Three-Dimensional Geometric Morphometric Analysis of the Intermediate Cuneiform in Anthropoids

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Abstract

The primate foot exhibits substantial morphological variation associated with locomotor behaviour, substrate use, and phylogenetic history. Despite its central role in load transmission, stability, and mobility during locomotion, the intermediate cuneiform remains one of the least studied tarsal bones in comparative morphology. This study uses three-dimensional geometric morphometrics (3DGM) to investigate variation in intermediate cuneiform morphology among anthropoids and assess the extent to which shape variation reflects locomotor behaviour, functional adaptation, and/or phylogenetic relationships. The sample for this study consists of 403 intermediate cuneiforms across various anthropoid species and focuses specifically on the facets that articulate with the navicular and second metatarsal bones and their impact on intermediate cuneiform shape. Digital 3D models derived from previously acquired laser scans of primate intermediate cuneiforms were analyzed using 3DGM of landmark and semi-landmark data. Analyses were conducted using generalized Procrustes analysis (GPA), principal component analysis (PCA), and Procrustes analysis of variance (PERMANOVA). Across all analyses, the first few principal components captured a substantial proportion of total shape variation, with the first three components explaining over half of the total variance. The results demonstrated that intermediate cuneiform morphology largely reflects phylogeny rather than any simple relationship with locomotor behaviour alone. Closely related taxa generally clustered together, whereas more distantly related taxa with similar locomotor behaviours frequently occupied different regions of morphospace. Atelids and colobus monkeys, for instance, clustered at opposite ends of the morphospace, despite both being primarily arboreal quadrupeds. The Procrustes analysis of variance further supports the interpretation that variation in the intermediate cuneiform is structured by phylogeny as well as locomotor behaviour, as it

indicated that taxonomy and locomotor behaviour both explain a substantial proportion of total shape variation among anthropoids. Atelids, in particular, have short and stout intermediate cuneiforms that are unlike any other anthropoid in this study. Gorillas (and colobus monkeys to a degree) also have distinctive intermediate cuneiforms that are tall and narrow in shape. In addition to strong separation from other taxa, gorillas exhibit unusually high levels of interspecific and intraspecific variation in intermediate cuneiform morphology, suggesting that this variation is likely caused by lineage-specific evolutionary history. Unexpectedly, modern humans and fossil hominins occupied a relatively central position within the morphospace rather than forming a highly distinct cluster and consistently overlapped or clustered near orangutans despite major differences in locomotor behaviour. Overall, humans and most other anthropoids follow a similar structural framework for intermediate cuneiform morphology, with only minor differences occurring in the shape of this bone between species. These results suggest that the intermediate cuneiform is morphologically constrained, with phylogenetic history acting as the primary driver of variation while locomotor behaviour contributes secondarily.

Introduction

The comparative anatomy and locomotor behaviours of anthropoids (i.e., humans, apes, and monkeys) provide valuable insights into the evolution of locomotion, particularly the emergence of habitual terrestrial bipedalism in the hominin lineage. However, interpretations of fossil foot function are constrained by the incomplete hominin postcranial record. Individual elements of the foot are often fragmentary, and small pedal bones are less frequently recovered than larger skeletal elements, as they are particularly susceptible to destruction, fragmentation, and loss during fossilization and excavation, meaning that complete or identifiable tarsal elements are uncommon in many hominin assemblages (Lorenzo et al., 2015; Pablos, 2015).

Consequently, establishing a detailed understanding of the morphology and functional significance of individual pedal elements in extant primates is essential for providing a comparative framework through which the limited fossil record can be interpreted.

Considerable comparative research has been focused on several of the larger and more functionally prominent tarsal bones such as the navicular, talus, calcaneus and cuboid (Blomberg et al., 2021; Deane et al., 2017; Knigge et al., 2015 Monclús-Gonzalo et al., 2023; Nozaki et al., 2021a; Nozaki et al., 2021b; Püschel et al., 2018; Turley and Frost, 2013). These elements have been investigated using a variety of morphological and geometric morphometric approaches to evaluate relationships between shape, locomotor behaviour, and phylogeny. For example three-dimensional geometric morphometric studies of the talus have demonstrated that talar shape reflects differences in locomotor behaviour among primates, with variation in features such as the trochlea, articular surfaces, and talar head associated with differences in arboreal and terrestrial behaviours (Püschel et al., 2018). Püschel et al. (2018) used 3D geometric morphometrics alongside other methods to distinguish locomotor categories among extant platyrrhines and infer the locomotor behaviour of Miocene fossil taxa from talar morphology. Their results showed that different locomotor categories could be distinguished using talar shape. Likewise, the calcaneus has received considerable attention because its morphology is closely associated with foot-ground interaction and the mechanical demands of locomotion. Blomberg et al. (2021) used 3D geometric morphometrics and sliding semilandmarks to examine calcaneal shape in humans, nonhuman primates, and early hominins, finding relatively weak phylogenetic signal and interpreting much of the observed variation in relation to locomotion and body size. They found that humans have a larger calcaneus and more distinctive cuboid facet associated with a rigid midfoot, while more arboreal apes had a cuboid facet associated with greater midfoot

mobility. Similarly, Nozaki et al. (2021a) applied 3D geometric morphometrics to the calcanei of humans and great apes and found clear interspecific differences corresponding to degree of arboreality. More recently, the navicular has begun to receive attention. Monclús-Gonzalo et al. (2023) used 3D geometric morphometrics and quantified locomotor data to demonstrate a significant relationship between navicular shape and locomotor behaviour. Their analysis showed that navicular shape has a strong functional signal and can be used to infer locomotor behaviour in extinct primates. Together these studies demonstrate that individual tarsal elements preserve distinct morphological signals associated with locomotor behaviour, while also highlighting differences in the extent to which particular bones have been investigated.

In comparison, the intermediate cuneiform has received considerably less comparative attention. The element is represented in the fossil record, and its morphology has been documented in several early hominins, including *Ardipithecus*, *Australopithecus*, *Homo erectus*, *Homo naledi*, *Homo floresiensis* (DeSilva et al., 2019). However, much of the work on this bone has focused on describing individual specimens rather than characterizing three-dimensional shape variation across a broad comparative sample. This gap in the research is notable because the intermediate cuneiform occupies a central position within the distal tarsal row, articulating proximally with the navicular, distally with the second metatarsal, and medially and laterally with the other cuneiforms (Kent, 2006; White, 1991) (Figure 1, Figure 2). Despite its small relative size, the intermediate cuneiform contributes to both the medial longitudinal and transverse arches of the foot (Kent, 2006; White, 1991). Its position in the arch of the foot has a tight fit in the tarsometatarsal joint because the base of the second metatarsal wedges proximally between the three cuneiforms, thus making the midfoot more stable and creating support for both the medial longitudinal and transverse arches (Suzuki et al., 2020). This tight joint configuration

locks the foot during the “push-off” phase of bipedal locomotion, allowing for a more efficient transfer of force between the hindfoot and the forefoot (McNutt et al., 2018). Its morphology therefore contributes to the mechanical demands of the forefoot and midfoot (McNutt et al., 2018; Suzuki et al., 2020).

The relative lack of research on the intermediate cuneiform may have several explanations, including the limited number of well-preserved specimens available for comparative study. Although intermediate cuneiforms are represented in the hominin fossil record, they remain relatively sparsely represented compared with other pedal elements, with DeSilva et al. (2019) documenting intermediate cuneiforms from only a limited number of fossil taxa and specimens. Individual specimens can provide important information about the evolution of the human midfoot; however, the fossil record for this element is more limited than what is needed to establish its functional and evolutionary trajectory. The small size of the intermediate cuneiform may also contribute to its comparatively low representation in the fossil assemblages, and adds to the more practical aspect of building large comparative samples. These factors, together, may have led to less interest in developing the extensive comparative datasets that now exist for some other pedal elements. However, the absence of large fossil samples increases the need for a robust comparative framework based on extant taxa. Developing such a framework is particularly important because intermediate cuneiform morphology may provide information that cannot be fully captured by studies of other elements.

