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Locomotion in Extant and Extinct Nonhuman Hominidae: Implications for Hominin Bipedalism

Lokomoce žijících a vyhynulých nelidských Hominidae: Implikace pro bipedii homininů

Bachelor's thesis

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Poděkování:

Chtěla bych vyjádřit velké díky svému školiteli Mgr. Martinu Horovi Ph.D. za ochotu a trpělivost při vedení mé závěrečné práce.

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze,

Podpis

Abstract

The purpose of this thesis is to examine extinct and extant nonhuman Hominidae locomotion, through analysis of observational and fossil postcranial research. The extant genera reviewed were *Pongo*, *Gorilla*, and *Pan*. Knucklewalking is the primary locomotor form observed in African great apes while suspension predominates in Pongo. Less prominent are palmigrade quadrupedalism, bridging, vertical climb, scrambling, and other forms of suspensory behavior. Bipedalism, primarily assisted, is found in all examined extant apes with *Pongo* utilizing it the most. Extinct genera were selected based on the recent, thoroughgoing phylogenetic study by Pugh (2022), categorizing probable stem hominids, stem hominids, pongines, and hominines. Main forms of locomotion utilized were quadrupedalism, vertical climb, and suspensory behavior. *Kenyapithecus* and *Sivapithecus* are suggested to have used, along arboreal quadrupedalism, knucklewalking. Most of the discussed hominines, phylogenetically closest to our chimpanzee-human last common ancestor (CHLCA), have limited postcranial data and locomotion could not be concluded. *Danuvius guggenmosi*, *Lufengpithecus lufengensis*, and *Ouranopithecus macedoniensis* are thought to have employed bipedalism. *Lufengpithecus* and *Danuvius* further show signs of recently termed extended limb clambering, which along with bipedalism is a promising hypothesis for the locomotor form of the CHLCA.

Key words: Apes, bipedalism, postcranial, quadrupedalism, suspension, CHLCA

Abstrakt

Cílem této práce je analýza pohybu vyhynulých a současných nelidských Hominidae prostřednictvím publikovaných pozorování a postkraniálního fosilního záznamu. Zkoumané žijící rody byly *Pongo*, *Gorilla* a *Pan*. Nejrozšířenější formou lokomoce u afrických hominidů je kotníkochodectví a u rodu *Pongo* je to zavěšování. Dále méně častá je palmigrádní kvadrupedie, přemosťování, vertikální lezení, lpění a skákání, a další formy zavěšené lokomoce. Bipedie, především asistovaná, je využívaná u všech probíraných žijících lidoopů, přičemž u rodu *Pongo* nejvíce. Vyhynulé rody byly vybrané dle recentní, ucelené fylogenetické analýzy od Pugha (2022), kategorizované do pravděpodobných basálních hominidů, basálních hominidů, ponginů a homininů. Hlavní formou lokomoce u vyhynulých rodů byla kvadrupedie, vertikální lezení a zavěšování. *Kenyapithecus* a *Sivapithecus* mohli též využívat, vedle arboreální kvadrupedie, kotníkochodectví. Většina zmíněných homininů, nejbližších k našemu poslednímu společnému předku s šimpanzi (CHLCA), nemá dostatečná postkraniální data a lokomoci není možné popsat. U *Danuvius guggenmosi*, *Lufengpithecus lufengensis* a *Ouranopithecus macedoniensis* je možná bipedie. *Lufengpithecus* a *Danuvius* dále vykazují známky recentně kategorizovaného pohybu *extended limb clambering* což spolu s bipedií tvoří slibnou hypotézu o lokomoci CHLCA.

Klíčová slova: Lidoopi, bipedie, postkraniální, kvadrupedie, zavěšování, CHLCA

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1 Introduction

There is a longstanding debate regarding the human locomotor origins. The emergence of bipedalism is described by several evolutionary hypotheses including a knucklewalking ancestor (Makedonska & Strait, 2015), suspensory ancestor (Thorpe et al., 2007), terrestrial quadruped with climbing abilities (Prang, 2019), arboreal quadrupedal ancestor (Lovejoy et al., 2009; Prang, 2019), or even a recently proposed extended limb clamberer (Böhme et al., 2019). Whether it was a phylogenetically linear path from these hypothetical forms of movement to the habitually bipedal locomotion remains a mystery. Transitioning from the locomotion in taxonomically more basal hominids, through the chimpanzee-human last common ancestor (CHLCA), leading up to first hominins is not yet resolved. *Sahelanthropus tchadensis* (Daver et al., 2022) and *Orrorin tugenensis* (Pickford et al., 2002) are believed to be the oldest hominins to have supposedly employed habitual bipedalism. An analysis of the locomotor repertoire of phylogenetically proximate group of hominids to first hominins could ameliorate the search for possible missing links towards habitual bipedalism. Taking also into consideration stem hominid groups would enlarge the locomotor scope through which a better understanding of the CHLCA possible locomotion could emerge. Furthermore, reviewing locomotion utilized in the extant great apes, therefore, *Pan*, *Gorilla*, and *Pongo* could also serve as a valuable outline of potential CHLCA locomotor repertoire, given our genetic proximity (Mohammad-Ali et al., 1995). There is an ambiguity behind bipedal origins in terms of environment, whether it emerged in terrestrial or arboreal settings (Crompton et al., 2010; Drummond-Clarke, 2023). Viewing where set genera utilize their locomotion, in this case bipedalism, could counter this ambiguity with found data. Presenting various forms of locomotion within many groups of the nonhuman Hominidae could potentially serve as a theoretical framework for further research regarding the CHLCA and its locomotor range.

2 Goals

The goal of this thesis is to analyze locomotion of extinct and extant genera within the Hominidae family and present a general assortment of utilized locomotor forms. It will be achieved through examination of published observational studies regarding extant species, therefore *Pongo*, *Gorilla*, *Pan*. As for the extinct genera, postcranial fossil evidence with specific anatomical properties linked to certain locomotor forms will be scrutinized as well. Discussed extinct genera will be selected based on newest and most complete phylogenetic research conducted by Pugh (2022). Extinct species will be reviewed extensively due to the secondary objective of this work on detecting possible bipedal behavior appearance throughout the Hominidae evolution leading up to the chimpanzee-human split and origins of bipedalism.

3 Defining the Hominidae

The Hominidae is a taxonomic family, alternatively referred to as the great apes. It consists of four extant genera: *Homo*, *Pan*, *Gorilla*, *Pongo*, and several extinct ones. The taxonomic classification has undergone a lengthy evolution and has been a subject of debate over the past centuries. Carl von Linné stands at the beginning of this taxonomic ambiguity, placing humans among other animals and classifying them in the Quadruped class and Antropomorpha order. This order encompassed *Homo* (humans), *Simia* (apes), and *Bradypus* (sloths) (Linné et al., 1792). Eventually, he would rename both the class and the order as Mammals and Primates (Charmantier, 2020). Several naturalists, including Johann Friedrich Blumenach, disagreed with the taxonomic placement, assigning humans to the order Bimana and apes to the order Quadrumana, creating a potent barrier (Blumenach, 1825). Thomas Henry Huxley, who laid down the structural differences between humans and apes, concluded with no need of separating the two into distinct orders (Huxley, 1886). Charles Darwin concurred as well, arguing in Linné's favor, upholding the term Primates for both humans and apes (Darwin, 1889).

Until around the 1960s, humans and apes were distinctly separated within the superfamily of Hominoidea. Humans, referred to as hominids, placed in the Hominidae family, and apes, on the other hand, in the Pongidae family (Straus, 1946). New phylogenetic studies revealed a closer relationship between humans and apes, thereby classifying them in the same family, the Hominidae. With molecular advancement in the 1970s, research had shown that the genera *Homo*, *Pan*, and *Gorilla*, are genetically proximate, while orangutans stand as an outgroup in the Hominidae family (Mohammad-Ali et al., 1995). Therefore, only orangutans could be classified as pongids leading to a new division of subfamilies, the *Homininae*, with *Homo*, *Pan*, and *Gorilla* and *Ponginae* comprising *Pongo* (Goodman, 1974). Today, the consensus stands at Hominidae, a family, consisting of two subfamilies, *Homininae* and *Ponginae*. *Homininae* is further divided into two tribes, *Hominini* with *Homo* and *Pan*, and *Gorillini*, with *Gorilla* (Goodman et al., 1989).

3.1 Evolutionary Background and Hominoid Origins

There has been a long-standing debate over the origins of the primate order. Molecular data and physical fossil finds suggest different times of emergence. The molecular clock points at a much older period than fossils, the Cretaceous, therefore placing the first primate-like species as far as 90 Ma (Janecka et al., 2007). The fossil record of undisputable primates, however, stands at 56 Ma (Silcox et al., 2017), implying a large dissonance between the data. Steiper & Seiffert (2012) propose the hypothesis of convergent rate slowdown as an explanation for this discordance. Furthermore, they offer a new time of primate appearance to the K-Pg boundary. As for the physical evidence behind primate evolution, we are presented with another uncertainty due to geographical distribution of fossils. As mentioned before, primate fossil record appears at the Paleocene-Eocene boundary (56-55 Ma) coinciding with the climatic Thermal Maximum (Smith et al., 2006). Fossil discoveries of the Haplorhini, however, appeared synchronously in North America and Eurasia, proposing a question of

geographical origins (Smith et al., 2006). Smith *et al*. (2006) reference the omomyid *Teilhardina* as the oldest primate known, spanning the North American and Eurasian continent. Another Eocene Haplorhine from the infraorder Tarsiiformes is described from China (55 Mya), with a discovery of a nearly complete skeleton. Furthermore, this fossil primate narrows down the timeframe of Tarsiiformes and Anthropoidea divergence (Ni et al., 2013). The Oligocene period (34–23 Ma) is suggested by molecular data as the time of Cercopithecoidea-Hominoidea divergence, however, fossil record remains insufficient (Stevens et al., 2013).

Early Miocene (23–17 Ma) presents a favorable climatic environment in which the catarrhine primates proconsuloids, a possible ancestorial link to hominoids, thrived (Harrison, 2010). Period between ca. 17 to 15 Ma marks a warming trend referred to as the Miocene Climatic Optimum (MCO). This period of warmer climate is also accompanied by low seasonality (Methner et al., 2020), and forest expansion, which proved to be beneficial to the modern ape ancestor radiation. It is exactly during the time of MCO when the Hylobatid-Hominid divergence occurs and when undisputable hominoids appear (Pozzi et al., 2014). Around ca. 14 Ma, seasonality increased, leading to the decrease of proconsuloid diversity and resulting in cercopithecoids and hominoids becoming the prevailing taxa, largely due to their dietary and locomotor adaptations (Harrison, 2010). Gradual cooling in Mid-Miocene led to unfavorable biome changes, followed by the Vallesian Crisis (9.6 Ma) which marked a decline in forest-adapted taxa (Casanovas-Vilar et al., 2005). Most hominoids had become extinct by 5 Mya, except for the extant lineages restricted to the present-day geographical localities (Begun et al., 2012).

3.2 Fossil Record of Extinct Genera

First modern-like apes are thought to appear before the last marine transgression in Eurasia around 17 Ma at sites in Germany and Turkey (Heizmann & Begun, 2001). The classification of modern apes and their taxonomic placements remain subjects of debate, thus this thesis offers insights based on the latest research discoveries made by Pugh (2022), who distinguishes found fossil Hominidae into categories of *probable stem hominids*, *stem hominids*, *pongines*, and *hominines*. Stem hominids, in this context, constitute a paraphyletic group of extinct genera, displaying resemblance to the nearest crown group (comprising the last common ancestor and all its descendants). Both geographical and chronological data of further mentioned fossil finds are presented in Fig. 1 and detailed list of genera in Table 1.

