thumb, and pronounced apical tufts appearing on the ends of the fingers (Tocheri et al. 2008; Kivell et al. 2011; Kivell et al. 2015). Bone mineralisation within the hands became far more uniform reflecting reduced bone remodelling due to repetitive loading, and joint stability within the hand increased, particularly

between bones such as the capitate and third metacarpal (Zeininger et al. 2011; Rein and Harvati 2013). These changes track the reduced arboreality (and thus highly loading function of the fingers) and increased tool use with a precision grip between thumb and fingers in later hominin species (Kivell et al. 2011; Kivell et al. 2015; Selby et al. 2016).

### Feet and ankle

Later hominins are fairly unique among primates in having forelimbs and hindlimbs that perform distinctly different roles due to the adoption of bipedalism, one set based on locomotion and the other on manipulation and tool use (Susman 1983). This was not the ancestral form, as arboreal primates have grasping capabilities with all their limbs, and use them all for both tasks. For example the majority of primates possess a flexible mid-foot, otherwise known as a mid-tarsal break (Crompton et al. 2008; Meldrum et al. 2011; Holowka et al. 2017). This is useful for climbing as it allows very high degrees of ankle dorsiflexion (foot towards shin; this can exceed 45° as seen in extant chimpanzees) and inversion (twisting the foot to the side, sole inwards), enabling full foot contact with a tree during vertical climbing (Conroy and Rose 1983; DeSilva 2009; Holowka et al. 2017). Metatarsal torsion describes how the phalanges of the feet are oriented among many non-human primates, with the first metatarsal (the big toe) being everted while metatarsals 2-5 are inverted (Wunderlich and Ischinger 2017- figure 10). This further helps conform the phalanges to a round arboreal substrate, and aids in the grasping between the first and second digits (Wunderlich and Ischinger 2017).



**Figure 10:** Illustration depicting the morphology of a chimpanzee foot versus a modern human foot. The key difference involves metatarsal torsion seen in chimpanzees- how the first metatarsal (the big toe) is everted while the remaining toes are inverted. Along with retaining long toes, this generates a foot form far more alike to their hands than a human possesses, enabling strong grasping capabilities of the feet useful in climbing. The human foot however has elongated, with shorter toes that all point forwards, which creates greater efficiency for terrestrial walking and running.

In modern humans the flexible mid-foot is entirely lost, replaced with substantially reduced mobility of the tarsal joints, creating a rigid longitudinal arch along the length of the mid-foot and a metatarsal break which is highly useful for efficient terrestrial bipedalism (Susman 1983; Crompton et al. 2008; Meldrum et al. 2011). The foot has also lengthened in humans to create a longer lever, while the phalanges themselves have shortened and digits 2-5 have become more everted (in line with big toe) all to further aid walking (Susman 1983; Wunderlich and Ischinger 2017- figure 10). This form of the hominin foot seems to have arisen by the time of *Homo habilis* (ibid.) The earlier Australopithecines display an intermediate condition ideally suited to neither walking nor climbing but instead representing a compromise between the demands of both, as displayed most famously by the 3.6my old Laetoli footprints from Tanzania (Susman 1983; Meldrum et al. 2011). In terms of ankle dorsiflexion, DeSilva (2009) has found the tibia of even early hominins such as *A. africanus* to be significantly less inverted than that of extant chimpanzees, thus they would likely not have been able to dorsiflex their ankles like modern apes. Although they were surely climbing based on other morphology, their feet thus suggest that early hominins were doing so in a unique way (DeSilva 2009).

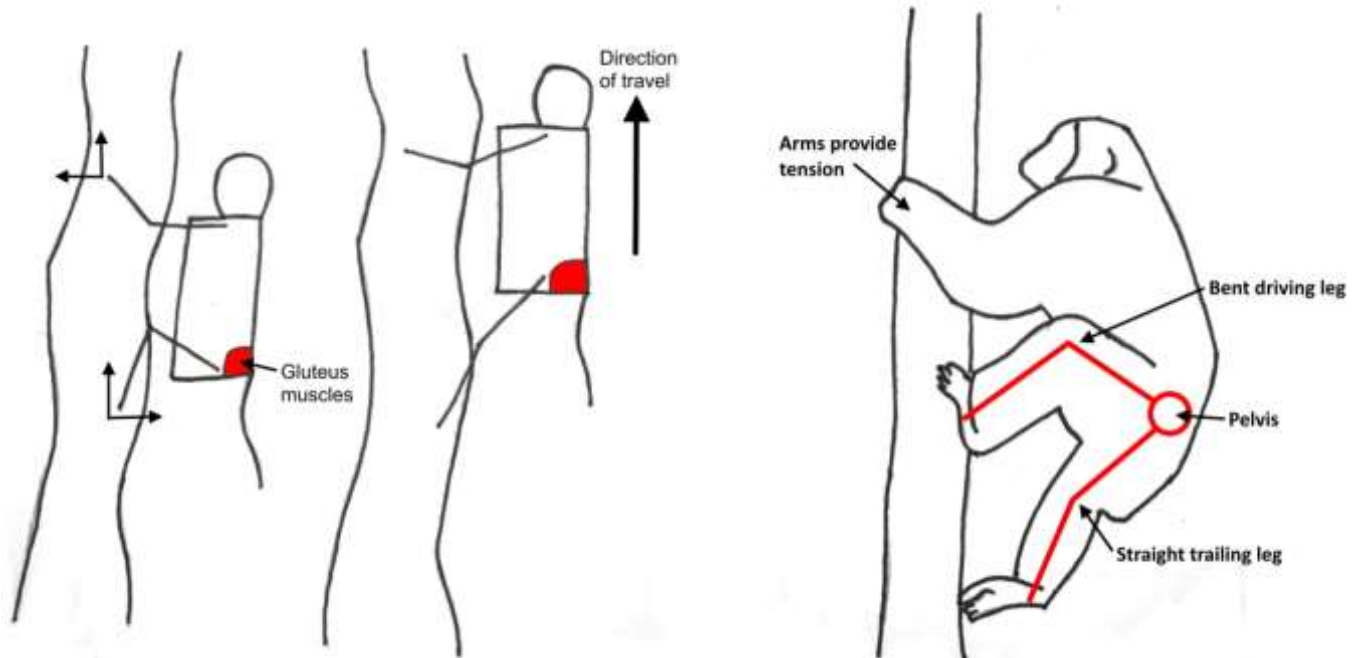
As previously discussed some modern human groups have developed impressive levels of ankle mobility to climb very effectively, therefore morphology of the ankle may not actually be a limiter on climbing performance (Kraft et al. 2014). Further evidence for this is provided by Holowka *et al.* (2017), finding that chimpanzees exhibit high levels of ankle joint motion during both climbing and walking, suggesting that one should not gauge arboreality vs terrestriality based on ankle flexibility.

### **The trunk and pelvis**

For the purpose of this review, the trunk describes the region of the body between the scapula and the glutes. The shape of the ribcage is important for climbing ability and efficiency, as the wider it is the greater compression is experienced in the upper torso, reducing mechanical advantage and general comfort (Hunt 1996). In combination with a more cranially-oriented glenoid fossa, a narrow ribcage further enables a weight-bearing arm to be closer to the midline of the body while hanging, a form that resembles hanging from the point of a teardrop, compared with a wide ribcage which resembles hanging from the corner of a rectangle (Hunt 1996- figure 6).

The orientation of certain muscles of the trunk, such as craniocaudal positioning of the serratus anterior (on the side of the chest) and a clavicular origin of the pectoralis major, have been shown to aid in certain climbing behaviours in a range of primates (Stern et al. 1980a; Stern et al. 1980b). Modern humans retain such characteristics, resembling those of non-human brachiators enabling adeptness at arm raising activities, although these adaptations are probably not specifically climbing focussed due to the adoption of bipedalism and other upper body activities such as load carrying and throwing (Stern et al. 1980a; Stern et al. 1980b)

Although it is often assumed that the upper body contributes most to climbing (notably via the arms) this statement is quite incorrect. Much like a modern human climbing a ladder the legs actually provide the majority of the propulsive force for non-human primates while vertically climbing, while the arms function to keep tension with the support (Preuschoft 2002; Hanna et al. 2017- figure 11).



**Figure 11:** Illustrations depicting a model primate climbing a vertical support (left) and a chimpanzee doing the same (right). They demonstrate the use of the legs during climbing, which provide driving force up and away from the support, as indicated by the arrows on the left most image. Extension of the legs is aided by powerful gluteal muscles of the pelvis. As the legs extend the arms provide tension with the support, pulling the body inwards towards it, while also aiding in upwards propulsion. Much like a human walking the driving leg alternates up the support from right to left. Figure produced using information from Preuschoft (2002).

As such the contribution of the legs to successful climbing cannot be ignored. Much of the power of the legs comes from the pelvis, which varies considerably in morphology depending on locomotory behaviour. The shape of the acetabulae (the 'socket' for articulation with the femoral head) has been shown to be different among powerful leaping primates, slow cautious climbers and bipeds such as modern humans, as it must withstand different specific loading patterns (San Millán et al. 2015). The gluteal muscles are important stabilisers of the pelvis during many different forms of locomotion, helping to minimise side-to-side motion, while also providing considerable muscular force for extension, abduction and rotation of the hips (Hogervorst and Vereecke 2015). Using electromyography Stern and Susman (1981) found that gluteal activity and recruitment was very similar in bipedal walking and climbing. This has been further proven more recently by Bartlett *et al.* (2014), who found no significant difference in gluteal muscle activity between individuals while running and ladder climbing. The importance of the glutes for climbing may have been an important pre-adaptive factor for the transition towards bipedalism, as the muscular capabilities of the pelvis were already present (Stern, and Susman 1981; Yamazaki and Ishida 1984). Other regions of the leg seem

to support this idea, such as the tricep surae and Achilles tendon, which appear to have similar morphology among a large range of climbing primates as well as humans, suggesting that the modern human form of the lower leg could be ancestral, and pre-adaptive for bipedalism (Hanna and Schmitt 2011a; Aerts et al. 2018). Yamazaki and Ishida (1984) found that in gibbons vertical climbing promotes and develops the knee and hip extensors, helping create and maintain erect posture in the body, all of which are useful for bipedalism, furthering this point. Modern humans have seen significant expansion and remodelling of the gluteal muscles, notably due to these muscles being the strongest hip extensors enabling bipedalism, but also potentially due to predator avoidance (sprinting away from large carnivores present throughout hominin evolution) and other activities such as projectile throwing (Bartlett et al. 2014; Hogervorst and Vereecke 2015). Indeed a great number of other muscles such as the various hip flexors and hamstrings have been remodelled for bipedalism- see Hogervorst and Vereecke (2015) for further detail.

## Conclusions

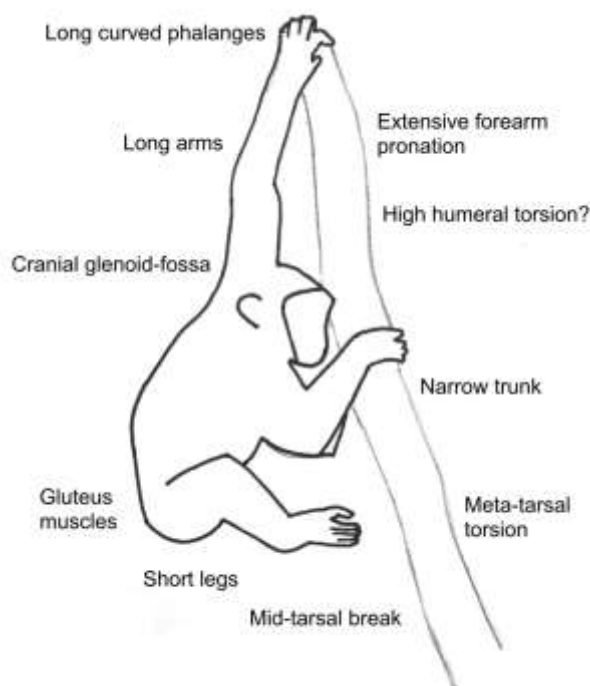
Table 1 and figure 12 below summarise the key physiological and anatomical features seen in hominids relating to climbing behaviour, as discussed within the review. The overall conclusions of this review are as follows:

- From an evolutionary perspective, climbing within hominids has been a fundamental behaviour enabling an arboreal lifestyle within forested environments.
- Due to climatic shifts towards the end of the Miocene, tree cover in Africa began to reduce. Hominid species present were constricted to smaller pockets of rainforest, forced to spend more time moving terrestrially between fragmented habitats.
- Although primitive bipedalism had likely already arisen within the genera *Sahelanthropus* and *Orrorin*, walking bipedal slowly became more efficient within the earliest hominin species- with *Ardipithicus ramidus* and later the Australopithecines displaying a mosaic of climbing and walking related anatomy.
- The genus *Homo* arose as the first obligate bipeds, with climbing behaviour substantially reduced, although likely still providing some use for foraging and escaping predation. This use has maintained all the way into the modern day with a few remaining modern hunter-gatherer groups.
- Modern humans have lost the majority of the climbing-enabling features of their ancestry. Such features displayed by extant apes are generally focussed upon the strength and mobility of the upper body, as well as the hands and feet. However some features of the leg, such as the gluteus musculature, seem to be useful for both climbing and walking.



**Table 1:** Summary of key aspects of hominid anatomy and biomechanics relating to arboreal behaviour.

Climbing adaptations	Summary
Cranially-oriented glenoid fossa	More cranial orientation of the shoulder more evenly loads the ligaments of the shoulder during overhead weight-bearing. It also corresponds to an upwards-pointing scapula spine and thus narrow infraspinatus muscle of the shoulder, more suited to climbing
Long arms	This improves reach and security during bridging moves in the canopy, while also improving pendulum motion during arm-swinging
Extensive forearm pronation	Enables good flexibility grasping supports in different orientations, while also allowing below branch hang feeding, rotating on the arm
Humeral torsion	A higher level of torsion enables more internal rotation of forearm, useful for negotiating a complex arboreal environment?
Long curved phalanges	Curvature resists bending strain on bones associated with long fingers, while greater length aids security grasping even large supports
Mid-tarsal break	Enables prehensile grasping of the foot, while also aiding dorsiflexion and inversion of the ankle
Metatarsal torsion	Everted big toe enables the foot to better conform to a round support, and allows grasping capability between the big toe and other digits
Ankle dorsiflexion/ inversion	Ankle flexibility allows full foot contact with the support, increasing surface area and thus security
Narrow trunk	A narrow ribcage aids a cranial glenoid fossa in making a hanging arm closer to the midline of the body, generating less strain
Gluteus muscles	These provide stabilisation of the hips during movement, while also powerful extension helping drive the hips upwards



**Figure 12:** Summary annotated illustration detailing key features of hominids relating to arboreal climbing behaviour, as inferred by table 1 and the information in this review.

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## **Section 2- Squatting**

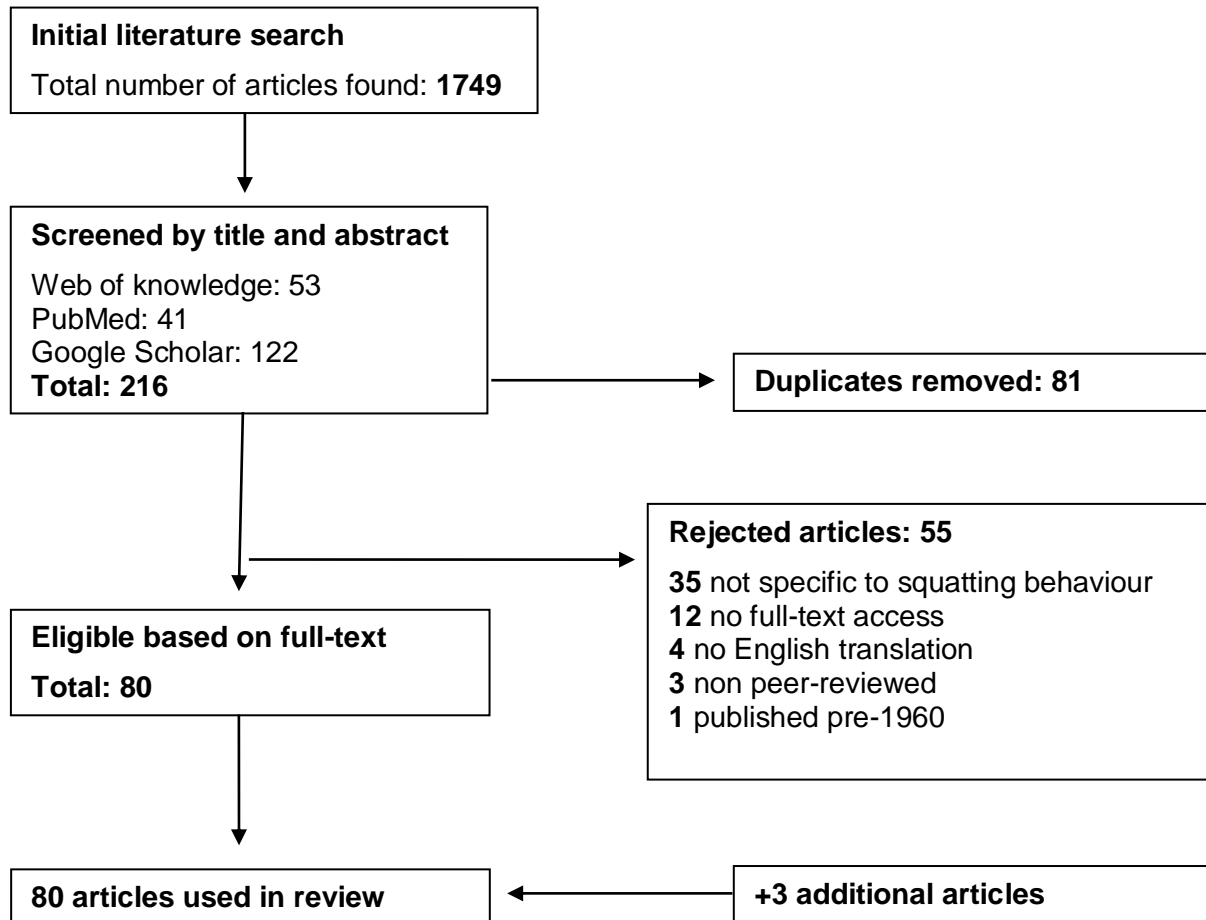
### **Overview**

This second systematic review concerns the evolutionary significance of a deep squatted posture. It begins with a broad background to this behaviour in the modern day, before exploring the evidence we have for it in the fossil record. Alternatives to this posture are considered, especially in reference to the wide adoption of chairs in recent times. Then the two major ancestral uses of squatting (besides simple resting) childbirth and defecation, and their adaptive implications are reviewed in depth. It ends with a brief section on potential squatting anatomy and biomechanics. The overall aim of this section is to evaluate the origin, usefulness and anatomical markers of a prolonged deep squatted position.

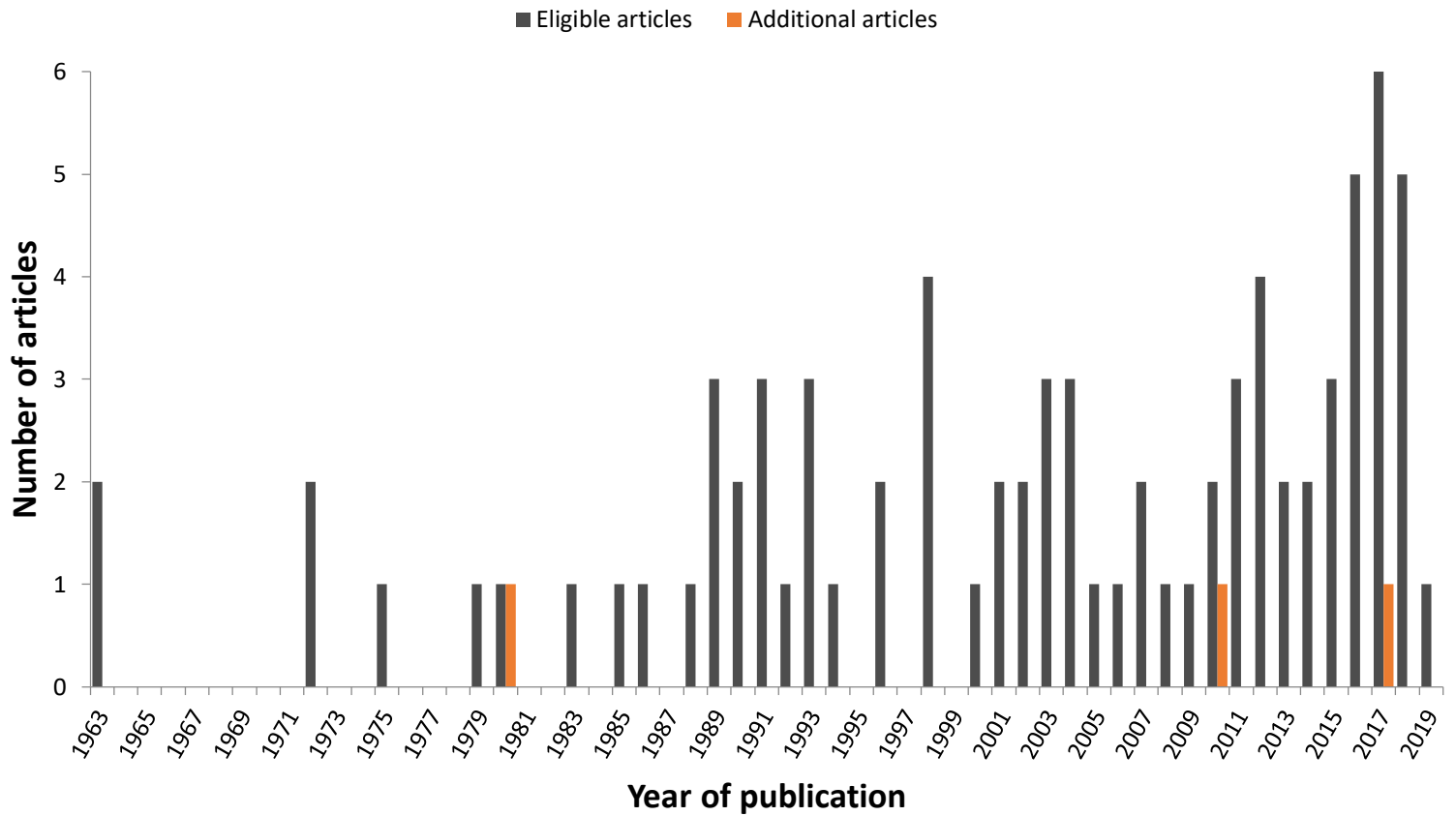
Figure 13 below summarises the steps undertaken to acquire the literature base for this section. The initial search of the squatting literature identified 1749 articles, of which 216 were screened (and thus deemed relevant) by title and abstract. Once duplicates were removed (81) this left 135 articles to check for eligibility. A total of 55 articles were excluded in this second round of screening: 35 lacked specific reference to a squatted posture, 12 articles were not-accessible in full text, 4 articles had no English translation, 3 articles were non-peer reviewed works and a final paper was published pre 1960. This left a total of 80 eligible full-text articles used in this review.

An additional 3 papers were added at the end of the writing process, to provide further evidence within specific topics that was seemingly lacking from the systematic search. These were sourced via targeted searching of Web of knowledge, PubMed and/or Google Scholar. The first of these papers concerned squatting kinematics in relation to exercise performance, while the other two were observational studies detailing the birthing process in chimpanzees and gelada monkeys.

As demonstrated by figure 14 below, included articles were published across a broad timeline from 1963 to 2019, although with a greater inclusion of articles from 1989 onwards.



**Figure 13:** Flow diagram illustrating the steps undertaken to acquire the literature base for the squatting section of this thesis. Eligibility of articles following a full-text read through was based on specific criteria stated within the methods section previously in this thesis. Additional articles were sourced from Web of knowledge, PubMed or Google Scholar where gaps in the research base were revealed, as outlined in the introductory text above.



**Figure 14:** Graph showing the range of literature by year of publication that was sourced for the squatting section of this thesis. Literature was sourced in accordance to the methods section previously, as diagrammed by figure 13 above. Eligible articles are shown in grey, representing the core relevant literature sourced by the systematic searching process. Additional articles are shown in orange, representing the further literature sourced to provide extra detail or reference at the end of the writing process. The articles range along a linear scale from 1963 to 2019.

## **Background**

The deep squat is a commonly used resting posture in primates, characterised by full flexion of the knees and hips, and hyper-dorsiflexion of the ankles (feet bent towards the shins) to place the centre of gravity low and over the feet (Bridger 1991; Kasuyama et al. 2009; Narayanan et al. 2018). In human society this posture is practiced by millions of people worldwide, although generally focussed in lower income and/or less-Westernised countries of Africa and Asia where use of furniture such as chairs is not yet widespread due to socio-economic and/or cultural influence (Bridger 1991; Ingold 2004). For example in a Chinese study involving over 2000 people, 40% of men and 68% of women (aged 25) reported that they squatted for at least an hour a day, representing a significant activity for a large portion of people (Zhang et al. 2004). Other than as a simple resting posture, squatting is utilised in many industries around the world where working at or near the ground is typical, such as farming, shipbuilding and welding jobs (Chung et al. 2003).