This research gap is significant because the anthropoid foot should not be understood as a collection of functionally independent bones. Locomotion emerges from interactions between the tarsals, metatarsals, and joints of the foot as an integrated system. An incomplete understanding of any individual element limits our ability to evaluate how the morphology of the foot as a

whole evolved in response to different locomotor demands. The intermediate cuneiform may be particularly informative because its position links the navicular to the second metatarsal and plays an important role in how weight is distributed across the foot. Establishing how its morphology varies among taxa with different evolutionary histories and locomotor repertoires can therefore provide an additional component to the comparative framework already established for other pedal elements.

The significance of studying the intermediate cuneiform goes beyond filling a taxonomic or anatomical gap. A better understanding of its normal range of morphological variation among extant anthropoids provides a basis for evaluation of fossil specimens that fall outside or within those patterns of variation. Such a framework may help distinguish morphological similarities associated with shared ancestry from those associated with similar functional demand, further contributing to interpretations of locomotor evolution in extinct hominins. More broadly, examining an understudied element within the context of the entire primate foot can help clarify whether patterns associated with locomotion are repeated across the foot or whether different pedal elements record different aspects of locomotor adaptation.

This study addresses a fundamental gap in our understanding of anthropoid foot evolution by quantitatively characterizing three-dimensional shape variation in the intermediate cuneiform across a broad sample of extant anthropoids and fossil hominins. By establishing a comparative framework for this poorly studied tarsal element, this study aims to determine the extent to which intermediate cuneiform morphology reflects phylogenetic relationships, locomotor behaviour, or an interaction between the two.

Primate Locomotion

Primates move around their environments in incredibly diverse ways, and these locomotor patterns are a defining characteristic of the Order (Table 1). They have adapted to moving on various substrates, from the narrow tops of trees to the open forest floor, which has shaped their anatomy in distinct ways (Schmitt et al., 2018). Primates are primarily arboreal, but every primate is capable of terrestrial locomotion, despite very few doing so habitually (Schmitt et al., 2018). More specifically, no platyrrhines, and very few strepsirrhines, are committed terrestrial quadrupeds, which means they do not travel on the ground regularly; in contrast, there are many semiterrestrial or primarily terrestrial catarrhines, including baboons, macaques, and great apes (Schmitt et al., 2018).

Primate locomotor behaviours can be broadly, and somewhat loosely, divided into two major categories: arboreal and terrestrial, with further subdivisions in each category, including quadrupedalism, brachiation, suspension, climbing, knuckle walking, and bipedalism. It is important to note that all primates engage in a varied locomotor behavioural repertoire; thus, these categories are generalized and do not necessarily include all of the ways a given primate species locomotes. Rather, they group primates based on similar behavioural characteristics and the locomotor patterns most frequently used by each species.

The intermediate cuneiform plays an essential role in stabilizing the medial longitudinal and transverse arches of the foot. Its position in the midfoot, articulating with the navicular and second metatarsal, is critical during the push-off phase of bipedal and quadrupedal locomotion. Additionally, the bone contributes to shock absorption and weight bearing during all types of locomotion. Thus, this bone is crucial to study different locomotor behaviours and may provide insights into the evolutionary transition between having feet adapted for arboreal locomotion and having feet adapted for bipedal locomotion. The morphology of the intermediate cuneiform may

vary between primates that use different locomotor strategies and thus have feet adapted for various environments.

Arboreal Quadrupedalism

Arboreal quadrupedalism is a common primate locomotor behaviour in which the forelimbs and hindlimbs are used together to move across branches and other elevated substrates. Unlike terrestrial locomotion, which generally occurs on relatively continuous and stable surfaces, arboreal locomotion requires primates to move along irregular and discontinuous surfaces that can vary substantially (Youlantos, 2018). These demands place particular importance on the ability of the foot to maintain secure contact with the substrate while accommodating changes in branch shape and orientation (Young et al., 2015). During arboreal quadrupedalism primates rely on their grasping feet to provide support, balance, and propulsion, with the hind limbs and feet contributing substantially to maintaining a secure grip on uneven substrates (Patel et al., 2015). The foot of an arboreal quadruped combines sufficient mobility to grasp uneven substrates with enough stability during weight bearing (Youlantos, 2018; Young et al., 2015). The intermediate cuneiform is critical in this case, as it is situated in the region of the foot where much of this flexibility occurs; the shape of this bone and how it articulates with the navicular and second metatarsal bones could contribute to the primate's ability to maintain a flexible and balanced foot hold on thin, narrow branches.

Climbing

Climbing is one of the most fundamental forms of locomotion among primates, forming the foundation for many other arboreal and terrestrial locomotor behaviours. Nearly all primates climb to some degree, although the manner in which they climb, the frequency with which they engage in this behaviour, and the morphological demands of climbing vary strongly between

taxa (Hanna et al., 2017; Hanna and Schmidt, 2011). Climbing allows the primate to move vertically along tree trunks. As with other types of arboreal locomotion, the hands and feet of climbing primates are adapted to maintain a strong grip (Hanna et al., 2017; Hanna and Schmidt, 2011; Neufuss et al., 2018; Runestad et al., 1993). The morphology of the intermediate cuneiform provides a unique opportunity, as it plays a role in the mechanics of the foot responsible for maintaining stability and flexibility during climbing. Variation in the shape of the intermediate cuneiform may reflect the locomotor specialization for climbing, with a more flexible midfoot compared to the more rigid midfoot of a terrestrial quadruped.

Terrestrial Quadrupedalism

Terrestrial quadrupedalism is a locomotor behaviour where primates move on all four limbs across the ground. Although many primates occasionally move terrestrially, habitual terrestrial quadrupedalism is particularly common among several catarrhine taxa, including baboons, macaques, patas monkeys, mandrills, chimpanzees, bonobos, and gorillas (Schmitt et al., 2018). Because primates evolved primarily in arboreal environments, terrestrial quadrupedal taxa generally retain aspects of the grasping hands and feet characteristic of their arboreal ancestry rather than possessing the highly specialized morphology seen in many other terrestrial mammals. However, moving across relatively stable terrestrial substrates places different mechanical demands on the foot than navigating narrow and irregular branches. Terrestrial locomotion requires the foot to provide a stable platform for weight transmission while accommodating repeated loading during walking and, in some taxa, relatively rapid travel over long distances (Schmitt, 1998). These specific adaptations for moving along the ground may be reflected in the intermediate cuneiform morphology, and it is crucial to study this bone in relation to midfoot stability in terrestrial quadrupeds.

Knuckle Walking

Knuckle walking is a rare form of terrestrial quadrupedalism among primates, with only the African apes (gorillas, chimpanzees, bonobos), and some orangutans participating in this behaviour (Simpson et al., 2018). This is a specialized form of terrestrial quadrupedalism where the primate walks using their feet and their knuckles rather than the palms of their hands (Sarringhaus et al., 2022; Simpson et al., 2018). Knuckle-walking is associated with a suite of anatomical features that facilitate repeated terrestrial loading while allowing African apes to retain the mobility required for arboreal locomotion (Richmond et al., 2001; Simpson et al., 2018). The intermediate cuneiform will be interesting to study in this context, as the feet of African apes are not uniquely adapted to knuckle walking, as these adaptations are mainly in the forelimbs. African ape feet retain features associated with arboreal locomotion; thus, the intermediate cuneiform shape may be similar to that of other arboreal primates.

Bipedalism

Bipedalism is a mode of terrestrial locomotion in which an organism habitually moves using only its two hindlimbs, maintaining an upright posture. This is a hallmark feature that sets humans apart from most species, living and extinct. Humans are the only living primate to use bipedal locomotion and one of just a few animals on Earth that move using only two legs. In humans, bipedalism is obligate, distinguishing it from the facultative or occasional bipedal behaviours observed in some nonhuman primates (Harcourt-Smith, 2010). This form of locomotion is incredibly energetically efficient, allowing us to move over long distances. Nonhuman primates are capable of bipedal locomotion over short distances and do move bipedally often, although this mostly occurs in arboreal contexts, but their musculoskeletal anatomy is adapted for arboreal locomotion and quadrupedal or suspensory behaviours (Aerts,

2023; Larson, 2018). Human postcranial anatomy, however, including the pelvis, knee, ankle, and foot, exhibits a number of derived traits that facilitate efficient terrestrial bipedalism over long distances.