Table 1. List arrangement of fossil apes mentioned in the text. Table is based on the work of Begun (2010) and Pugh (2022). Danuvius guggenmosi *is placed within stem hominids, but phylogeny is not yet agreed upon.*

Phylogenetic placement	Genera	Fossil find dating (Ma)	Localities of discovery
Probable stem hominids			
	Griphopithecus	16.0–16.5	Germany, Turkey
	Kenyapithecus	16.0–16.5, 13.5	Turkey, Kenya
Stem hominids			
	Dryopithecus	12.0–12.5	France
	Anoiapithecus	11.9–12.3	Spain
	Pierolapithecus	12.0	Spain
	Danuvius guggenmosi	11.6	Germany
	Hispanopithecus	10.0–11.0	Spain
	Rudapithecus	9.8–10.3	Hungary
	Lufengpithecus hudienensis	7.2–8.2	China
Pongines			
	Sivapithecus	12.5	Pakistan
	Khoratpithecus	9.0–12.5	Thailand
	Ankarapithecus	10.0	Turkey
	Indopithecus	8.9	India
	Lufengpithecus lufengensis	6.2–6.9	China
	Gigantopithecus	2.0–0.3	China
Hominines			
	Nakalipithecus	9.8–9.9	Kenya
	Ouranopithecus macedoniensis	8.7–9.6	Greece
	Ouranopithecus turkae	7.4–8.7	Turkey
	Graecopithecus	7.2	Greece

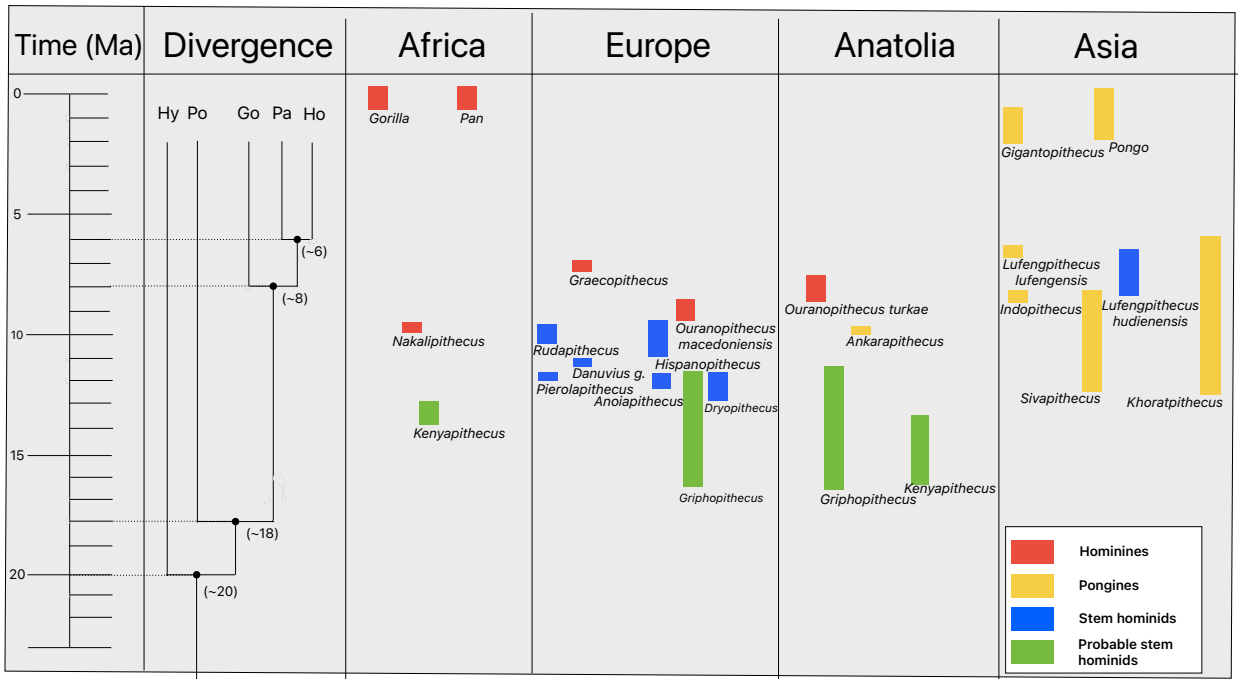

Figure 1. Geographical and chronological dispersal of fossil finds of extinct and extant nonhuman Hominidae and assumed lifespans. Figure is based on the work of Pugh (2022), added genera with alternative dating are based on Ji et al. (2013) and Böhme et al. (2019a).

The earliest modern ape fossil discovered in Eurasia is *Griphopithecus* emerging 16 to 16.5 Ma, believed to represent a stem hominid (probable) (Casanovas-Vilar et al., 2011). The first sites of its discovery are in Germany, Turkey, and later in Africa. *Kenyapithecus*, another assumed stem hominid, was discovered in both Europe and Africa as well (Kelley et al., 2008). The European *Kenyapithecus* discovery, from Paşalar in Turkey, dated around 16 to 16.5 Ma predates the African findings, from Fort Ternan in Kenya, which are approximately 13.5 milion years old (Andrews & Kelley, 2007; Begun & Geraads, 2003; Leakey, 1961).

Among the generally accepted stem hominids proposed by Pugh (2022), the first known is *Dryopithecus* believed to have appeared 12 to 12.5 Ma, discovered at the St. Gaudens site in France (Begun, 2005; Pilbeam & Simons, 1971). Initially grouped together with other apes, for instance with *Sivapithecus* (Begun, 2005), under a single genus, current discoveries suggest this categorization was incorrect. *Anoiapithecus*, another stem hominid, was found in the region of Els Hostalets de Pierola on the Iberian Peninsula, dating back to 11.9–12.3 Ma (Alba et al., 2013; Moyà-Solà et al., 2009). Both chronologically and geographically proximate to *Anoiapithecus* is *Pierolapithecus*, an ape discovered in Spain, now estimated to be 12 million years old (Pugh et al., 2023). The younger *Hispanopithecus*, also a stem hominid from the Iberian Peninsula, dates back to 10 Ma (Alba et al., 2012). Pugh (2022) and Casanovas-Vilar (2011) suggest even earlier emergence (11 Ma). In Hungary's Rudabánya site, a discovery was made of *Rudapithecus*, an ape estimated to be 9.8–10.3 million years old (Casanovas-Vilar et al., 2011). The last putative Miocene stem hominid is *Lufengpithecus hudienensis*. It is younger than the above mentioned apes, dating 7.2 to 8.2 Ma (Pan et al., 2021), discovered in southwestern China in the Yuanmou basin. *Danuvius guggenmosi* is a recently discovered Miocene

ape (dating 11.6 Ma, Germany) that has been placed within stem hominids, but needs more phylogenetic analysis for concurrence (Böhme et al., 2019). It is included, despite its uncertainty, due to the importance of found postcranial evidence.

Pongines, also referred to as Asian hominids, encompass several extinct genera and a single extant genus, *Pongo*. The oldest pongines, currently agreed upon, are *Sivapithecus* and *Khoratpithecus*. *Sivapithecus* was first unearthed in Pakistan and the findings date back circa 12.5 Ma (Kappelman et al., 1991). *Khoratpithecus* emerged between 9 and 12.5 Ma in Thailand (Chaimanee et al., 2019). A sole European pongine *Ankarapithecus* extends furthest west and was found in Turkey from deposits at Sinat Tepe and overlaps geographically with both *Dryopithecus* and *Griphopithecus* (Chaimanee et al., 2019). The *Ankarapithecus* fossils discovered date back approximately 10 million years (Begun & Geraads, 2003). *Indopithecus*, an extinct ape from India dated around 8.85 Ma (Pillans et al., 2005) was previously linked to *Gigantopithecus*, however, its distinct position is now well resolved. *Lufengpithecus* is another fossil ape that falls into the pongine category, however, only one specie. Pugh (2022) differentiates and classifies this taxa, that consists of two species, into two distinct categories. *Lufengpithecus hudienensis* among stem hominids and *Lufengpithecus lufengensis* among pongines (Pugh, 2022). The species *lufengensis* was found in the Lufeng basin in southwestern China and originated around 6.2–6.9 Ma (Ji et al., 2013). The last and probably the most renowned genus of extinct pongines, due to its enormous size, is *Gigantopithecus*. Discoveries were made in caves in southwestern China and the unearthed remains date from 2 Ma to 300 Ka, spanning the Early and Middle Pleistocene (Zhang & Harrison, 2017).

As of the extinct apes assigned to the subfamily *Homininae*, it has been concluded with three genera, the oldest of which is *Nakalipithecus*, discovered in Nakali, Kenya, from Late Miocene approximately 9.8–9.9 Ma (Kunimatsu et al., 2007). Following is another genus, *Ouranopithecus*, represented by two species. The earlier emerging *Ouranopithecus macedoniensis*, found in Greece, is dated back to 8.7–9.6 Ma (de Bonis & Koufos, 2014; Kunimatsu et al., 2007). The younger, *Ouranopithecus turkae*, from central Anatolia, is dated between 7.4 and 8.7 millions ago (Güleç et al., 2007). The last genus is *Graecopithecus*, discovered in Pyrgos Vassilissis, Greece, estimated to 7.2 Ma (Fuss et al., 2017).

The diversity of extinct ape lineages surpasses that of the extant ones. There are solely three surviving genera: *Pongo*, *Gorilla*, and *Pan*. The only one outside Africa and the sole extant member of *Ponginae* is *Pongo*, with three species, all resorted to southeastern Asia. It is also the oldest living ape, emerging around 1.2–2 Ma under the specie *P. weidenreichi* (Harrison et al., 2014; Wang et al., 2014) found at sites in China. *Pan* and *Gorilla* are both classified under the subfamily *Homininae* and are assumed to be younger, due to the lack of fossil evidence (Steiper & Young, 2006). The pongine-hominine divergence is thought to have occurred between 16-20 Ma (probably around 18 Ma) (Steiper & Young, 2006), followed by the *Gorillini-Hominini* split around 6–10 Ma (Katoh et al., 2016) and the *Pan-Homo* around 5–7 Ma (Locke et al., 2011). While *Pan* and *Gorilla* inhabit Africa, there are no

certain fossil taxa identified as members of their evolutionary lineages. The only possible fossil finds are related to the chimpanzee clade, from Kenya, traced back to Middle-Late Pleistocene (approx. 500 Ky) (McBrearty & Jablonski, 2005).

4 Locomotion forms in the Hominidae

Various forms of locomotor behavior proved to be an important ecological adaptation acquired by taxa when facing changing environments (Behrensmeyer, 2006). Late Miocene cooling brought drier climate in Western Eurasia and the subtropics, resulting in the transition from broadleaved evergreen forests to more open woodlands and C4 grasslands (Agustí et al., 2013; Herbert et al., 2016). Along with geographic transitions due to climate change, development of locomotor versatility stands at frontline in obtaining a successful and sustainable ecology (Habinger et al., 2022). Further discussed will be the locomotor and positional repertoire of the extinct and extant Hominidae genera with addition of anatomical factors linked to specific movements. Postcranial evidence is the main method of examining locomotor behavior of extinct species.

4.1 Anatomical properties

Locomotion variety in the Hominidae spans both arboreal and terrestrial environments. Along with different ecologies propelling various forms of movement, evolutionarily flexible anatomical plans are key in viewing different strategies utilized by both the extant and extinct genera. One of the significant anatomical features is the presence of either pronogrady or orthogrady in both posture and body plan (Almécija et al., 2021). The pronograde posture refers to a horizontal position of the body, or specifically the trunk, during locomotion or positional behavior. On the other hand, orthogrady is a position where the body is vertical. The orthograde body plan is scarcer among primates and includes, for example, a coccyx as a remnant of the tail, dorsoventrally shallow and mediolaterally broad rib cage, and dorsally placed scapulae (Almécija et al., 2021). The pronograde body plan contains a deep, narrow ribcage, laterally placed scapulae, and a tail as seen in Fig 2. (Almécija et al., 2021).

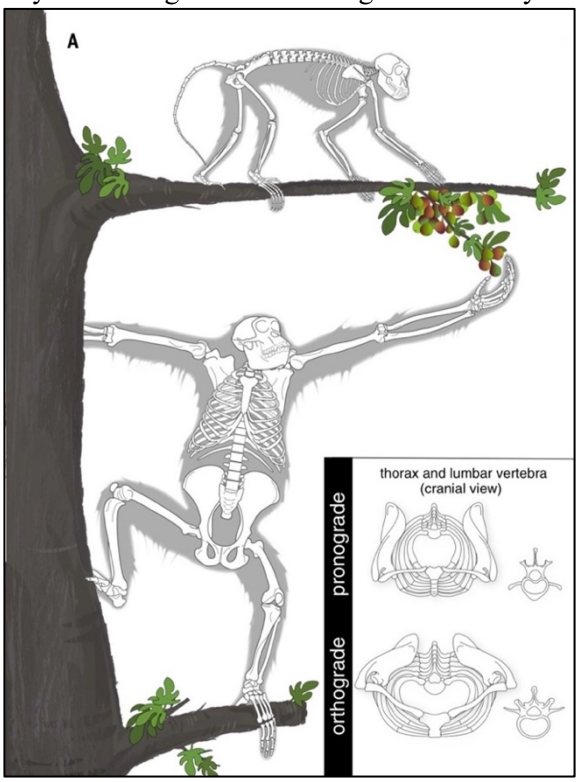

Figure 2. Pronograde (above, monkey) versus orthograde (below, ape) posture and thorax. Taken from Almécija et al. (2021).