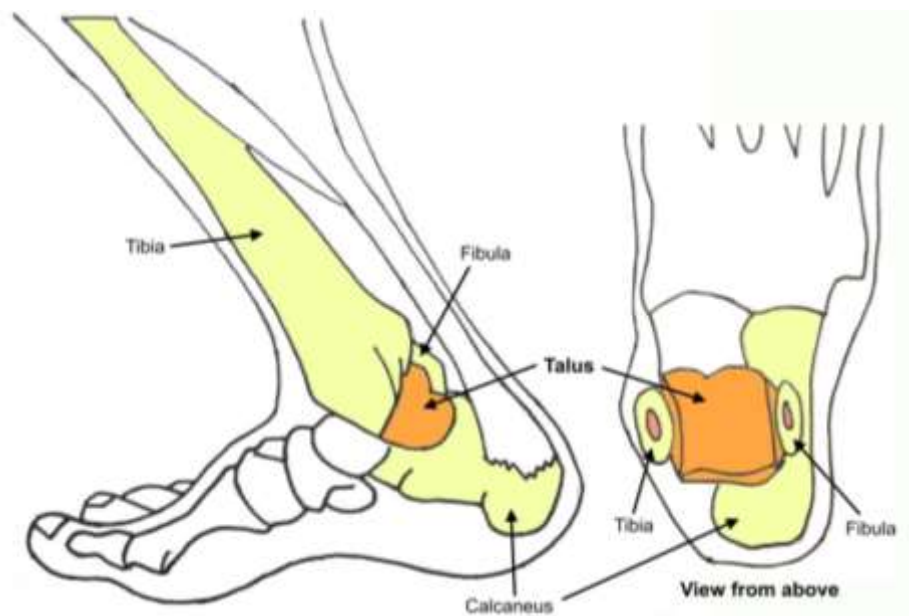
Among non-human primates, squatting is a highly common posture for foraging close to the ground, perched upon tree branches, or simply for resting (Alexander 1994; Tuttle et al. 1998). The benefits of this posture over sitting on the ground are many, including being in a more elevated position for comfortable access to higher forage, while keeping one's body detached from whatever substrate may be on the ground, and also being in a more convenient position to stand and suddenly move off (Tuttle et al. 1998). These benefits are presumably the reason why most non-human primates habitually adopt a deep squatted position rather than a sit. Such behaviour among extant primates alludes to the origin of squatting among humans. As it's likely that humans evolved from a chimpanzee-like primate (see climbing review previously), the squatting behaviour of extant great-apes and wider primates for foraging, rest, defecation and childbirth shows us our ancestral use of this posture.

In modern human society squatting is widely utilised as part of dynamic exercises or a static posture to build strength and improve muscular control (Platek et al. 2011). As part of a stretching regime it has even been found to improve the angle of lumbar lordosis, potentially reducing lower back related pains (Kadono et al. 2017). However extended periods of squatting have also been shown to achieve the opposite, altering joint kinematics and recruitment to increase the likelihood of lumbar dysfunction, demonstrating the existence of an upper threshold beyond which excessive squatting can be damaging to health (Lui et al. 2018). This is often reported in occupational squatters, those that work in awkward squatted positions for long periods of time, who at best simply generate musculoskeletal discomfort, or at worst may experience more debilitating conditions such as compression of the peroneal nerve (Yilmaz and Bodur 2015; Maity et al. 2016; Salve and Amitabha 2016). A squatted posture is also utilised for two key behaviours in primates, childbirth and defecation, which are discussed later in great depth.

## **Evidence from squatting facets**

Articular facets provide the majority of evidence for squatting in pre-history, with archaeological accounts of such features being commonplace in the literature (Boulle 2001a; Ari et al. 2003; Baykara et al. 2010). Squatting facets are described as changes to the shape and form of bones at articular

surfaces (joints), brought about by continuous loading from habitual movement patterns (Trinkaus 1975; Nelson 2011). Plasticity in the form of bones enables them to respond to the mechanical stresses being placed upon them, and thus perform in a manner more suited to a particular activity (Narayanan et al. 2018). For squatting the notable facets appear at the ankle due to hyper-dorsiflexion at this joint, which is a biomechanical position of the foot rarely seen under any form of locomotion or resting- see figure 17 later (Narayanan et al. 2018). Generally these present as a lunate-shaped groove on the distal end of the tibia, and/or medial and lateral flattening of the talus (Boulle 2001a; Nelson 2011- figure 15). Tibial retroversion can also sometimes be seen at the knee due to full flexion at this joint when one squats, and the subsequent contact between the patella ligament and the anterior proximal portion of the tibia (Boulle, 2001a). Indeed a large range of other more minor modifications can also be displayed at these joints, either together or separately, in habitual squatters. The complexity of interpreting squatting facets is best exemplified by studies such as Blau (1996) and Anjaneyulu *et al.* (2014). It is beyond the scope of this review to discuss the plethora of different facets possible.



**Figure 15:** Annotated illustration detailing the location of the talus of the ankle in modern humans, at the junction between the Tibia and Fibula of the lower leg and the foot. As deep squatting requires substantial ankle dorsiflexion (foot towards shin), habitually loading the talus in this way leaves facets upon the bone-ridging and flattening as certain surfaces wear with prolonged contact with other bones. Therefore the morphology of the talus within a fossil sample provides insight into the squatting habits of the particular individual represented.

There are many studies reporting the incidence of squatting facets within various historical populations, with percentage presence generally varying considerably depending on many cultural influences. In their study of French populations from the 1<sup>st</sup> to 18<sup>th</sup> centuries, Boulle (2000) found that incidence of a lateral squatting facet on the talus ranges between 26 and 45%. Facet presence in Indian populations has been extensively studied, probably because squatting is still a commonly used posture in this society. For the most common lateral squatting facet, a range between 37 and 90%

presence has been reported, demonstrating the variation possible even within the same society, brought about by differences in occupational posture, traditions and wealth (Jeyasingh et al. 1979; Pandey and Singh 1990; Dixit et al. 2012; Garg et al. 2015; Narayanan et al. 2018). For more minor facets, presence has been reported even higher, sometimes above 90% (Kumar and Koranne 1983). Similar wide levels of variation in squatting facets have been reported from a plethora of literature, from Africa (Kostick 1963; Satinoff 1972; Dewar and Pfeiffer 2004; Dlamini and Morris 2005), Europe (Castellana and Malgosa 1993; Baykara et al. 2010), and Byzantine populations (Oygucu et al. 1998; Ari et al. 2003). Additionally facets from similar postures such as kneeling have also been identified and described, demonstrating the depth of the facet-related literature (Lai and Lovell 1992). Interestingly, work by Dlamini and Morris (2005) found that later stone-age foragers from South Africa had a lower incidence of squatting facets compared with iron-age farmers, perhaps reflecting the increase in stationary manipulative tasks such as grain-grinding with the transition to agriculture, and thus the greater need to squat or kneel for prolonged periods of time (osteological evidence discussed by Molleson (1989)). Although it should be noted that due to rather different sample sizes between foragers and farmers in Dlamini and Morris (2005), this hypothesis should remain speculative until further study.

Although wide variation exists, the common incidence and general high percentage presence of squatting facets (particularly within more traditional societies) provides robust historical evidence for habitual squatting in humans. Before *Homo sapiens* the evidence base for squatting is less extensive. Neanderthals appear to have habitually squatted, based on the very dated yet comprehensive work by Trinkaus (1975). Furthermore the similar morphology and seemingly fundamental use of a squatted position for childbirth and defecation in humans (discussed later) and extant primates points towards this posture probably being common for all hominids (Alexander 1994).

Rather than being gained only by individuals that habitually squat, squatting facets may actually have an embryonic origin, and only be retained by people who habitually adopt a squatted position into adulthood (Singh 1963; Kidd and Oxnard 1998; Boule 2001b). Therefore the presence of squatting facets is the derived state, and their absence is the modified state brought about by a change in movement patterns in adolescence and early adulthood (Kidd and Oxnard 1998). As such squatting facets are more prevalent in Asian and African cultures than in Europe and North America, mainly because of the retention of habitual squatting way into adulthood in more traditional less-industrialised societies (Dixit et al. 2012). There is also often a sex component to squatting facets, due to the occupational differences between males and females within traditional society. Female prevalence of facets is higher as they generally perform more stationary manipulative activities throughout the day, often on the floor in a squatted or semi-squatted position (Pandey and Singh 1990; Maity et al. 2016). The presence/ absence of squatting facets could have wider implications for the hominin fossil record. Kumar (2011) has suggested that as facets are only present in habitual squatters, and quadrupeds are physiologically unable to squat, the presence of facets in a fossil sample suggests bipedalism. Although yet to be substantiated and with some clear challenges to face concerning other non-human primates that are both squatters and predominantly quadrupeds, this line of thought may have merit for future study.



### **Evidence from osteoarthritis**

A link between habitual squatting and osteoarthritis has been noted by several authors, and is sometimes used to infer the postural behaviour of a fossil sample (Zhang et al. 2004; Lieverse et al. 2007; Nelson 2011; Billard 2016). Osteoarthritis is a highly common joint condition in humans, characterised by loss of cartilage and bony lesions at joint surfaces (Lieverse et al. 2007). It's linked closely with levels of physical activity, particularly repeated motions, and builds up over time so that it is most often displayed in older individuals, although not exclusively so (Lieverse et al. 2007).

Extreme flexion at the knees and hips during squatting is thought to contribute to osteoarthritis over time, as is clear from bony lesions on archaeological samples, and modern humans from cultures such as China that still practice this posture (Zhang et al. 2004; Lieverse et al. 2007; Nelson 2011; Billard 2016; Maity et al. 2016).

Interestingly the opposite connection between squatting and/or activities that require full flexion of joints and osteoarthritis has also been made in the literature. Although modern humans can achieve an impressive range of motion of the hips and knees with practice, it is still far inferior than those of other primates. Alexander (1994) found that closely related great apes such as chimpanzees and orang-utans fully utilise their joints range of motions far more than modern humans, mainly due to their demanding arboreal lifestyle and the increasing comforts of modern human living. This may have a bearing on osteoarthritis, as the underutilisation of joint movement ranges has been linked with the onset of this condition, in a case of inherited form and function not matching up with current biomechanical demand (Alexander 1994). Conflicting opinion here suggests another avenue for future research.

### **Squatting today and the rise of chairs**

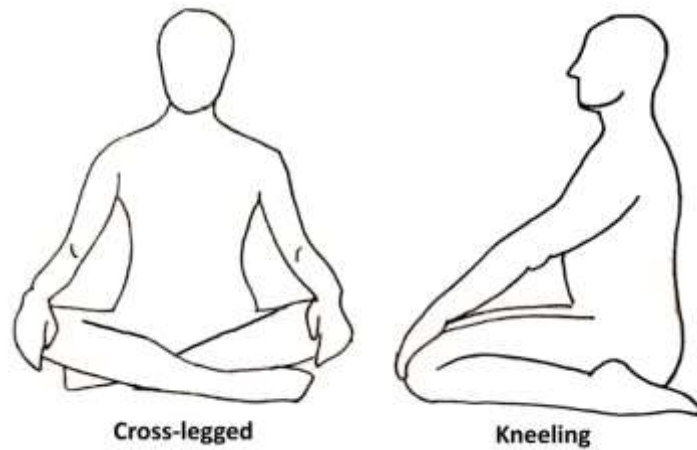
Evidence of humans' squatting ancestry today lies mainly with those cultures of Asia that still practice this posture (40-68% of people for at least an hour a day, outlined previously (Zhang et al. 2004)), and with the remaining traditional societies of Africa that maintain a hunter-gatherer lifestyle, such as the Dope !Kung foragers of the Kalahari (Dewar and Pfeiffer 2004). This tribe has a rich historic and photographic account of postural squatting, in line with other groups of this region (Dewar and Pfeiffer 2004).

The invention of the chair within the early civilisations of Ancient Greece and/or Egypt marked an important transition in the postural habits of humans, where it was heralded as a symbol of higher social class and authority (Bridger 1991). This trend has continued throughout much of human history since, with the advent of chairs in the western world in the 16<sup>th</sup> century, though only among the wealthiest few (Ingold 2004). Chairs have only been commonplace in the last 200 years, a similar time scale as the advent of footwear (Ingold 2004). Habitual sitting- particularly for extended periods of time and with poor posture- has been linked with a number of conditions common in the 21<sup>st</sup> century, including lower back pain and general inflexibility of the hips and legs, brought about by muscle atrophy, imbalance and shortening (Hargovan 2012; O'Sullivan et al. 2012; Sung 2013; Gabel et al. 2018).

People who have been brought up with the use of chairs find the deep squat a difficult position to adopt and maintain (Ingold 2004). Indeed in their study of 71 Japanese college students, Kasuyama, Sakamoto and Nakazawa (2009) found that 22.5% of them were unable to squat at all, a statistic likely to be even higher within a more 'westernised' culture. For instance in a study of 125 Australian women, only 54 of them were able to sustainably maintain a deep squat, the rest either could only hold it for less than thirty seconds (51) or not get into the position at all (19) (Rane and Corstiaans 2008). The use of a low stool (10cm high) has been shown to be effective in reducing the discomfort levels of squatting while enabling the same posture, demonstrating that there are solutions for those who find it particularly difficult to maintain (Chung et al. 2003). All children can squat for long periods of time happily, however it seems that their ability reduces as they get older, probably due to the increased use of chairs thus reduced use of a deep squatted position (Rane and Corstiaans 2008). Although modified functional biomechanics such as reduced ankle dorsiflexion are the main reason for lack of squatting ability (see squatting anatomy section below), body weight and BMI also have an influence, with higher numbers correlating with reduced ability to squat, possibly due to increased thickness of the thigh and calf, which makes it difficult to maintain stability and full knee flexion (Kasuyama et al. 2009).

### **Other forms of 'floor sitting'**

Although chairs are ubiquitous today in the western world, a variety of other forms of 'floor sitting' (resting without the aid of furniture) other than squatting are practiced by certain cultures or for specific uses (Bridger 1991). These include the cross-legged style of Korea (or western primary school), kneel sitting/ the prayer position commonly used in Japan and the Islamic world, and an array of postures intermediate between them (Bridger 1991; Hargovan 2012; McNeill 2017; Moon et al. 2018- figure 16). As with squatting, these postures involve considerably greater flexion of the hips and knees than sitting using a chair, and as such require varying degrees of long-term habituation before they can be adopted and comfortable for extended periods of time (Bridger 1991; Ingold 2004; McNeill 2017). In comparison with squatting, they generally require lesser muscular control and are less demanding on the joints, making them more sustainable for the majority of people (Okada 1972; Nag et al. 1986; Maity et al. 2016). There are also many potential biomechanical benefits of these postures, like producing a spinopelvic orientation more like that of standing (as in kneel sitting) so as to potentially reduce posture-related back pain, or simply improving flexibility and range of motion (McNeill 2017; Moon et al. 2018).



**Figure 16:** Illustration depicting two forms of 'floor sitting' - resting postures without the aid of furniture- other than deep squatting that are regularly practiced across the world. Cross- legged sitting involves sitting upon your glutes with your ankles crossed in front of you and your knees splayed out wide. It is a common posture in Korea, although is utilised globally by all manner of cultures, especially among children. Kneeling involves resting upon your shins with both knees together in front of you, and your ankles in full plantar flexion. It is a key pose of the Islamic world where it is used for prayer, while also being a commonly utilised posture for anyone working low to the ground, such as builders and farmers.

### The ancestral functions of squatting

#### Childbirth

Other than as a simple resting posture, squatting has two major ancestral functions seen in virtually all primates- as a posture utilised for childbirth and defecation. Although these uses may not involve extended periods of squatting, they are nevertheless likely to be important enough to ensure that relevant elements of anatomy and biomechanics remain selected for.

Posture and position during childbirth is a topic which attracts wide opinion and is highly influenced by culture and belief, as there is little consensus as to what is optimal for mother and child. Sitting, kneeling, squatting, semi-reclining, lying down and standing are all postures utilised for childbirth across the world, demonstrating some of this variation (Liu 1989; Rosenberg and Trevathan 2002). Due to the increased proportional size of the skull (to fit the brain), many primates are faced with a significant biomechanical challenge to the pelvis while giving birth, epitomised by humans with our extreme brain volume increase, in addition to obligate bipedalism and the delivery of truly helpless young (Rosenberg and Trevathan 2002).

In comparison with monkeys who seek solitude to give birth, human mothers nearly always look for assistance due to the physiological demands imposed upon them, making posture potentially very important to ensure ease of delivery (Rosenberg and Trevathan 2002). In the western world a semi-recumbent position upon a birthing bed is most commonly adopted, as it is the most convenient in a modern hospital environment, enabling easy monitoring of the birthing process (Liu 1989; Gupta et al. 2004). Elsewhere a deep squatted position is still utilised for childbirth, with a considerable body of literature championing the benefits of doing so (see upcoming references). The second stage of labour has been reported to be shorter during squatted deliveries than in semi-recumbent ones, which

is obviously generally preferred by the mother and any helpers present (Gardosi et al. 1989; Liu 1989; Golay et al. 1993; Dani et al. 2015). There are many explanations for this, the simplest being that more upright positions improve the action of the force of gravity on the descending baby, providing extra 'push' and requiring less expulsive force from the mother (Golay et al. 1993; Dani et al. 2015). Although not always reported in the past (see Gupta *et al.* (1991)), recent literature has shown that pelvic dimensions are altered in a squatted position compared with a supine one, potentially improving the alignment and size of the birth canal (Roberts 1980; Hemmerich et al. 2018; Hemmerich et al. 2019). In terms of the use of instrumentation such as birthing forceps, squatting mothers generally require less mechanical assistance, and the prevalence of complications such as perineal tears is lower (Gardosi et al. 1989; Terry et al. 2006; Nasir et al. 2007; Sayed Ahmed and Youssef 2015). Finally the perception of pain is also reportedly lowest in a squatted position (Valiani et al. 2016).

The disadvantages of a squatted position when giving birth are far less evident. They mainly centre on the lack of access for any birth attendants, both from a visual monitoring perspective and in order to perform medical intervention, however this is more of a commonly held myth than actual fact (Romond and Baker 1985; Waldenström and Gottvall 1991). With willing hospital staff there is plenty of scope for normal monitoring and delivery of a baby while squatting, providing the staff can kneel or squat to the same level as the mother (Romond and Baker 1985). In societies where squatting is not commonplace, such as Europe and North America, few women will be able to maintain this position for long enough to deliver a child, due to lack of long term conditioning (Rosenberg and Trevathan 2002). This can easily be seen as a fairly major problem for this posture's use in a modern hospital environment. However the use of a birthing cushion (a semi-upright back support) on a conventional hospital bed has been shown to enable a mother to adopt a squatted position while being supported, providing the biomechanical benefits without requiring the squatting conditioning (Gardosi et al. 1989). Other furniture aids such as the birthing stool serve the same function (Waldenström and Gottvall 1991). Therefore, a lack of squatting ability in the western world should not be a limiting factor regarding birthing posture. In terms of medical complications, increased blood loss from a squatted birth has been found by a couple of studies, probably due to the increased effect of gravity compared with a supine position (Waldenström and Gottvall 1991; Gupta et al. 2004). Some cases of peroneal neuropathy have been reported in squatting mothers after birth, caused by compression of the peroneal nerve and the head of the fibula (Reif 1988; Babayev 1998). This condition manifests as weakness and numbness of the lower extremity, with patients often unable to lift their toes or feet, although the recovery rate is normally very good (Babayev 1998). Although fairly rare among mothers, this condition is common among habitual squatters, and generally can be prevented at labour by only squatting during contractions, utilising other positions in-between to relieve pressure on the nerve (Reif 1988; Babayev 1998).

In terms of literature support, the case for squatting when giving birth thus seems overwhelmingly positive. In addition, non-human primates such as chimpanzees and geladas (an old-world monkey) usually adopt a squatted or crouched position during birth, as observed and recorded by Goodall and Athumani (1980) and Nguyen et al. (2017). This suggests that this posture is the likely 'natural' choice

for giving birth. However in their Cochrane review of various birthing postures, Gupta, Hofmeyr and Smyth (2004, p.8) concluded that due to a lack of scientific certainty “mothers should be encouraged to give birth in the position they find most comfortable”. Although somewhat out of date, this demonstrates that more work needs to be done concerning the pros and cons of specific birthing postures.

## **Defecation**

Along the same lines as childbirth, squatting is the ancestral posture for defecation that was utilised worldwide prior to the invention of the toilet in the 19<sup>th</sup> century, and is still practiced in many cultures of Asia and Africa (Sakakibara et al. 2010). The fundamental difference between using a conventional toilet and squatting is the hip angle produced, which is far tighter (hips fully flexed) in the latter (Edgar et al. 2017). Through experimentation with different sitting postures, the tighter hip angle of squatting has been shown to enlarge the rectoanal angle, essentially straightening out the rectal canal and thus requiring less abdominal pressure (straining) to effectively defecate (Sikirov 2003; Sakakibara et al. 2010). As well as less strain, satisfactory emptying is achieved far faster while squatting, probably also due to the straighter line of rectal passage (Sikirov 2003). Use of a low stool placed in front of a conventional toilet to raise the feet and thus mimic a squatted position has been shown to produce the same biomechanical benefit (Edgar et al. 2017). Alternatively, bending the upper body forwards towards the feet while toileting seems to have a similar effect, a posture that has been named ‘The Thinker’ due to its resemblance to Auguste Rodins’ famous sculpture (Takano and Sands 2016). There are several potential medical benefits of squatting at defecation. The first is a reduced risk of developing haemorrhoids- a common condition involving a bulging vein protruding from the anus- as it is generally linked with straining (Dimmer et al. 1996). Indeed researchers working with rural African populations in the 1950s found little if any incidence of haemorrhoids, possibly reflecting their postural habits at defecation, as well as their diets (Sikirov 2003; Tanjung et al. 2013). Tanjung *et al.* (2013) found that incidence of constipation to also be lower in Sumatran children who squatted compared with those who sat, most likely due to the straighter rectal passage in a squatted position. Therefore squatting may be a viable treatment for constipation and other similar conditions such as obstructive defecation syndrome (Rane and Dilgir 2017). Straining at defecation can have far more dangerous consequences, such as cardiovascular events brought about by excessive straining via the ‘Valsalva maneuver’ (expulsive effort against a closed airway), leading to alarming spikes in blood pressure and potentially heart attack in those that are vulnerable (Sikirov 1990). Therefore any means of reducing straining, such as switching to squatting, should be seen as very beneficial for one’s health. Other conditions and diseases such as stretch-induced injury of the pelvic nerves and colorectal cancer may reduce in incidence within squatting populations, although there are as of yet no significant results under experimental study (Lam et al. 1993; Sohrabi et al. 2012).

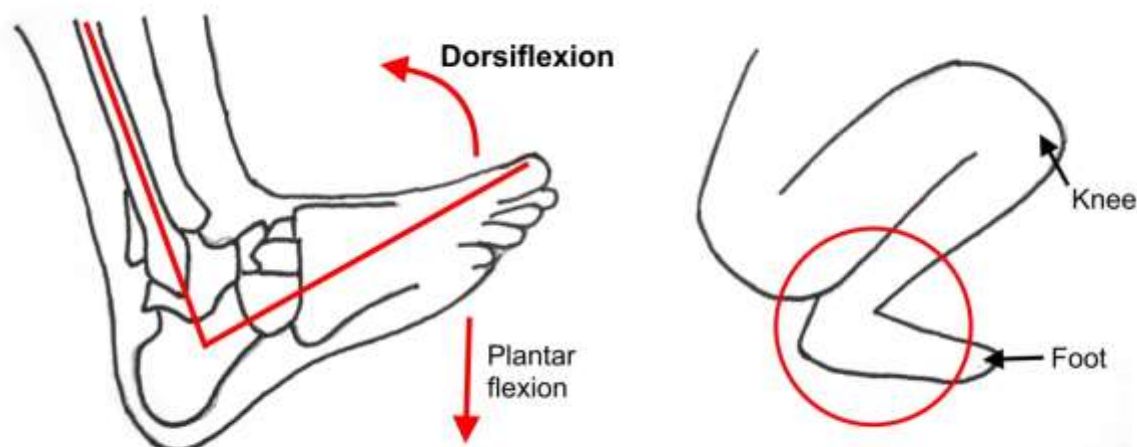
Proposed disadvantages of a squatted position at defecation are generally hard to come by. However Chakrabarti *et al.* (2002) found significant incidence of stroke while squatting at defecation among an Indian population (36% of 100 consecutive stroke patients), suggesting that this posture certainly does not eliminate cardiovascular events. Such risk may be unavoidable regardless of posture. A

comparison in anorectal bleeding between squatting and sitting did produce a significant result, with squatting causing increased bleeding due to increased pressure on the rectal region (Shekokar and Borkar 2017). This makes it clear that in certain cases squatting should be avoided. Once again, lack of physical ability to squat can be seen as a significant disadvantage here. However as previously discussed furniture aids such a low stool in conjunction with a conventional toilet produces similar biomechanical effect, therefore lack of ability to squat should not be seen as a limiter to gain the same health benefits (Rane and Corstiaans 2008; Edgar et al. 2017).