Fossil evidence suggests that bipedalism emerged early in hominin evolution, preceding many other hallmarks of humanity. Currently, the oldest record of possible bipedalism in the hominin evolutionary timeline is with *Sahelanthropus tchadensis* in Chad, around 7 million years ago (Daver et al., 2022; Williams et al., 2026). This species had an upright posture, where the head sat on top of the spine, suggesting the species was likely capable of bipedal posture, but this evidence is debated as no leg or foot bones were found (Daver et al., 2022; Williams et al., 2026). More likely evidence of bipedalism comes from *Ardipithecus* and *Australopithecus*. *Ardipithecus* for instance, had a short and broad upper pelvis, much like modern humans, but the lower pelvis was still more ape like, in addition to this, this genus had a more rigid midfoot, a slight longitudinal arch, but still possessed an abducted big toe, thus it was capable of walking upright but this was likely inefficient (Harcourt-Smith, 2010; Lovejoy et al., 2009; Prang, 2019). *Australopithecus* was even better adapted for bipedal locomotion, with a short and wide pelvis, and a stiff midfoot with a longitudinal arch, this genus also had an adducted big toe, that was not capable of grasping, thus, *Australopithecus* who provides strong evidence for habitual bipedalism but still possesses some features for climbing trees (Stern and Susman, 1983; Ward, 2002; Ward et al., 2011). While early hominin feet retained some grasping capacity, particularly in the hallux, later hominins evolved a foot increasingly specialized for weight support, shock absorption, and propulsion during bipedal gait (Drapeau and Harmon, 2013; Holowka et al., 2017b). It is not well understood if bipedalism evolved from suspensory, quadrupedal, or terrestrial behaviours, but factors such as tool use, thermoregulation, and predator avoidance

seem to be keystones in the push for evolving bipedal posture (Harcourt-Smith, 2010; Watson et al., 2008). The fossil record demonstrates that the traits needed for bipedalism evolved gradually and in a mosaic fashion, underscoring the complexity of bipedal evolution.

During bipedal walking, the foot performs several biomechanically demanding tasks, such as absorbing shock during heel strike, supporting the body's weight, balancing on a single limb, and generating enough propulsive force during toe off for forward motion. These functions require a fine balance between flexibility and rigidity, with the foot being mobile enough to adapt to uneven ground, but rigid enough to effectively move bipedally (Jung et al., 2021; Schmitt, 2003; Venkadesan et al., 2020). Features that are vital to this balance of movement and stability include an adducted hallux, short and straight toes, the presence of transverse and longitudinal arches, midfoot stiffness, and a large and robust calcaneus (Harcourt-Smith and Aiello, 2004; Harper et al., 2021; Harper et al., 2022; MacGregor and Byerly, 2020; Venkadesan et al., 2020). These pedal adaptations do not function in isolation, instead they work in tandem to support stable and efficient bipedalism, working collectively to enable the human foot to operate as a rigid lever during propulsion while retaining sufficient flexibility for balance and shock absorption. Understanding these adaptations provides essential context for interpreting both fossil hominin feet and variation within modern primate clades.

The Primate Foot

All primates share a suite of pedal traits that distinguish them from other mammals and reflect adaptations for grasping. Primates have five pedal digits, nails rather than claws, and a combination of skeletal and muscular morphology that allows the foot to grasp substrates during arboreal locomotion (Soligo and Müller, 1999). There are 26 bones in the anthropoid foot: seven tarsals, five metatarsals, five proximal phalanges, four intermediate phalanges, and five distal

phalanges (Standring, 2020). The tarsal bones form the hindfoot and midfoot and include the talus, calcaneus, navicular, cuboid and three cuneiforms. These bones articulate with each other to form a rigid platform that stabilizes the foot (MacGregor and Byerly, 2020). Additionally, tarsal bones have a combination of features that provide flexibility and stability (White, 1991). The metatarsals are long, tubular bones positioned between the tarsals and the pedal phalanges (i.e., toes), and together with the latter form the forefoot. The first metatarsal articulates proximally with the medial cuneiform and distally with the 1st proximal phalanx, which articulates distally with the 1st distal phalanx. Together, this first ray of the foot is known as the hallux. The 2nd and 3rd metatarsals articulate proximally with the intermediate and lateral cuneiforms, respectively, and distally with their respective proximal phalanx. The 4th and 5th metatarsals articulate proximally with the cuboid and distally with the 4th and 5th proximal phalanges, respectively. Finally, the hallux has two phalanges (proximal and distal) whereas the remaining digits have three phalanges: proximal, intermediate, and distal. This generalized pedal architecture is shared across primates, but the proportions, orientation, and mobility of these elements vary substantially among lineages in association with differences in substrate use and locomotor behaviour.

The hallux is particularly important to the generalized primate foot. In most nonhuman primates, the hallux is divergent and opposable, allowing the foot to function as a grasping structure during climbing and suspension (Goodenberger et al., 2015). Primates also generally retain a mobile midfoot, enabled by flexible tarsometatarsal joints and a functional midtarsal break. This mobility allows the foot to conform to uneven or irregular substrates and is particularly advantageous during arboreal locomotion (DeSilva, 2009; Greiner and Ball, 2014). Additionally, the presence of nails is particularly important for arboreal locomotion, as they

provide a broad, flat surface that enhances precision gripping, thus improving control and reducing the risk of slipping on narrow or irregular substrates (Soligo and Müller, 1999; Toussaint et al., 2020).

The foot plays a crucial role in climbing, serving as both a stabilizer and a means of grasping. Climbing primates use their feet to anchor and balance themselves on irregular substrates; and the mobile midfoot allows the foot to flex and conform around tree trunks or branches (DeSilva, 2009). The calcaneus is less robust and longer than that of modern humans, allowing for greater shock absorption when transitioning between supports (Nozaki et al., 2021a). The talus is also uniquely adapted for increased mobility, allowing the entire plantar surface of the foot to make contact with supports, thereby improving grip and balance on uneven surfaces (DeSilva, 2009). Arboreal primates also typically have relatively long and curved phalanges, which enhance grasping of narrow substrates. In some taxa, particularly suspensory species, increased phalangeal curvature provides additional support when grasping branches. A divergent hallux can oppose the lateral digits to produce a pincer-like grip, a feature that is especially pronounced in platyrrhines and allows multiple points of contact during climbing (Fleagle et al., 2024). Although these characteristics broadly define the generalized primate foot, they are not equally developed across all primates. Most terrestrial primates are plantigrade, although some, such as patas monkeys, occasionally demonstrate a digitigrade posture that may represent an adaptation for increased speed (Zeininger, 2022; Zihlman and Underwood, 2013). Similarly, the degree of pedal mobility, digit curvature, hallux divergence, and calcaneal robustness varies according to the relative importance of arboreal and terrestrial locomotion. Thus, rather than representing a single morphological type, the primate foot provides a flexible anatomical framework that has been modified repeatedly in response to different locomotor

demands. Together, these features characterize primate feet broadly, but there is substantial variation among humans, apes and monkeys, reflecting differences in substrate use and degrees of terrestriality or arboreality.

The Monkey Foot

Monkeys retain many of the generalized grasping characteristics of the primate foot, but exhibit substantial morphological variation associated with differences in habitat use and locomotor diversity. In particular, many monkeys retain a divergent hallux and lack a pronounced longitudinal arch resulting in relatively flat and flexible soles (Greiner and Ball, 2014; Oku et al., 2021). The calcaneus is generally smaller and more angled than in humans and often contacts the ground simultaneously with the midfoot during locomotion (Harper et al., 2021; Nozaki et al., 2021a; Oku et al., 2021). The midfoot remains highly mobile, with a functional midtarsal break that allows the foot to conform to narrow or irregular arboreal substrates (DeSilva, 2009).

Most monkeys are either arboreal or semi-terrestrial quadrupeds. During above branch postural behaviours, arboreal monkeys use their hindlimbs to hold most of their bodyweight; this contrasts sharply with nonprimate arboreal mammals, which evenly distribute their body weight on both the hindlimbs and forelimbs (Patel et al., 2015). The pedal morphology of monkeys reflects these demands. Many arboreal species have highly curved pedal phalanges, with curvature increasing in suspensory species and providing greater support when grasping narrow substrates. In contrast, terrestrial species tend to have less curved digits and a reduced degree of hallux divergence (Schmitt et al., 2018; Wennemann et al., 2022). Additionally, arboreal species tend to have a shorter and more gracile calcanei compared to terrestrial primates, whereas monkeys that are more terrestrial, or travel on wider supports, show longer and more robust

calcanei that aid in propulsion and shock absorption when moving terrestrially and are more similar to the great apes (Harper et al., 2021; Nozaki et al., 2021a). These changes likely contribute to propulsion and shock absorption during terrestrial locomotion. To reduce the concentration of pressure on the sole, arboreal quadrupeds also tend to have a soft, cushioned, and thick foot pad, compared to their terrestrial counterparts, this improves grip and adds shock absorption when moving across unstable branches (Cartmill, 1974).