Many primates while possessing either a pronograde or an orthograde body plan may still exhibit locomotion that extends beyond their inherent body plan. All extant great apes display an orthograde body plan (Almécija et al., 2021). The great apes share anatomical features that permit various forms of locomotion from suspensory to bipedal variants.

The hominoid torso has many properties that allow such possibilities. Compared to monkeys, apes evolved tail-lessness and possess short and broad lumbar vertebrae, three to five depending on the genus (Spear et al., 2023). This column reduction was due to sacralization (last lumbar vertebra fused with the sacrum), resulting in apes having a shorter back than the Cercopithecoidea (Spear et al., 2023). Apes therefore have 7 lumbar vertebrae, advantageous to countering buckling forces in arboreal environments (Hunt, 2016). The pelvis differs to the one of monkeys as well, being tall and broad, also resisting buckling strain and further maintaining hip extensions. The hip mobility is further characterized by factors such as rounded femoral head or shallow acetabulum (Hunt, 2016). The ape upper torso is significantly distinguishable from that of the monkeys. As further seen in Fig. 2, the ribs are tightly curved and the sternum is broad, all of which reduces stress on thorax and facilitates arm raising and force-bearing during arm-hanging (Hunt, 2016).

Hominoid forelimb and hindlimb anatomy is quite distinguishable from that of monkeys and can differ between the great ape genera. Generally, apes have elongated upper limbs compared to lower limbs (Hunt, 2016). This facilitates suspensory behavior, vertical climbing and increases foraging reach. The so called intermembral index is a forelimb-hindlimb length comparative ratio suggesting either a suspensory or quadrupedal forms of locomotion (Moyà-Solà & Köhler, 1996). Hunt (2016) suggests that owing to the expanded, globular humeral head and scapulae dorsally placed, large shoulder mobility is achieved, furthermore, the ulnar articular surface wraps around the trochlea and thus allows the body weight to be borne by bone rather than muscle, beneficial during suspension.

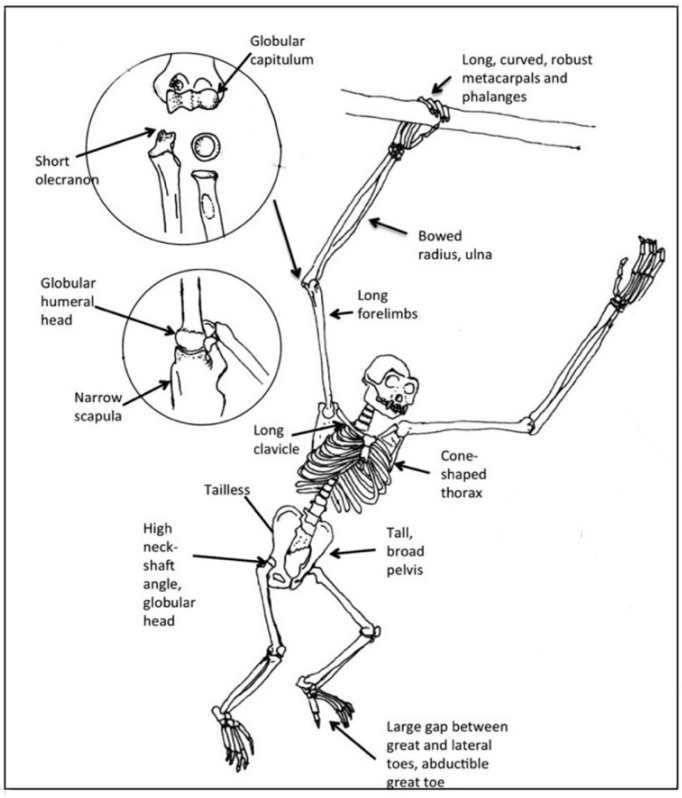

Figure 3. Anatomical scheme of a suspending great ape. Modified version taken from Hunt (2016).

The ape olecranon process is reduced, allowing full elbow extension during arm-swinging (Hunt, 2016). Great apes have the ability to pronate and supinate, allowed, for example, by the bowed

radius and ulna, and the possession of a circular radial head allowing 150 degree wrist rotation compared to 90 degrees in monkeys (Hunt, 2016; O'Connor & Rarey, 1979), depicted in Fig. 3.

The ape hand is variable and serves as a reflector of different ecologies. The phalanges and metacarpals have various degrees of curvature (See Figure 4.), more so is seen in orangutans, given their arboreal lifestyle, and less in the more terrestrial gorillas or chimpanzees (Howell, 1917; Matarazzo, 2008). Furthermore, secondary phalangeal shaft characters such as ridges are present in suspensory apes enabling muscle and tendon attachment (Almécija et al., 2007).

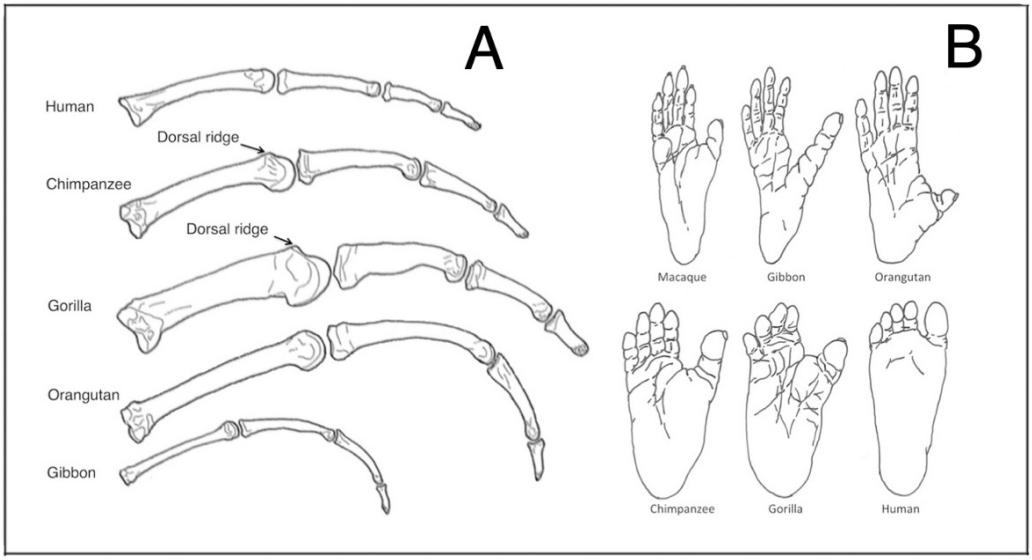

Figure 4. A: variation in primate phalangeal curvature, B: diversity in primate foot morphology with different degrees of hallux abduction. Both images taken from Hunt (2020).

Hominoid hindlimbs, as previously mentioned, are shorter than forelimbs, however, facilitate great amount of mobility and operate quite dexterously. Due to the large globular femoral head and high femoral neck-shaft angle, as presented in Fig. 3, apes achieve substantial hip mobility (Hunt, 2016). The ape foot contains an important locomotive adaptation, being the opposable hallux, enabling grasping (Schultz, 1950). The degree of big toe abduction varies within genera (Fig. 4.). As well as in the hand, finger curvature is present in hominoid feet too.

4.2 Extant Genera

As previously noted, the sole living members of the nonhuman Hominidae are orangutans (*Pongo)*, gorillas (*Gorilla)*, chimpanzees and bonobos (*Pan)*. These genera are described ahead of the extinct ones, due to the broader availability of data regarding them, most importantly due to the fact we can presently still observe them. Chapters following, are detailed in locomotion utilized by set genera, further summarized in Figure 5.

4.2.1 Pongo

The genus *Pongo* currently encompasses three species, all restricted to Southeast Asia. *Pongo pygmaeus* occupies the island of Borneo and *Pongo abelii* along with *Pongo tapanuliensis* the Sumatra

Island. *Pongo tapanuliensis* was described in 2017 (Nater et al., 2017) and thus available data is greater in the two former species. Orangutans live in lowland rain forests, inhabiting tree canopies abundant with fruit (Djojosudharmo & Schaik, 1992; Galdikas, 1988). Time spent on the ground is minimal with most activities and travel occurring high up in the canopy. However, terrestrial locomotion does occur, notably more so among males (Ashbury et al., 2015; Djojosudharmo & Schaik, 1992). The orangutan is the largest primarily tree-dwelling mammal and must operate with its substantial body mass in the canopy (Galdikas, 1988).

Suspensory behavior, precisely below-branch suspension, is the primary locomotion and posture utilized by this genus (Hunt et al., 1996). Dominating postural mode is the orthograde suspension with the use of forelimbs, often together with hindlimb compression for further support, termed orthograde clambering (Hunt et al., 1996), making up 46% of total movement in Sumatran *Pongo abelii* (Thorpe & Crompton, 2005) and 48% in Bornean *Pongo pygmaeus* (Manduell et al., 2011). Hindlimb suspension is also observed, given the anatomical property of their grasping feet, but less commonly than the forelimb variation (Cant, 1987). Furthermore, ipsilateral suspension variation has been recorded as well (Thorpe & Crompton, 2005).

Brachiation is a form of a pendulum-like movement employed during the branch-to-branch or tree-to-tree transfers and is categorized under the orthograde suspension mode. Pronograde suspension is seen as well, more so among younger individuals (Manduell et al., 2011; Thorpe & Crompton, 2005). Bridging is another locomotive form used, but scarcely seen. During bridging, orangutans suspend themselves and reach out to grasp a branch and pull their body towards it (Manduell et al., 2011). Additionally, orangutans utilize compressive pronograde postures, pressing their bodies against surfaces to navigate through confined spaces (Thorpe & Crompton, 2006), a behavior more associated with feeding rather than travelling (Manduell et al., 2011). Oscillation is another form of locomotion used by orangutans more frequently observed in the *pygmaeus* species (Manduell et al., 2011; Thorpe & Crompton, 2005). Oscillation combines tree sway and ride motion during tree-to-tree transitions (Thorpe & Crompton, 2005). Tree sway is a form of movement where the animal uses either its body weight to accumulate enough force to bend a branch one way or swings with the branch back and forth in oscillations with increasing magnitude and finally grasping the destination branch (Thorpe & Crompton, 2005). Ride is very similar to tree sway but is reserved for tree-to-ground travel. Orangutans have been recorded oscillating branches, trees, and lianas (Mackinnon, 1974).

Another significant locomotive form is climbing, encompassing both ascending and descending movements, and is not restricted to the canopy, but also utilized during ground-to-tree travel and vice-versa. Orangutans travel on the ground less frequently compared to African apes, resulting in climbing being less prevalent within the *Pongo* genus and primarily facilitating food acquisition (Thorpe & Crompton, 2005). Climbing accounts for 24% within the *P. abelii* locomotion and 8% in *P. pygmaeus* (Manduell et al., 2011; Thorpe & Crompton, 2005).

Next to suspensory locomotion, quadrupedalism as the most prevalent locomotion within the primate order is greatly observed in great apes (Rose, 1973). In the case of orangutans, it is both a terrestrial and an arboreal form of movement. Arboreal quadrupedalism on branches is exhibited more in higher levels of the canopy and during feeding rather than during travel (Thorpe & Crompton, 2005). On the ground Pongo utilizes classic palmigrade quadrupedalism (fist walk has been identified as well (Hunt et al., 1996), and occasionally adopts a tripedal walk, compressing hindlimbs and using a forelimb for additional support (Hunt et al., 1996). Orangutans do not have a defined running gait. When in danger however, quadrupedal run may be seen as well (Hunt et al., 1996).

Bipedalism, movement on two legs, is seen within this genus more often than within other great apes (Thorpe et al., 2007). Unassisted bipedalism is present but not frequently observed, however, assisted bipedalism is more commonly seen, with locomotion on hindlimb with assisted forelimb branch gripping. Some authors suggest it is a mere extension of the orthograde clamber locomotion (Thorpe & Crompton, 2005), others define assisted bipedalism as a distinct form of travel, specifically within the canopy. Thorpe & Crompton (2006) in their study find *P. pygmaeus* to use bipedalism in 2% of total locomotion and assisted bipedalism in 6%. In contrast, Manduell et al. (2011) suggest 0.1% and 3.1%.