### **Squatting anatomy and biomechanics**

From the evidence base above it's clear that squatting has a rich history in hominin evolution. However literature testing and reporting on the physiological demands of this posture are few, especially in terms of a deep static hold rather than a dynamic squat-to-stand movement such as people might do at the gym. Therefore it is difficult to ascertain potential adaptations in the human form that may have come about as a result of habitual use of this posture, as I have done for the other activities reviewed within this thesis. None-the-less, some specific adaptations to squatting can be suggested based on the data we already have, and these are discussed below, though no summary-table has been included due to the general lack of relevant information.

Firstly the degree of ankle dorsiflexion one possesses is a key predictor of squatting performance, as it is crucial to lean the trunk forwards thus maintaining a stable centre of gravity over the feet (Kasuyama et al. 2009- figure 17). With limited dorsiflexion the only way of staying stable is by flexing the trunk and hips forwards, however this tends to lift the thigh from the calf generating a fairly demanding position that cannot be maintained for any period of time (Kasuyama et al. 2009). As discussed in the 'squatting facets' section, osteological evidence of prolonged squatting is found at the ankle in a large percentage of historical samples, up until around the middle ages where it's use progressively declines (Bouille, 2001a). Despite this, all modern humans have the biomechanical potential to adequately dorsiflex their ankles for a deep squat, as is evident from children who can all adopt this posture, traditional societies who habitually use it way into adulthood, and people of modern more-industrialised countries who use it as an exercise to increase range of motion and strength (Dewar and Pfeiffer 2004; Rane and Corstiaans 2008; Platek et al. 2011). However lack of squatting practice in more Westernised societies makes the posture far more challenging to adopt, due to reduced ankle flexibility. Ankle dorsiflexion appears to therefore be a plastic trait rather than an inherited adaptation, something that can be maintained through life via habitual flexion of the ankle as in squatting.



**Figure 17:** Illustration depicting the human ankle, showing the difference between dorsiflexion (foot towards shin) and plantar flexion (pointing the toes down). Squatting requires ankle dorsiflexion in order to keep your centre of gravity low and over your feet, preventing you from toppling backwards.

Although the ankle appears crucial to maintaining stability while squatting, having adequate joint flexibility elsewhere in the body is also important, such as in the knees, hips and spine. This is evident from studies looking at the kinematics of a dynamic squat exercise such as Schoenfeld (2010), who demonstrate that full joint mobility within the knees, hips and ankles is necessary for proper form of a squat. However literature directly addressing the kinematics of a static squatting posture is lacking, demonstrating a need for future research.

As well as a number of other extant primates, humans possess large robust heels to their feet, which for squatting are crucial to provide a stable platform. The heel clearly holds a key role in bipedalism, particularly for the heel-strike mechanics of walking. However the fact that closely related great apes such as gorillas spend a significant amount of time squatting while feeding (and are not habitually bipedal), it's possible that the heel developed in an ape-like hominin before the rise of habitual bipedalism (Tuttle et al. 1998). By this logic, squatting (particularly in an arboreal environment) would be the primitive selective force for heel morphology, while the resulting anatomy was then exapted for bipedal locomotion later. This is an interesting theory, although unsubstantiated and now fairly dated, making it difficult to draw any conclusions from it.

## Conclusions

The overall conclusions of this review are as follows:

- Squatting is a behaviour fairly commonly adopted in the modern age, particularly within cultures of eastern Asia and lesser-industrialised societies.
- Historically it seems highly likely that squatting was practiced even more extensively, based on the common occurrence of facets upon the talus of archaeological samples from varied

timescales and locations. The invention and wide adoption of the chair may have been a key factor in reducing time spent squatting in recent times.

- Childbirth and defecation are two behaviours in which a squatted posture is commonly utilised in less-industrialised society. The current research base championing the health benefits of squatting for these behaviours seem to outweigh the negatives, although with several notable unknowns.
- In terms of the anatomy and biomechanics enabling squatting, the research base is lacking, especially as a static long-term posture. Research is needed to ascertain how habitual squatting might affect human biomechanics.



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### **Section 3- Endurance running**

#### **Overview**

The evolution of endurance running has been of notable research interest in recent years, with a handful of extensive reviews detailing our current understanding. Despite its well-reviewed nature, endurance running is included as a review section of this thesis, as it played a major role in shaping the anatomy and physiology of our own species (which is the key exploratory aim of this thesis), and the topics/ regions of the body covered within the endurance running literature are highly relevant to the other behaviours considered herein. Furthermore, despite its research bias, if one is to approach evolutionary biomechanics holistically then running must be included. This review therefore is not designed as a deep-dive into the topic, but an overview summarising the findings of the major review articles currently published on endurance running. The overall aim is to ascertain the evolutionary origin of this behaviour, how and why it may have been useful, and what features of the body may have seen adaption for it.

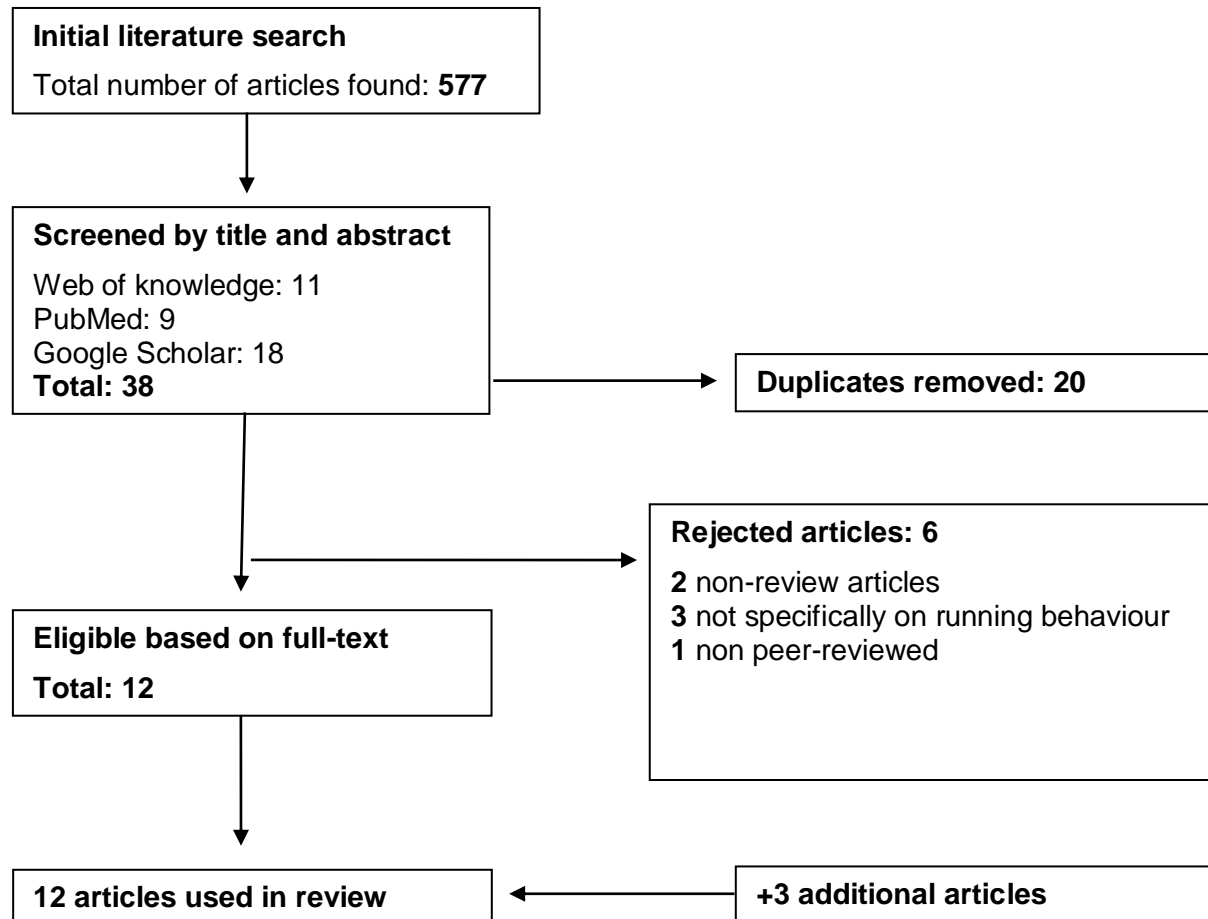
It begins with a brief look at how bipedalism (enabling running) came about, although greater detail for this can be found in the climbing review previously presented. It then explores the usefulness of running for hunting techniques such as persistence hunting and scavenging, before delving into those aspects of human physiology, anatomy and biomechanics that have arisen in order to best perform this behaviour.

It should be noted that 'barefoot running', another related and literature dense topic, has been left out of this review. The reason for this is that although some of it is relevant to understanding the evolution of endurance running, it opens up a plethora of literature that is less so, being focussed upon injury prevention and shoe design in the modern day. These sorts of topics will be covered within the discussion of this thesis, therefore barefoot running has been left out here.

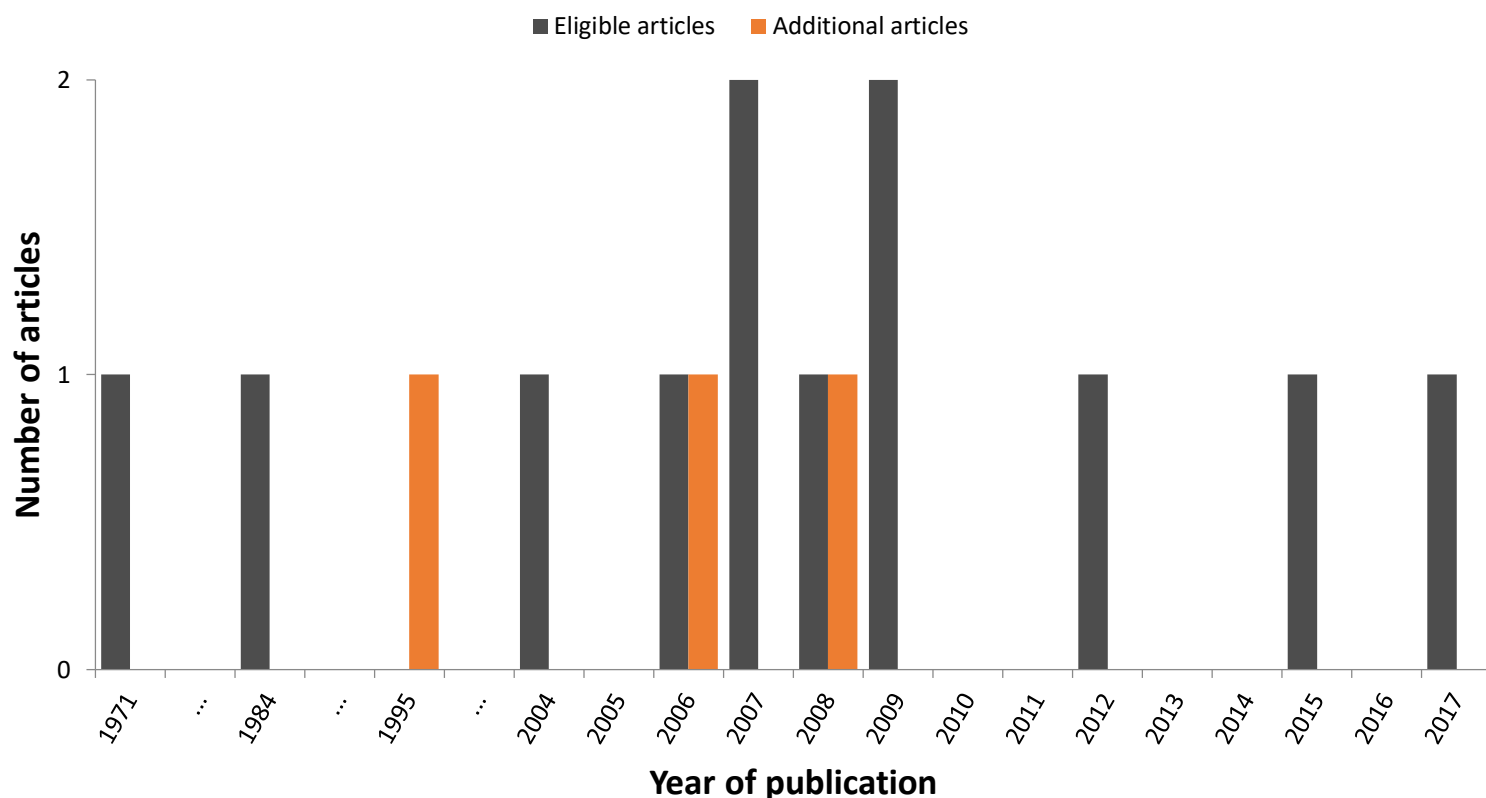
Figure 18 below summarises the steps undertaken to acquire the literature base for this section. A total of 577 articles were found with the initial literature search for endurance running articles. Of these, 38 articles were screened by title and abstract. Once duplicates were removed (20) this left 18 articles to check for eligibility. In total 6 articles were rejected after a full read: 2 were not review articles (which, as mentioned above, were the preferred choice here), 3 were not focused specifically on running but on general energetics and 1 other was not peer reviewed. This left a total of 12 eligible full-text articles that are used in this review.

In addition to these, despite trying to focus entirely on endurance running review articles (as outlined in the methods) 3 extra papers were added at the end of the writing process, to provide extra evidence that was lacking and to make this review flow more coherently. One was taken from the climbing literature search, providing detail on the earliest hominins. Another concerned the role of the gluteus maximus in running, and was sourced via the reference list of one of the eligible papers herein. The final extra article concerned hominin brain evolution.

As demonstrated by figure 19 below, with the exception of three articles published in the late 1900s, the included literature was published between 2004 and 2017, with a particularly abundant period between 2006 and 2009.



**Figure 18:** Flow diagram illustrating the steps undertaken to acquire the literature base for the endurance running section of this thesis. Eligibility of articles following a full-text read through was based on specific criteria stated within the methods section previously in this thesis. Additional articles were sourced where gaps in the research base were revealed, as outlined in the introductory text above.



**Figure 19:** Graph showing the range of literature by year of publication that was sourced for the running section of this thesis. Literature was sourced in accordance to the methods section previously, as diagrammed by figure 18 above. Eligible articles are shown in grey, representing the core relevant literature sourced by the systematic searching process. Additional articles are shown in orange, representing the further literature sourced to provide extra detail or reference at the end of the writing process. The year of publication of the three earliest articles- 1971, 1984 and 1995- considerably predate the others, and as such have been placed on the far left of the scale, with non-linear distances between them (denoted by ...). The remaining articles range along a linear scale from 2004 to 2017.

## Bipedalism and Environmental change

The transition to habitual bipedalism while on the ground was a major shift in hominid evolution that occurred around 6mya, probably with origins of the genera *Sahelanthropus* and *Orrorin* (Crompton et al. 2008). Many theories exist as to the selective benefit of bipedalism, as discussed in the previous climbing review, including that it provided a means to reach higher food resources by standing on your hind legs, or to improve locomotory efficiency while travelling for sustained periods along the ground (Lieberman 2015). Both of these theories pivot around gradual environmental change and the thinning of the rainforests, with a greater distance between trees. This savannah environment started developing a little over 2.5mya in Africa with an uneven and patchy distribution, and was generally widespread by 1.8mya- a similar time period as the emergence of *Homo erectus* within the fossil record (Pickering and Bunn 2007; Lieberman et al. 2009). With the gradual emergence of widespread savannah, hominins began transitioning towards being habitual bipedal walkers and facultative climbers, in stark contrast to their rainforest-dwelling ancestors. Key genera include *Ardipithecus* (~5mya) and *Australopithecus* (~4-2mya). These hominins while remaining good climbers with their relatively long arms, shrugged shoulders for arm mobility and curved phalanges, also slowly acquired characteristics for improved bipedal efficiency, such as a rigid mid-foot with a partial arch, and a laterally oriented ilium enabling gluteal hip abduction (Lieberman 2015). It wasn't until the emergence of the genus *Homo* that modern-human like locomotory efficiency came about, perhaps with *Homo habilis* (~2.3ma) and certainly with *Homo erectus* (~1.8ma), with their enlarged gluteal muscles, long striding gait and fully developed plantar arch- among many other modern features (Lieberman 2015).

## Why run?

The actual reason why hominins began running is unclear, especially as to whether it was either simply be a side product of being a striding biped, or a selectively advantageous activity in its own right (Bramble and Lieberman 2004; Lieberman and Bramble 2007). No doubt many of the 'running adaptations' discussed below have also been considered for walking e.g. large articular surfaces, sweating etc. However several key ones, such as the elastic potential of human leg tendons, cannot be explained by walking alone as they are virtually unused during this activity (Bramble and Lieberman 2004). Considering that humans retain elastic tendons today, this suggests that endurance running has somehow been useful within the evolution of hominins, useful enough for natural selection to adapt us to its stresses and for us to retain these adaptations long-term. Watanabe (1971) provides one of the very first reviews of evolutionary locomotion in humans, considering many forms of movement including swimming, crawling and running. Running seems to have been useful for both close-range ambush opportunities when hunting, and more long range pursuing hunts of potentially 20 miles or more (Watanabe 1971; Liebenberg 2006). Plenty of ethnographical evidence within hunter gatherer societies- both extinct and still around today- exists to support this. For example the Chipewyan Indians of North America, the Tarahumara of Mexico and Australian Aborigines all have an extensive historical record of utilising long distance running in order to hunt (Watanabe 1971; Carrier et al. 1984; Liebenberg 2006). More recent literature has described the two major theories as to how running has been useful to humans- persistence hunting and scavenging.

## Persistence hunting

Originally named the 'run-down' method of hunting, persistence hunting describes how consistent on-foot pursuit can eventually lead a human hunter to overtaking and dispatching a larger mammalian prey (Watanabe 1971). When one considers humans within the animal kingdom we generally do not think of ourselves as excellent runners, especially when compared with the obvious speed and agility of many quadrupeds such as dogs and horses. Speed and agility has never been hominins speciality, but at endurance speeds we are comparable with the best of the animal kingdom. Human endurance speeds range from 2.3 to 6.5m/s in a well trained individual, the top end exceeding the trot-gallop transition of many quadrupeds which sits at around 4m/s (Bramble and Lieberman 2004; Lieberman and Bramble 2007; Pontzer 2017). Essentially this means that conditioned humans can travel faster within their comfortable endurance zone than other mammals such as horses, which at a lower speed have to gallop- a far more metabolically strenuous gait (Lieberman et al. 2009). At the same time, unlike most mammals human running is equally energetically costly across their range of endurance speeds, meaning that they can tailor their pace to the environment or need without fear of substantial energetic penalty (Carrier et al. 1984; Liebenberg 2006). The upper end of this 'endurance zone' is known as VO<sub>2</sub>max- the organisms' maximum rate of oxygen consumption- beyond this point conditions become anaerobic and a build up of lactate occurs within the working muscle, which is the key contributor to fatigue during hard exercise (Pontzer 2017).

Persistence hunting is a theory for how hominins were able to hunt large mammalian herbivores, utilising their impressive range of endurance speeds along with a novel form of cooling. Running produces a great deal of heat that must be expelled in order to maintain a safe core body temperature, a fact which holds true for all mammals (Carrier et al. 1984). To cool themselves most mammals have to pant, a highly effective cooling mechanism in which the mammal takes hundreds of very short and sharp breaths, utilising the evaporation of water in the upper respiratory tract to cool down (Lieberman 2015). Panting can only be carried out while travelling relatively slowly due to the minimal gaseous exchange that occurs- i.e. reduced oxygen intake and a build up of bodily carbon dioxide (Lieberman et al. 2009; Lieberman 2015). A mammal galloping is unable to pant and therefore will either have to slow to a trot or eventually collapse due to heat exhaustion (Carrier et al. 1984). Humans (along with a few other mammals like horses and camels) are able to sweat to reduce heat instead, decoupling the thermoregulatory and respiratory systems, enabling us to run at endurance speeds for very long periods of time (Carrier et al. 1984).

All that was needed to turn these physiological facts into a successful hunting tactic was for a group of hunters to begin pursuing their mammalian game (normally the weakest individual- injured or old) during the hottest part of the day at a comfortable endurance speed (Liebenberg 2006). The prey animals would gallop away, and once out of sight would likely stop to pant and cool themselves, but crucially not for long enough to fully recover before the hunters were upon them once more (Liebenberg 2006). Given enough time and probably a good helping of skill and luck in tracking the prey, one of the weaker animals would collapse due to heat exhaustion, making for an easy kill (Lieberman and Bramble 2007; Lieberman et al. 2009).

This is a contentious theory, especially as little solid evidence exists- most of such evidence being based simply on physiological theory and/ or some historical ethnographic records. Liebenberg (2006) has reported firsthand accounts of persistence hunts in the central Kalahari, however these records are now over 30years old. It's quite possible that this lack of historical record is due to researchers simply not picking up on this form of hunting, as there are few visible cues (weapons, stalking) and is spontaneous in nature (Liebenberg 2008). But without record it is difficult to ascertain how important it might have been in selecting for the endurance running capabilities in humans. In the literature, the claims of Liebenberg (2006) about the importance of persistence hunting have been debated by Pickering and Bunn (2007), who claim that too much staging has taken place in modern ethnographic records, and that a lack of any sort of weaponry pre 400ka plus little evidence for the levels of intelligence required to track animals in the savannah would make persistence hunting almost impossible until much more recently.

Nonetheless it must be noted that there is plenty of evidence suggesting that hominins were hunting and eating large game as far back as 2mya, far prior to the invention of sophisticated weaponry (Lieberman 2015). Persistence hunting provides a potentially viable theory as to how hominins were able to do this.

### **Scavenging**

The scavenging hypothesis is a simpler idea, stating that hominins utilised running as a means of reaching a recently deceased animal before other carnivores such as hyenas moved in (Lieberman et al. 2009). In the same way as postulated for the thermoregulatory mechanics of persistence hunting, adeptness at endurance running would potentially give hominins an advantage over other mammalian scavengers, enabling them to reach and exploit the food source first (Lieberman et al. 2009; Lieberman 2015). At some point they would undoubtedly come into contact with such competition, and anatomically would be very inadequate against the claws and teeth of a lion. However in numbers and with the use of projectiles such as stones and throwing weapons (once they had been invented) they would be able to drive them off, just as has been recorded in modern hunter-gatherer groups such as the Hadza of Tanzania (Pickering and Bunn, 2007; Lieberman *et al.*, 2009).

A large range of ethnographical data supports the scavenging theory, and it was likely hominins first exposure to significant meat resources, making it the oldest selection force for endurance running (Lieberman 2015). Once again Pickering and Bunn (2007) have contested this idea, stating that hominins were unlikely to be fiercely competing for scavenging opportunity, and even if they were, endurance running would have had little selective benefit in driving off a pack of hyenas. Low-competition scavenging by hominins certainly had its place, perhaps in the early semi-wooded environments before the open savannahs expanded where carcasses could easily be overlooked, but it's role in selection for endurance capabilities is contentious (Pickering and Bunn 2007).

## Endurance running physiology, anatomy and biomechanics

As discussed by Pontzer (2017), the initial transition to bipedalism likely incurred an endurance cost of potentially as much as 22% reduced  $\text{VO}_{2\text{max}}$ , due to the isolation of the hind limbs for locomotion (and thus lack of contribution from the fore limbs). Considering that with conditioning humans today can become excellent endurance athletes, a significant amount of adaptation must have ensued in the millions of years since. This is especially the case as in comparison with mammals of a similar size, human running is over twice as metabolically costly (Carrier et al. 1984). Although these adaptations probably started within the *Australopithecus* species who displayed a fairly economical bipedal gait, major improvements in endurance specifically did not come about until *Homo erectus*, whose almost human-like body form probably made him a formidable endurance athlete (Pontzer 2017). Adaptations possessed by humans that are useful for endurance running can generally be placed into four major categories: energetics, skeletal strength, stabilisation and thermoregulation, as laid out most succinctly by Bramble and Lieberman (2004). The brain has also undoubtedly also been important, as discussed by a couple of papers in this review. Here, I will address each category in turn.