Despite these general similarities, monkey pedal morphology varies between major groups, particularly between platyrrhines (New World monkeys) and cercopithecids (Old World monkeys). Firstly, platyrrhines exclusively live in Mexico, Central, and South America, where many taxa occupy tropical forest environments and are highly arboreal (Schmitt et al., 2005). Some platyrrhine lineages, primarily the atelines, such as the spider and woolly monkeys, have prehensile tails that function as an extra limb, providing additional support when moving across tree branches (Schmitt et al., 2005). The use of a prehensile tail can reduce the mechanical demands placed on the feet during some arboreal behaviours, although the feet retain the grasping morphology characteristic of highly arboreal primates.

Cercopithecid monkeys, in contrast, possess nonprehensile tails and include a greater diversity of terrestrial and semi-terrestrial species. Baboons and some macaques are relatively terrestrial, whereas colobine monkeys include highly arboreal specialists (Fleagle, 2013). Cercopithecids are native to Africa and Asia and inhabit a much wider range of habitats than New World monkeys do, thus contributing to their wider range of locomotor behaviours (Fleagle, 2013). This ecological diversity is reflected in their pedal morphology. More terrestrial cercopithecines, including baboons and macaques, exhibit modifications of the midfoot and calcaneus associated with terrestrial locomotion and propulsion, whereas arboreal colobines

retain a more typical grasping foot with increased midfoot mobility (Greiner and Ball, 2014; Strasser, 1992). Thus, while monkeys broadly retain the flexible, grasping pedal configuration of the generalized primate foot, their morphology demonstrates how this configuration can be modified in response to increasing terrestriality.

The Ape Foot

Nonhuman apes (chimpanzees, bonobos, gorillas, orangutans, and gibbons) retain many of the grasping adaptations found in monkeys but exhibit further modifications associated with their combination of arboreal climbing, suspension, and terrestrial locomotion. Ape metatarsals and phalanges are much longer than in humans, and the phalanges are typically more curved, enhancing the ability to grasp branches (Fernández et al., 2016; Thorpe et al., 2009). The hallux remains fully opposable and is abducted from the lateral digits, allowing the foot to function in a manner similar to a hand during climbing and suspension. In great apes, including chimpanzees, bonobos, gorillas, and orangutans, the hallux and elongated, curved lateral digits work together to provide a secure grasp of branches and maintain balance during arboreal locomotion (Fernández et al., 2016; Thorpe et al., 2009).

A defining characteristic of the ape foot is the continued mobility of the midfoot. Unlike the human foot, nonhuman apes lack a rigid longitudinal arch and retain highly mobile articulations between the tarsals and metatarsals, this mobility produces a pronounced midtarsal break, allowing the foot to flex, supinate, and pronate around branches and other irregular substrates (Fernández et al., 2016; Holowka et al., 2017a; Thorpe et al., 2009). Rather than functioning as a rigid lever during push-off, the ape foot remains capable of conforming to uneven substrates. Consequently, nonhuman apes lack a longitudinal arch, and thus generate less propulsive force through the foot than humans and, particularly during climbing, rely heavily on

the forelimbs for propulsion rather than generating force through a rigid toe-off mechanism as humans do(Fernández et al., 2016; Holowka et al., 2017a; Holowka et al., 2017b).

The degree to which these grasping features are expressed varies among apes according to their locomotor ecology. Gibbons and orangutans are highly arboreal and use their feet as a second set of hands, grasping branches during climbing and suspension and, in some contexts, moving bipedally across the tops of branches (Thorpe et al., 2009; Vereecke and Aerts, 2008). Gibbons in particular rarely come to the ground and rely extensively on their feet for grasping, suspension, and movement between branches. Their feet therefore retain a pronounced midtarsal break and a particularly flat and flexible configuration suited to grasping branches (Vereecke and Aerts, 2008). The increased flexibility of the ape midfoot also influences terrestrial locomotion, with much of the body's weight being placed on the calcaneus and rearfoot rather than distributed across a rigid, arched foot as in humans (Fernández et al., 2016; Holowka et al., 2017a).

The African apes, chimpanzees, bonobos, and gorillas provide an important intermediate comparison between the highly arboreal ape foot and the specialized human foot. Compared with the more arboreal apes, these taxa experience greater terrestrial locomotor demands while retaining substantial arboreal abilities. Chimpanzees and bonobos combine terrestrial knuckle-walking with climbing and other arboreal behaviours, whereas gorillas are more terrestrial but retain the ability to climb. Their feet consequently combine a relatively robust morphology suited to terrestrial loading with long, grasping phalanges and a mobile midfoot that remain useful during climbing (Fernández et al., 2016; Harper et al., 2021; Holowka et al., 2017a). Their robust calcanei contribute to shock absorption during terrestrial locomotion, while the retention of a divergent hallux and mobile midfoot preserves the ability to grasp and conform to arboreal substrates (Fernández et al., 2016; Harper et al., 2021; Holowka et al., 2017a). The

African apes therefore illustrate how a primate foot can become more robust and adapted for terrestrial locomotion without developing the rigid fully adducted configuration characteristic of humans.

The Human Foot

The human foot represents a substantial departure from the generalized grasping configuration retained by monkeys and nonhuman ape. Rather than primarily functioning as a grasping structure, the human foot supports the full body mass and acts as a stable and efficient lever during habitual upright walking and running. This functional shift is reflected in changes to the hallux, metatarsals, calcaneus, and midfoot, as well as the development of rigid longitudinal and transverse arches. Together, these modifications allow the human foot to meet the distinctive biomechanical requirements of bipedalism, including supporting body weight, absorbing and redistributing forces, maintaining stability, and efficiently transmitting forces during propulsion.

Compared with other primates, human metatarsals are shorter and wider, supporting the arches and contributing to the overall stiffness of the foot during push off (MacGregor and Byerly, 2020). Humans also possess relatively short toes, reducing bending movements during toe-off and improving energetic efficiency (White, 1991). Most notably, the hallux is fully adducted and aligned with the other pedal digits rather than being divergent and opposable. The human hallux is also relatively robust and works together with the stiff midfoot to create an effective lever during push-off (Harcourt-Smith and Aiello, 2004). These modifications increased the efficiency of bipedal walking and running but substantially reduced the ability of the foot to grasp arboreal substrates (Schmitt, 2003).

The calcaneus is also relatively large and robust in humans, reflecting the importance of heel strike during bipedal locomotion. During human walking, the heel contacts the ground first

and must therefore absorb substantial forces (Harper et al., 2021; Harper et al., 2022). The enlarged calcaneus provides a broad surface for load transmission and serves as an attachment site for the Achilles tendon, contributing to efficient force generation during push-off (Harper et al., 2021; Harper et al., 2022; Mahan et al., 2020). This heel-strike pattern contrasts with the forefoot or midfoot strike observed in many nonhuman primates (Harper et al., 2021; Harper et al., 2022). Thus, changes to the calcaneus represent another component of the transition from a flexible, grasping foot to a robust, load-bearing foot adapted for habitual bipedalism.

The human foot must support the entire body weight during standing, walking, and running, making its capacity for load bearing crucial for balance, stability, and efficient movement (Lieberman, 2012; Winter, 1995). During these activities, the foot is exposed to substantial ground reaction forces. During walking, these forces can reach approximately 1 – 1.5 times body weight, while during running they can increase to approximately three times body weight (Kirby, 2017). The ability of the human foot to withstand and efficiently transmit these forces depends largely on the coordinated function of the arches and the structural rigidity of the midfoot. Thus, the transition from the highly mobile midfoot of nonhuman primates to the relatively rigid human midfoot represents an important functional adaptation for habitual bipedalism.