4.2.2 Gorilla

The *Gorilla* genus constitutes of two species, the western gorilla (*Gorilla gorilla*), and the eastern gorilla (*Gorilla beringei*). Furthermore, the eastern gorilla subdivides into the mountain and lowland gorillas and the western gorilla into lowland and cross river gorillas (Thompson, 2021). The localities of the two species are separated by the Congo River, where the western gorilla occupies west central Africa and the eastern gorilla the eastern part. Habitat distribution is various, especially in terms of elevation ranges (Sarmiento, 2002). However, it is the subtropical and tropical forests biomes this genus inhabits. Gorillas are considered to be the most terrestrial of the nonhuman Hominidae (Fuh et al., 2022; E. Sarmiento, 1994). Arboreal travel is mainly reserved for food acquisition, and is more prevalent within female and immature gorillas (Hunt, 2016).

A gorilla's primary form of locomotion is quadrupedalism, specifically knuckle-walking which can be seen in the *Pan* genus as well (Kivell & Schmitt, 2009). Given gorillas' dominant terrestrial ecology, quadrupedalism makes up the majority of observable locomotion, with approximately 96% (Doran, 1997). In this percentage, quadrupedalism, movement employing all four limbs, encompasses knuckle-walking (sometimes fist-walking) and palmigrade quadrupedalism, present in both terrestrial and less frequently arboreal environments. Palmigrade quadrupedalism, moving on palms, is frequently seen within infants (Doran, 1997). The dominating knuckle-walking, with 85% of total quadrupedal locomotion, is primarily in adult gorillas (Doran, 1997). Knuckle-walking is a form of movement where the forelimbs bare weight on the dorsal side of middle phalanges (II-V) (Tuttle, 1967). As opposed to the Chimpanzee form of knucklewalking with an

extended wrist posture, gorillas utilize a “columnar” form, with the hand and wrist joins aligning in a straight, neutral position (Kivell & Schmitt, 2009).

As mentioned before, arboreality is observable, and more so within the western lowland gorillas (Tocheri et al., 2011). Gorillas utilize quadrumanous climbing, in both ascend and descend. Furthermore, gorillas utilize scrambling and bridging, as well (Doran, 1997). Scrambling is a form of movement with unpatterned gaits, combining varying combinations of climbing and crawling, generally used to maneuver difficult areas (Hunt et al., 1996). Climbing is the second most utilized form of locomotion and accounts for approximately 20% of arboreal locomotion (Doran, 1997; Remis, 1995). Suspensory behavior is not common, nonetheless suspension can be observed in females and juveniles (Remis, 1995). Lastly, both unassisted and assisted bipedalism is seen within this genus. Less so than in orangutans, and mainly used as a means to show dominance, or carry objects (Hunt, 2016).

4.2.3 Pan

Panins comprise of two extant species, the *Pan troglodytes* and *Pan paniscus*. Both species are sub-Saharan natives but occupy different localities. *Pan paniscus*, also called bonobo, spans the Congo Basin south of the Congo river and inhabits moist, mixed, forests and forest-savanna mosaics, in elevations ranging between 300 and 700 m (Fruth et al., 2016). *Pan troglodytes*, the chimp, is found in both central and western Africa. Chimpanzees live in lowland, swamp, dry, submontane and montane forests and also in savanna woodlands (Humle et al., 2017). The *Pan* genus is quite terrestrial but arboreal environments are more prominent. Nest building is typically arboreal, for instance (Tédonzong et al., 2020).

Chimpanzees, like gorillas, utilize quadrupedal locomotion the most. It accounts for about 77% of their locomotor behavior (Sarringhaus et al., 2014), and some authors state even more (Hunt, 1992). Within this locomotor form, palmigrade quadrupedalism and knucklewalking is frequently observed. As compared with the knucklewalking form seen in gorillas, chimpanzees have a less columnal arm position and a more extended wrist (Püschel et al., 2020). To reach food or nests that are located high in the canopy, vertical climb and further descent is observable within this genus as well (Henke & Tattersall, 2015; Sarringhaus et al., 2014). Suspensory locomotion is seen with postural orthograde suspension as the most prominent, along with the lesser utilized clambering and brachiation (Hunt, 1992). Chimpanzee infants are found is this postural-locomotive mode very frequently (Sarringhaus et al., 2014). Bipedalism, with 1.8% occurrence, is seen within the chimpanzee locomotor spectrum as well with hand-assisted flexed bipedal walk as the most common, followed by hand-assisted bipedal scramble (Sarringhaus et al., 2014). Infants are the ones who walk bipedally the most with about 6% of total locomotive occurrence (Sarringhaus et al., 2014). Bridging, dropping, ride and sway are all locomotor forms that are utilized, but all together account for about 4% of total movement (Sarringhaus et al., 2014).

Bonobos, as compared to chimpanzees, are more arboreal (Doran, 1993), therefore, most studies and observed data cover arboreal environment rather than terrestrial. Most frequently observed form of locomotion within this specie is arboreal quadrupedalism and vertical climb and descent (Susman et al., 1980). Within the canopy, bonobos move quadrupedally utilizing palmigrade quadrupedalism (Doran, 1993). On the ground, knucklewalking can be observed as well and is like the form seen in chimpanzees. Climbing is one of the most prominent bonobo locomotor forms with approximately 48% of overall movement (Doran, 1993). Suspensory locomotion is more frequent in bonobos than chimpanzees and bipedalism is less frequent in bonobos with a about 1.3% occurrence, therefore 0.5% less than chimps (Doran, 1993). Leaping is another locomotor behavior more frequently seen in bonobos than chimpanzees with about 3.8% (Doran, 1993). Leaping is a form of movement where the body is abruptly propelled off the ground, followed by suspension, and then landing again (Demes et al., 1995).

4.3 Extinct Genera

The extinct members of the Hominidae have been introduced in previous chapters. Fossil finds have been discovered, but due to the inability to observe exact movements utilized by these species, anatomical indications serve as the only possible clue to determine locomotor forms which had been used. These anatomical properties are compared with other fossil finds and extant primates to assemble a valid hypothesis for locomotor behavior. Following descriptive chapters, is Figure 5 summarizing employed locomotion.

4.3.1 Probable Stem Hominids

There is not much available fossil data that would enable extensive analysis of locomotor versatility of the *Griphopithecus* genus. The only indications have been assessed from the Paşalar site in Turkey (Kelley et al., 2008). Number of phalanges have been discovered and based on their curvature and width/height index evaluated as non-suspensory, given greater height and robustness. Furthermore, there is a non-cercopithecoid-like dorsal side expansion of the proximal articular surface of the proximal phalanges indicating pronograde quadrupedalism (Ersoy et al., 2008).

Kenyapithecus has more postcranial evidence and thus better chance at interpretation. Owing to fossil discoveries in Maboko and Nachola, Kenya, there are possible locomotor patterns that could be assigned to this genus (Rose et al., 1996). Hominoid-like features of *Kenyapithecus* include its humeral properties like the size of the humeral head, the bone's gracility, or great shoulder joint mobility. These properties suggest scansorial movements, with forelimb-dominated forms, such as vertical climbing, or hoisting (Mccrossin et al., 1998). Hoisting refers to raising the body upwards using arms and grasping hands. Furthermore, anatomically similar to the *Pan* or *Gorilla* genus, the distal radioulnar joint and the metacarpophalangeal joint suggest knuckle-walking ability (Mccrossin

et al., 1998). Overall, *Kenyapithecus* can be concluded as a primarily arboreal quadruped, including some suspensory locomotor forms, with semi-terrestrial lifestyle (Nakatsukasa, 2004).

4.3.2 Stem Hominids

Postcranial discoveries of *Dryopithecus* are limited. Owing to that fact, pronogrady versus orthogrady cannot be concluded. Nevertheless, fossil finds from Saint-Gaudens propose various locomotor forms. Above-branch quadrupedalism remains as the dominant movement with supporting arguments of proximal projection of the greater trochanter or rounded femoral head with deep articular surface aiding hindlimb abduction (Pina et al., 2019). Suspensory behavior remains unresolved with no exact adaptations discovered (Alba et al., 2011), furthermore, secondary shaft characters on phalanges associated with suspension, such as ridges, pits or scars showing ligament and muscle attachment, were not found either (Begun, 1994). Some authors, however, still believe suspensory activities were present (Böhme et al., 2019b). As opposed to extant great apes, *Dryopithecus* has a long, curved, muscular pollical phalanx suggesting great grasping capabilities associated with cautious vertical climbing (Almécija et al., 2012).

Pierolapithecus has been discovered at the beginning of the century with about 80 bones allowing a reconstruction of a largely complete body plan (Moyà-Solà et al., 2004). It has been concluded that this genus possessed an orthograde body plan based on the degree of rib curvature, clavicle length, or the morphology of the lumbar region, all suggesting broad and shallow thorax (Moyà-Solà et al., 2004). Phalanges and metacarpals are relatively short but show signs of power-grasping capabilities with the assistance of the pollex or hallux (Moyà-Solà et al., 2004). Furthermore, phalanges are not curved and thus this genus does not conclude as suspensory, but some forms of this locomotion are possible (Deane & Begun, 2010). A patella has been found and associated with that of great apes, suggesting knee joint mobility associated with climbing (Pina et al., 2014). With all factors brought into consideration, this genus is concluded to be somewhat between an above-branch quadruped and a suspensory ape, with an orthograde body plan (Deane & Begun, 2010). It is proposed that forms of vertical climbing had been utilized (Moyà-Solà et al., 2004). Below-branch suspensory behaviors are unresolved. The anatomical properties of the phalanges and metacarpals do not support suspensory movements, but some authors believe they were present based on its positional behavior (Deane & Begun, 2008).

Hispanopithecus, like *Pierolapithecus*, has been concluded to possess an orthograde body plan with a broad, shallow thorax, and a rigid lumbar region. Its long, compressed acromion process and craniocaudally compressed ribs support this body plan (Alba, 2012). A straight humerus and a curved radius and ulna suggest versatile movement such as pronation, abduction, and flexion, all of which is associated with suspension and vertical climbing (Moyà-Solà & Köhler, 1996). Above branch quadrupedalism is, however, still at forefront in this genus' locomotor repertoire. The phalangeal shafts exhibit insertions indicating powerful grasping capabilities (Almécija et al., 2007) . The large femoral head in comparison to the neck and shaft also propose great hip mobility (Moyà-Solà &

Köhler, 1996). Lastly, the intermembral index, which compares the length of forelimbs and hindlimbs and expresses a ratio indicating an either arboreal suspensory or quadrupedal lifestyle, is high, and thus proposes suspensory adaptations for this genus (Moyà-Solà & Köhler, 1996). *Hispanopithecus* is one of the oldest hominoids with an orthograde body plan with below-branch suspensory capabilities (Alba, 2012).

The recently discovered *Danuvius guggenmosi* has sufficient postcranial evidence and thus its locomotor repertoire can be assessed. This genus has diaphragmatic vertebra placement with a longer lumbar region, aiding with placing the center of mass over the extended hips, knees, and feet (Böhme et al., 2019). This anatomy suggests some form of bipedalism given the possibility of hip and knee extension and orthograde body plan but further analysis must be done to conclude (Williams et al., 2020). The upper limb is adapted for below-branch suspensory behavior as well. Danuvius further possesses a grasping hallux and curved phalanges. Böhme et al. (2019) proposes extended limb clambering as a unique locomotor form extensively utilized by this genus. It combines patterns of orthograde suspension as well.

Rudapithecus has limited fossil data available, but an extensive analysis of a partial pelvis from Hungary has been conducted and further observation of several other postcranial bones enabled locomotor reconstruction (Ward et al., 2019). Ward (2019) suggests the bone morphology proposes an orthograde body plan. With a great hip, elbow, and wrist mobility, *Rudapithecus* is thought to resemble the range of motion typical for orangutans (Ward et al., 2019). A shallow acetabulum and thus less coverage of the femoral head enables this great hip mobility (Hammond, 2014). The elbow with trochlea and capitulum separated by *zona conoidea* and a medially-projecting medial epicondyle enables a plethora of positions the ape could adopt (Ward et al., 2019). Supination and pronation were possible as well (Begun, 1992). Furthermore, *Rudapithecus* had long, curved, ridged phalanges (Begun, 1992). Altogether, there is a clear indication for below-branch suspensory behavior along with vertical climbing, given the phalangeal morphology grasping capabilities, and bridging (Ward et al., 2019). Above branch quadrupedalism had been utilized as well (Ryan et al., 2012). Unlike extant great apes, *Rudapithecus* has a more flexible lower lumbar region, suggesting when on ground, could move in a more upright position that them, however, more fossil data is needed to address hypothetical forms of bipedalism within this genus' locomotor repertoire (Ward et al., 2019).