### Energetics

A number of features of the human musculoskeletal system reduce the metabolic cost of sustained endurance running. Spring- like tendons of the lower legs are possibly the most significant energy-savers that humans possess, providing propulsive energy for the runner by recycling impact forces from the ground (Lieberman and Bramble 2007; Pontzer 2017). The Achilles tendon is a prime example, stretching from the plantar flexors of the foot to the heel and the bodies of the gastrocnemius muscles at the back of the calf (figure 20). The arch of the foot is the other classically cited example, which by its very shape compresses under the loading of foot strike, before the multiple plantar tendons that support the arch recoil and propel the foot forwards, reportedly returning 17% of the initial energy (Bramble and Lieberman 2004, figure 20) . Unfortunately it is difficult to estimate tendon length and form from fossils, as only the attachment sites on bone are preserved (ibid.). Nonetheless, scientists have predicted that the Achilles tendon and plantar arch developed sometime after 3mya within the genus *Homo* (Bramble and Lieberman 2004; Lieberman et al. 2009) Long legs provide another mechanical advantage for running (and walking), by enabling increased ground contact time during gait, which is useful as lower ground contact times increase the metabolic costs of running (Bramble and Lieberman 2004). This feature first appears in the fossil record with *Homo erectus*, whose long legs are much like our own, and far longer than any species that came before (Bramble and Lieberman 2004). The musculature of the human leg is also well suited for endurance activity. In contrast to most other mammals who seem to possess more fast-twitch type 2 muscle fibres (predominantly for escaping predation, or being the predator), with training humans can greatly develop their slow-twitch type 1 fibres, and thus their aerobic potential (Lieberman *et al.*, 2009). In comparison with chimpanzees, humans have up to 3 times more type 1 muscle fibres in

their calves alone, demonstrating this apparent muscle specialism for endurance activity (Pontzer 2017).



**Figure 20:** Illustration detailing the locations of the two key spring-like tendons of the foot and ankle- the Achilles tendon and the longitudinal plantar arch. Both of these serve to reduce the impact from the ground while running, by recycling much of the impact-force into forward propulsion through elastic recoil.

### **Skeletal strength**

When compared with walking, running is a highly impactful activity that heavily loads the bones and joints of the lower extremity. Enlarged articular surfaces of several joints such as the knees and sacroiliac joint of the hips ensures robustness of the body under sustained loading such as running, helping to prevent brakeage or dislocation (Bramble and Lieberman 2004; Pontzer 2017). These stress reducing features seem to be unique to the genus *Homo*, proving to be considerably more robust in the lower body when compared with the Australopithecines and extant Chimpanzees (Bramble and Lieberman 2004). Currently the earliest fossil evidence for enlarged articular surfaces is found in *Homo erectus* (ibid.).

### **Stabilisation**

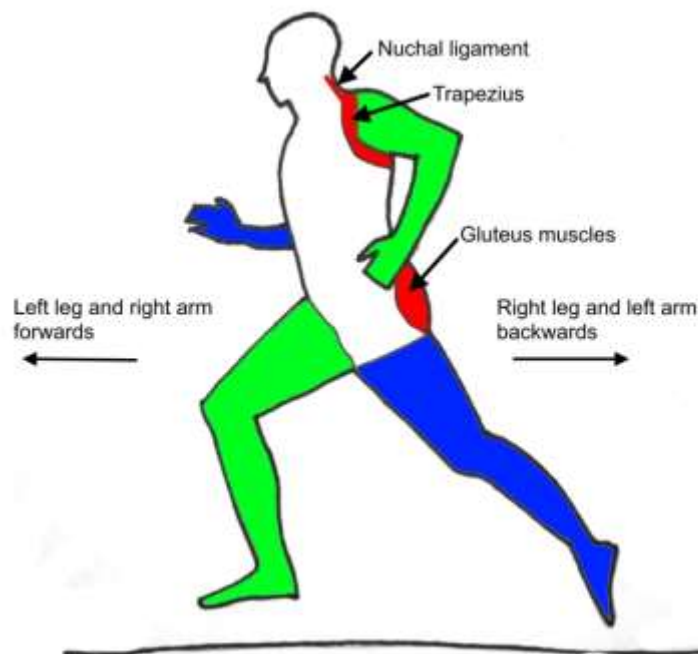
Stabilisation refers to how the body maintains a consistent upright form and posture while running. Biomechanically this is challenging due to the considerable forces produced by fast swinging legs and the impact that travels through the body at foot strike (figure 21).

The human head requires great stabilisation while running, due to its considerable weight and impulse to pitch forwards with the impact of foot strike (Bramble and Lieberman 2004; Lieberman et al. 2009). Decoupling of the head and shoulders, barring the cleidocranial portion of the trapezius and nuchal ligament, stabilises the head by utilising the swing of the arms (Lieberman *et al.*, 2009). This is achieved by firing the trapezius before heel strike on the forward leg side, which links the mass of the swinging arm with the head via the nuchal ligament (Bramble and Lieberman 2004; Lieberman et al.



2009- figure 21). Swinging arms (in combination with low-wide shoulders) are also important for stabilising the entire trunk, by counteracting the force of the swinging leg, and are aided by a second decoupling between the shoulders and waist that allows the entire trunk to rotate with the swinging arm (Lieberman *et al.*, 2009). Seeing as strong connections between the head, shoulders and waist are advantageous for climbing, as seen in many other primates such as chimpanzees, it's probable that decoupling occurred sometime after the slow climber *Australopithecus*, and early within the genus *Homo*.

Another important stabiliser the gluteus muscles, which are significantly enlarged in humans in comparison to both previous hominin species such as the Australopithecines and extant great apes (Bramble and Lieberman 2004; Lieberman *et al.* 2006). These muscles of the pelvis extend the hips forwards (helping enable bipedalism), counteract side-to-side pitching of the body during movement, and provide significant forwards propulsion of the driving leg during running (and walking although less so) (Lieberman *et al.* 2006).



**Figure 21:** Illustration depicting a human running, detailing a number features that aid in stabilising the body. Firstly marked in green and blue are the arms and legs, which swing in opposition to each other (left side of body marked in green, right in blue). This helps to counteract the force of the swinging legs, keeping the trunk stable. Swinging arms also help stabilise the head, by firing the trapezius muscle on the forwards leg side before heel strike, which links with the head via the nuchal ligament, keeping it upright. Finally the gluteus muscles of the pelvis provide forwards propulsion as well as countering side-to-side pitching of the hips.

### Thermoregulation

Running is metabolically costly, and produces a great deal of heat that must be expelled. Simply becoming bipedal might have been the first thermoregulatory adaptation of hominins, as it substantially reduces the surface area exposed to maximum solar radiation compared with a typical quadruped due to being tall and thin (Lieberman 2015). However as previously discussed there were

likely greater selective forces driving bipedalism (see the beginning of this review and the climbing section previously).

Sweating is a far more important mechanism that humans have evolved in order to quickly cool the body. This is made possible by mass multiplication and better neuronal control of eccrine sweat glands across the body's surface, plus almost entire loss of body hair (Carrier et al. 1984; Lieberman and Bramble 2007). In comparison with our closest cousin the chimpanzee, humans have at least 50% more eccrine glands across the bodies surface allowing significantly higher secretion of liquids- which is around 80 g/m<sup>2</sup>/h in chimpanzees, versus up to 884 g/m<sup>2</sup>/h in humans (Lieberman 2015). This mass multiplication seems to have come at the expense of apocrine glands, whose ancient function is to secrete certain lipids as an olfactory communication, and are now only found in the axillary and pubic regions in humans (Lieberman 2015). Sweating secretes water onto the surface of the skin, which in turn evaporates and cools the surface via convection (Lieberman 2015). Although effective this process is highly demanding on water and salt levels within the body, making excessive sweating potentially dangerous without adequate nutrition (Lieberman *et al.*, 2009). Being a sweating, hairless runner further improves the dissipation of heat via convection as you are moving through the air, something that cannot be said for thick-coated mammals, whose fur almost completely negates this affect (Carrier et al. 1984; Lieberman 2015).

Sweating on the face- which is often most excessive when exercising hard- cools the blood vessels beneath the surface of the skin, helping to cool the face (Bramble and Lieberman 2004; Lieberman 2015). Although more *in vivo* research is needed to prove this theory, it's thought that the body further utilises this cooled blood by using it to reduce the temperature of blood within the major carotid artery before it reaches the brain, a process known as cranial venous circulation (Bramble and Lieberman 2004; Lieberman 2015).

Apart from sweating, nasal cooling is another thermoregulatory mechanism that humans possess. This uses the inner portion of the nasal cavity to either warm or cool air to the bodies' core temperature before it reaches the lungs, while also adding moisture- a process that helps ensure that extreme temperature air that has been inhaled does not change body temperature (Lieberman 2015). Humans have uniquely capitalised on this cooling mechanism by developing a series of valve-like cartilage structures in the outer nose that generate turbulence at airflow, while also being the only mammal to transition to breathing orally during highly intense exercise, a behaviour that further dumps excess heat (Lieberman 2015).

## **The brain**

With the emergence of the genus *Homo* around 2mya brain size began to increase quite dramatically. Aiello and Wheeler (1995) have hypothesised that such an increase correlates with more complex foraging behaviours (perhaps involving running) and a higher quality of diet, thus increasing the available energy to grow a larger brain. They named this the 'expensive tissue hypothesis', as gut size (another metabolically costly tissue) seems to have decreased as brain size increased, probably due to reduced bulk and more rapid assimilation of their foods (Aiello and Wheeler 1995).

Mattson (2012) has linked the extensive encephalisation of hominins with endurance running, as a positive correlation between maximum metabolic rate and brain size has been recorded in many mammal species. Higher maximum levels of metabolism improve your ability to exercise for extended periods of time, as a greater amount of oxygen is reaching the working muscles. This link with the brain potentially works both ways, with the brain providing adaptive advantages for running, and running providing a strengthening response for the brain. The former is quite easy to understand, as hunting in a complex and potentially dangerous savannah environment would be made significantly more manageable with good cognitive abilities- for example being able to judge the age of animal tracks, estimating the distance needed to run for a scavenging opportunity, or keeping track of the weather so as not to get caught out in a storm (Mattson 2012). At the same time endurance activity strengthens the brain by stimulating the production of neurotrophic factors, improving the connections between synapses (ibid.). As the brain is the control centre of the body, this has a multitude of positive effects, including improved memory, decreased heart rate and insulin sensitivity- all of which further improve your ability to run (Mattson 2012).

Stimulation of the brain by running has been further explored by Sands and Sands (2009), who claim that running might have created some kind of 'horizontal awareness' in early savannah hominins, keeping them in touch with the intricacies of the environments they lived in. This stimulation might have been enhanced by the natural pain and reward system, something known as 'runners high'- a heightened sense of consciousness or euphoria that is experienced by athletes performing a wide range of different sports, but was first described in runners (Sands and Sands 2009). Such a high is caused by the release of neurochemicals such as endorphins which block pain receptors, a highly selectively advantageous trait for a Palaeolithic hominin, not just in enabling them to run for longer, but also heightening their awareness for when it really mattered, e.g. spotting an approaching predator or landing the killer throw while hunting (ibid.). Once again, just as with Mattson (2012), a positive feedback loop is created, where running provides adaptive advantages to the hominin brain by stimulating certain chemicals to release, which in turn enhances running ability due to reduced pain response, causing them to run more and begin the cycle once more (Sands and Sands 2009).

## Conclusions

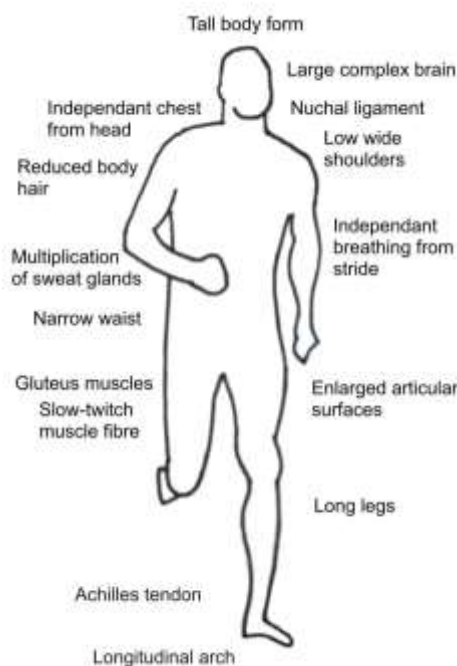
Table 2 and figure 22 below summarise the key physiological and anatomical features seen in hominins relating to running behaviour, as discussed within this review. The overall conclusions of this review are as follows:

- Endurance running capabilities developed within the genus *Homo*, either as a by-product of being a striding biped, a selectively advantageous hunting tactic, or likely a mixture of both.
- The theory of persistence hunting where by a human hunter could out-last a quadrupedal prey over a long distance, and its usefulness for scavenging already deceased animals provide viable solutions as to the selective advantage of endurance running.
- Due to the energetic penalty of becoming a biped (no forelimb locomotary contribution), a substantial range of physiological and anatomical features have developed in *Homo* to aid in efficient running.

- These adaptations relate to energetics (increasing the efficiency of running), skeletal strength (to resist the stresses and forces associated with running), stabilisation (ensuring the body remains erect), thermoregulation (keeping the bodies' core cool even during hard exertion) and some aspects of brain development.

**Table 2:** Summary table detailing the range of anatomical and physiological adaptations seen in humans that are geared towards the stresses of endurance running.

ER physiology/anatomy	Summary
Spring mechanism	Spring-like tendons utilise elastic energy, creating propulsion without muscular force, thus reducing metabolic cost
Long legs/ stride length	Long legs increase ground-contact time, reducing volume of muscles utilised at every step
Breathing rate	Breathing independently of stride means efficient air exchange regardless of speed or terrain
Slow-twitch muscle fibre	Slow-twitch muscles fibres are fatigue resistant performing at endurance levels
Enlarged articular surfaces	Help dissipate impact energy from the ground
Trunk stabilisation	Musculature of the trunk and pelvis provide stabilisation, stopping the upper body pitching forwards or to the side
Narrow waist	Allows the upper body to rotate independently of hips, helping facilitate arm swing, which counteracts the force of moving legs
Independent pectoral girdle and head	Further helps facilitate arm swing as above, while helping to keep the head stable
Low, wide shoulders	Aids arm swing by creating extra moving mass
Head stabilisation	Elastic linkage between the head, nuchal ligament and trapezius keeps the head stable
Reduced body hair	Increases convection rates, allowing heat to be readily lost
Sweat glands	Mass multiplication of sweat glands allows great amounts of heat to be lost via evapotranspiration, further enhanced by reduced body hair
Tall, narrow body form	Large body surface area to dissipate heat
Cranial venous circulation	Utilising blood that has been cooled by surface sweating of face to cool hot arterial blood before it reaches the brain
Nasal cooling	Using the inner portion of the nasal canal to cool air before it reaches the lungs
Mouth breathing	Increases airflow thus gaseous exchange
Large, complex brain	Enhances navigation due to improved memory recall, among many benefits



**Figure 22:** Illustration depicting a human running, detailing the range of anatomical and physiological adaptations seen in humans that are geared towards the stresses of endurance running.

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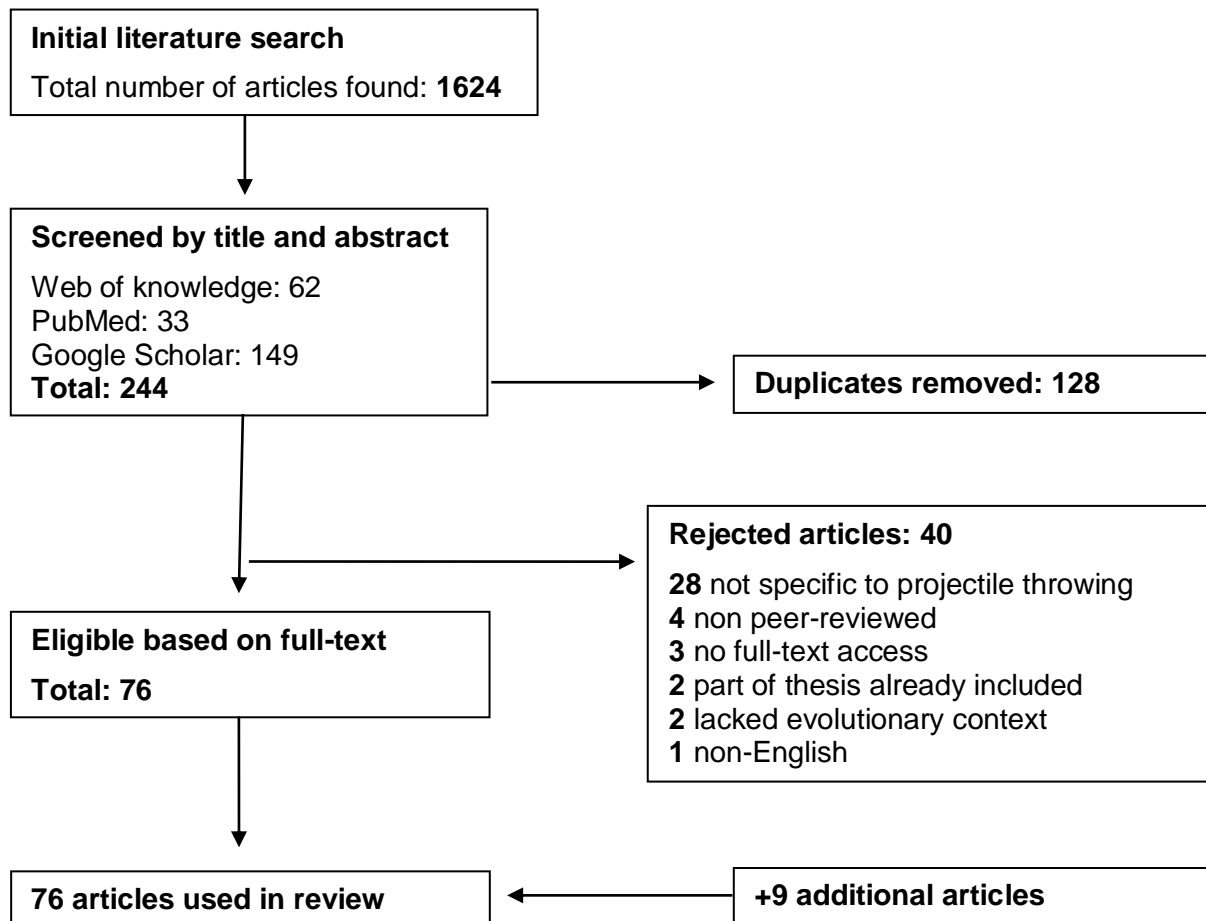
## **Section 4- Projectile throwing**

### **Overview**

This review concerns the evolution of thrown projectiles among hominids. It begins by introducing the species and time periods involved, both of extinct hominins and wider hominids, suggesting why using projectiles has been such a valuable behaviour in our ancestry. The evolution of projectiles themselves is then considered in depth, from stones to spears to bows, including a section covering the plethora of literature considering the likely throwing ability of the Neanderthals. Finally the physiology, anatomy and biomechanics of throwing is explored, beginning with sections explaining the importance of handedness and sexual dimorphism for this behaviour, before ideal specific morphologies for projectile throwing are reviewed. The overall aim of this review is to explore the evolutionary origin and usefulness of an overhead throwing motion among hominids, and to determine what features of the body may have developed in order to most efficiently perform this behaviour. Figure 23 below summarises the steps undertaken to acquire the literature base for this section. The initial search of the literature for projectile throwing related papers identified 1624 articles, of which 244 were screened by title and abstract. Once duplicates were removed (128) this left 116 articles to check for eligibility. A total of 40 articles were rejected: 28 did not specifically concern projectile throwing, 4 were not peer-reviewed works, 3 could not gain full-text access, 2 were part of a research thesis already included, 2 lacked evolutionary context and one didn't have an English translation. This left a total of 76 eligible full-text articles that are used in this review.

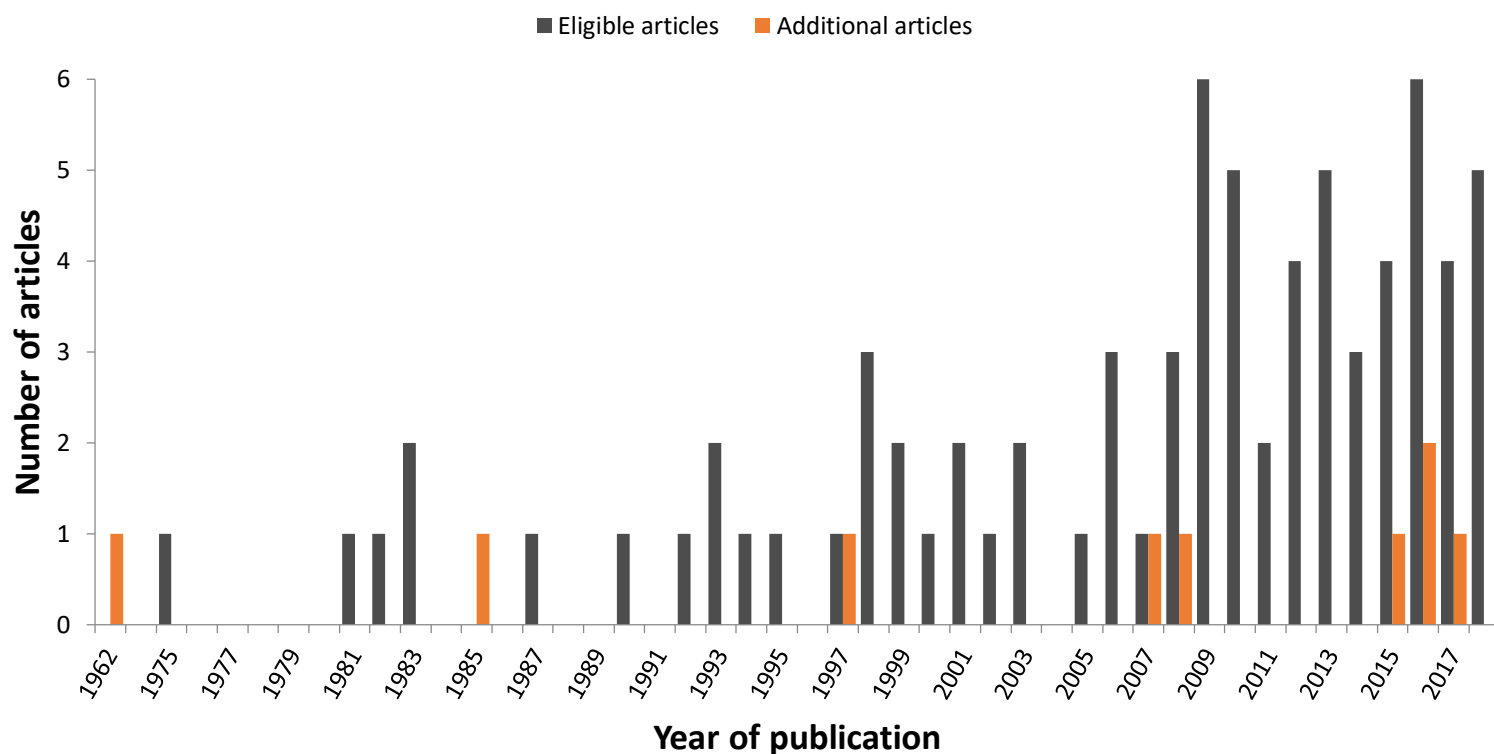
Towards the end of the writing process an additional 9 articles were added to provide further evidence within specific topics that was seemingly lacking from the systematic search. These were sourced via targeted searching of Web of knowledge, PubMed and/or Google Scholar. Two of these papers were the original articles uncovering and describing the findings of the Lomekwian and Oldowan tools, thus providing credit to the original authors. Further articles concerned climate change and Neanderthal extinction (2), projectile weapon technology among the Hadza hunter-gatherers (2), more sophisticated projectile weapons such as the crossbow in recent times (1), the biomechanics of a modern day baseball pitcher (1), and finally the biomechanics of the human hand (1).

As demonstrated by figure 24 below, with the exception of a single article published in 1962, the included literature was published across a broad timescale from 1975 to 2018. Although the period from 1975 to 2005 produced a fair quantity of papers, most were published within the last 15 years since 2006.



**Figure 23:** Flow diagram illustrating the steps undertaken to acquire the literature base for the projectile throwing section of this thesis. Eligibility of articles following a full-text read through was based on specific criteria stated within the methods section previously in this thesis. Additional articles were sourced from Web of knowledge, PubMed or Google Scholar where gaps in the research base were revealed, as outlined in the introductory text above.





**Figure 24:** Graph showing the range of literature by year of publication that was sourced for the throwing section of this thesis. Literature was sourced in accordance to the methods section previously, as diagrammed by figure 23 above. Eligible articles are shown in grey, representing the core relevant literature sourced by the systematic searching process. Additional articles are shown in orange, representing the further literature sourced to provide extra detail or reference at the end of the writing process. The year of publication of the earliest article (1962) considerably predated the others, and as such has been placed on the far left of the scale, with a non-linear gap to the others. The remaining articles range along a linear scale from 1975 to 2018.