The human foot is further distinguished by the presence of two relatively rigid longitudinal arches, the medial and lateral arches, as well as the transverse arch. In contrast, nonhuman primates generally lack rigid longitudinal arches, with the medial longitudinal arch being absent or weak (MacGregor and Byerly, 2020; Venkadesan et al., 2020). These arches function together as a spring-like system that bears weight, absorbs shock, and redistributes forces during bipedal locomotion (Sorrentino et al., 2023; Venkadesan et al., 2020). During

initial contact and stance, controlled deformation of the arches allows the foot to absorb and redistribute forces, while subsequent recoil contributes to the return of stored elastic energy (Conconi et al., 2023). The transverse arch is particularly important for distributing loads across the midfoot, preventing forces from becoming concentrated in a single structure (Asghar and Naaz, 2022; Chauhan and Taqi, 2022).

The medial longitudinal arch is the most prominent and spans from the calcaneus through the talus and navicular, into the cuneiforms and to the base of the first three metatarsals (MacGregor and Byerly, 2020; Venkadesan et al., 2020). This arch contributes to shock absorption and weight bearing and acts as a spring-like structure during bipedal locomotion (Schmitt, 2003; Thorpe et al., 2007a; Thorpe, 2009). The lateral arch is formed by the calcaneus and cuboid together with the fourth and fifth metatarsals and is substantially flatter than the medial arch (MacGregor and Byerly, 2020; Venkadesan et al., 2020). It contributes to stability and weight transmission, while the two longitudinal arches work together to support and propel the body during bipedal locomotion (MacGregor and Byerly, 2020; Jung et al., 2021; Venkadesan et al., 2020). The stiff, longitudinal arches evolved after the hallux became more robust as well as fully adducted and in line with the lateral pedal digits (Negishi et al., 2021; Schmitt, 2003). This adaptation in particular is vital to creating a rigid lever during the push-off motion of walking, greatly reducing the amount of work needed for forward movement (Venkadesan et al., 2020). Finally, the transverse arch is formed by the distal tarsals and the base of the metatarsals and curves around the midfoot and forefoot (Venkadesan et al., 2020). Although the evolutionary development of this arch is not well understood, it contributes to load distribution, shock absorption, and the spring-like behaviour of the foot during push-off (Venkadesan et al., 2020). Together, the longitudinal and transverse arches transform the foot

into a stable but dynamic platform for weight bearing and forward propulsion during bipedal locomotion (Jung et al., 2021; Schmitt, 2003; Venkadesan et al., 2020). The development of these rigid structures represent a major functional contrast with the flexible midfoot of monkeys and nonhuman apes.

Midfoot rigidity is particularly important during the push-off phase of bipedal locomotion. As the body moves over the foot, the medial longitudinal arch, supported by the lateral and transverse arches, becomes increasingly stiff and allows the foot to function as a rigid lever for forward propulsion (Conconi et al., 2023; Sorrentino et al., 2023; Venkadesan et al., 2020). Dorsiflexion of the toes further contributes to this process. Extension of the toes stretches the plantar aponeurosis, tightening the longitudinal arch and increasing midfoot stiffness, thereby locking the foot into a rigid lever during push-off (Fernández et al., 2016; Sichting et al., 2020; Sorrentino et al., 2023). In great apes, loading of the foot instead tends to produce a midfoot break, reflecting their more flexible midfoot and lack of a rigid medial longitudinal arch (Fernández et al., 2016; Sorrentino et al., 2023). In humans, midfoot rigidity prevents this collapse and allows forces to be transmitted from the hindfoot through the tarsals and into the metatarsals, rather than being dissipated through excessive midfoot deformation.

The bones of the midfoot are therefore particularly important for maintaining this rigid load-bearing column. The medial longitudinal arch comprises the calcaneus, talus, navicular, three cuneiforms, and first three metatarsals. The navicular is an important component of this arch, articulating proximally with the talus and distally with the three cuneiforms and forming a central region of weight transfer between the hindfoot and medial longitudinal arch (Kirby, 2017; Sorrentino et al., 2023). The articulation between the navicular and cuneiforms is also important

to midfoot stability, functioning as a coordinated hinge-like structure that contributes to the mechanics of bipedal locomotion (Welte et al., 2023).

Within this system, the intermediate cuneiform occupies a central position in the midfoot and contributes to the distribution of forces between the tarsals and metatarsals (Kirby, 2017). During load-bearing activities, there is relatively little movement between the cuneiforms and metatarsals, allowing forces to be transferred efficiently through the midfoot (Conconi et al., 2023). Mobility between the navicular and cuneiforms varies across the three cuneiforms, decreasing from the medial to the lateral cuneiform (Conconi et al., 2023). The relative restriction of movement between these elements contributes to the stiffness of the medial longitudinal arch and facilitates efficient transfer of forces through the tarsal and metatarsal column. The second metatarsal further reinforces this structure by being tightly wedged between the medial and lateral cuneiforms, creating a relatively stiff central column between the tarsals and forefoot (Conconi et al., 2023; Welte et al., 2023). The intermediate cuneiform therefore forms part of an integrated midfoot platform with the navicular, adjacent cuneiforms, and second metatarsal, contributing to the structural integrity and stability of the foot during loading (Asghar and Naaz, 2022; Chauhan and Taqi, 2022). Together, these articulations allow the midfoot to transmit loads from the hindfoot toward the forefoot.

The rigid midfoot architecture contrasts strongly with the flexible midfoot of monkeys and nonhuman apes. In arboreal primates, midfoot mobility allows the foot to conform to branches and irregular substrates, while in great apes the midfoot break permits substantial deformation under load. While this is advantageous for grasping and climbing, it reduces the ability of the foot to function as a rigid propulsive lever. In humans, the rigid midfoot, combined with the non-opposable hallux, shortened metatarsals, robust calcaneus, and pedal arches, allows

the foot to support body weight, distribute and absorb loads, and efficiently transmit forces during push-off. The presence of the longitudinal arches, non-opposable hallux and rigid midfoot are among the most distinctive features separating the human food from those of other primates (Sorrentino et al., 2023). These features work together to distribute body weight throughout the midfoot column during bipedal standing, walking, and running while providing the rigidity necessary for efficient propulsion. Fossil hominin feet are rare, but those that are preserved reveal a mosaic of pedal features that document the gradual emergence of these adaptations.

Fossil evidence suggests that early hominin feet shifted from a more ape-like flexible morphology to the stiff, robust configuration that is characteristic of modern humans. While there is little evidence as to exactly when this shift occurred, the order in which these changes evolved is better understood. Current evidence suggests that the foot first evolved an elongated tarsal region, with improved stability in the midfoot and the ankle, followed by changes in the rest of the foot that resulted in an even more derived configuration (McNutt et al., 2018). The midfoot first became more rigid and a stiff lateral arch was formed, then the metatarsal length was reduced prior to the hallux becoming fully adducted (Harcourt-Smith and Aiello, 2004; Negishi et al., 2021; Sorrentino et al., 2023). Species in the genus *Homo* were fully bipedal, the shape and structure of their feet reflect this preference for upright locomotion. However, some variation exists among species in the genus *Homo,* but the functional differences in the foot morphology of this genus are not yet known (Harcourt-Smith and Aiello, 2004).

Taken together, the comparative morphology of the primate foot demonstrates a broad transition from a flexible, grasping structure to a rigid, load-bearing platform. The generalized arboreal primate foot is characterized by a divergent hallux, mobile midfoot, and curved digits that facilitate grasping and conforming to irregular substrates. Monkeys retain this configuration

but have some modifications associated with different degrees of arboreality and terrestriality. Apes retain the grasping hallux and mobile midfoot while developing greater pedal robustness in association with their diverse locomotor strategies, with the African apes representing an important intermediate condition characterized by both terrestrial and arboreal adaptations. Finally, humans represent the most derived condition in this comparison, with a fully adducted hallux, shortened metatarsals and phalanges, robust calcaneus, and rigid longitudinal and transverse arches that collectively transform the foot into an efficient structure for habitual bipedal locomotion. This provides an anatomical and functional framework for interpreting variation in individual pedal elements, including the intermediate cuneiform, within an evolutionary context.