Lufengpithecus hudienensis has scarce cranial fossil evidence. Furthermore, its own taxonomical classification is relatively new (Qi et al., 2006). More available data regarding the postcranium and locomotion is known of the *Lufengpithecus lufengensis* specie.

Anoiapithecus, one of the extinct hominids found on the Iberian Peninsula, has got no postcranial evidence that would suggest any form of locomotor repertoire, thus this genus remains unresolved (Miguel, 2016).

4.3.3 Pongines

Sivapithecus, the long-debated genus in terms of phylogenetic placement, is thought to had been both arboreal and terrestrial. Cranially, it resembles the genus *Pongo*, postcranially it differs (Begun & Kivell, 2011). Proximally it appears to have terrestrial Cercopithecoid anatomical properties, distally arboreal suspensory ones (Begun & Kivell, 2011). Two humeri were discovered, one described as robust, medially inclined, with flat deltoid plane and no torsion, the other slender, with straight lateral side and no indication of a flat deltoid plane (Moyà-Solà & Köhler, 1996). Furthermore, its' thorax is mediolaterally compressed. Both quadrupedalism, more probable pronograde, and suspensory behavior are a valid hypothesis regarding the locomotor repertoire. Vertical climbing has been suggested as well (Moyà-Solà & Köhler, 1996). Newer studies, however, add knuckle-walking as another possibility. Based on the discovered carpal bones, similarities with African apes were proposed. An analysis of the capitate and hamate, two carpal bones, has been conducted and supports the knuckle-walking argument (Begun & Kivell, 2011). The capitate morphology is like that of a primitive hominid, with low mobility and possible compressive loading abilities. Furthermore, in terms of size, it resembles that one of *Pan* or *Gorilla* (Begun & Kivell, 2011). Overall, the locomotor and positional behavior of *Sivapithecus* remains unresolved with further data necessary for classification.

Khoratpithecus, a hominoid from Thailand and Myanmar, has been described from several cranial fossil discoveries. Postcranial data is missing and thus locomotor behavior cannot be concluded. Based on available cranial data, however, this genus closely resembles the extant *Pongo* (Chaimanee et al., 2006).

The same goes for *Indopithecus*, a hominoid from India. No sufficient postcranial data and therefore, no clear locomotor behavior. Based on its predicted size however, terrestrial lifestyle is highly probable (Patnaik et al., 2014).

Ankarapithecus has scarce evidence as well. The only postcranial features unearthed are one radius and two distal fragments of phalanges. It has been debated that overall, this genus exhibits rather non-hominoid like characteristics such as straight phalanges with poor curvature and ridge development (Andrews, 2004). It has been proposed that *Ankarapithecus* was probably both an arboreal and terrestrial pronograde quadruped. Suspensory behavior was not present (Andrews, 2004)

Lufengpithecus lufengensis is limited in fossil evidence likewise, but more data is available than the few above mentioned genera. This genus is thought to perform suspensory behavior based on found proximal phalanx which resembles that of *Pongo*, in both curvature, shape, and articular morphology (Kelley, 2002). Furthermore, later found scapula, clavicle, and radius support this argument as well. It is evident *Lufengpithecus* had great hip mobility based on the proximal femur and distal first metatarsal anatomy (Kelley, 2002). Grasping capabilities were prominent as well. Altogether this genus' locomotor variety includes forelimb suspension, vertical climbing, above-branch quadrupedalism, clambering, and even possibly above-branch bipedalism, based on a recent

analysis of discovered bones of the inner ear (Zhang et al., 2024).

Lastly, *Gigantopithecus*, thought to be the greatest in size of all hominoids in history, is also solely known from several mandibles and teeth. The search for postcranial material is extensive, but unsuccessful so far. Therefore, there is no certainty about this genus' locomotion. However, the proposed diet based on the discovered teeth and the enormous body size would suggest terrestrial lifestyle (Zhang et al., 2024).

4.3.4 Hominines

Nakalipithecus, discovered in Nakali, Kenya, is known from dental fossils and postcranium has not yet been discovered. Locomotion is therefore not possible to determine. Based on the data available, this hominine is believed to be related to the younger *Ouranopithecus* and thus serves as a link between Late Miocene African hominids and Eurasian ones (Begun, 2009). Another hypothesis proposes *Nakalipithecus* as the basal genus of the gorilla lineage (Katoh et al., 2016).

Ouranopithecus macedoniensis was discovered in Greece and for a long time only known from cranial elements. The first postcranial finds, two phalanges, were unearthed only recently. The found phalanges are short, robust, and with low curvature. Furthermore, ridges for muscle attachment are poorly developed suggesting no suspension, climbing, or any significant grasping capabilities (de Bonis & Koufos, 2014). When compared to African knucklewalkers, differences are apparent as well, such as more dorsally flexed hand and short phalangeal ridges. The locomotor form utilized by this genus could be terrestrial quadrupedalism, but some form of bipedalism is being considered as well (de Bonis & Koufos, 2014). For clarification, more data must be assessed. *Ouranopithecus turkae* has no postcranial data available and thus cannot be surely determined, although similar locomotor forms to *O. macedoniensis* are predicted (Güleç et al., 2007).

Graecopithecus, considered to be an important piece in the African ape-*Homo* lineage, has got no postcranial fossil finds and locomotion is thereby, unfortunately, not assessable (Fuss et al., 2017)

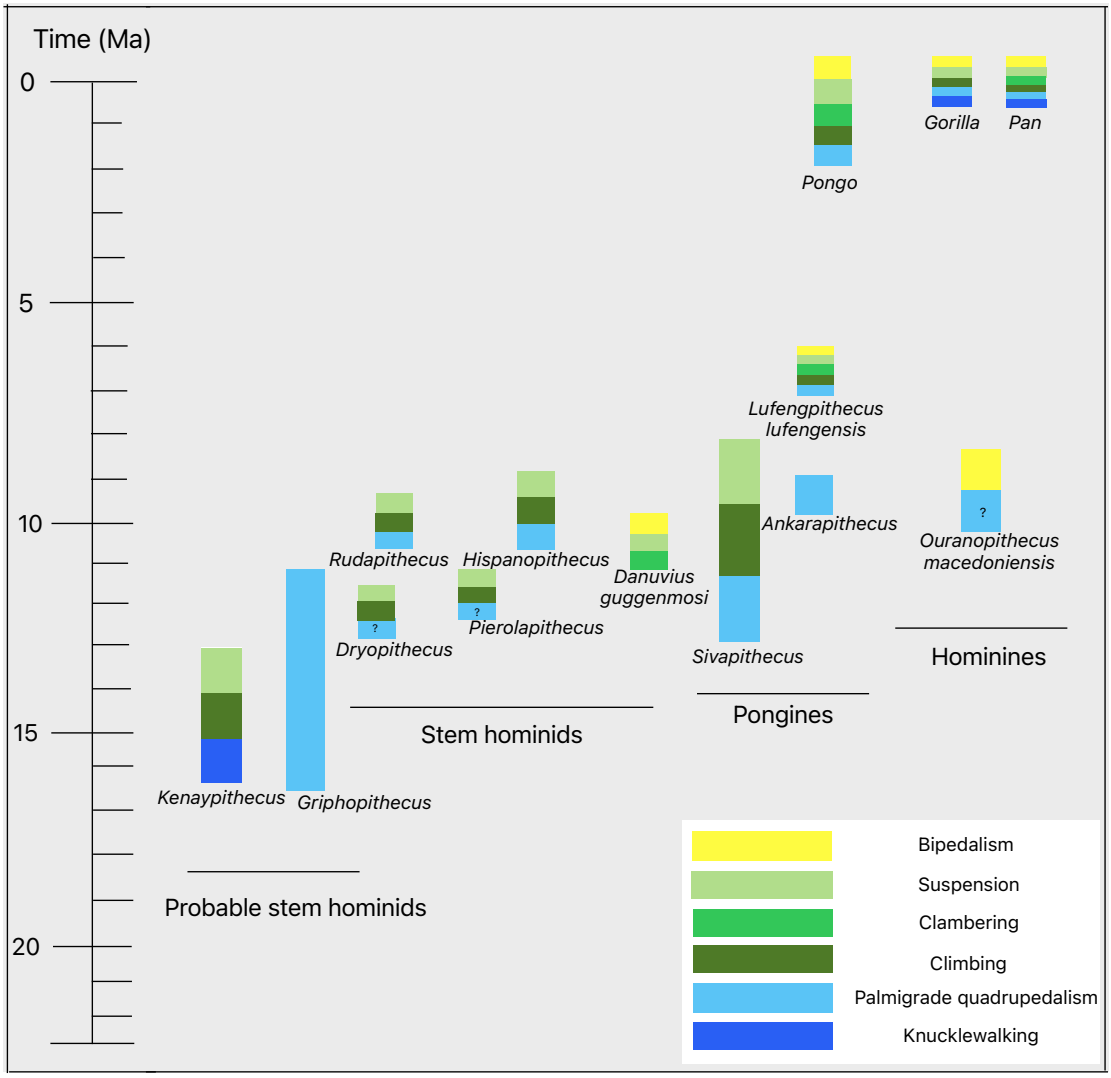

Figure 5. Color-coded representation of main forms of locomotion utilized within both extinct and extant nonhuman Hominidae.

4.4 Implications for Hominin Bipedalism

There are many hypotheses regarding the origin of bipedalism and from which locomotor form it developed. Some propose it evolved from knucklewalking, given our closest ape relatives (*Pongo*, *Gorilla*) who utilize this form of movement (Makedonska & Strait, 2015). Others suggest a generalized terrestrial quadrupedalism and climbing (Prang, 2019), arboreal bipedalism and suspension (Thorpe et al., 2007), or recently proposed extended limb clambering (Böhme et al., 2019).

The knucklewalking theory has long been debated, but many paleoanthropologists today do not support it given other more plausible hypotheses and newer fossil data, such as probable mobile lower back region, as opposed to the rigidity found in extant African apes (Lovejoy, 2009). The human vertebral spinous process morphology is also like that of the extinct *Pierolapithecus* and transitional vertebra placement similar to Orangutans, rather than to the African apes (Machnicki & Reno, 2020). Generalized palmigrade terrestrial quadrupedalism, as another possible origin theory, is proposed based on the *Ardipithecus ramidus* (considered bipedal) foot fossil and its similarity to the African ape foot with retained arboreal adaptations such as grasping capabilities (Prang, 2019).

Many researchers lean towards the arboreal bipedal and suspensory chimpanzee-human last common ancestor (CHLCA), given the fact *Pongo* is the most bipedal of all extant great apes. Furthermore, first bipedal Hominin genera are still adapted to arboreal lifestyle (Stamos & Alemseged, 2023). The recently discovered *Danuvius guggenmosi* is thought to have used extended limb clambering as a dominant locomotor mode and it is proposed as a missing link, having adaptations for both bipedalism and suspension (Böhme et al., 2019). Further research is needed to concur this locomotor scheme, however. Recent discoveries have also suggested *Lufengpithecus*-like locomotor repertoire as representative of the possible CHLCA (Zhang et al., 2024). This proposes orthograde posture with forelimb-dominated suspension, vertical climbing and clambering, and possibly above-branch bipedalism (Zhang et al., 2024).

Paleoanthropologists are pulling away from the initial savannah hypothesis and its treeless grassland evolutionary pressures aiming at bipedalism (Harcourt-Smith, 2010). Arboreal origin of bipedalism is based on fossil data of both extinct apes and first hominins who retained several arboreal adaptations (Drummond-Clarke, 2023). Along with *Lufengpithecus*, *Ouranopithecus macedoniensis*, categorized under hominines, is considered bipedal at times as well, but differing from locomotive forms of both African apes and suspensory apes (de Bonis & Koufos, 2014). Phylogenetically closest hominines and their locomotor variety could ameliorate potential evolutionary direction towards the CHLCA and its employed locomotor behavior, however, more postcranial data must be obtained. Among extant great apes, all show bipedalism, mostly in the form of assisted bipedalism above branches (Crompton et al., 2010).