## Background

The transition to bipedalism freed up the forelimbs of hominins, allowing them to perform more complex manipulatory tasks and evolve specific upper body adaptations without the constraints of locomotion (Lombardo and Deaner 2018a). Indeed throwing itself has been proposed as a selective force driving bipedalism, however with little if any archaeological evidence of throwing such as throwing favoured morphology (discussed later) or preserved projectiles, at this transition this remains speculative (Knüsel 1992). Certainly *Australopithecus* had some anatomical features that would enable somewhat accurate throwing, such as a hand that could hold a forceful precision grip, however their other anatomy implies that throwing wouldn't have been a common activity for them (Isaac 1987; Lombard 2015). Forceful over-arm throwing with the potential to cause lethal damage evolved later, perhaps with the emergence of *Homo erectus* (~2mya) who is the first hominin to display some modern human like adaptations for throwing, although the orientation of the shoulder- specifically the glenoid fossa- does not seem indicative of forceful high speed throwing (Roach et al. 2013; Lombardo and Deaner 2018a). Nonetheless there must have been some selective advantages to efficient throwing as far back as *Homo erectus*, otherwise these traits would less-likely have evolved. There are two major possibilities: that throwing was useful in warfare/ agonistic interaction, or that throwing was useful for hunting and scavenging, although it's most probable that both are true (Lombardo and Deaner 2018a). In both warfare and hunting projectiles offer distinct advantages over hand weaponry, most notably enabling striking at a distance which offers both the element of surprise and reduced risk of injury to the thrower through prey/ opponent retaliation (Lombardo and Deaner 2018a). Of course other behaviours carried out by hominins at this time such as endurance running will have also influenced their morphology, which will be considered in the discussion of this thesis.

Besides the fashioning of stone tools (although it's linked) throwing may well have been the first major complex skill for hominins to acquire and begin to perfect, beginning the transition from an ecology and hierarchy based on brute force and power to one based on skill (Darlington 1975; Bingham 1999). This would make it the first 'social equaliser', favouring the selection of cooperation over individual force, therefore perhaps also marking the beginnings of altruism and group selection (Darlington 1975; Bingham 1999). Similarly, the significance of projectiles in aiding the geographical expansion of humans is potentially extensive. *Homo sapiens* first expanded from Africa around 45ka, and evidence from the Levant (the Europe-Africa land bridge) suggests that projectile technology was important in aiding this dispersal (Shea and Sisk 2010). Projectiles broadened their dietary niche (useful for survival in the colder European climates), helping make early humans more ecologically versatile and true generalists of the animal kingdom, owing to our ability to colonise an array of very different environments (Shea and Sisk 2010; Sisk and Shea 2011).

## Non-human throwing

A variety of different primate species engage in habitual throwing. Great apes such orang-utans and chimpanzees routinely toss branches or rocks with fair accuracy, normally as a display of power or aggression, but rarely with any lethal force (Knüsel 1992; Kühl et al. 2016; Lombardo and Deaner 2018a). Kühl *et al.* (2016) have reported interesting findings of chimpanzees cumulatively throwing

rocks at particular trees, creating piles beneath them that resemble ritualistic sites, although their purpose is unknown.

Smaller primates are perhaps better known for their throwing behaviour. Japanese macaques are well known to habitually throw rocks and other objects, almost always underarm and with little force or accuracy, although their intention is unknown (Leca et al. 2008). Capuchin monkeys have easily attracted the greatest research interest. These species have been recorded throwing during their proceptive phase (females at males), as a means of food sharing between individuals and throwing at humans and food buckets in experimental studies (Westergaard and Suomi 1994; Westergaard et al. 1998; Cleveland et al. 2003; Falótico and Ottoni 2013). Just as in humans, a throwing hand bias almost always exists in capuchin monkeys, although it's highly variable between individuals and not predominantly right handed (Westergaard and Suomi 1994; Westergaard and Suomi 1995). In terms of accuracy and sex, and distinct from what we see in humans male capuchins are not reportedly any more accurate at throwing than females (Westergaard et al. 2000; Watson 2001).

Despite the throwing behaviour of these species, none-other than humans throw with our form, accuracy and speed, or as a means of dispatching prey, making these traits uniquely human (Lombardo and Deaner 2018a). This therefore suggests that selection for throwing ability has been far more important in humans than any other primate (Watson 2001; Lombardo and Deaner 2018a). Furthermore, much has been speculated about hominin evolution by studying throwing in other primates. For instance the brain size, general physiological form and environmental niche of chimpanzees and orang-utans represents the closest extant comparison with the Australopithecines, letting us speculate that they probably had a similar throwing ability and style (Knüsel 1992). On the basis of stone flaking ability in capuchins and archaeological findings, it's also been suggested that *Homo habilis* was able to throw fairly well- including adjusting to specific target demands and projectile weight- although certainly not with the same deadly ability of later *Homo* species (Westergaard and Suomi 1995).

## **The evolution of projectiles**

### **Stones**

Hominids have likely been tossing stones and branches for millions of years, as is predictable from a range of behavioural studies like the ones above documenting this behaviour in closely related primates. The use of stones as weapons however is unique to later hominins, and marked the beginning of the evolution of projectile technology. A stone can be a deadly projectile weapon; a 500g stone thrown by a proficient baseball player equals the kind of force produced by a revolver pistol (~200Nm), demonstrating this point (Cannell 2002). The weight of a potential throwing stone is important, as humans seem to possess an innate ability to select the perfect projectile. Studies have found a weight of around 500g and 320g for males and females respectively to be what feels most 'right' to us, and suggest that given the choice of a range of stones humans will most often choose these weights (Cannell 2002; Zhu and Bingham 2008). Zhu and Bingham (2011) have found humans to exhibit a 'size-weight illusion', where by a person will nearly always perceive that a larger item (in raw size) is heavier than a smaller one, even when the masses are actually the same. This illusion

might be functional, representing humans' innate desire to select items that are optimised for throwing distance and power, as even though the items are the same mass, the smaller one would be easier to throw (Zhu and Bingham 2011).

Such unconscious ability even in modern humans that have no need to throw further lends support to the suggestion that this activity is of evolutionary significance for hominins. Wilson *et al.* (2016) reports findings of perfectly weighted spherical stones (spheroids) that are of a mass so as to inflict maximal damage while still being physically throw-able. These 'spheroids' are found at multiple African and Asian sites dating back as far as 1.8mya, perhaps representing some of the first projectile weapons to be selected and stored by hominins for future hunting (Zhu *et al.* 2008; Wilson *et al.* 2016). Such simple projectiles are also widely present in the modern ethnographic record, with stones and compacted balls of mud frequently being used by indigenous islanders such as the Polynesians during the colonial age to ambush and kill foreign explorers (Isaac 1987; Lombardo and Deaner 2018a). Such records show the usefulness of throw-able stones.

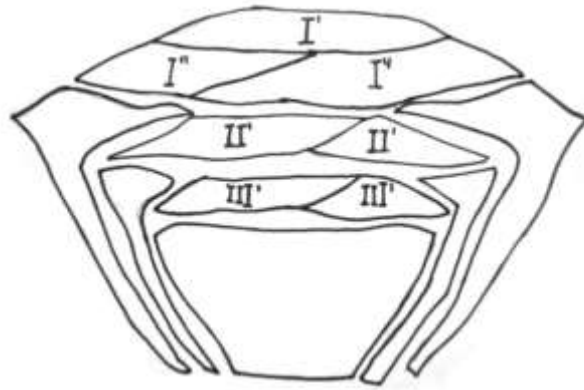
## **Spears**

The earliest throwing spears currently known date from around 400ka, found in Schöningen, Germany (Thieme 1997; Cannell 2002; Villa and Soriano 2010; Schoch *et al.* 2015). Nine spruce or pine spears were found at this site, ranging from 1.8- 2.5m in length, fashioned from old trees (~50-60 years old) and heavily worked to remove the bark, cut out knots and sharpen the ends (Schoch *et al.* 2015). The weapons vary in form, although three of the most obvious spears have been tooled so that there is greater weight towards the point, mimicking a modern javelin (Thieme 1997). The sophistication of these weapons' design has been demonstrated in experimental studies, where they have been shown to be well balanced, travelling up to 35m and with significant close range penetration (Schoch *et al.* 2015).

Wooden spears were a start for the fashioning of projectiles, but they would have lacked damage at range. The shaping of stone, flint, bone and antler fragments which could be hafted onto wooden shafts made a significantly more deadly weapon, as they made a larger entry wound thus improving the stopping power of the spear (Lenoir and Villa 2006; Villa and Soriano 2010). Such points are frequently present by around 200ka in the fossil record, although much debate exists as to whether they were truly thrown or simple hand-held cutting and scraping tools (Villa and Soriano 2010). Even older points have been reported, for instance from the Ethiopian Rift dating from >279ka, and micro-fracture and morphometric analysis confirms that many of them were thrown, suggesting that the careful knapping and shaping of projectile spear points is not a uniquely human trait as previously assumed (Sahle *et al.* 2013).

Indeed, stone tooling has a rich history in hominins, with current archaeological findings dating back as far as 3.3mya with the Lomekwian finds from Kenya (Harmand *et al.* 2015), and the better known Oldowan tools of Ethiopia (2.5mya, Semaw *et al.* 1997). These were simple scraping and cutting stones produced by striking a round pebble against a thinner flake and gradually rotating to remove cone-shaped chunks, producing a sharpened edge (Ambrose 2001). Acheulean technology (1.5mya) brought about larger more sophisticated designs, such as 10cm handaxes, with bilateral symmetry

and standardisation in shape indicating good cognitive skill in the maker (Ambrose 2001). Towards the end of the Acheulean technological period, the Levallois core technique (which appeared ~0.5mya) revolutionised point production, enabling multiple flakes to be gained from a single stone core with careful striking, reducing waste and improving productivity, demonstrating even higher cognitive ability (Ambrose 2001- figure 25).



**Figure 25:** Illustration depicting the cross section of a rock cracked apart using the Levallois core technique. By doing so multiple flakes of successively smaller sizes could be produced from a single piece of rock, improving productivity and reducing waste. Roman numerals mark each usable flake, with the top layer consisting of three flakes, and the next two consisting of two. Figure produced using information from Ambrose (2001).

Distinguishing between thrusting and projectile points in the archaeological record is of importance to determining what weapons the hominins present were using. Micro-fracture and use-wear analysis are two key techniques used to do this, relying on the fact that spear points will change in form with use, wearing, scarring and possibly breaking at differential rates and/or locations depending on the delivery of the weapon (Rots and Plisson 2014; Iovita et al. 2016). This information can be gained by recreating lithic points en masse, and firing them at comparable velocities to the proposed historical weapon system at an experimental prey item, before analysing any change in the point (Iovita et al. 2016; Rios-Garaizar 2016). Morphometric analysis is normally used in tandem with a variety of other metrics to determine a tool's use, such as the width, penetrating angle, tip cross-sectional area, weight and thickness, before a comparison with archives of previous findings (Lenoir and Villa 2006).

## Neanderthals

The hominin origin of the first throwing spears is much debated, especially as to whether the Neanderthals exhibited this behaviour- a key part of the projectile throwing literature. The Schöningen spears are thought to have been wielded by *Homo heidelbergensis*, demonstrating that Neanderthals' direct ancestor clearly had the capacity to produce sophisticated weaponry (Shea and Sisk 2010). There is also plenty of archaeological evidence for Neanderthals hafting large robust stone-tipped spears, showing that they had a need to hunt meat in the colder environments of Europe, and had the intelligence to do so (Shea and Sisk 2010). There is even evidence suggesting they were hunting very large dangerous prey, the sort that might incentivise developing projectile weaponry so as not to risk getting too close (Shea 2009). All this aside, direct evidence of Neanderthal throwing is weak. It's

possible that the reason for this was anatomical or physiological, that is that either the shorter arms and generally stockier build of Neanderthals was non-adaptive for throwing, or their higher calorific requirements made laborious hafting of sophisticated weaponry impossible, instead favouring obtaining quicker simpler meals (Shea and Sisk 2010). Perhaps the cost-benefit calculus for Neanderthals hunting large game simply did not add up with the inclusion of projectile technology, and their robust thrusting spears were a means of improved meal reliability (Shea 2006; Shea and Sisk 2010). Anatomically the gleno-humeral joint (where the humerus meets the shoulder) of Neanderthals has been described as long, narrow and high, generally thought to be non-adaptive to the high reaction forces of over-arm throwing, and in opposition to the wide glenoid form of humans (Churchill and Trinkaus 1990; Churchill and Rhodes 2009; Rodriguez-Perez et al. 2018). This would potentially make throwing injurious for Neanderthals, as discussed in greater depth in the 'throwing adaption' section below. In light of such evidence, the traditional belief is that Neanderthals did not habitually throw (Rhodes and Churchill 2009; Rios-Garaizar 2016).

However, with greater research interest the evidence base is growing, and although the physical and mental capabilities of Neanderthals are much argued, a growing body of thought is now suggesting that they were more advanced than they've been credited for in the past. Hardy *et al.* (2013) have reported complex foraging and hafting behaviour in Neanderthals from archaeological sites in south-eastern France, including the findings of a collection of potential projectile spear-points. These points are generally thin (~100mm<sup>2</sup> tip cross-sectional area), thus too fragile to have been used as thrusting spears, and many bear the hallmarks of hafting and re-touching of their edges suggesting long use-lives (Hardy et al. 2013). Lazuén (2012) report a similar cache of potential projectile points in northern Spain, at a time well before the colonisation of humans (>150ka), suggesting Neanderthal use. In addition, Neanderthals hafting technology was seemingly highly sophisticated, utilising fire to melt balls of sandy bitumen to form a glue, or intense heating of birch bark (<340°) under anaerobic conditions to produce pitch- a powerful adhesive (Villa and Soriano 2010). The argument that Neanderthal thrusting spears would have been too heavy to throw has been easily countered, as Roman and Greek soldiers are known to have thrown javelins three times their weight (2-4kg) with lethal effect at 15m (Lenoir and Villa 2006; Villa and Soriano 2010). Neanderthals were certainly robustly built, thus there is no reason to believe that they couldn't physically match a Roman soldier, especially when going hungry was the alternative (Lenoir and Villa 2006). At an experimental level, Neanderthal spear points such as these have been shown to be quite effective at close range (>10m), although with great variability depending on the length of the shaft and weight and cross section of the point (Rios-Garaizar 2016). Nonetheless, these lines of evidence suggest a greater utilisation of throwing by Neanderthals than previously thought.

The adoption of projectile weaponry to some degree by Neanderthals seems logical. Failure to do so would have had competitive implications, particularly with the expanding *Homo sapiens* from Africa, who would have been able to exploit a generally larger dietary niche, while also possessing a significant lethal advantage in any aggressive encounter (Shea 2006; Shea 2009; Shea and Sisk 2010). Therefore, although projectile weaponry- or its lack- may well have contributed to the demise of the Neanderthals, evidence of projectile points in this species suggests it may not have been very

significant, or perhaps it was just one of several factors. Extreme climatic shifts within Neanderthals' European habitat (like the most recent 'ice age'- ~115 to ~11ka) were probably also factors, forcing them south towards their final Iberian strongholds (Jiménez-Espejo et al. 2007). Neanderthals may have therefore been one of the many large mammals of Pleistocene Europe to first become bottlenecked within the warmer southern climates before going extinct during this period of glaciation, as also happened to the hippopotamus, straight-tusked elephant and rhino (Stewart 2008).

### **The atlatl and bow**

Projectile technology has evolved alongside hominins, giving rise to what are known as 'complex projectiles'- essentially utilising another tool to propel a projectile with more leverage or elasticity, reducing the physical demand on the user. The spearthrower or atlatl is a short length of wood, notched at one end to take a long wooden dart. They extend the leverage possible from the arm by creating a fulcrum with the wrist, allowing greater distance, accuracy, propulsion and thus penetration of a projectile without expending extra force (Frayser 1981; Peterson 1998; Maki 2013). They're often associated with a transition towards hunting much smaller prey, yet at a truly impressive distance of up to 40metres with accuracy (Churchill 1993; Maki 2013). Interestingly, the atlatl was the favoured weapon of the Australian aborigines, who never adopted the bow and arrow despite it being known in Australia, as is evident from their rich tradition of rock paintings (Walsh and Morwood 1999; Grund 2017). The earliest atlatl is known from southern France, dating somewhere between 19 and 17ka (Lenoir and Villa 2006).

The bow and arrow replaced the atlatl at multiple time scales across the world, and no general consensus on a date exists. Although micro points found in Africa might indicate an origin of bow technology as early as 70ka, robust evidence from Stellmoor Germany provides the earliest known direct findings at 11ka (Grund 2017; Pontzer et al. 2017). This weapon is of simple construction, a length of wood (often yew in Europe, or *Dombeya kirkii* or *Grewia bicolor* in Africa) slightly bent tip to tip with string or a similar fine strong material such as mammal nuchal ligament or sinew, utilising the elastic properties of the wood when the string is drawn and released to project a short fletched dart (an arrow) (Pontzer et al. 2017). The bow and arrow is a highly flexible weapon with key advantages over the throwing spear and atlatl. It is useful for dispatching prey of various sizes from a variety of different postures including crouched, as arrows can be fired with superior distance and accuracy without significant motion, and in quick succession improving success rates should the first fail to hit its mark (Frayser 1981; Churchill 1993; Hughes 1998; Peterson 1998).

These are distinct advantages offered by the bow over the obligate upright athletic stance of throwing. Maximum distance for a bow and arrow shot is approximately 185m, however accurate shooting distance for the Palaeolithic sits at around 25metres (these were short lower-powered bows), considerably less than with the atlatl, although generally with far greater accuracy due to aiming and firing from a fixed position (Churchill 1993; Maki 2013). Pontzer *et al.* (2017) found that archers among the Hadza hunter-gatherers possess formidable bows, with draw weights (power required to pull the string back) higher than those used by Olympic archers, enabling lethal hunting at distances up to 50m. Therefore although the Hadza are not Palaeolithic hunter-gatherers, as a good proxy they

demonstrate the potential the bow and arrow would have had for improved hunting success. The atlatl also retained some advantages, such as possessing greater penetrating ability, which led to its retention for warfare in certain historical indigenous populations, such as the Aztecs of South America (Churchill 1993). Furthermore, the atlatl has been shown to be easier to learn than the bow, thus more accessible to younger individuals, potentially making it favourable in certain demographics (Grund 2017). No matter, bow and arrow technology- especially in terms of range and penetration with larger higher powered bows, improved steadily throughout history to become a ubiquitous weapon of war (Gorman 2016). The evolution of the bow culminated with more complex designs such as recurve bows and crossbows, helping to forge many major civilisations all the way up until the invention of gunpowder (Gorman 2016).

Complex projectiles likely helped to further expand the dietary niche of humans, and began the gradual decline of the throwing spear. Despite this, throwing behaviour is known to have persisted for a long time, for instance the Natufian people of Jordan and Palestine were still habitually throwing some 11,000 years ago based on archaeological data (Peterson 1998). There may be good reason for this, as heavier throwing spears can sometimes inflict greater damage to a thick-skinned animal, as has been noted by hunters in the Kalahari (Hughes 1998). In more recent times, the javelin has been used globally in warfare including by formidable civilisations such as the Romans and Greeks, and was retained as a weapon of war well into medieval times (Villa and Soriano 2010). However in the modern day, ethnographic records of recent hunter gatherer groups throwing are few, suggesting that it is now a rare behaviour (Churchill 1993).

## **The physiology, anatomy and biomechanics of throwing**

### **Handedness**

Effective and efficient throwing requires practice, as does a variety of manipulative tasks such as fashioning tools, which in turn strengthens thus adapting the musculature (and the coordination of the brain) to the particular activity (Lombardo and Deaner 2018a). A distinct preferred handedness has developed in humans, which most often favours the right arm (~90%), and as such this arm is generally stronger and more robust than the left (Peterson 1998; Cannell 2002; Sparacello et al. 2017). As overhead throwing specifically requires a single arm grasping the projectile (see below for a description of throwing biomechanics), it's reasonable to assume that throwing within human evolution has contributed to this handedness (Churchill and Rhodes 2009; Lombardo and Deaner 2018a). Plenty of evidence for dominant handedness in the fossil record exists, for instance Nariokotome boy- the famous *Homo erectus* skeleton (~1.6mya) had a longer right ulna and clavicle, both of which increase leverage during over arm throwing, suggesting right handedness (Cannell 2002). Sparacello et al. (2017) analysed a sample of Late-Pleistocene forelimbs for asymmetry (>100 individuals), finding that 83% had stronger right humeri compared with their left. Further evidence can be gleaned from the presence of musculoskeletal stress markers or 'enthesopathies' at muscle attachment sites of the upper limbs, which are more often present in the right limb of prehistoric samples (Villotte et al. 2010). In modern times this dominant preference has been shown in habitual throwing athletes, such as cricketers who display greater robusticity and rigidity in their throwing arm compared with the other



(Shaw and Stock 2009). Sládek *et al.* (2016) have synthesised the shifts in humeral asymmetry (both length and breadth) since the Pleistocene, reporting a general reduction in asymmetry through time, reflecting the changes in hunting technology (less spear-throwing and more use of bow and arrow) and later the rise of agriculture. Reduced bilateral activity over time has helped even out the humeral strength in each arm, so that asymmetry is less pronounced in modern humans (Sládek *et al.* 2016). Although generally more pronounced in males, right-hand preference is true of humans regardless of sex, and a key theory explaining it is that of infant carrying. Human females- as well as those of a range of other primates- most often carry their infants in their left arm, closest to the heart and left breast which is thought to offer more milk, therefore leaving only their right arm free (Hopkins *et al.* 1993; Cannell 2002). Furthermore it might also reflect specialisation of the left hemisphere of the brain for motor skills and cognitive ability, explaining why a mother would choose to cradle with her left arm, as she has better motor control of the right (Hopkins *et al.* 2005). Alternatively, the hunting capacity of females may have been overlooked, as has been recorded in several ethnographical samples, such as in hunter-gatherer groups of higher-latitudes where acquiring game is particularly difficult, or among the Agta peoples of the Philippines (Sparacello *et al.* 2017). Although it is unlikely to have been wide-spread, hunting in females may have influenced their right hand bias just as in males. Of course other regular activities involving reaching and hand manipulation, including small tool use and foraging, will likely have further influenced this handedness bias (Cavanagh *et al.* 2016). Throwing is just one of many behaviours that exhibit right-hand bias in hominids.

### **Sexual dimorphism**

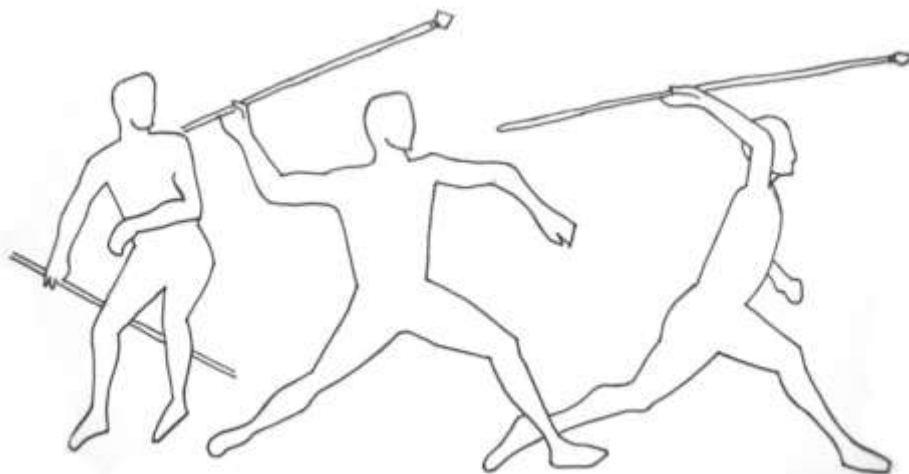
Due to the link with warfare and hunting, and a general bias in ethnographical data for males more commonly performing these activities, projectile throwing is often cited as a particularly male adaptation (see refs following). Males generally have longer arms and broader shoulders than females, creating greater leverage for propulsion, and their muscle mass is significantly higher, especially of the upper body which is not only bigger but also contains a greater proportion of fast-twitch type 1 muscle fibres (Lombardo and Deaner 2018b). These physiological facts help males throw with superior speed and accuracy than females, and this fact remains constant regardless of training, environment or culture, suggesting it reflects an innate capability (Jardine and Martin, 1983; Young, 2009; Lombardo and Deaner, 2018b). This is demonstrated in the development of children, who regardless of situation still develop the specific motor sequencing of over-arm throwing, and who by their late teens have a movement pattern very comparable to an elite thrower (Young 2009). During this developmental process, males and females progress at the same rate, but females plateau sooner at a lower level than males (Young 2009). Thomas *et al.* (2010) have found that Australian aboriginal girls are closer in their throwing ability to their male counterparts than US girls, suggesting that cultural influence, especially within less-Westernised cultures, can narrow the gap between genders. This seems intuitive as females in more traditional cultures are certainly more likely to throw than in western countries. Regardless, this sexual dimorphism overall is presumably the result of greater selection pressures on males as hunting and warfare have always been male dominated activities. This means males have simply had more reason to throw throughout hominin

evolution, thus more reason for positive selection for their throwing traits than occurs in females (Young 2009; Lombardo and Deaner 2018b).