The Role of Taxonomy in Skeletal Morphology

Given the central role of the intermediate cuneiform in force transmission and articulation between the tarsals and metatarsals, differences in locomotor behaviour would be expected to produce corresponding differences in its morphology. Species that rely on the distinct locomotor repertoires discussed previously, have different loading and functional demands across the midfoot. Consequently, it can be assumed that the morphology of the intermediate cuneiform will differ according to the primary ways in which a species uses their feet, reflecting adaptations that optimize stability, mobility, and force transmission for particular locomotor behaviours. This prediction, however, assumes that skeletal morphology primarily reflects functional adaptation. If other evolutionary processes exert stronger influences on skeletal morphology, species with similar locomotor behaviours may not possess similar intermediate cuneiform morphologies, while closely related taxa may retain similar morphologies despite differences in locomotor repertoire. Based on the positioning of the intermediate cuneiform, as well as its role in stability,

load bearing, and mobility within the foot, it can be assumed that its shape will be highly influenced by locomotor behaviour, but this may not be the only, or even the primary cause of morphological variation between species.

Although locomotor behaviour is an important influence on primate postcranial morphology especially when it comes to the foot, skeletal shape is not determined by function alone. Morphological variation can also reflect phylogenetic history, shared ancestry, convergent evolution, developmental constraints, and developmental abnormalities. Thus, similar locomotor behaviours do not always produce identical skeletal morphologies. Closely related taxa may have similar foot shapes even when their locomotor behaviours differ. The shape of different bones is created through multiple interacting factors rather than just a simple relationship with locomotor behaviour. This is especially relevant when studying the intermediate cuneiform, a tarsal element that occupies a structurally important but relatively constrained position within the midfoot. The bone contributes to both stability and mobility of the mid foot, thus its shape may reflect a balance between functional demands and broader evolutionary patterns seen across multiple anthropoid species. Variation in intermediate cuneiform morphology, while likely influenced at least to a degree by locomotor behaviour, is likely also influenced by taxonomy. Combined, these factors are essential for shaping how the morphology of the intermediate cuneiform varies across extant and fossil anthropoids.

An additional factor influencing skeletal morphology is developmental integration. Individual skeletal elements do not evolve in isolation, they share common developmental pathways and have shared functional interactions (Hallgrímsson et al., 2009; Klingenberg, 2009). Bones within the postcrainal skeleton are part of complex integrated systems, where changes in one bone may cause changes in neighboring bones (Lovejoy et al., 2003; von Cramon-Taubadel,

2022). This is especially true for bones like the intermediate cuneiform, which are part of the complex structure that make up the foot. This bone is likely to exhibit developmental integration because it occupies a central position within the tarsal complex. During movement the tarsals and metatarsals function together to maintain the structural integrity of the midfoot, facilitating load transmission between the tarsals and metatarsals. Therefore, changes to the intermediate cuneiform, or other bones in the foot may influence the morphology of the intermediate cuneiform even if selective pressures are not acting directly on the bone itself. Thus, variation in the intermediate cuneiform may reflect broader patterns of foot evolution rather than adaptations of this bone alone. Further, the intermediate cuneiform, like many other bones of the foot may follow a generalized anthropoid pattern, where extreme changes to its shape are constrained by the demands of the foot that are shared by all anthropoid species. Locomotor behaviour influences the form and function of the foot as a whole, but the response of any individual tarsal bone is constrained by its developmental and functional relationships with the surrounding bones.

Yet another factor that may influence the morphology of any particular bone in the skeleton is convergent evolution. Species with widely differing locomotor repertoires may have similar skeletal morphologies as a result of convergent evolution. Convergent evolution is a fundamental evolutionary process where similar anatomical characteristics evolve independently in distantly related taxa as a result of functional or environmental pressures, rather than shared ancestry (Losos, 2011; Stern, 2013). Morphological similarities do not always indicate close evolutionary relationships, or similar behavioural adaptations, but similar biomechanical demands may drive the repeated evolution of similar skeletal features in multiple lineages (Losos, 2011). Being able to distinguish between traits inherited from a common ancestry and a

trait produced through convergence is an important factor that needs to be considered in these types of studies.

Several examples of convergent evolution have been documented throughout the postcranial skeleton in primates reflecting the repeated evolution of similar locomotor strategies across independent lineages, like the atelid and colobus monkeys, which both participate primarily in arboreal quadrupedalism and share many skeletal elements as a result of their shared locomotor behavior, despite being distantly related (Fleagle, 2013). If locomotor behaviour is a dominant driver of intermediate cuneiform morphology, these distantly related taxa that have similar locomotor behaviours should exhibit convergent intermediate morphologies. However, if phylogenetic history has a stronger influence, these species may have differing intermediate cuneiform morphologies, despite their shared locomotor repertoires. Adaptations associated with suspension, climbing, terrestrial and arboreal quadrupedalism have evolved multiple times and often have comparable functional morphologies despite having differing origins (Fleagle, 2013b; Larson, 2018; Youlatos and Meldrum, 2011). At the same time, phylogenetic history influences skeletal morphology through inherited developmental patterns and evolutionary constraints, meaning that morphology reflects a combination of functional adaptation and shared ancestry rather than being a result of just one of these factors on its own (Hallgrímsson et al., 2009; Lovejoy et al., 2003; Klingenberg, 2009). When interpreting variation in individual elements of the postcranial skeleton, one should consider both phylogenetic and functional factors.

These evolutionary processes suggest that intermediate cuneiform morphology is unlikely to be determined solely by locomotor behaviour. Rather, the shape of the bone may reflect a combination of functional adaptation to specific locomotor behaviours, phylogenetic history, developmental integration, skeletal abnormalities, and convergent evolution. This thesis aims to

understand how much these factors contribute to intermediate cuneiform morphology and the overall shape of the anthropoid foot, and to see the extent to which intermediate cuneiform morphology can be used to infer locomotor behavior in both extant and fossil primates.

Objectives

Understanding the morphology of the human foot and that of our ancestors provides important insight into the evolution of the modern human foot and terrestrial bipedal locomotion. However, the hominin foot fossil record is fragmentary, and the small individual elements of the foot are often poorly preserved or rarely recovered. Developing a clearer understanding of the comparative morphology of individual pedal elements can therefore provide an important framework for interpreting the limited fossil material that is available. Extant anthropoids provide a valuable comparative framework for this purpose because they encompass substantial taxonomic and locomotor diversity, including platyrrhines and catarrhines that vary in their use of arboreal and terrestrial environments.

The intermediate cuneiform is one of the least studied of the primate tarsal bones, despite its position within the central midfoot and its articulations with the navicular and second metatarsal. Its morphology may therefore provide information about the functional and evolutionary factors that shape the primate midfoot. This uses three-dimensional geometric morphometrics (3DGM) to characterize intermediate cuneiform shape variation across a broad sample of extant anthropoids and several fossil hominin specimens. Although 3DGM has been used extensively to investigate the morphology of other tarsal elements in anthropoids (e.g., Knigge et al., 2015; Turley and Frost, 2013; Stanković et al., 2018; Nozaki et al., 2021a, 2021b; Friesen et al., 2022), relatively little work has examined the intermediate cuneiform specifically,

with Belance et al. (2025) providing one of the only other comparative 3DGM analyses of this element.

The primary objective of this study is to characterize the pattern and extent of intermediate cuneiform shape variation among extant anthropoids and fossil hominins and to evaluate the extent to which this variation corresponds with phylogenetic relationships and locomotor behaviour. Two complementary hypotheses are examined: (1) intermediate cuneiform morphology reflects phylogenetic history, thus closely related taxa exhibit greater morphological similarity; and (2) intermediate cuneiform morphology reflects locomotor behaviour thus taxa experiencing similar locomotor demands exhibit similar morphological characteristics, including similarities that may result from convergent evolution. These hypotheses are not mutually exclusive and the morphology of the intermediate cuneiform may reflect a combination of shared ancestry and functional adaptation.

Phylogenetic Hypothesis

If phylogenetic relationships are the primary influence on intermediate cuneiform morphology, taxa that are more closely related are predicted to exhibit greater morphological similarity than distantly related taxa. Taxonomic groups are predicted to show recognizable patterns of clustering in the morphospace, with differences expected between major anthropoid groups such as platyrrhines and catarrhines, and between monkeys and apes. Greater morphological similarity is also predicted among closely related species within these groups. Conversely, if distantly related taxa exhibit similar intermediate cuneiform morphology despite substantial phylogenetic differences, this may indicate that factors other than shared ancestry, such as locomotor behaviour have contributed to the observed similarity.