Conclusively, it is apparent that with the arrival of bipedalism, it was a mosaic-like repertoire of several different locomotor forms and postures, both arboreal and terrestrial, like it is with all above-mentioned Hominidae (Harcourt-Smith & Aiello, 2004). The ancestral mosaic-like form of locomotion is still disputed, however, comparing extinct ape genera and the genera close to the CHLCA, therefore *Sahelanthropus tchadensis* and *Orrorin tugenensis*, we can see several overlaps in terms of locomotion variety. Newest studies suggest that both *Sahelanthropus* and *Orrorin* were habitually bipedal, with the latter more certainly (Daver et al., 2022; Pickford et al., 2002). *Sahelanthropus tchadensis* is older and thus closer to the chimpanzee-human divergence and the origins of bipedalism (Macchiarelli et al., 2020). New fossil discoveries suggest that *Sahelanthropus* was habitually bipedal in terrestrial environments yet retained adaptations for arboreal lifestyle (Daver et al., 2022). Specifically, it is believed that this genus manifested both pronograde and orthograde clambering along with bipedalism. Quadrupedalism is ruled out within these new studies (Daver et al., 2022). Based on the extinct genera mentioned in this thesis, closest ones to this *Sahelantropus*-like form of locomotion are *Lufengpithecus* and possibly *Danuvius*. Both genera are primarily arboreal with possible bipedal forms of movement above branches, which could be associated with locomotion seen in *Sahelanthropus*, who employed habitual bipedalism within its more terrestrial environment.

This sheds light on possible environmental origin of bipedalism, therefore being arboreal, and further down in evolution employed terrestrially.

5 Conclusion

This thesis sought to examine locomotor diversity in extinct and extant nonhuman Hominidae, utilizing postcranial fossil record as the main reconstruction tool. Extinct genera based on the phylogenetic work of Pugh (2022) were analyzed through anatomical properties linked to specific locomotive forms. Extant genera were primarily described based on published observational research. African great apes predominantly utilized knucklewalking with occasional employment of palmigrade quadrupedalism, vertical climb, scrambling, leaping, clambering, bridging, ride, and sway. Bipedalism was recorded within both *Gorilla* and *Pan*, commonly in the form of assisted bipedalism, but not as frequently as in *Pongo*. The *Pongo* genus further exhibits quadrupedalism, orthograde clambering, brachiation, bridging, oscillation, sway, ride, and climbing.

Determining extinct Hominidae locomotion is challenging due to limited fossil data, but forms of quadrupedalism, vertical climb, and suspension has been concluded. Probable stem hominids showed signs of pronograde quadrupedalism, vertical climbing, and even possible knucklewalking within the *Kenyapithecus* genus. Most stem hominids utilize above-branch quadrupedalism, vertical climbing, and forms of suspensory behavior, all concluded within *Hispanopithecus*, and *Rudapithecus*. The recently discovered *Danuvius guggenmosi* is thought to have been bipedal and utilized extended limb clambering. Pongines are thought to have used pronograde quadrupedalism, suspensory behavior, and vertical climbing. Furthermore, clambering and even possibly bipedalism was suggested for *Lufengpithecus lufengensis* and knucklewalking for *Sivapithecus*.

Hominines have limited postcranial data and thus locomotor variety could not be determined for *Nakalipithecus* nor *Graecopithecus*. *Ouranopithecus,* however, showed signs of terrestrial quadrupedalism and bipedalism. Based on new postcranial findings and proposed locomotor repertoire of *Sahelanthropus tchadensis*, a genus closely related to the chimpanzee-human last common ancestor (CHLCA), *Lufengpithecus* and *Danuvius,* appear as the most similar. Both *Lufengpithecus* and *Danuvius* exhibit forms of bipedalism and clambering which are thought to have been the main locomotor forms of the CHLCA. *Sahelanthropus* is described as habitually bipedal while retaining arboreal traits. *Lufengpithecus* and *Danuvius*, both arboreal, exhibit similar locomotive forms as *Sahelanthropus*, with the environmental distinction of arboreal-terrestrial habitats. Therefore, this presents a possible environmental model of bipedal origins. Described hominines (*Nakalipithecus, Graecopithecus, Ouranopithecus*), phylogenetically closest to the CHLCA, lack sufficient postcranial data and cannot serve as the linking trajectory towards bipedalism.

6 References

Agustí, J., Cabrera, L., & Garcés, M. (2013). The Vallesian Mammal Turnover: A Late Miocene record of decoupled land-ocean evolution. *Geobios*, *46*(1–2), 151–157. https://doi.org/10.1016/j.geobios.2012.10.005

Alba, D. M. (2012). Fossil apes from the vallès-penedès basin. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(6), 254–269. https://doi.org/10.1002/evan.21312

Alba, D. M., Almécija, S., Casanovas-Vilar, I., Méndez, J. M., & Moyà-Solà, S. (2012). A Partial Skeleton of the Fossil Great Ape Hispanopithecus laietanus from Can Feu and the Mosaic Evolution of Crown-Hominoid Positional Behaviors. *PLoS ONE*, *7*(6), e39617. https://doi.org/10.1371/journal.pone.0039617

Alba, D. M., Fortuny, J., Pérez de los Ríos, M., Zanolli, C., Almécija, S., Casanovas-Vilar, I., Robles, J. M., & Moyà-Solà, S. (2013). New dental remains of Anoiapithecus and the first appearance datum of hominoids in the Iberian Peninsula. *Journal of Human Evolution*, *65*(5), 573–584. https://doi.org/10.1016/j.jhevol.2013.07.003

Alba, D. M., Moyà-Solà, S., & Almécija, S. (2011). A partial hominoid humerus from the middle miocene of Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). *American Journal of Physical Anthropology*, *144*(3), 365–381. https://doi.org/10.1002/ajpa.21417

Almécija, S., Alba, D. M., & Moyà-Solà, S. (2012). The thumb of Miocene apes: New insights from Castell de Barberà (Catalonia, Spain). *American Journal of Physical Anthropology*, *148*(3), 436–450. https://doi.org/10.1002/ajpa.22071

Almécija, S., Alba, D. M., Moyà-Solà, S., & Köhler, M. (2007). Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: First steps towards great ape suspensory behaviours. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1624), 2375–2384. https://doi.org/10.1098/rspb.2007.0750

Almécija, S., Hammond, A. S., Thompson, N. E., Pugh, K. D., Moyà-Solà, S., & Alba, D. M. (2021). Fossil apes and human evolution. *Science*, *372*(6542), eabb4363. https://doi.org/10.1126/science.abb4363

Andrews, P. (2004). Geology and Paleontology of the Miocene Sinap Formation, Turkey. *Journal of Human Evolution*, *46*(5), 645–646. https://doi.org/10.1016/j.jhevol.2004.02.001

Andrews, P., & Kelley, J. (2007). Middle Miocene Dispersals of Apes. *Folia Primatologica; International Journal of Primatology*, *78*, 328–343. https://doi.org/10.1159/000105148

Ashbury, A. M., Posa, M. R. C., Dunkel, L. P., Spillmann, B., Atmoko, S. S. U., Van Schaik, C. P., & Van Noordwijk, M. A. (2015). Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan. *American Journal of Primatology*, *77*(11), 1216–1229. https://doi.org/10.1002/ajp.22460

Begun, D. R. (1992). Phyletic diversity and locomotion in primitive European hominids. *American Journal of Physical Anthropology*, *87*(3), 311–340. https://doi.org/10.1002/ajpa.1330870307

Begun, D. R. (1994). Relations among the great apes and humans: New interpretations based on the fossil great ape Dryopithecus. *American Journal of Physical Anthropology*, *37*(S19), 11–63. https://doi.org/10.1002/ajpa.1330370604

Begun, D. R. (2005). Sivapithecus is east and Dryopithecus is west, and never the twain shall meet. *Anthropological Science*, *113*(1), 53–64. https://doi.org/10.1537/ase.04S008

Begun, D. R. (2009). Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. *Geodiversitas*, *31*(4), 789–816. https://doi.org/10.5252/g2009n4a789

Begun, D. R. (2010). Miocene Hominids and the Origins of the African Apes and Humans. *Annual Review of Anthropology*, *39*(1), 67–84. https://doi.org/10.1146/annurev.anthro.012809.105047

Begun, D. R., & Geraads, D. (2003). Dispersal patterns of Eurasian hominoids: Implications from Turkey. *Deinsea*, *10*.

Begun, D. R., & Kivell, T. L. (2011). Knuckle-walking in Sivapithecus? The combined effects of homology and homoplasy with possible implications for pongine dispersals. *Journal of Human Evolution*, *60*(2), 158–170. https://doi.org/10.1016/j.jhevol.2010.10.002

Begun, D. R., Nargolwalla, M. C., & Kordos, L. (2012). European Miocene Hominids and the Origin of the African Ape and Human Clade. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(1), 10–23. https://doi.org/10.1002/evan.20329

Behrensmeyer, A. K. (2006). Climate Change and Human Evolution. *Science*, *311*(5760), 476–478. https://doi.org/10.1126/science.1116051

Blumenach, J. F. (1825). *A manual of the Elements of Natural History*. W. Simpkin & R. Marshall.

Böhme, M., Spassov, N., Fuss, J., Tröscher, A., Deane, A. S., Prieto, J., Kirscher, U., Lechner, T., & Begun, D. R. (2019a). A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature*, *575*(7783), 489–493. https://doi.org/10.1038/s41586-019-1731-0

Cant, J. G. H. (1987). Positional behavior of female bornean orangutans (*Pongo pygmaeus*). *American Journal of Primatology*, *12*(1), 71–90. https://doi.org/10.1002/ajp.1350120104

Casanovas-Vilar, I., Alba, D. M., Garcés, M., Robles, J. M., & Moyà-Solà, S. (2011). Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences*, *108*(14), 5554–5559. https://doi.org/10.1073/pnas.1018562108

Casanovas-Vilar, I., Moyá-Solá, S., Agustí, J., & Köhler, M. (2005). The geography of a faunal turnover: Tracking the vallesian crisis. In A. M. T. Elewa (Ed.), *Migration of Organisms* (pp. 247–300). Springer-Verlag. https://doi.org/10.1007/3-540-26604-6_9

Chaimanee, Y., Lazzari, V., Chaivanich, K., & Jaeger, J.-J. (2019). First maxilla of a late Miocene hominid from Thailand and the evolution of pongine derived characters. *Journal of Human Evolution*, *134*, 102636. https://doi.org/10.1016/j.jhevol.2019.06.007

Chaimanee, Y., Yamee, C., Tian, P., Khaowiset, K., Marandat, B., Tafforeau, P., Nemoz, C., & Jaeger, J. (2006). *Khoratpithecus piriyai* , a Late Miocene hominoid of Thailand. *American Journal of Physical Anthropology*, *131*(3), 311–323. https://doi.org/10.1002/ajpa.20437

Charmantier, I. (2020, September 3). *Linnaeus and Race*. The Linnean Society. https://www.linnean.org/learning/who-was-linnaeus/linnaeus-and-race

Crompton, R. H., Sellers, W. I., & Thorpe, S. K. S. (2010). Arboreality, terrestriality and bipedalism. *Philosophical Transactions: Biological Sciences*, *365*(1556), 3301–3314.

Darwin, C. (1889). *The Descent of Man and Selection in Relation to Sex* (New edition, revised and augmented, Vol. 1). D. Appleton and Company.

Daver, G., Guy, F., Mackaye, H. T., Likius, A., Boisserie, J.-R., Moussa, A., Pallas, L., Vignaud, P., & Clarisse, N. D. (2022). Postcranial evidence of late Miocene hominin bipedalism in Chad. *Nature*, *609*(7925), 94–100. https://doi.org/10.1038/s41586-022-04901-z

de Bonis, L., & Koufos, G. D. (2014). First discovery of postcranial bones of Ouranopithecus macedoniensis (Primates, Hominoidea) from the late Miocene of Macedonia (Greece). *Journal of Human Evolution*, *74*, 21–36. https://doi.org/10.1016/j.jhevol.2014.05.015

Deane, & Begun. (2008). Broken fingers: Retesting locomotor hypotheses for fossil hominoids using fragmentary proximal phalanges and high-resolution polynomial curve fitting (HR-PCF). *Journal of Human Evolution*, *55*(4), 691–701. https://doi.org/10.1016/j.jhevol.2008.05.005

Deane, & Begun, D. R. (2010). Pierolapithecus locomotor adaptations: A reply to Alba et al.'s comment on Deane and Begun (2008). *Journal of Human Evolution*, *59*(1), 150–154. https://doi.org/10.1016/j.jhevol.2010.04.003

Demes, B., Jungers, W. L., Gross, T. S., & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *American Journal of Physical Anthropology*, *96*(4), 419–429. https://doi.org/10.1002/ajpa.1330960407

Djojosudharmo, S., & Schaik, C. (1992). Why are orang utans so rare in the highlands? Altitudinal changes in a Sumatran forest. *Tropical Biodiversity*, *1*, 11–22.