### Throwing adaptations

Humans are excellent throwers, with Dharmadhikari and Chatterjee (2018) finding that even compared with 20,000 optimised robots, the human arm alone (or an anthropomorphic digital version of one) fell consistently at the 96<sup>th</sup> percentile, demonstrating great proficiency of the throwing motion. The mechanics of throwing consist of a launch, flight and penetration phase (Hughes 1998). The latter two phases are taken care of by projectile design- many of the things discussed previously such as the weight and length of the shaft of a spear, or the penetrating ability of the hafted stone point. The launch phase however is purely athletic, relying on the practiced technique and physical form of the thrower.

This launch phase is known from extensive studies of baseball pitchers and consists of six stages, for great detail see Maki (2013). Firstly the thrower 'winds up' shifting their weight back on the throwing side, then they stride forwards with their non-throwing-side leg, cocking their arm back to full extension, where it accelerates forwards in unison to their forwards twisting trunk to maximum reach before release of the projectile, followed by full body deceleration of the forwards momentum (Young 2009; Maki 2013- figure 26). Such a complex series of movements requires great practice and biomechanical optimisation, which is explored in this section.



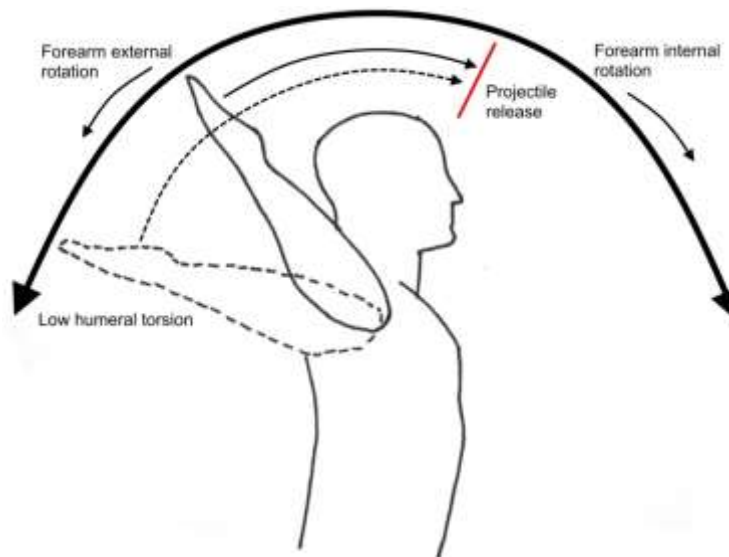
**Figure 26:** Illustration depicting a human throwing as three successive phases. First the wind up (far left figure), twisting the weight back on the throwing side, followed by the forwards stride of the non-throwing side leg, lifting the projectile up and back culminating in full extension of the forearm (far right image) before whipping the arm forwards in unison a twisting trunk to release the projectile. Figure produced using information from Young (2009)

### The shoulder

Due to the very nature of over-arm throwing, the shoulder is a highly important region of the body and thus has seen much modification to aid in this activity. The length of the clavicle is often cited as a key contributor to throwing performance, with longer clavicles being advantageous as they provide greater leverage between the pectoral girdle and the arm, which allows you to throw further and faster without expending extra force (Knüsel 1992; Maki 2013). The *Homo erectus* skeleton of Nariokotome boy has

a relatively short clavicle, which sparked the debate on this morphological feature, with some stating that he must have had an anteriorly positioned shoulder and therefore poor throwing performance (Larson, 2007, 2009; Roach and Richmond, 2015a). However short clavicles are seen today in certain heat-adapted African populations such as the Nilotic peoples of Kenya, and within the Daasanach tribe of this region there has been found to be no significant relationship between clavicle length and throwing speed (Roach and Richmond, 2015a). Therefore there are clearly more influences on throwing proficiency than clavicle length alone.

Humeral torsion describes the positional difference between the articular surface of the humeral head and the axis of the elbow, and is generally lower in the dominant arm of proficient throwers, enabling greater external rotation of the elbow by as much as 20° (Rhodes and Churchill 2009; Roach et al. 2012; Maki 2013; Roach et al. 2013; Kuhn 2016- figure 27). A trade-off exists where by decreased torsion improves external rotation while reducing internal rotation, and visa-versa (Roach et al. 2012). More external rotation allows the hand (and projectile) to be further behind the body during the 'cocking' phase, thus generating more elastic energy as it is whipped forwards (Roach et al. 2013- figure 27). This sudden internal acceleration of the humerus occurs staggeringly fast- with record velocities as high as 9000degrees per second- and as such is the fastest motion that the human body can produce (Pappas et al. 1985; Roach et al. 2013). Ontogenetically, humeral torsion begins very low and increases throughout childhood and adolescence until full skeletal development, where it stabilises (Roach et al. 2012). As such there is likely a relationship between habitual throwing during childhood and lower humeral torsion as an adult (Rhodes and Churchill 2009).



**Figure 27:** Illustration depicting a human with their arm aloft and forearm pointing towards the sky. It demonstrates how having a larger degree of forearm external rotation- known as having low humeral torsion- is useful for projectile throwing as it enables the forearm to extend further behind the body, thus creating a longer throwing arch to apply force and extra elastic energy before release. Figure adapted from Roach et al. (2013).

The glenohumeral joint is the junction between the humerus of the upper arm and the scapular, and is significantly more laterally orientated (lower and to the side) in humans than other primates (Maki 2013; Roach et al. 2013). Lower orientation of this joint enables the pectoralis major muscle of the

chest to contract along the same axis as the rotation of the trunk during throwing, maximising potential propulsion (Roach et al. 2013). This is made possible by the tall mobile waist of humans, which is decoupled from the shoulders, allowing a good range of twisting motion and the utilisation of the large muscles of the trunk (see next section) (Roach et al. 2013). The glenoid of humans is also relatively wide and pear shaped, in order to maximise possible external rotation of the forearm, and to resist the considerable transverse forces that are inflicted upon this joint during throwing (~400N), and thus prevent injury and/or delay the onset of osteoarthritis (Churchill and Rhodes 2009; Maki 2013; Kuhn 2016).

*Homo erectus* was the first hominin to display lateralised shoulders, along with very low humeral torsion (Roach and Richmond, 2015b). Although Larson (2007, 2009) has argued that this low torsion will have modified the orientation of the shoulder (more anteriorly, as mentioned) perhaps inhibiting manipulatory tool use, Roach and Richmond (2015b) have proved by looking at throwing athletes today that lateralised shoulders, low dominant-arm humeral torsion and normal manipulative abilities can all occur together, lending evidence to modern human like shoulders in *Homo erectus*.

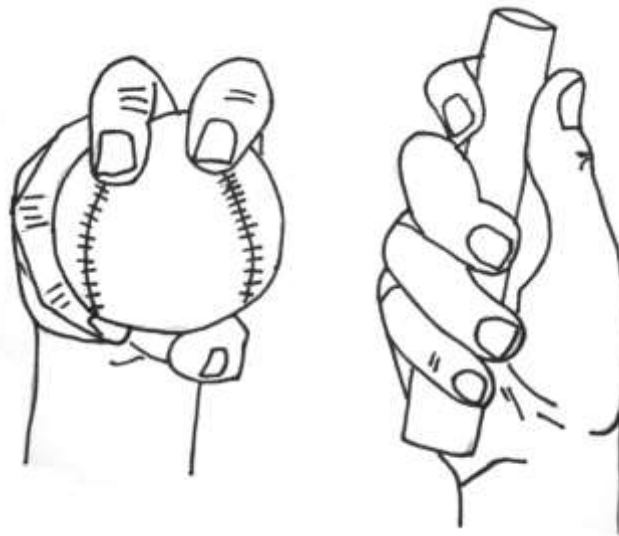
### **The trunk and hips**

As mentioned, humans possess a tall and mobile trunk (the 'torso' of the body between shoulders and legs), which is the powerhouse of the throwing motion. The muscles of hip rotation such as gluteus medius, minimus and maximus, tensor fasciae lata and piriformis (among others) rotate the body back on the throwing side during the cocking phase (Roach and Lieberman 2014). This rotation indirectly loads the elasticity of several muscle groups. First the hips rotate forwards with the trunk lagging behind, generating elastic energy in the abdominals, which in turn thrusts the trunk forwards with the arm lagging, loading the elasticity of the pectorals of the chest (Serrien and Baeyens 2017). Such sequencing of movements to utilise the elastic potential of the body enables greater power generation in throwing. In an experimental situation utilising braces to restrict movement, the musculature of the hips has been shown to produce almost all (~90%) of the power required to throw, and if immobilised causes a reduction in elastic potential upstream in the shoulders and arms (Roach and Lieberman 2014). Power from the legs pushing off from the ground in the wind-up and stride phases of throwing has also been shown to contribute to throwing velocity, with bigger legs and longer stride length correlating with more forceful throwing (Maki 2013).

### **The hand**

The human hand possesses notable advantages for throwing over that of most other typical primates. Where a chimpanzee hand has long curved fingers and a short thumb, humans have developed a much longer and more muscular thumb, in combination with shorter straight fingers and broad distal pads (Young 2003). Phalanx rotation is also improved in humans, allowing each finger to pitch inwards towards the thumb, creating two enhanced human grips- a precision grip and a power grip- first described and diagrammed by Napier (1962). The precision grip consists of a pincer movement between the index, middle finger and the thumb, allowing one to hold a ball-sized object carefully away from the palm (Young 2003; Wolfe et al. 2006; Rohde et al. 2010- figure 28). The power grip

utilises all digits to fully grasp an object towards the palm- as one might hold a club or spear- notably aided by the squeezing action of the thumb generating a firm grip (Young 2003; Wolfe et al. 2006; Rohde et al. 2010- figure 28). These two grips are probably pronounced only in the genus *Homo*- although they certainly began evolving in *Australopithecus*- and would have enabled hominins to carry out more complex manipulatory tasks, including the fashioning and hafting of spears as well as projectile throwing (Wolfe et al. 2006). Over-arm throwing requires a precision grip, although with enough 'squeeze' to maintain hold of the projectile during rapid acceleration of the arm before release (Young 2003). As well as squeezing, humans have impressive neurological control of their fingers, able to subtly alter the abduction of the thumb and extension of the fingers just before release to finalise the trajectory of the projectile (Young 2003).



**Figure 28:** Illustration depicting two human hands performing two distinct grip types. The left hand is a precision grip, where a relatively small object such as a tennis ball is held away from the palm using a pincer-like movement between the thumb, fore and middle fingers. This allows dexterity, useful in the evolution of humans for making tools and clothes, or playing ball games in the modern day. The right hand is a power grip, holding a potentially large object into the palm utilising all four fingers and the thumb to fully squeeze. The thumb can either rest in line with the object (as above) for a looser grip, or fully wrap around over the fore and middle fingers. This secure grip is useful for holding weapons such as clubs, spears and bows, where keeping hold of the object under impact is important. Figure produced using graphical reference from Napier (1962) and Young (2003).

The wrist of humans is also fairly unique among primates, and is generally poorly understood in terms of the rotation and contribution of individual bones (Wolfe et al. 2006). Humans have what has been named a 'dart throwers' level of wrist mobility, from full radial extension to ulna flexion- an exceptional range of lateral movement (Rohde et al. 2010). This is quite different from the ball and socket configuration seen in habitually arboreal primates such as gibbons, or the far more rigid form of the knuckle walking primates (Rohde et al. 2010). As the name suggests, the dart throwers motion is very useful for over-arm throwing and clubbing, as the flexibility inherent to it allows the projectile/ weapon to be oriented in a huge array of different positions, allowing subtle movement to improve accuracy or power (Wolfe et al. 2006; Rohde et al. 2010). To account for this wrist mobility, the human extensor muscles of the forearm are well developed, far more so in most individuals than the flexors which

would be useful for climbing (Wolfe et al. 2006). Bharambe *et al.* (2017) have found there to be great variation in the extensor muscles and tendons of the forearm between individuals, via a large sample dissection project. They hypothesise that duplication of tendons and muscles in the human forearm- and the loss of some (see paper for specifics)- reflects the evolutionary pressure for throwing and other tooling over the last few million years (Bharambe et al. 2017). The wrist and fingers (particularly the index and middle) are thought to provide the final thrust of force to a projectile before it is released, explaining why such extensor ability in the forearm would be advantageous (Bharambe et al. 2017). Roach and Lieberman (2014) have attempted to test the power contribution of the wrist during throwing via an immobilising wrist brace, and although the detrimental effects of wrist immobilisation were severe, this may have been due to the added weight at the hand rather than a reduction in range of motion *per se*. Such an experimental outcome speaks to both the complexity of the wrists contribution to throwing performance, and general lack of consensus.

### **The brain**

Accurate throwing requires the co-ordination of three different moving objects- yourself as the thrower, the object being thrown and the target, and thus requires a far greater level of cognitive ability than the majority of daily tasks- especially for an early hominin (Darlington 1975; Calvin 1983). In essence, during about 1 second of throwing time, a thrower must judge his own muscular movement in order to generate the correct force in sequence, the trajectory of the thrown object through space (variables such as distance and wind) and the estimated movement of the target (Calvin 1982). Such complex and interweaving trajectories creates a very narrow 'launch window' for success, thought to be achieved via redundancy of neural timing circuits within the human brain, essentially the staggered firing of neurons so as not to overload the system (Calvin 1982; Calvin 1983). As successful projectile throwing has been a significant selective force throughout recent hominin evolution, and is demanding of cognitive performance, it's reasonable to suggest that projectile throwing may have been crucial to the rapid growth of the hominin brain- which has tripled in volume over the last few million years (Calvin 1983). Such a theory is supported by research into handedness, which finds that habitual throwing with the right arm (which is most common), and the subsequent development of the left hemisphere of the brain, improves other capabilities of the organism in addition to the motor skills that are also associated with the left hemisphere- such as speech and language (Hopkins et al. 2012). Projectiles may also have developed the teaching abilities of hominins, as parents would have an obvious need to educate their children on how to use these new weapons so that they could help in the future with hunting and warfare, and generally improve their chances of survival (Lombard 2015). To teach you need theory of mind- understanding of someone else's level of knowledge, knowledge of what gaps they need to fill, and capacity to formulate a strategy to effectively help them learn (Lombard 2015). Projectiles presented a selective need to educate, made far easier by the development of speech and language, further improving the cognitive abilities of hominins (Lombard 2015). Gärdenfors and Lombard (2018) present a model for this cognitive evolution, stating that the transition towards increasingly more complex projectile weapons within hominin evolution- from thrusting spears to poisoned arrows- reflects the gradual

increase in cognitive understanding over the same time period. They grade this understanding, with the 7<sup>th</sup> grade being 'causal network understanding', the highest form of reasoning that was only achieved by humans by around 70ka with the advent of poisoned tips and spring traps (Gärdenfors and Lombard 2018). As part of their evidence base they cite Williams, Burke and Lombard (2014) and their landmark pilot study into the neurological demands of throwing a spear versus shooting a bow and arrow. Although with a very small sample size, they found that working memory (e.g. attention, context updating and memory rehearsal among others) was enhanced while shooting a bow compared with throwing a spear (Williams et al. 2014). This suggests that more complex projectiles require greater cognitive effort, lending support to the model and presenting a plausible hypothesis as to how cognitive abilities developed in hominins as they invented increasingly more innovative projectile technologies.

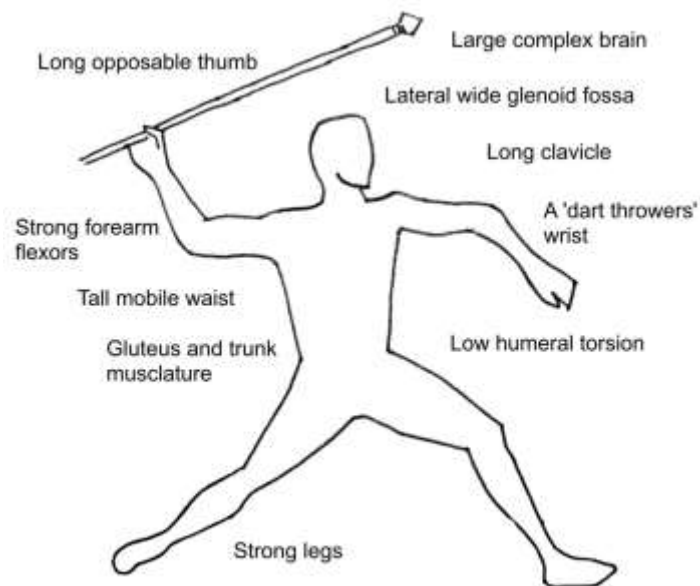
## Conclusions

Table 3 and figure 29 below summarise the key physiological and anatomical features seen in hominins relating to projectile throwing, as discussed within the review. The overall conclusions of this review are as follows:

- Although likely all hominids (and wider primates) toss and throw objects routinely, the evolution of accurate high-speed throwing occurred relatively recently, perhaps within *Homo erectus* at the earliest.
- Projectile throwing with the ability to cause deadly harm will have proved selectively advantageous for both hunting and warfare, helping to broaden their dietary niche and better fend-off competition.
- Blunt objects such as stones were likely the first projectiles. Later a series of cognitive and technological improvements led to carefully hafted throwing spears, and much later more complex projectiles such as the bow and arrow.
- As throwing is such as bilateral activity it may have contributed to the handedness bias seen in modern humans, most often of their right arm.
- Due to its link with hunting and warfare, adaptations for throwing are most notable in males, likely as they were more often performing these activities, thus more prone to the positive selection of throwing-enhancing traits.
- Throwing physiology and anatomy can be seen throughout the modern human form, from the flexibility and strength of the arm, the twisting mobility of the trunk, the fine neurological and biomechanical manipulations of the hand and wrist, and finally even within the motor-capabilities of the brain.

**Table 3:** Summary table detailing the range of physiological features and anatomy seen in humans that are geared towards the stresses of projectile throwing.

Throwing adaptations	Summary
Long opposable thumb	Enables precision grip between thumb and forefingers, improving security of grasping projectiles and accuracy at release
A 'dart throwers' wrist	Full movement from extension to flexion and ulna to radial flexion of the wrist allows great flexibility in the orientation of the projectile, while also providing extra leverage at release
Forearm musculature	Strong flexors of the forearm enable powerful flexion of the wrist and fingers, providing the final propulsion of a projectile before release
Pelvis musculature	Stabilisation muscles of the pelvis such as the gluteus group help to rotate the trunk back on the throwing side, generating elastic energy
Low humeral torsion	Higher rotational angle of the humerus relative to the elbow enables a greater range of motion of the forearm behind the head, useful for 'cocking' the arm back, providing greater arc to apply force
Lateral, wide glenoid fossa	A wide glenoid fossa better dissipate high energy strain on the shoulder, while being lateral improves throwing mechanics
Long clavicle	Generates greater leverage between the pectoral girdle and the arm
Tall mobile waist	Enables the trunk to twist round on the throwing side, utilising large muscles of the trunk to generate extra propulsion
Strong legs	Provides a sturdy platform from which to throw from, while also pushing off from the ground to provide extra propulsion
Large, complex brain	Allows calculation of trajectory and required force of a projectile, generally improving accuracy



**Figure 29:** Summary figure detailing the range of physiological features and anatomy seen in humans that are geared towards the stresses of projectile throwing.



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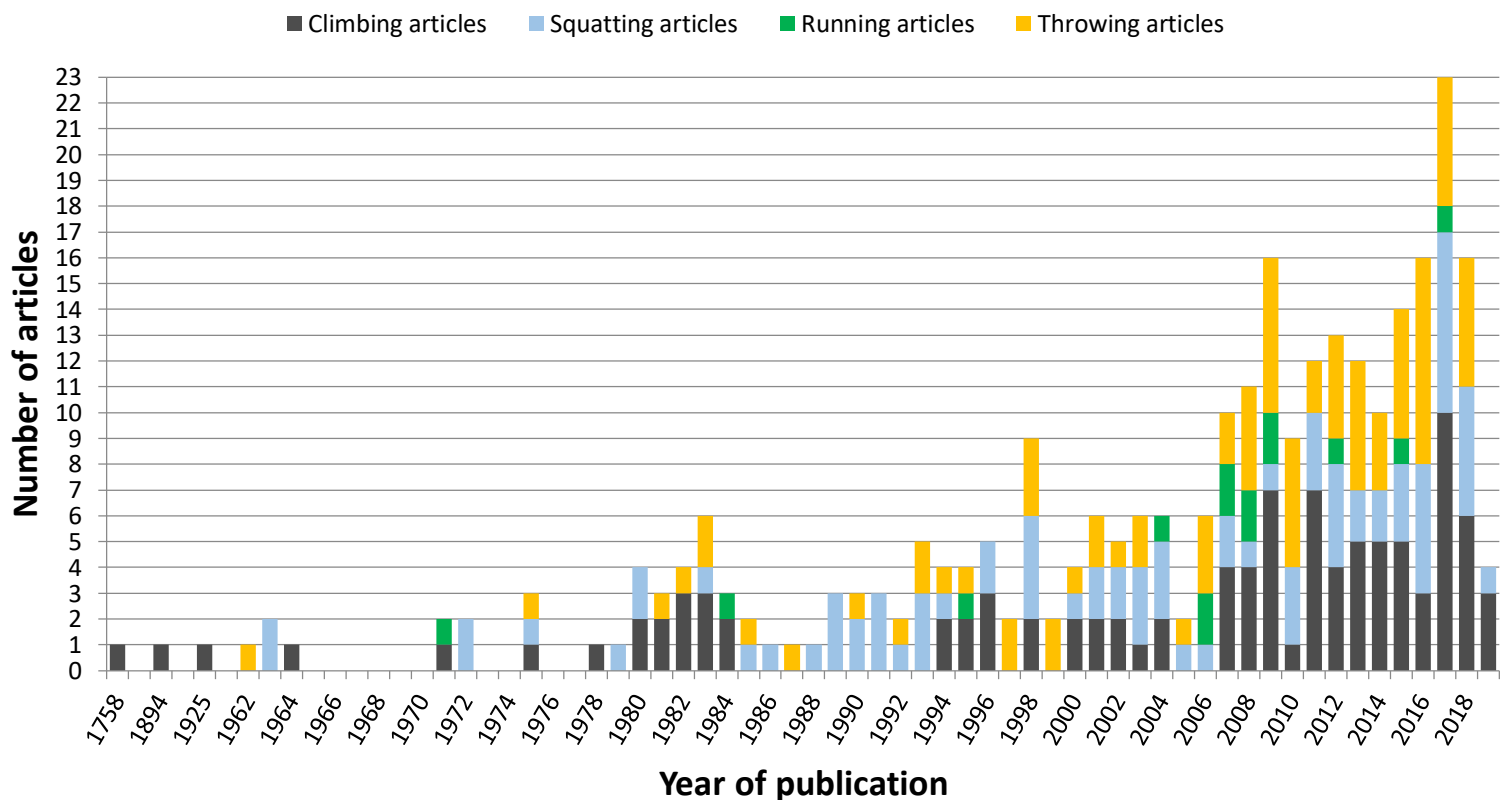
Zhu, Q. and Bingham, G.P. 2008. Is hefting to perceive the affordance for throwing a smart perceptual mechanism? *Journal of Experimental Psychology: Human Perception and Performance* 34(4), pp. 929–943. Available at: <http://doi.apa.org/getdoi.cfm?doi=10.1037/0096-1523.34.4.929> [Accessed: 4 January 2019].