Locomotor Hypothesis

If locomotor behaviour influences intermediate cuneiform morphology, taxa that regularly experience similar mechanical demands during locomotion are predicted to exhibit greater morphological similarity, regardless of their phylogenetic relationships. In particular, arboreal and terrestrial quadrupedal taxa are predicted to differ in intermediate cuneiform shape if their contrasting locomotor demands have influenced the structure of the midfoot. Arboreal taxa are expected to exhibit morphological characteristics associated with greater midfoot mobility and flexibility, whereas taxa that rely more heavily on terrestrial locomotion are expected to exhibit characteristics associated with increased midfoot stability and resistance to loading. Therefore, similarities among distantly related taxa that share comparable locomotor behaviours would provide evidence for possible functional convergence. The study also evaluates taxa with more specialized locomotor behaviours including climbing, suspension, and bipedalism. Where these behaviours have distinctive mechanical demands on the midfoot, taxa exhibiting these behaviours are predicted to occupy distinct regions of the morphospace or to exhibit morphological characteristics that distinguish them from predominantly quadrupedal taxa. However, because many anthropoid species use multiple locomotor behaviours, locomotor categories are expected to overlap to some degree rather than forming completely discrete morphological groups.

Hominin Predictions

The morphology of modern humans is examined within this broader comparative framework to evaluate whether habitual bipedalism is associated with distinctive intermediate cuneiform morphology. If the functional demands of habitual terrestrial bipedalism have substantially influenced the shape of the intermediate cuneiform, modern humans are predicted to occupy a distinct region of the morphospace relative to all other nonhuman anthropoids.

Alternatively, substantial overlap between humans and nonhuman anthropoids would suggest that the intermediate cuneiform retains a morphology that is shared more broadly among anthropoids or that the effects of bipedalism are not strongly expressed in this particular element. Fossil hominins are predicted to exhibit varying degrees of morphological similarity to modern humans and nonhuman anthropoids. Fossil specimens that share locomotor adaptations may exhibit greater similarity to nonhuman anthropoids. These comparisons provide an opportunity to assess whether intermediate cuneiform morphology can contribute to interpretations of locomotor behaviour in the hominin fossil record.

Analytical Approach

By using 3DGM, this study will explore small to large-scale differences in the shape of this bone and create a comparative framework that highlights any variation in shape found between or within species. 3DGM provides a quantitative means of testing these hypotheses by capturing and comparing differences in intermediate cuneiform shape among individuals and taxa. By analyzing the three-dimensional configuration of anatomical landmarks and semilandmarks, 3DGM permits shape variation to be examined independently of differences in position, orientation, and scale. This approach is particularly appropriate for the intermediate cuneiform because it allows subtle differences across the complex three-dimensional surfaces of the bone to be quantified within a common comparative framework. In this study semilandmarks are concentrated on the articular surfaces of the intermediate cuneiform that contact the navicular and second metatarsal. These regions are particularly relevant to the functional role of the bone because they form part of the articulations through which forces are transmitted across the midfoot during locomotion. Examining variation in these regions therefore provides a means of

evaluation whether differences in intermediate cuneiform morphology correspond with differences in locomotor behaviour and functional demands.

Overall, this study tests whether intermediate cuneiform morphology is structured primarily by phylogenetic relationships, locomotor behaviour, or a combination of both. By establishing the pattern of intermediate cuneiform shape variation across extant anthropoids and fossil hominin, this study aims to provide a comparative framework for understanding the functional and evolutionary significance of this understudied element of the foot and to assess its potential for informing interpretations of locomotion and evolutionary relationships in the fossil record.

Methods

Samples

The 3D models in this study were obtained by laser scanning skeletal collections at several institutions. All scanning and modelling steps were conducted previously by Dr. Matthew W. Tocheri and Dr. Thomas C. Prang. Three-dimensional surface models were generated following established protocols for the digital preparation of primate skeletal elements (Prang and Tocheri, 2024; Tocheri, 2009; Tocheri et al., 2011). Specimens were scanned from multiple orientations to capture the complete external surface, with individual scans aligned and merged to produce a triangular surface mesh (Prang and Tocheri, 2024; Tocheri, 2009; Tocheri et al., 2011). The resulting models were digitally cleaned to remove unnecessary data and correct imperfections in the mesh, while preserving the morphology of the original specimen (Tocheri, 2009). Finally, where necessary, models were further prepared and segmented to isolate the relevant anatomical surfaces prior to landmarking and subsequent 3DGM analysis (Tocheri, 2009). The comparative sample of extant primates consisted of 399 specimens of monkeys, apes,

and modern humans, as well as four fossil hominins (Table 2). All bones were analyzed from the right side of the body; those from the left were reflected using the mirror surface function in Stratovan Checkpoint version 2024.03.07 (Stratovan Checkpoint, 2024) prior to data collection.

3DGM provides a robust quantitative framework for comparatively analyzing shape variation of particular biological structures (in this case, a bone in the midfoot) independently of other shape information such as size, position, and orientation (Slice, 2006). This methodology. 3DGM quantifies variations in the shape of biological structures across predetermined groups such as taxonomic groups or populations (Adams et al., 2004; Slice, 2006). 3DGM uses a series of anatomical landmarks or semilandmarks (virtual points that are attributed to x, y, and z coordinates), which are placed along the surfaces of the 3D biological structure of interest (Figure 3). This method captures shape variation through a Generalized Procrustes Analysis (GPA), which removes size, position, and rotational information in each sample, allowing the structure to solely be analyzed by its shape (Slice, 2006). This is followed by Principal Component Analysis (PCA), which is used to analyze a large dataset and compare the specimens based on morphological differences or similarities to find patterns of variation (Adams et al., 2004; Slice, 2006; Bartoli et al., 2013).

Phylogenetic Considerations

Because morphological variation may reflect both locomotor adaptations and shared evolutionary history, phylogenetic relationships among taxa represent an important consideration when interpreting comparative morphological data. The analyses employed in this study, including principal component analysis (PCA) and Procrustes-based analysis of variance, were used to evaluate patterns of morphological variation and differences among taxonomic and locomotor groups; however, they did not explicitly account for phylogenetic relatedness among

specimens. The effects of shared evolutionary history could not be statistically separated from those associated with locomotor behaviour using the chosen methods of analysis. Therefore, phylogenetic comparative methods were not incorporated into the analyses. However, this could be an important avenue for future research to further evaluate the contributions of phylogeny and locomotor behaviour to intermediate cuneiform morphology.

Landmarks

Landmarking consisted of applying two patches to each of the 403 intermediate cuneiforms using Stratovan Checkpoint version 2024.03.07. One patch was applied to the facet that articulates proximally with the navicular, and the other was applied to the facet that articulates distally with the second metatarsal base. These two patches were considered sufficient for the purposes of this study because 1) the intermediate cuneiform has a relatively simple shape compared with other tarsal bones, 2) the navicular and second metatarsal facets cover the entirety of the bone's proximal and distal ends, respectively, and are key for distributing proximo-distally directed loads during locomotor behaviours, and 3) the remaining four surfaces (i.e., medial, lateral, dorsal, and plantar) vary to such a degree (not just between species but within species as well) that consistent, reliable identification of homologous landmarks is essentially impossible. Each patch consisted of 169 semilandmarks (338 per bone), with four of these on each of the four corners of the surface. For consistency, patches were applied to each intermediate cuneiform using Stratovan Checkpoint's template function, which ensured homogeneity as it kept the semilandmark density (13 x 13), point rotation, and position of the patches consistent across all the samples. The resulting data consist of a set of x, y, and z coordinates for each intermediate cuneiform that were then saved as individual .nts files. These landmarks were then imported into R for geometric morphometric analysis as multiple .csv files.

Once all of the bones were patched, an .nts file was created in Excel that contained each of the sample IDs, which were subsequently numbered with the following sequence: 001, 002, 003, etc. This NTS file also included group designations for each sample named based on the species (e.g., human, mountain gorilla, chimpanzee). Additional .nts files were created with more specific group designations, including the locomotor behaviour of each species, and broader group designations (e.g., great ape, lesser ape, monkey), which were used for further analysis. These .nts files assigned a specific numerical value and a group designation for each of the 403 samples, which made analysis easier, as each individual was grouped with other individuals in its own species, rather than having to do so manually.