Doran, D. M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology*, *91*(1), 83–98. https://doi.org/10.1002/ajpa.1330910106

Doran, D. M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, *32*(4), 323–344. https://doi.org/10.1006/jhev.1996.0095

Drummond-Clarke, R. C. (2023). Bringing trees back into the human evolutionary story: Recent evidence from extant great apes. *Communicative & Integrative Biology*, *16*(1), 2193001. https://doi.org/10.1080/19420889.2023.2193001

Ersoy, A., Kelley, J., Andrews, P., & Alpagut, B. (2008). Hominoid phalanges from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution*, *54*(4), 518–529. https://doi.org/10.1016/j.jhevol.2007.08.004

Fruth, B., Hickey, J., Andre, C., Hart, T., Hart, J., Kühl, H., Maisels, F., Nackoney, J., Reinartz, G., Sop, T., Furuichi, T., Thompson, J., & Williamson, L. (2016). Pan paniscus. The IUCN Red List of Threatened Species 2016. In *IUCN Red List of Threatened Species*.

Fuh, T., Todd, A., Feistner, A., Donati, G., & Masi, S. (2022). Group differences in feeding and diet composition of wild western gorillas. *Scientific Reports*, *12*(1), 9569. https://doi.org/10.1038/s41598-022-13728-7

Fuss, J., Spassov, N., Begun, D. R., & Böhme, M. (2017). Potential hominin affinities of Graecopithecus from the Late Miocene of Europe. *PLOS ONE*, *12*(5), e0177127. https://doi.org/10.1371/journal.pone.0177127

Galdikas, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, *9*(1), 1–35. https://doi.org/10.1007/BF02740195

Goodman, M. (1974). Biochemical Evidence on Hominid Phylogeny. *Annual Review of Anthropology*, *3*(1), 203–228. https://doi.org/10.1146/annurev.an.03.100174.001223

Goodman, M., Koop, B. F., Czelusniak, J., Fitch, D. H. A., Tagle, D. A., & Slightom, J. L. (1989). Molecular phylogeny of the family of apes and humans. *Genome*, *31*(1), 316–335. https://doi.org/10.1139/g89-050

Güleç, E. S., Sevim, A., Pehlevan, C., & Kaya, F. (2007). A new great ape from the late Miocene of Turkey. *Anthropological Science*, *115*(2), 153–158. https://doi.org/10.1537/ase.070501

Habinger, S. G., Chavasseau, O., Jaeger, J.-J., Chaimanee, Y., Soe, A. N., Sein, C., & Bocherens, H. (2022). Evolutionary ecology of Miocene hominoid primates in Southeast Asia. *Scientific Reports*, *12*(1), 11841. https://doi.org/10.1038/s41598-022-15574-z

Hammond, A. S. (2014). *In vivo* baseline measurements of hip joint range of motion in suspensory and nonsuspensory anthropoids. *American Journal of Physical Anthropology*, *153*(3), 417–434. https://doi.org/10.1002/ajpa.22440

Harcourt-Smith, W. E. H., & Aiello, L. C. (2004). Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, *204*(5), 403–416. https://doi.org/10.1111/j.0021-8782.2004.00296.x

Harcourt-Smith, W. H. E. (2010). The First Hominins and the Origins of Bipedalism. *Evolution: Education and Outreach*, *3*(3), Article 3. https://doi.org/10.1007/s12052-010-0257-6

Harrison, T. (2010). Apes Among the Tangled Branches of Human Origins. *Science*, *327*(5965), 532–534. https://doi.org/10.1126/science.1184703

Harrison, T., Jin, C., Zhang, Y., Wang, Y., & Zhu, M. (2014). Fossil Pongo from the Early Pleistocene Gigantopithecus fauna of Chongzuo, Guangxi, southern China. *Quaternary International*, *354*, 59–67. https://doi.org/10.1016/j.quaint.2014.01.013

Heizmann, E. P. J., & Begun, D. R. (2001). The oldest Eurasian hominoid. *Journal of Human Evolution*, *41*(5), 463–481. https://doi.org/10.1006/jhev.2001.0495

Henke, W., & Tattersall, I. (Eds.). (2015). *Handbook of Paleoanthropology*. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-39979-4

Herbert, T. D., Lawrence, K. T., Tzanova, A., Peterson, L. C., Caballero-Gill, R., & Kelly, C. S. (2016). Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience*, *9*(11), 843–847. https://doi.org/10.1038/ngeo2813

Howell, J. A. (1917). An experimental study of the effect of stress and strain on bone development. *The Anatomical Record*, *13*(5), 233–252. https://doi.org/10.1002/ar.1090130502

Humle, T., Maisels, F., Oates, J., Plumptre, A., & Williamson, L. (2017). *Pan troglodytes. The IUCN Red List of Threatened Species 2016*. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en

Hunt, K. D. (1992). Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology*, *87*(1), 83–105. https://doi.org/10.1002/ajpa.1330870108

Hunt, K. D. (2016). Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *Journal of Anatomy*, *228*(4), 630–685. https://doi.org/10.1111/joa.12454

Hunt, K. D. (2020). *Chimpanzee: Lessons from our Sister Species* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781316339916

Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates*, *37*(4), 363–387. https://doi.org/10.1007/BF02381373

Huxley, T. H. (1886). *Evidence as to Man's Place in Nature*. D. Appleton and Company.

Janecka, J., Miller, W., Pringle, T., Wiens, F., Zitzmann, A., Helgen, K., Springer, M., & Murphy, W. (2007). Molecular and Genomic Data Identify the Closest Living Relative of Primates. *Science (New York, N.Y.)*, *318*, 792–794. https://doi.org/10.1126/science.1147555

Ji, X., Jablonski, N. G., Su, D. F., Deng, C., Flynn, L. J., You, Y., & Kelley, J. (2013). Juvenile hominoid cranium from the terminal Miocene of Yunnan, China. *Chinese Science Bulletin*, *58*(31), 3771–3779. https://doi.org/10.1007/s11434-013-6021-x

Kappelman, J., Kelley, J., Pilbeam, D., Sheikh, K. A., Ward, S., Anwar, M., Barry, J. C., Brown, B., Hake, P., Johnson, N. M., Raza, S. M., & Shah, S. M. I. (1991). The earliest occurrence ofSivapithecus from the middle Miocene Chinji Formation of Pakistan. *Journal of Human Evolution*, *21*(1), 61–73. https://doi.org/10.1016/0047-2484(91)90036-U

Katoh, S., Beyene, Y., Itaya, T., Hyodo, H., Hyodo, M., Yagi, K., Gouzu, C., WoldeGabriel, G., Hart, W. K., Ambrose, S. H., Nakaya, H., Bernor, R. L., Boisserie, J.-R., Bibi, F., Saegusa, H., Sasaki, T., Sano, K., Asfaw, B., & Suwa, G. (2016). New geological and palaeontological age constraint for the gorilla–human lineage split. *Nature*, *530*(7589), Article 7589. https://doi.org/10.1038/nature16510

Kelley, J. (2002). *The hominoid radiation in Asia* (pp. 369–384).

Kelley, J., Andrews, P., & Alpagut, B. (2008). A new hominoid species from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution*, *54*(4), 455–479. https://doi.org/10.1016/j.jhevol.2007.08.007

Kivell, T. L., & Schmitt, D. (2009). Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proceedings of the National Academy of Sciences*, *106*(34), 14241–14246. https://doi.org/10.1073/pnas.0901280106

Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Hyodo, M., Hyodo, H., Itaya, T., Nakaya, H., Saegusa, H., Mazurier, A., Saneyoshi, M., Tsujikawa, H., Yamamoto, A., & Mbua, E. (2007). A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proceedings of the National Academy of Sciences*, *104*(49), 19220–19225. https://doi.org/10.1073/pnas.0706190104

Leakey, L. S. B. (1961). A new Lower Pliocene fossil primate from Kenya. *Annals and Magazine of Natural History*, *4*(47), 689–696. https://doi.org/10.1080/00222936108651194

Linné, C. von, Linné, C. von, Gmelin, J. F., Kerr, R., & Archer, J. (1792). *The animal kingdom, or zoological system, of the celebrated Sir Charles Linnæus. Containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the mammalia, or animals which give suck to their young* (pp. 1–686). Printed for A. Strahan, and T. Cadell, London, and W. Creech, Edinburgh. https://doi.org/10.5962/bhl.title.57940

Locke, D., Hillier, L., Warren, W., Worley, K., Nazareth, L., Muzny, D., Yang, S.-P., Wang, Z., Chinwalla, A., Minx, P., Mitreva, M., Cook, L., Delehaunty, K., Fronick, C., Schmidt, H., Fulton, L., Fulton, R., Nelson, J., Magrini, V., & Wilson, R. (2011). Comparative and Demographic Analysis of Orang-Utan Genomes. *Nature*, *469*, 529–533. https://doi.org/10.1038/nature09687

Lovejoy, C. O. (2009). Reexamining Human Origins in Light of *Ardipithecus ramidus*. *Science*, *326*(5949), 74. https://doi.org/10.1126/science.1175834

Lovejoy, C. O., Suwa, G., Simpson, S. W., Matternes, J. H., & White, T. D. (2009). The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes. *Science*, *326*(5949), 100–106.

Macchiarelli, R., Bergeret-Medina, A., Marchi, D., & Wood, B. (2020). Nature and relationships of Sahelanthropus tchadensis. *Journal of Human Evolution*, *149*, 102898. https://doi.org/10.1016/j.jhevol.2020.102898

Machnicki, A. L., & Reno, P. L. (2020). Great apes and humans evolved from a long-backed ancestor. *Journal of Human Evolution*, *144*, 102791. https://doi.org/10.1016/j.jhevol.2020.102791

Mackinnon, J. (1974). The behaviour and ecology of wild orang-utans (Pongo pygmaeus). *Animal Behaviour*, *22*(1), 3–74. https://doi.org/10.1016/S0003-3472(74)80054-0

Makedonska, J. A., & Strait, D. S. (2015). Are Humans Descended from a Knuckle-Walking Ancestor? In Wiley, *Encyclopedia of Life Sciences* (1st ed., pp. 1–5). Wiley. https://doi.org/10.1002/9780470015902.a0026161

Manduell, K. L., Morrogh-Bernard, H. C., & Thorpe, S. K. S. (2011). Locomotor behavior of wild orangutans (*pongo pygmaeus wurmbii*) in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia. *American Journal of Physical Anthropology*, *145*(3), 348–359. https://doi.org/10.1002/ajpa.21495

Matarazzo, S. (2008). Knuckle walking signal in the manual digits of *Pan* and *Gorilla*. *American Journal of Physical Anthropology*, *135*(1), 27–33. https://doi.org/10.1002/ajpa.20701

McBrearty, S., & Jablonski, N. G. (2005). First fossil chimpanzee. *Nature*, *437*(7055), 105–108. https://doi.org/10.1038/nature04008

Mccrossin, M., Benefit, B., Gitau, S., Palmer, A., & Blue, K. (1998). *Fossil evidence for the origins of terrestriality among Old World monkeys and apes* (pp. 353–396).