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## Discussion

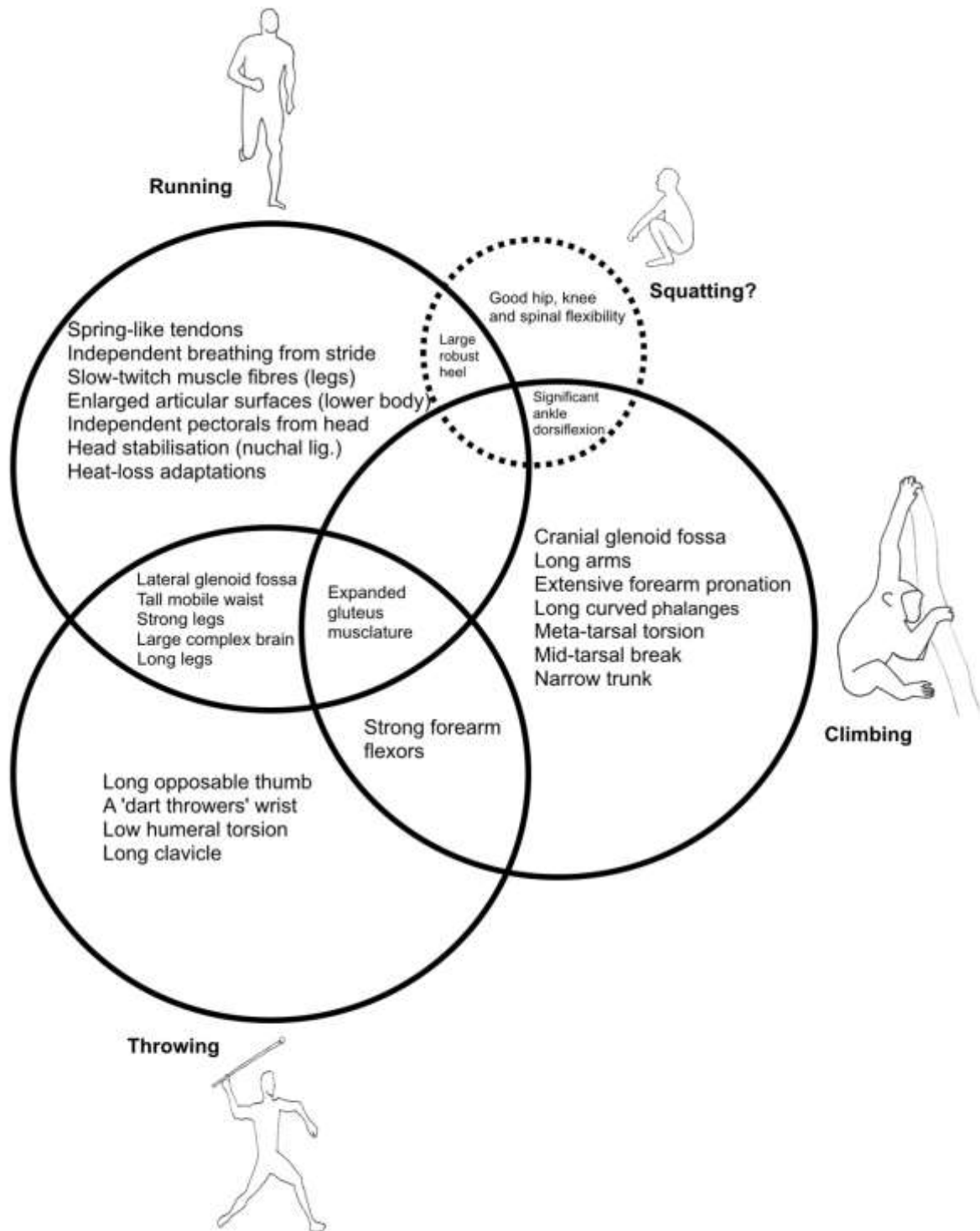
This thesis has pulled together a very large body of literature within the evolutionary anthropology/ biomechanics realm- a total of 284 articles within the main four sections. Figure 30 below shows the distribution of articles by year of publication, split by the four different sections. Foremost it shows that academic interest in this topic has increased substantially over time, as you can expect to find with many scientific fields today, particularly within the last 15 years. Secondly it shows that the distribution of articles between the three behaviours searched in their entirety- climbing, squatting and throwing- show a broadly similar range. Academic interest in these topics seems to have begun in the late 1970s, with between one and three papers published yearly until around 2005, where the quantity rises. However, squatting and throwing articles have been published fairly consistently every year since 1980, whereas climbing seems to have attracted fair research interest in the early 1980s, before a period of 10 years of zero publications. Of course these analyses should be taken with care, as Figure 30 only shows articles picked up by this particular literature review, which will certainly not be every article out there on these topics- discussed later.



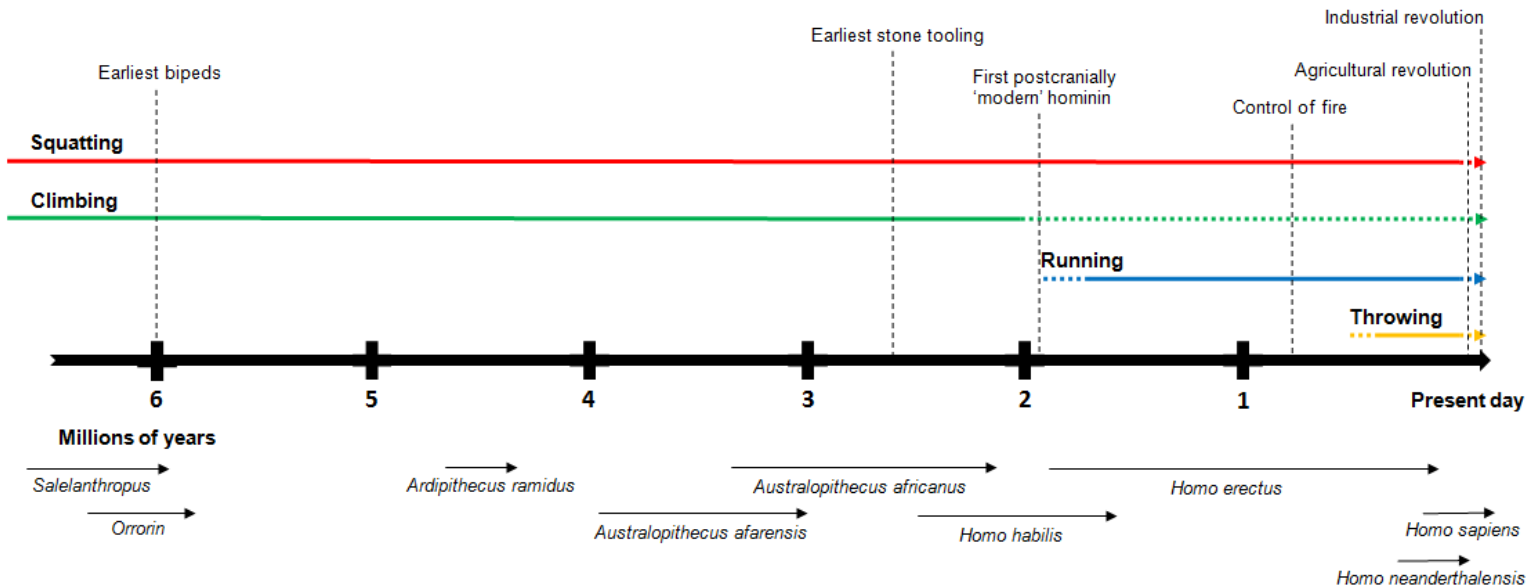
**Figure 30:** Graph showing the range of literature by year of publication that was sourced for this thesis, divided by each section- climbing, squatting, running and throwing. Eligible articles and additional articles have been merged for the purposes of this graph. The year of publication of the earliest articles- 1758, 1894 and 1925- considerably predated the others, and as such have been placed on the far left of the scale, with non-linear gaps between them. The remaining articles range along a linear scale from 1962 to 2019.

The four physical activities reviewed in this thesis represent key behaviours within the evolution of hominins (~6mya) and in some cases even earlier (back to the origin of hominids). Figure 31 below is a summary bringing together the specific adaptations shown by hominins for each behaviour, and the commonalities and differences between them. Figure 32 is a timeline of hominin evolution, detailing the periods of time these behaviours were practiced, by which species and how they overlapped. Of the four activities, climbing and squatting are the most ancient, as their origin although unknown seems to significantly pre-date that of hominins. Climbing adaptations are very different to running and throwing adaptations, as displayed by figure 31 below. These arboreal-focussed adaptations notably include adaptations of the upper body for load bearing, such as the more cranial glenoid fossa orientation, curved phalanges and a narrow trunk, all aiding in efficient body weight bearing during arboreal activity, but totally unnecessary for bipedal behaviours such as running. The squatting review herein revealed a potentially important posture with a long evolutionary history, but mostly disregarded by the academic literature. Perhaps as a result of its long time scale of effect, it shares some biomechanical features with both climbing (ankle dorsiflexion) and running (large robust heel), although far more work is needed to verify this, as is discussed later. Running and throwing are far more recent behavioural ventures, likely reaching only as far back as *Homo erectus*, the first hominin species to have human like bipedal efficiency. These behaviours share several associated anatomical features, such as a more lateralised glenoid fossa and tall mobile waist, perhaps due to their both involving obligate upright postures. Where they differ is in more specific features relating to the activity, running favouring elasticity and robustness of the lower body and heat-loss adaptations, while throwing is more determined by the strength, dexterity and flexibility of the arm. These adaptations occur together in modern humans, i.e. we can be both good runners and throwers with practice, epitomised by sports such as baseball and cricket which require not only good throwing ability but also a good deal of running after the ball or between bases/ wickets. A common feature thought to be useful for climbing, running and throwing appears to be increased importance of the pelvic musculature, particularly the gluteus group which provides extension and thus propulsion of the hips either vertically up a tree, forwards along the ground or rotationally for the biomechanics of throwing. This commonality will also be discussed later.

What's made clear by figure 32 is that at some point within the evolution of hominins all four of these activities have co-occurred, though this is of course dependant on local cultural traditions and geography, especially for climbing which likely varied considerably in usefulness in different parts of the world over the last two million years. The behavioural transition from climbing to running to throwing was likely made necessary by a changing climate (discussed in previous reviews), with a reduction in tree cover necessitating long-distance running and walking (and less climbing), and much later the adoption of throwing providing an effective way to dispatch prey and widen your diet in a more open habitat (probably also reducing the need to run) (Susman et al. 1984; Senut et al. 2018). Squatting has been a different case, likely practiced throughout this entire set of transitions.



**Figure 31:** Summary Venn diagram collating the physiological, anatomical and biomechanical findings from the previous four reviews on the evolutionary impacts of climbing, squatting, running and throwing. Each circle corresponds to a different behaviour. Where a feature is written in the overlap between circles this means it has been useful for multiple behaviours. Squatting has been included in a dashed circle due to the lack of conclusive literature found in that review.



**Figure 32:** Timeline stretching back six million years, detailing the persistence of the four behaviours reviewed herein—climbing, squatting, running and throwing, within the context of hominin evolution. A solid coloured line for each behaviour indicates when it was likely performed, a dashed one indicates either uncertainty as to its origin or the behaviour becoming little used. Along the bottom are estimates of key hominin species durations, allowing the inference of their behavioural repertoire. Note that not all hominin species have been included here, just the notable ones referred to within this thesis.

## Humans today

In comparison with our evolutionary history it's undoubtable that the way we use our bodies today has vastly changed, notably since the invention of agriculture 10,000 years ago, and particularly within the last few centuries of industrialisation. This review has revealed four activities commonplace within our evolutionary history and/or that of our ancestors, as is evident from our retaining a host of physiological features that help us perform them. This demonstrates the generally physically demanding lifestyle of hominins of the past. However today (typically in the more developed western world) activities such as running, throwing, climbing and squatting are no longer components of our daily routines, instead being reserved for totally voluntary planned exercise. The amount of exercise one performs daily varies wildly in uptake between individuals and populations, discussed in depth later. A key reason for such a lack of physical activity is that modern humans have become the first mammal for whom acquiring food and shelter no longer requires much energy expenditure, due to technological innovation and social organisation (Cordain et al. 1998). For example, a minority number of farmers use mass-machinery and fertilisers (among many technological enhancements) to produce food for supermarkets, which the general public can acquire for very little energetic cost. No longer is the energetic cost of acquiring food placed upon the consumer.

Even as recently as the 18<sup>th</sup> century, our relationship with physical exertion was radically different, with famous figures such as the musician Sebastian Bach reportedly walking up to 60 miles in order to attend performances (Walker et al. 2003). Without the automobile and other modern-day transport solutions, having to walk long distances was a seemingly normal undertaking if one wanted to get anywhere (Walker et al. 2003). Although perfectly capable of such an endeavour, the thought of

covering such distances on foot today is reserved purely for keen athletes and eccentrics. Because of the lack of requirement to hunt your meals and general alienation from physical exertion, the daily energy expenditure levels of an average western human are significantly lower than our Palaeolithic counterparts- around 35% lower if estimations from modern hunter-gatherer communities such as the !Kung and Ache are comparable to ancient hunter-gatherers (Cordain et al. 1998). Note that not all modern hunter gatherers have been shown to have higher energy expenditures, the Hadza being a case in point (Pontzer et al. 2012).

Today within the developed world the kinds of physical activities you do and postures you adopt depends largely upon your age, your profession and what can be termed your 'sportiness'; all three of which are discussed in turn below. Your age and level of physical activity are fundamentally linked as they are in any mammal, as aging imposes a complex suite of interacting biological, morphological and functional processes upon the body that generally produce a decline in physical ability (Sebastião et al. 2017). Therefore levels of physical exertion tend to be high as children (think of the playground) and taper off throughout life due to aging as well as increased work and family responsibilities. Of course this is not always the case, with many people maintaining consistent activity levels throughout their lives, or picking up a new sport when they retire and have more time. Doing so has overwhelming research support in terms of retaining physical and mental capabilities and staving off disease (McAuley and Rudolph 2016; McPhee et al. 2016).

The division of labour today has proceeded so far that levels of physical exertion between and within working sectors can be drastically different. One thing common however is the rise of heavily computer reliant employment; for instance 'computer occupations' accounted for nearly 45% of jobs within the science, technology, engineering and maths sector (STEM) in the US in 2015 (Fayer et al. 2017). Furthermore, despite not being technically classed as a 'computer occupation', basically every other subsector within the STEM group also probably places high reliance on computers, such as for mathematicians, architects and managerial roles (Fayer et al. 2017). Computers and related technology such as automation machinery are designed to swap human musculature and brain power for mechanical power, which reduces the physical and mental strain on the workforce (Hallal et al. 2012; Autor 2015). As such this rise in technology has led to a reduction in jobs in sectors such as agriculture and labouring, particularly within the last 100 years, and a transition towards more people performing professional, technical and managerial occupations (Autor 2015). This follows the trend of increased worldwide urbanisation, which in countries such as China has led to a dramatic drop in physical activity levels due to the transition from a traditional agricultural lifestyle to urban living, something that African countries are now also beginning to experience (Kohl et al. 2012). More people than ever now have desk-based employment and thus spend a significant amount of time unmoving in a seated position. For instance an Australian study of workplaces within the city of Melbourne found the median total sitting time of people to be 9 hours per day, ~56% of that time being in the work environment (Bennie et al. 2015). Although there is generally motivation among office workers to get up and move around occasionally, among many professions such as software engineers there is a commonly held belief that continuous long hours of concentration sat at the computer are required in order to be most efficient and avoid distractions (Cole et al. 2015). At the

same time employees often don't utilise their breaks for active purposes, choosing to eat lunch still at the desk, and using their free time to surf the internet rather than getting some fresh air (Cole et al. 2015). A seated posture is unavoidable within today's developed societies, in the workplace but also the transport sector (cars, trains, planes etc all design themselves around sitting) and in the home environment, where comfort and convenience has been taken to the max with furnishings such as reclining chairs.

Of course a sedentary lifestyle is not shared by everyone today, with some people employed within very physically demanding sectors such as that of construction and labouring, or other employment in which being active and 'on your feet' is common for most of the day, such as factory delivery line workers. At the same time, with increased scientific understanding of the benefits of exercise, and crucially the costs of not doing enough, more people than ever now engage in improving their health and fitness. Popular methods for this include frequenting a local gym in-between their work commitments, or partaking in a sport. For example a large scale Australian study found that between 2001 and 2010 participation in any sport or recreation rose from 80% to 83% in males, and 76% to 81% in females (Eime et al. 2015).

Generally 'sufficient' physical activity levels for adults are defined as 150 minutes of aerobic activity, plus two days with some form of muscle strengthening such as gym work, as part of a typical week (Piercy et al. 2018). Unfortunately even with promising sports and recreation statistics, the number of people globally not meeting such guidelines for physical activity (and thus defined as physically inactive) is growing and now stands at 31% of adults globally, or 1.5 billion people (Hallal et al. 2012). In some countries such as America the statistics are even more damning, with 80% of adults and adolescences classed as physically inactive as of 2018 (Piercy et al. 2018).

A lack of adequate physical activity in comparison with our evolutionary past is leading to a decline in human health, both in terms of reduced aerobic fitness due to a general lack of daily endurance exercise, and as a result of subsequent increased weight gain aided by over-consumption of readily available energy-rich foods (Cordain et al. 1998; O'Keefe and Cordain 2004; O'Keefe et al. 2011). Accordingly percentages of overweight and obese people within a country's population has become staggeringly high- in excess of 65% among adults in some developed countries such as America- leading to an increased risk of a plethora of diseases and conditions including diabetes, stroke and coronary heart disease (O'Keefe and Cordain 2004; O'Keefe et al. 2011). Physical inactivity is now number four in leading causes of death worldwide (Kohl et al. 2012). As such the number of people recommended physical activity by a doctor or physician is growing, 22% of adults in the year 2000 compared with 32% just ten years later (in America), in an attempt to combat such diseases (Barnes and Schoenborn 2012).

### **Evolutionary mismatch**

Although cardio-vascular disease and diabetes (among many others) represent the most life threatening conditions associated with physical inactivity, there are other risk factors associated with our apparent failure to 'live up' to our evolutionary history. Evolutionary mismatch is one such concern already outlined within the introduction to this thesis. This section of discussion is going to concern

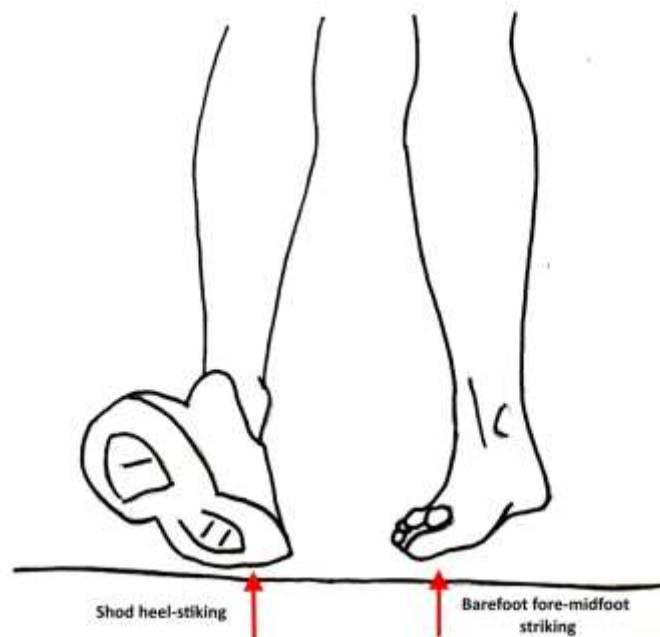
some of the mismatches possible within the context of the reviews in this thesis, and includes both well-established mismatches and ones that are more speculative or less certain.

### **Barefoot running**

By far the most extensively researched and widely discussed evolutionary mismatch is that of barefoot running, a highly popular topic over the last decade among both athletes and academics, aided by hit titles such as 'Born to run' (McDougall 2010). Modern humans are well suited to the demands of endurance running- as this review has shown- however the advocates of the barefoot running movement suggest that humans today are running in a way vastly unsuited to our bodies' adaptations, notably due to the adoption of footwear. Humans probably didn't invent footwear until around 45,000 years ago, and these shoes would have been very minimal, much like sandals today (Lieberman 2012; Tam et al. 2014). In fact the highly supportive shoes that we know today were not invented until the 1970s (Lieberman 2012). Therefore throughout the vast majority of our evolutionary history our own species (as well as our ancestors) have been running, walking and carrying out all of our daily activities completely barefoot or perhaps in minimal sandals until around 50 years ago. That's hundreds of thousands of years worth of natural selection for adaptable and robust feet, highly capable in their 'naked' form, that today we constrict within a shoe and expect to perform just as well. However shoes can impose significant changes to the human gait, specifically at foot-strike with the ground, and can adversely impact anatomy and health.

As discussed, the human foot is a marvel of energy dissipating design, with elastic-like tendons such as that of the Achilles and longitudinal arch serving to reduce the impact forces that travel through the kinetic chain at foot-strike, from foot to ankle to knee and beyond (Bramble and Lieberman 2004). In order to utilise such design a barefoot runner needs to land on their fore to mid-foot, something that will feel natural if one takes off their shoes, mainly due to the pain experienced if you land too far towards the heel (Lieberman 2012; Tam et al. 2014). The design of modern athletic shoes generally do not facilitate this same foot-strike, due to a vast range of different impact-absorbing and stability controlling features that have been imagined, such as a large cushioned heel designed to absorb impact energy (Murphy et al. 2013). Such shoes enable the user to lengthen their stride and adopt a more rear-foot strike known as 'heel striking', made possible by the cushioned heel which prevents the pain associated with landing on such a bony structure (Almeida et al. 2015). Heel striking negates the mechanical capabilities of the longitudinal arch and Achilles tendon, and although a cushioned running shoe heel provides some impact dissipation (albeit to a contentious degree), much of the associated stress still travels further up the kinetic chain to joints such as the knees and hips (Lieberman 2012; Fong Yan et al. 2013). With such information it is no wonder that rates of running injuries today are scarily high- perhaps as high as 80% of runners pick up an injury annually, even with a multi-billion pound athletic shoe industry with their plethora of sophisticated technology (Lieberman 2012; Perkins et al. 2014). The differences between heel-striking and fore to midfoot striking are illustrated by figure 33 below.

Advocates of the barefoot running movement propose that transitioning away from highly cushioned shoes towards those with minimal thickness, support and no drop from toe to heel (mimicking the naked foot) may be the best way to reduce running related injury (Rixe et al. 2012; Murphy et al. 2013). Injury could be reduced in a variety of different ways other than by adjusting basic foot-strike, including by encouraging softening of the knees, pre-activation of the tricep surae and greater somatosensory feedback at the feet, all of which would aid in reducing impact forces and improving muscular control (see summary tables in Rixe *et al.*, 2012). Furthermore there is reason to believe that running performance may even improve with 'less shoe', due to improved economy through greater utilisation of elastic fibres and less weight attached to the foot, both of which reduce oxygen consumption, enabling a greater workload (Cheung and Ngai 2015; Fuller et al. 2015). In this classic case of evolutionary mismatch modern society tells us we should only run in the latest tech-laden shoes, when in truth they could be the issue causing many impact-related injuries, and preventing the human foot from functioning as it has been evolutionary adapted. Of course plenty of caution should be used when considering this theory, as there is great variation in foot-strike with some favouring heel striking when barefoot even on hard surfaces, and as of yet no scientific consensus as to whether it influences injury rates at all (Nigg and Enders 2013). Therefore, currently the barefoot running movement is based purely on theory with solid biomechanical reasoning and some anecdotal evidence. Hopefully in the future long-term study will find the truth regarding possible injury prevention.



**Figure 33:** Illustration depicting two human legs running, one clad in a typical athletic shoe and the other barefoot. Both are the forwards foot, i.e. the one about to strike the ground in front, with the red arrow indicating what part of the foot will strike first. The shod leg (left) is heel-striking, a common sight among runners as they lengthen their stride and fully utilise the foam shock-absorption provided by the heels of the majority of modern running shoes. The barefoot leg (right) is fore to midfoot striking, a technique fairly crucial to barefoot running in order to avoid painfully landing on your bony heel. The transition towards athletic shoes in modern times has been associated with more heel-striking, which only poorly utilises the elastic tendons of the foot and ankle such as the Achilles, and causes the impact energy to travel higher up the kinetic chain.



## **Chairs and squatting**

This review has revealed the deep evolutionary history of a squatted posture, as a means of resting and for important behaviours such as defaecation and childbirth, probably stretching far back to the very origin of hominids. Chair sitting has by no means been a long standing component of humans' evolutionary history, with the wide-scale adoption of chairs perhaps starting just 200 years ago, piling in comparison to >20million years of hominid evolution (Ingold 2004). When compared to the barefoot running mismatch, although shod running and chair sitting are similar in that they have come about within a relatively short and similar time period, hominids have probably been squatters for 20mya+ based on the postures utilisation among most primates, significantly longer than they have been runners (~2mya) (Alexander 1994; Bramble and Lieberman 2004). This points towards a potentially huge and long-lived evolutionary mismatch in modern humans, which is mostly disregarded within the developed world.

It has previously been noted herein that prolonged chair-sitting is commonplace within the developed world, and often unavoidable. However such a posture has been linked with a number of debilitating health issues, even in seemingly healthy individuals that meet or exceed recommended exercise levels (Owen 2012). Although our understanding of such conditions is surely incomplete, related health issues include all manner of cardio-vascular disease generally brought about by obesity, as well as increased risk of cancer, diabetes and a host of musculoskeletal disorders (van Uffelen et al. 2010; Dunstan et al. 2012; Owen 2012). Staggeringly there is evidence to suggest that for every hour you spend watching television (a typical seated activity) after the age of 25, you reduce your life expectancy by 22minutes (Veerman et al. 2012). Obesity related disease as a result of prolonged sitting is fairly easily understood, as it is such a sedentary activity requiring very little muscular activity and thus energy expenditure, enhancing calorific imbalance and the chances of putting on weight (Hamilton et al. 2007). Although certainly the most life threatening, conditions such as heart disease are not the most globally common complaints associated with sitting- these are musculoskeletal disorders such as lower back pain.

Lower back pain (LBP) is a highly common condition affecting up to 90% of people during their lifetimes, thought to be brought about by a number of physiological factors including overuse and/or injury of muscles, tendons and ligaments within the lumbar area of the spine and pelvis (Roffey et al. 2010; Sung 2013; Gabel et al. 2018). Although it is widely believed that excessive time spent sitting promotes LBP- with plenty of anecdotal evidence- a rigorous scientific link has yet to be established through systematic review (Hartvigsen et al. 2000; Chen et al. 2009; Roffey et al. 2010). Instead the posture adopted while sitting has become the main academic focus, with a tall but not overextended 'neutral spine' posture generally being considered most healthy by medical professionals (O'Sullivan et al. 2012). More 'slumped' postures with greater flexion of the lumbar and thoracic spine generally require less muscular control, and have been associated with LBP in a number of studies (O'Sullivan et al. 2006; Meziat Filho et al. 2015). This may be because they promote a lack of endurance in the stabilising muscles of the lower spinal region, rendering them inactive sooner while sitting and thus putting greater strain on the spinal cord itself causing pain (O'Sullivan et al. 2006). Alternatively muscles of the lumbar region might be over-active as a means of protecting the spine at the end of its

lumbar flexion, a subconscious response to a seated posture that can aggravate pain symptoms over time (Dunk and Callaghan 2010; Schinkel-Ivy et al. 2013). When compared with non-sufferers those with LBP display differential neuromuscular control of the lumbar region, and as might be expected struggle to maintain consistent posture while seated- 'fidgeting' far more often (Dunk and Callaghan 2010; Lui et al. 2018). Other causes of LBP associated with sitting can originate from the gluteal region, with conditions such as piriformis syndrome. Here the piriformis muscle (a deep external rotator of the hips) impinges or entraps the sciatic nerve, causing pain in the buttock and lower back area, and possibly radiating further down the legs (Papadopoulos and Khan 2004; Cass 2015). This condition can be attributed to trauma or excessive use of hip rotation, as well as prolonged sitting particularly on hard surfaces (Papadopoulos and Khan 2004).

As these health issues and musculoskeletal disorders can be attributed fairly convincingly at least in part to prolonged sitting, and this has only recently become a component of human behaviour, they are the result of an evolutionary mismatch. Being sedentary has never been a common hominin activity, mainly due to the need to hunt and find shelter in a world without agriculture and technology, which necessitates physically demanding behaviours such as climbing, running and throwing.

Therefore counteracting this mismatch seems fairly straightforward, requiring a concerted effort to reduce the amount of time you spend sat at a desk or on the sofa- perhaps breaking it up at intervals- and increasing the amount of physical activity you do during the day (Larsen et al. 2014). A seemingly simple task that is all too soon derailed by the modern age, with work commitments requiring long hours at the desk and little time or energy afterwards to devote towards physical activity. A potential solution here is to follow the blueprint of the barefoot running movement, and habitually adopt squatting, which hominins have done for millions of years. This would certainly seem radical to most and require a paradigm shift in how we think, behave and design our work and leisure lives.

Furthermore the idea is not aided by the fact that the health implications of habitually adopting a prolonged squatted position are generally unknown due to a lack of research focus, something that would need to be remedied before any robust recommendations could be made. Nonetheless there are certain encouraging insights to be taken from the current squatting related literature. Firstly the health benefits of squatting for defaecation and childbirth are fairly convincing (see squatting section for detail), the former being a regular daily activity that everyone performs, and the latter being a matter of comfort, pain and ultimately survival for both mother and child, demonstrating that these are not menial issues. Secondly squatting is a common behaviour during childhood and seemingly easy at young ages, however it appears to become more difficult through adolescence and beyond (Rane and Corstiaans 2008). If this is as a result even in part to the cultural adoption of chairs at later ages, then maintaining habitual daily squatting into adulthood might help retain some of that childhood flexibility, which would be useful for mobility later in life. Finally the adoption of squatting need not be so radical due to our understanding of other similar 'floor sitting' postures that are practiced generally by Asian cultures. Postures such as sitting 'cross-legged' or kneeling are similar to squatting in that they require deep flexion of the knees and hips thus culturing flexibility, but are generally easier to adopt. Taken together just these three points accentuate the need for further squatting-related

research, particularly work focussing on the biomechanical effects of this posture and how it can be implemented in modern society.

### **Strength, flexibility and modern sport**

Alexander (1994) performed an interesting study comparing the utilisation of different joints by humans and chimpanzees during normal behaviour. The study found underutilisation in every joint group looked at in humans, notably due to a lack of arboreal activity and knuckle walking, perhaps relating to the onset of conditions such as primary osteoarthritis (Alexander 1994). It demonstrates that in comparison with our extant relative the chimpanzee modern humans do not place nearly the same strain on their bodies. This can be extended to the activities reviewed in this thesis, all of which while playing important roles in shaping the evolution of the modern human form, are underutilised today, and thus our strength, flexibility and general health are inferior to our ancestors. For example, running is a strenuous activity which imposes great demands upon the lower body for propulsion and impact absorption, and the upper body as it stabilises the entire body in order to maintain a consistent erect form (see running review herein). As such running strengthens the muscles of the legs and gluteus group, increases bone density to better withstand impact and generates heightened cardiovascular health and fitness, among many benefits (Michel et al. 1992; Rector et al. 2008; Lee et al. 2014; Lee et al. 2017). Indeed in terms of all-cause mortality, runners reduce their risk of early death by 25-40%, and crucially reduce the risk of developing a cardiovascular disease by as much as 70% when compared with non-runners (Lee et al. 2017). Climbing is a similarly strenuous behaviour requiring not only raw power from the upper body but also great stability from the trunk and legs in order to move safely and efficiently. It develops not only muscular strength (particularly in the upper limbs) but also flexibility and balance as one must maintain stability upon small supports, and has some cardio-vascular benefits during longer or interval-style sessions (Gallotta et al. 2015; Siegel and Fryer 2017). From a physiological perspective the highly stressful nature of climbing may have some anxiety and mood control benefits, helping to train mind relaxation and create more positive thinking, as has been found in multiple different sports (Gallotta et al. 2015). These examples demonstrate how the physically demanding lifestyle of hominin hunter-gatherers helped make them generally robust, highly capable athletes, something that cannot be said for the majority of modern society.

However, today exercise trends and classes such as yoga, Pilates and Tai Chi (among many others) go some way to remedy this deficiency, and are highly popular. These movement routines often have ancient origins and involve varying static and semi-static postures aimed to challenge strength, mobility and flexibility, as well as mindfulness components through meditation and breath control (Sorosky et al. 2008; Kloubec 2010; Ross and Thomas 2010). In their review comparing the health benefits of yoga and other exercise, Ross and Thomas (2010) found the health effects of yoga to be overwhelmingly positive in both well and diseased people. Kloubec (2010) found similar results for Pilates, with a 12 week program significantly improving abdominal endurance, hamstring flexibility and upper-limb muscle endurance. These modern day exercises mimic the kind of whole-body strain of a hunter-gatherer lifestyle, and go a long way towards promoting the same kind of physical wellness

when integrated into a generally more sedentary lifestyle. As such they should be encouraged, and thankfully such classes are becoming commonplace in fitness centres with encouraging participation statistics- such as in America 15 million people practicing yoga more than three times per week in 2003 (Sorosky et al. 2008).

To a certain extent modern sport also fills the void of this lack of physical exertion, with several sports closely mimicking or matching hunter-gatherer energetics, such as endurance running, throwing sports like baseball or cricket and rock climbing. Indeed thanks to our ancestors demanding lives shaping our physiology and anatomy, elite athletes today are of staggering ability, with the first sub-two-hour marathon having just been run as of October 2019, and the world record javelin distance standing at a little over 100metres, to give a couple of examples (Chiu 2009).

Unfortunately due to the inherent competitive nature of human beings, and a general lack of awareness among most as to how to most successfully train the body, injuries in modern sport are commonplace. In running I have already mentioned this within this discussion, with perhaps as many as 80% of runners experiencing an injury annually. Although the shoes we wear and the way we run likely has an influence on this injury rate (see 'barefoot running' above), probably equally important is simply doing too much too soon. Our hunter-gatherer ancestors were undoubtedly very capable athletes, however their athleticism was purely necessary for the most part, not based around competition and sport but predicted on improving the survival of yourself and your close kin, by finding food, water and shelter (Malina and Little 2008; O'Keefe et al. 2010). As such physical health would have been paramount, and even minor injury such as a twisted ankle could have had life threatening consequences, due to missed hunting/ foraging opportunity among other potential losses (O'Keefe et al. 2011). From this understanding it's logical to assume that hunter gatherers' relationships with physical exertion would have been conservative and controlled, only doing what was necessary and 'listening' intently to inner signs of fatigue in order to not overstress the body. Modern humans for the most part no longer have this relationship with physical exertion, and instead push towards athletic goals as a means of competing with others or themselves, always reaching for new heights. Overuse injury is common, even within systems that are robust and supposedly 'well adapted' as with the activities reviewed herein. Common running overuse injuries include tendonopathy (failed healing response of tendons) within the Achilles or patellar tendons, tibial stress syndrome (failed muscular healing), plantar fasciitis (mid-foot inflammation) and bone stress fracture (Kozinc and Sarabon 2017). All of these injuries and more can be explained by a training regime that exceeds the individuals' current level of robusticity, essentially doing too much too soon, before the body is able to adapt to the demands imposed upon it (Malisoux et al. 2015; Kozinc and Sarabon 2017). Of course other explanations exist, such as that of shoe type worn, degree of cross-training within other sports, previous injury, body weight and age, making overuse injury difficult to specifically diagnose (Malisoux et al. 2015). Within throwing sports overuse injuries to the shoulder and arm are also common, with an Australian study finding that 25% of an elite cricket team sustained an injury within the 07/08 season, and potentially as many as 58 of every 100 professional baseball players in America picking up an injury annually (Saw et al. 2011; Lin et al. 2018). A plethora of injuries are possible in the throwing athlete, including damage to the shoulder joint capsule itself, inflammation or breakage of

the tendons surrounding the joint, or tears within the muscles themselves, such as those of the rotator cuff (Lin et al. 2018). Similarly to running, the amount of throwing that we do (throws per week) seems to be a key predictor of such injury, with a significantly heightened risk of injury if athletes perform more than 75 throws within a week (Saw et al. 2011).

Among traditional hunter-gatherer societies men would typically hunt one to four days per week depending upon demand and the season, with females gathering every two or three days, and average daily mileage equalling around nine miles, or ~135minutes of moderate to vigorous activity per day (Cordain et al. 1998; Raichlen et al. 2017). Although this may seem a lot these peoples would have traded days of intense physical labour with days of rest doing more menial tasks (Cordain et al. 1998; O'Keefe et al. 2010; O'Keefe et al. 2011). Running might have been reserved for just one or two days per week when the hunt was necessary, likely with a stop-start nature due to the need to track through challenging terrain, perhaps culminating in a throw to dispatch a prey item. The key here is that although the physical workload of hunter-gatherers was consistently high the vast majority of this work would have been at low intensities, with short bouts of higher exertion followed by rest (O'Keefe et al. 2011). Therefore the training regime of a typical modern athlete can be seen quite confidently as an evolutionary mismatch, as the sheer volume of intense runs or throws in a week vastly exceeds those likely for our hunter-gatherer ancestors, which helps to explain overuse injury. The best athletes today mimic hunter-gatherer energetics by generating a training plan that alternates between high intensity intervals and rest, demonstrating how important knowledge of evolutionary activity is to athletic performance today (O'Keefe et al. 2010; O'Keefe et al. 2011).

Cross-training is an interesting point, in that it has been speculated (with some experimental support) in modern athletes that those who diversify across a range of different sports rather than becoming specialists are less likely to become injured, probably due to increased robusticity of the musculoskeletal system through exposure to varied physical stressors (Brenner 2007; O'Keefe et al. 2010; Hall et al. 2015; Malisoux et al. 2015). Cross-training is normal routine within hunter-gatherer societies simply as a part of daily life, as individuals might have to perform a range of different physical activities, all those reviewed herein plus a range of others such as load carrying, fashioning tools and building shelters (Malina and Little 2008; O'Keefe et al. 2010; Platek et al. 2011). This diversity in their physical workload helps explain their robusticity and apparent lack of injury, and indicates why cross-training in modern sports is effective and should be encouraged. Platek *et al.* (2011) report several key cross-training functional movements that hunter gatherers perform, such as the dead lift (lifting a weight from the ground to waist), the power clean (from the ground to shoulders) and dynamic squat to stand. By adding such movements into a training plan (along with more wholesome dietary choices) they report very successful health outcomes, including weight loss, improved flexibility, easier pregnancy and physiological benefits (Platek et al. 2011). This demonstrates the value of hunter-gatherer inspired movement in the modern day.

### **Co-evolution of physical activities**

A recurring theme within hominin research is the idea that an adaptation for a particular activity or behaviour can prove to be pre-adaptive for another, or to use Gould and Vrba (1982), can later be

exapted for another as discussed in previous reviews. This concept provides a biomechanical launch pad for the exploration of new abilities, not foresight but simply the utilisation of a particular feature for a new purpose. An example of this is the postural feeding hypothesis described within the climbing section, where by the adoption of a tall upright position within the trees provided not only advantages in terms of feeding but also potentially biomechanical adaptation that aided the later transition towards bipedalism (Hunt 1996; Thorpe et al. 2007). Another is that of humans' low wide shoulders, almost certainly a result of the transition away from climbing behaviour, which aid arm swing during running to counteract the moving legs, while also providing a superior orientation of the shoulder musculature which was co-opted for projectile throwing in later evolution (Lieberman et al. 2009; Roach et al. 2013). Understanding this concept is aided by both figures 31 and 32 above, as they show firstly how much overlap there has been between the four behaviours of this thesis within hominin evolution, and secondly how the physiology and anatomy used for a particular behaviour can be shared by another.

This shows how the same biomechanical form can be useful for multiple functions. This is potentially important in the context of this thesis as it suggests possible biomechanical interactions between behaviours that evolved together, something that is true for climbing, running, throwing and squatting as has been established by the timeline herein (figure 32). Such an interaction would involve one activity providing biomechanical benefits for another, making them mutually beneficial of each other. An example of this might involve squatting and running, two behaviours that were likely performed regularly by hunter-gatherers over the last two million years. While squatting is certainly a 'resting' posture, it requires good levels of hip, knee and spinal flexibility, and crucially considerable ankle dorsiflexion in order to maintain stability. Hunter-gatherers would have rested in a squatted position in-between and probably during hunts, where running would have been a critical component. Under this theory perhaps the enhanced flexibility generated through habitual squatting was useful for some component of running biomechanics, enhancing the function of the ankle at foot-strike or increasing stride length for example. Visa-versa, the demanding nature of running (particularly barefoot) probably also provided some stability improvements for maintaining a deep squat for prolonged periods of time. Although purely speculation at this stage, an interaction such as this would have profound implications for our overall view of evolutionary mismatch and general health today, as it would be a mismatch not only to not be running and squatting in isolation but also not to be performing them *together* as part of daily life.

The gluteal muscle group perhaps demonstrates the best example of this. This group of muscles occupy the posterior portion of the pelvis, predominantly providing stabilisation of the body during movement, particularly since the adoption of bipedalism. Lieberman *et al.* (2006) found that the role of the gluteus maximus (the major muscle of the gluteal group) increased with speed travelled, and thus it becomes more active during running rather than walking. This is due to increasing forwards pitching forces with greater speed, which cause the gluteus maximus to become more active on the stance side each step to help maintain a consistent erect trunk (Lieberman et al. 2006). The gluteal muscles are also important for effective projectile throwing, acting as hip rotators to twist the trunk back, loading the elasticity of several muscle groups to provide extra propulsion (Roach and Lieberman

2014). Squatting in itself is passive in terms of gluteus activity, however rising from a deep squat to a full erect position requires substantial gluteus activity to extend the hips (Struminger et al. 2013). Finally, in climbing the gluteal muscles are important for both stabilisation and upwards propulsion, with activity levels similar to that of running, perhaps providing some sort of pre-adaption for the transition towards bipedalism in hominins as previously suggested (Stern, and Susman 1981; Bartlett et al. 2014). Foremost these four pieces of evidence demonstrate the great importance of the gluteal muscles for a variety of different movements, hence its central location in figure 31. Secondly it shows how performing one activity might be useful for another as there is great cross-over in muscular demands. For example, to return to the squatting-running connection suggested previously, if squatting was the predominant resting posture in-between active periods (which seems likely), then hunter-gathering hominins would have been recruiting and thus strengthening their gluteal muscles regularly throughout the day every time they rose from a squatted position. This gluteal strength would have then been useful for the demands of endurance running, which they were also likely utilising in order to hunt game, and perhaps also projectile throwing later in hominin evolution. This is but one potential example but it points towards interesting questions for modern day health and fitness. For instance, are runners who supplement their training with rock climbing or extended periods of squatting more capable athletes, and does this show in their performances? Questions such as this might make interesting avenues for future research. In essence this is a further call to understand the potential benefits of cross training within evolutionary activity, as has been shown in modern sports.

### **Phenotypic Plasticity**

Natural selection has acted throughout our evolutionary history, shaping hominins for highly active lifestyles. This is genetic change- positively selected mutations passed down through generations, however it is certainly not the only way in which an individual might seem to 'adapt' to their surroundings. First properly conceived by Bradshaw (1965) in plants, phenotypic plasticity describes how an organism can alter its phenotype in response to environmental conditions, without any genetic change. Since the 1960s this concept has become a stalwart component of the ecological literature, with plasticity being considered at every scale, from the variable expression of a single gene, within a single individual, to variable anatomies and behaviours in larger population of organisms (Forsman 2015). Within human biomechanics, a number of the 'adaptations' discussed within this thesis can be described as potentially at least partially plastic traits, i.e. those that are as a result of environmental or habitual biomechanical pressure on an individual rather than purely inherited genetics. For instance humeral torsion, described herein both in the throwing and climbing sections, is most certainly plastic in nature in that it varies wildly between individuals based on how much external rotation of the elbow they habitually perform, particularly how much they did throughout childhood while still developing (Churchill and Rhodes 2009; Roach et al. 2012; Roach et al. 2013). Along a similar vein, the degree of ankle flexibility an individual has, particularly dorsiflexion as discussed for squatting and climbing, is a result of the amount of time they spend at the extreme end of the ankles range of motion, as this actually modifies the articular surfaces helping facilitate the position (Dewar and Pfeiffer 2004).

These examples demonstrate instances where individuals are able, during development or through habits later in life, to subtly alter their biomechanics in order to improve their efficiency performing habitual movements. It testifies to the ability of humans to adapt to the specific demands imposed upon them, despite perhaps non-ideal morphology. Climbing ability today is a good example of this. As the climbing review herein outlined, the majority of the arboreal-focussed adaptations of ancestral hominins have been lost by modern humans, features such as a cranially-oriented glenoid fossa, a mid-tarsal break and metatarsal torsion, having been replaced with bipedal-focussed adaptations. Nonetheless rock climbing today is a rapidly growing sport, with top athletes displaying a staggering ability. Although there are parallels between climbing and more traditional endurance sports like running, such as requiring a high VO<sub>2</sub> max (maximum oxygen consumption) and being able to deal with high blood lactate, there are also some very different stresses (Sheel 2004). Increased hand grip strength and forearm extensor strength are two features fairly uniquely linked to climbing, and can become highly developed in well trained individuals, enabling them to climb vertically upon holds less than the size of their finger pads or on a wall that overhangs potentially more than 45° (Seifert et al. 2017). As such climbers have been recorded having higher levels of forearm/ handgrip endurance and raw finger strength compared with non-climbers in order to facilitate this ability (Giles et al. 2006). Whether these strengths are a result of phenotypic plasticity, retained abilities from our arboreal ancestry or simple hypertrophy of the musculature involved (or all three), it demonstrates that even without 'ideal' anatomy humans can climb very capably with training and practice. For our interpretation of the fossil record this insight could have profound implications, as it shows that apparent biomechanical optimisation for a particular physical activity does not mean that a particular group of hominins were incapable of performing others. So for example the apparent loss of climbing-focused adaptations with the emergence of the genus *Homo* (particularly *Homo erectus*) does not necessarily have to mean that climbing behaviour did not persist. The physical adaptability of humans today makes a case for never assuming the physical activity patterns of fossil hominins based on their biomechanics. Only work that is akin to this thesis in considering a range of different physical behaviours rather than a single one can hope to bring understanding as to the physical workload of the past.

### **Thesis strengths and limitations**

This thesis has brought together a very large body of highly varied literature on climbing, squatting, running and throwing. It has arranged it in a way designed to best review each behaviours evolutionary significance to hominids, what physiological and anatomical adaptation has occurred and changed over time, and how modern behaviour is often out of sync with our evolutionary adaptations. These were key aims outlined at the beginning of this thesis, for which it has successfully achieved. However a few limitations of this study should be discussed, as outlined below.

A systematic method of searching the literature was adopted, which proved very effective in providing a significant body of relevant literature on each behaviour. Unfortunately due to time and resource constraints, there was only one author to carry out the process of devising the search strategy and checking articles for eligibility, which in an ideal (and most robust) systematic review would be done



instead by three or more independent researchers. As such although this meant I benefited from a consistent view of what literature there was and how choices had been made regarding inclusion and exclusion in different sections, there may have been some inherent bias towards particular topics or themes due to a lack of a peer-review process. Although I do not believe this to be a detriment to my findings, it should be noted herein. On top of this, due to the same constraints the initial search of the literature was probably not as comprehensive as it could have been in an ideal world. Compiling the literature, reading it and then determining eligibility took on average over two months for each behaviour due to the sheer volume of articles and amount of time I had. As such initial searches had to be simple and broad to identify as much relevant material as possible, so I have no doubt that slightly more targeted searches might uncover additional more specific articles that were missed. To attempt to counter this, some more specific searches were carried out for each review towards the end of the writing process, targeting areas of particular interest that were lacking in evidence following the broad literature search. It was also part of the reason why Google Scholar was used as the third and final search engine, where its use is generally frowned upon in a systematic setting. Scholar's breadth enabled the identification of more niche literature, and was invaluable to the construction of this thesis.

Another point that should be considered here is behaviours not discussed by this thesis. The aim herein was to provide an up-to-date review of four major behaviours within the evolution of hominids, especially in terms of biomechanical optimisation, partly to reduce the bias that running related research has attracted in recent years. However climbing, squatting, running and throwing are not the only behaviours to have shaped the modern human form, with others that although less known are likely also significant, such as load carrying and flint/ general tool making. It was beyond the scope of this project to consider more such behaviours, although it points towards obvious future research avenues following this thesis.

## **Conclusions**

In terms of concluding this work, it can certainly be said that each one of these behaviours has been practiced significantly at some point within the evolution of hominids. As modern humans stem from an arboreal ape species, climbing ability can be seen as our original biomechanical selective pressure. However the length of time since arboreality was hominins major locomotory mode (~6mya+), plus the biomechanical shift towards bipedalism and more terrestrial behaviour that has occurred since then, has altered the majority of the physiological characteristics for climbing that our ancestors likely showed. As such a lack of climbing in people today should not be considered as much of an evolutionary mismatch, as the relevant adaptations do not still exist. Running and throwing are far more recent behaviours, with the host of features identified herein all being displayed by modern humans. A lack of running and/ or regular moderate endurance activity is confidently an evolutionary mismatch, as it was such a stalwart component of the energetic hunter-gatherer lifestyle and is widely neglected today, or is practiced rather differently as is the case with running shoes. A lack of throwing itself probably doesn't constitute mismatch, although the strength and mobility benefits of regular throwing need to be explored in order to prove this. Deep prolonged squatting is

also in need of further exploration, as the current evidence points towards a behaviour with an ancient origin, that once replaced by chairs led to a host of biomechanical disorders such as lower back pain. Understanding how it affects human biomechanics is crucial in determining any health benefits to be gained from it.

Overall this thesis contrasts with other work on evolutionary mismatch as it outlines how hominins have always performed a range of different physical behaviours, and as such modern humans are anatomically highly capable athletes, not 'born for' any single activity. A lack of consistent yet varied daily physical workload- including long-distance walking, running, carrying, foraging, climbing and potentially projectile throwing- is likely the most health-damaging evolutionary mismatch facing humans today. Yet it is also the most difficult to combat due to the structure of our modern lives and the machinery we use to help us. No longer do people live within walking distance of where they work, making physically devoid transportation such as cars and trains a necessity. In addition the indoor, sheltered desk-based employment that many of us find ourselves in further reduces our physical workload. The need for 'cross training' within modern society has never been greater, including varied physical stressors fit in-between the busy modern lifestyle, such as light running, yoga, Pilates and weight lifting. Although adopting a true hunter-gatherer way of life in the 21<sup>st</sup> century is impossible, such cross training goes a long way to mimicking the same kinds of physical stressors, vastly improving the health of our species today.

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