Methner, K., Campani, M., Fiebig, J., Löffler, N., Kempf, O., & Mulch, A. (2020). Middle Miocene long-term continental temperature change in and out of pace with marine climate records. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-64743-5

Miguel. (2016, June). *Unravelling the positional behaviour of fossil hominoids: Morphofunctional and structural analysis of the primate hindlimb*. Universitat Autònoma de Barcelona Research Portal. https://portalrecerca.uab.cat/en/studentTheses/unravelling-the-positional-behaviour-of-fossil-hominoids-morphofu

Mohammad-Ali, K., Eladari, M.-E., & Galibert, F. (1995). Gorilla and orangutan c-myc nucleotide sequences: Inference on hominoid phylogeny. *Journal of Molecular Evolution*, *41*(3). https://doi.org/10.1007/BF00186538

Moyà-Solà, S., Alba, D. M., Almécija, S., Casanovas-Vilar, I., Köhler, M., De Esteban-Trivigno, S., Robles, J. M., Galindo, J., & Fortuny, J. (2009). A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proceedings of the National Academy of Sciences*, *106*(24), 9601–9606. https://doi.org/10.1073/pnas.0811730106

Moyà-Solà, S., & Köhler, M. (1996). A Dryopithecus skeleton and the origins of great-ape locomotion. *Nature*, *379*(6561), 156–159. https://doi.org/10.1038/379156a0

Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., & Galindo, J. (2004). *Pierolapithecus catalaunicus* , a New Middle Miocene Great Ape from Spain. *Science*, *306*(5700), 1339–1344. https://doi.org/10.1126/science.1103094

Nakatsukasa, M. (2004). Acquisition of bipedalism: The Miocene hominoid record and modern analogues for bipedal protohominids. *Journal of Anatomy*, *204*(5), 385–402. https://doi.org/10.1111/j.0021-8782.2004.00290.x

Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., De Manuel, M., Desai, T., Groves, C., Pybus, M., Sonay, T. B., Roos, C., Lameira, A. R., Wich, S. A., Askew, J., Davila-Ross,

M., Fredriksson, G., De Valles, G., Casals, F., Prado-Martinez, J., Goossens, B., … Krützen, M. (2017). Morphometric, Behavioral, and Genomic Evidence for a New Orangutan Species. *Current Biology*, *27*(22), 3487-3498.e10. https://doi.org/10.1016/j.cub.2017.09.047

Ni, X., Gebo, D. L., Dagosto, M., Meng, J., Tafforeau, P., Flynn, J. J., & Beard, K. C. (2013). The oldest known primate skeleton and early haplorhine evolution. *Nature*, *498*(7452), 60–64. https://doi.org/10.1038/nature12200

O'Connor, B. L., & Rarey, K. E. (1979). Normal amplitudes of radioulnar pronation and supination in several genera of anthropoid primates. *American Journal of Physical Anthropology*, *51*(1), 39–43. https://doi.org/10.1002/ajpa.1330510105

Pan, L., Ji, X., Liao, W., Wang, W., Liu, J., & Xing, S. (2021). Premolar enamel thickness and distribution of a Miocene hominid Lufengpithecus hudienensis compared with Pleistocene and extant hominids. *Journal of Human Evolution*, *157*, 103030. https://doi.org/10.1016/j.jhevol.2021.103030

Patnaik, R., Cerling, T. E., Uno, K. T., & Fleagle, J. G. (2014). Diet and Habitat of Siwalik Primates *Indopithecus, Sivaladapis* and *Theropithecus*. *Annales Zoologici Fennici*, *51*(1–2), 123–142. https://doi.org/10.5735/086.051.0214

Pickford, M., Senut, B., Gommery, D., & Treil, J. (2002). Bipedalism in Orrorin tugenensis revealed by its femora. *Comptes Rendus Palevol*, *1*(4), 191–203. https://doi.org/10.1016/S1631-0683(02)00028-3

Pilbeam, D. R., & Simons, E. L. (1971). Biological Sciences: Humerus of Dryopithecus from Saint Gaudens, France. *Nature*, *229*(5284), 406–407. https://doi.org/10.1038/229406a0

Pillans, B., Williams, M., Cameron, D., Patnaik, R., Hogarth, J., Sahni, A., Sharma, J. C., Williams, F., & Bernor, R. L. (2005). Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: Implications for the age of the Miocene hominids Indopithecus and Sivapithecus, with a note on a new hominid tooth. *Journal of Human Evolution*, *48*(5), 507–515. https://doi.org/10.1016/j.jhevol.2004.12.003

Pina, M., Alba, D. M., Moyà-Solà, S., & Almécija, S. (2019). Femoral neck cortical bone distribution of dryopithecin apes and the evolution of hominid locomotion. *Journal of Human Evolution*, *136*, 102651. https://doi.org/10.1016/j.jhevol.2019.102651

Pina, M., Almécija, S., Alba, D. M., O'Neill, M. C., & Moyà-Solà, S. (2014). The Middle Miocene Ape Pierolapithecus catalaunicus Exhibits Extant Great Ape-Like Morphometric Affinities on Its Patella: Inferences on Knee Function and Evolution. *PLoS ONE*, *9*(3), e91944. https://doi.org/10.1371/journal.pone.0091944

Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., & Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *75*, 165–183. https://doi.org/10.1016/j.ympev.2014.02.023

Prang, T. C. (2019). The African ape-like foot of Ardipithecus ramidus and its implications for the origin of bipedalism. *eLife*, *8*, e44433. https://doi.org/10.7554/eLife.44433

Pugh, K. D. (2022). Phylogenetic analysis of Middle-Late Miocene apes. *Journal of Human Evolution*, *165*, 103140. https://doi.org/10.1016/j.jhevol.2021.103140

Pugh, K. D., Catalano, S. A., Pérez De Los Ríos, M., Fortuny, J., Shearer, B. M., Vecino Gazabón, A., Hammond, A. S., Moyà-Solà, S., Alba, D. M., & Almécija, S. (2023). The reconstructed cranium of *Pierolapithecus* and the evolution of the great ape face. *Proceedings of the National Academy of Sciences*, *120*(44), e2218778120. https://doi.org/10.1073/pnas.2218778120

Püschel, T. A., Marcé-Nogué, J., Chamberlain, A. T., Yoxall, A., & Sellers, W. I. (2020). The biomechanical importance of the scaphoid-centrale fusion during simulated knuckle-walking and its implications for human locomotor evolution. *Scientific Reports*, *10*(1), 3526. https://doi.org/10.1038/s41598-020-60590-6

Qi, G., Dong, W., Zheng, L., Zhao, L., Gao, F., Yue, L., & Zhang, Y. (2006). Taxonomy, age and environment status of the Yuanmou hominoids. *Chinese Science Bulletin*, *51*(6), 704–712. https://doi.org/10.1007/s11434-006-0704-5

Remis, M. (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*, *97*(4), 413–433. https://doi.org/10.1002/ajpa.1330970408

Rose, M. D. (1973). Quadrupedalism in primates. *Primates*, *14*(4), 337–357. https://doi.org/10.1007/BF01731356

Rose, Nakano, Y., & Ishida, H. (1996). Kenyapithecus Postcranial Specimens from Nachola, Kenya. *Afr Stud Monogr*, *24*.

Ryan, T. M., Silcox, M. T., Walker, A., Mao, X., Begun, D. R., Benefit, B. R., Gingerich, P. D., Köhler, M., Kordos, L., McCrossin, M. L., Moyà-Solà, S., Sanders, W. J., Seiffert, E. R., Simons, E., Zalmout, I. S., & Spoor, F. (2012). Evolution of locomotion in Anthropoidea: The semicircular canal evidence. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1742), 3467–3475. https://doi.org/10.1098/rspb.2012.0939

Sarmiento, E. (1994). Terrestrial traits in the hands and feet of gorillas. *Am. Mus. Novit.*, *3091*, 1–56.

Sarmiento, E. E. (2002). Distribution, taxonomy, genetics, ecology, and causal links of gorilla survival: The need to develop practical knowledge for gorilla conservation. In A. B. Taylor & M. L. Goldsmith (Eds.), *Gorilla Biology* (1st ed., pp. 432–471). Cambridge University Press. https://doi.org/10.1017/CBO9780511542558.020

Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2014). Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution*, *66*, 29–38. https://doi.org/10.1016/j.jhevol.2013.09.006

Schultz, A. H. (1950). The Physical Distinctions of Man. *Proceedings of the American Philosophical Society*, *94*(5), 428–449.

Silcox, M. T., Bloch, J. I., Boyer, D. M., Chester, S. G. B., & López-Torres, S. (2017). The evolutionary radiation of plesiadapiforms. *Evolutionary Anthropology: Issues, News, and Reviews*, *26*(2), 74–94. https://doi.org/10.1002/evan.21526

Smith, T., Rose, K. D., & Gingerich, P. D. (2006). Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene–Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences*, *103*(30), 11223–11227. https://doi.org/10.1073/pnas.0511296103

Spear, J. K., Grabowski, M., Sekhavati, Y., Costa, C. E., Goldstein, D. M., Petrullo, L. A., Peterson, A. L., Lee, A. B., Shattuck, M. R., Gómez-Olivencia, A., & Williams, S. A. (2023). Evolution of vertebral numbers in primates, with a focus on hominoids and the last common ancestor of hominins and panins. *Journal of Human Evolution*, *179*, 103359. https://doi.org/10.1016/j.jhevol.2023.103359

Stamos, P. A., & Alemseged, Z. (2023). Hominin locomotion and evolution in the Late Miocene to Late Pliocene. *Journal of Human Evolution*, *178*, 103332. https://doi.org/10.1016/j.jhevol.2023.103332

Steiper, M. E., & Seiffert, E. R. (2012). Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution. *Proceedings of the National Academy of Sciences*, *109*(16), 6006–6011. https://doi.org/10.1073/pnas.1119506109

Steiper, M. E., & Young, N. M. (2006). Primate molecular divergence dates. *Molecular Phylogenetics and Evolution*, *41*(2), 384–394. https://doi.org/10.1016/j.ympev.2006.05.021

Stevens, N. J., Seiffert, E. R., O'Connor, P. M., Roberts, E. M., Schmitz, M. D., Krause, C., Gorscak, E., Ngasala, S., Hieronymus, T. L., & Temu, J. (2013). Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes. *Nature*, *497*(7451), 611–614. https://doi.org/10.1038/nature12161

Straus, W. L. (1946). The principles o f classification and a classification of Mammals. By George Gaylord Simpson. Bull. Am. Mus. Nat. Hist., New York, vo1. 85, xvi + 350 pp., 1945. *American Journal of Physical Anthropology*, *4*(2), 243–248. https://doi.org/10.1002/ajpa.1330040218

Susman, R. L., Badrian, N. L., & Badrian, A. J. (1980). Locomotor behavior of *Pan paniscus* in Zaire. *American Journal of Physical Anthropology*, *53*(1), 69–80. https://doi.org/10.1002/ajpa.1330530111

Tédonzong, L. R. D., Willie, J., Makengveu, S. T., Lens, L., & Tagg, N. (2020). Variation in behavioral traits of two frugivorous mammals may lead to differential responses to human disturbance. *Ecology and Evolution*, *10*(8), 3798–3813. https://doi.org/10.1002/ece3.6178

Thompson, C. (2021). *Diversity Among Gorillas: Examining Ecology and Anatomy*.

Thorpe, S. K. S., & Crompton, R. H. (2005). Locomotor ecology of wild orangutans (Pongo pygmaeus abelii) in the Gunung Leuser Ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modelling. *American Journal of Physical Anthropology*, *127*(1), 58–78. https://doi.org/10.1002/ajpa.20151

Thorpe, S. K. S., & Crompton, R. H. (2006). Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *American Journal of Physical Anthropology*, *131*(3), 384–401. https://doi.org/10.1002/ajpa.20422

Thorpe, S. K. S., Holder, R. L., & Crompton, R. H. (2007). Origin of Human Bipedalism As an Adaptation for Locomotion on Flexible Branches. *Science*, *316*(5829), 1328–1331. https://doi.org/10.1126/science.1140799

Tocheri, M. W., Solhan, C. R., Orr, C. M., Femiani, J., Frohlich, B., Groves, C. P., Harcourt-Smith, W. E., Richmond, B. G., Shoelson, B., & Jungers, W. L. (2011). Ecological divergence and medial cuneiform morphology in gorillas. *Journal of Human Evolution*, *60*(2), 171–184. https://doi.org/10.1016/j.jhevol.2010.09.002

Tuttle, R. H. (1967). Knuckle-walking and the evolution of hominoid hands. *American Journal of Physical Anthropology*, *26*(2), 171–206. https://doi.org/10.1002/ajpa.1330260207

Wang, C.-B., Zhao, L.-X., Jin, C.-Z., Wang, Y., Qin, D.-G., & Pan, W.-S. (2014). New discovery of Early Pleistocene orangutan fossils from Sanhe Cave in Chongzuo, Guangxi, southern China. *Quaternary International*, *354*, 68–74. https://doi.org/10.1016/j.quaint.2014.06.020

Ward, C. V., Hammond, A. S., Plavcan, J. M., & Begun, D. R. (2019). A late Miocene hominid partial pelvis from Hungary. *Journal of Human Evolution*, *136*, 102645. https://doi.org/10.1016/j.jhevol.2019.102645

Williams, S. A., Prang, T. C., Meyer, M. R., Russo, G. A., & Shapiro, L. J. (2020). Reevaluating bipedalism in Danuvius. *Nature*, *586*(7827), E1–E3. https://doi.org/10.1038/s41586-020-2736-4

Zhang, Y., & Harrison, T. (2017). *Gigantopithecus blacki*: A giant ape from the Pleistocene of Asia revisited. *American Journal of Physical Anthropology*, *162*(S63), 153–177. https://doi.org/10.1002/ajpa.23150

Zhang, Y., Ni, X., Li, Q., Stidham, T., Lu, D., Gao, F., Zhang, C., & Harrison, T. (2024). Lufengpithecus inner ear provides evidence of a common locomotor repertoire ancestral to human bipedalism. *The Innovation*, *5*(2), 100580. https://doi.org/10.1016/j.xinn.2024.100580