Shape Analysis

All analyses were conducted in R using multiple packages created for 3D shape analysis (R Core Team, 2025). The required packages were installed and loaded using the **pacman** (Rinker and Kurkiewicz, 2018) package to ensure efficient package management. The main analytical packages used were **geomorph** (Adams et al., 2021), which was used for geometric morphometric analysis. **RRPP** (Collyer and Adams, 2018) was used for residual randomization permutation procedures; this evaluates the significance of variance by randomly shuffling residuals under the null hypothesis to compare variables, in this case, the morphology of the intermediate cuneiform across species. To visualize the data, **ggplot2** (Wickham, 2016) and **plotly** (Sievert, 2024) were used, and **ggConvexHull** (Martin, 2023) was used to create convex hulls to aid in data visualization and to make each cluster clearer. To visualize meshes and allow for data manipulation, **Morpho** (Schlager, 2017)**, rlg** (Murdoch et al., 2023), **FactoMineR** (Lê et al., 2008), **scatterplot3d** (Ligges and Mächler, 2003), and **Rvcg** (Schlager, 2023) were used.

After the above packages were installed and loaded, the working directory was set to the appropriate folder containing the .nts files; multiple directory paths were created depending on the taxonomic group under analysis (e.g., apes, monkeys, all species). Landmark data associated with these files was imported as a multi-specimen 3D array using the **readmulti.nts()** function in the **geomorph** package (Adams et al., 2021) and the data were reshaped into 338 landmarks x3 dimensions (X, Y, Z axes) for each species using the **two.d.array()** (Adams et al., 2021**)** and **arrayspecs** (Adams et al., 2021) functions. The **attributes()** function was used to inspect the first specimen's landmarks to ensure that each function performed as expected.

Finally, specimen metadata, such as taxonomic classifications and groups (e.g., locomotor preferences), were imported from the aforementioned .csv files using the **read.csv()** function. These additional data allowed for colour coding, specific shape distinctions, and grouping during further analysis, so that all categorical variables could be studied separately, or together in downstream analysis.

Generalized Procrustes Analysis

Most of the analysis conducted on the samples was through a generalized Procrustes analysis (GPA). A GPA is a statistical technique that aligns multiple data sets with a standardized reference frame (Bartoli et al., 2013). This process removes some shape data, such as size, positional, and rotational information and keeps only the remaining shape information for analysis (Bartoli et al., 2013). Thus, the variation of a specific biological structure across species can be analyzed by shape alone without factors such as the size of different individuals influencing the results. The GPA takes all the landmarked samples and creates a data set consisting of several points that show significant similarities, reducing the amount of data that needs to be explored (Bartoli et al., 2013). In this case, the goal is to take the landmark

information from several samples and translate it into a format that averages out the shape differences so that a principal component analysis (PCA) can be performed. The GPA was conducted using the **gpagen()** (Adams et al., 2021) function, which standardized all of the specimens into a shared coordinate system and aligned landmark (X, Y, Z) points. The GPA also calculated the centroid size, which is the sum of the squared distances of all the landmarks and the center point of each sample. Centroid size is used to determine how intermediate cuneiform shape varies based on overall size.

Principal Component Analysis

PCA is a statistical technique that seeks to identify correlations among measured variables and thus the directions of maximum variance in multivariate datasets (Bartoli et al., 2013). These directions of maximum variance are ordered as a new set of variables called components (Abdi and Williams, 2010). The first component represents the greatest variance, followed by the second PC, and so on (Abdi and Williams, 2010). PCA was performed on the previously aligned Procrustes coordinates using the **gm.prcomp()** (Adams et al., 2021) function, which reduces dimensionality and identifies the maximum shape variation. Eigenvalues were used to calculate the proportion of total shape variance explained by each component. A PCA of landmark coordinates for 403 samples results in 402 PCs, most of which explain only very small percentages of the total variance (i.e., <1%). In this study, only components that explained 5% or more of the total variance were examined in detail.

The function **ggplot2** (Wickham, 2016) was used to generate bivariate scatterplots of the various PCs of interest for each analysis and convex hulls were used to visualize group clusters based on taxonomy and/or locomotor behaviour (Abdi and Williams, 2010). Taxonomic groups were differentiated using combinations of colours and symbols to differentiate each group, and a

legend was generated for taxa and more specific groupings, such as locomotor behaviours. Standard bivariate plots were generated for several components (e.g., PC1 vs. PC2, PC3 vs. PC4), which were later saved for further analysis.

Shape Visualization

To visualize the morphological variation associated with the principal components, specimens representing the extreme positive and extreme negative scores for PC1, 2, and 3 were identified from the PCA results. For each component, the specimen that plotted furthest to the negative point and furthest to the positive point of the axis were selected to capture the full extent of shape variation represented by each component.

The corresponding 3D surface meshes were then opened in MeshLab (version 2025.07) (Visual Computing Lab, ISTI–CNR, 2025). Each intermediate cuneiform was oriented in a standardized anatomical position to ensure consistent comparison across the species, and views of the surfaces that articulate with the navicular, second metatarsal, medial and lateral cuneiformes were captured for both the positive and negative extremes of each principal component.

These images were compared qualitatively to identify anatomical differences (overall shape, mediolateral width, dorsoplantar height, differences in the navicular and second metatarsal articular facets) associated with the variation along each PC. By directly comparing specimens at opposing ends of each axis, the anatomical shape variation along each principal component could be interpreted in a biologically meaningful manner. This approach thus allowed visualization of real specimen morphology, rather than theoretical warps of the mean shape, which provided an interpretation of morphospace variation in real anatomical differences.

In addition to PC extremes, a representative specimen approximating the mean shape for each species was identified. These specimens were likewise opened in MeshLab, oriented in a standardized anatomical position, and views of the surfaces that articulate with the navicular, second metatarsal, medial and lateral cuneiforms were captured. These specimens representing the average intermediate cuneiform morphology in each species were compared across species to assess interspecific differences in overall morphology and to gain a better understanding of what the typical intermediate cuneiform morphology looks like in each of the species studied in this analysis. These figures were used to compare with the specimen representing each extreme on each of the principal components for all three analyses.

Procrustes ANOVA (PERMANOVA)

Finally, to statistically assess differences in intermediate cuneiform shape among taxonomic groups, a Procrustes analysis of variance (PERMANOVA) was conducted using the **procD.lm()** function in the **geomorph** package (Adams et al., 2021). This function implements a residual randomization permutation procedure (RRPP) which evaluates the significance of group-level differences in multivariate shape data. This analysis was conducted for each of the three analyses to individually assess differences between taxonomic groups as well as locomotor categories.

Prior to analysis, taxonomic groups and locomotor categories were coded as categorical factors in R. The Procrustes-aligned landmark coordinates were obtained from the generalized Procrustes analysis (GPA) and were used as the dependent variable, while taxonomic groups and locomotor categories were used as independent variables.

Significance was assessed using 5,000 permutations, which provides a robust estimation of p-values for high-dimensional geometric morphometric data. A total of 5,000 permutations

was selected as a compromise between statistical robustness and computational feasibility, as higher permutation numbers exceeded available memory due to the amount of specimens being analyzed and caused the analysis to fail. The purpose of this is to test whether among-group variation in the morphospace exceeds that expected under the null hypothesis of no group-level shape differences. Pairwise comparisons between taxonomic groups and between locomotor categories were conducted using the **pairwise()** function applied to the Procrustes ANOVA model. This procedure evaluates pairwise differences in mean shape between groups using permutation-based significance testing.

To account for multiple pairwise comparisons and reduce the likelihood of error, sequential Bonferroni-corrected p-values were calculated following the pairwise analyses. Pairwise comparison tables were extracted from the Procrustes ANOVA output and converted into a vector of p-values. The sequential Bonferroni correction method was then applied using the **p.adjust()** function. Corrected p-values were used to determine statistical significance among pairwise taxonomic comparisons of intermediate cuneiform morphology using an alpha level of 0.05.

Results

Monkeys

The first sixteen PCs collectively explain about 92% of the total variance observed in the dataset, with PCs 1 to 3 explaining 56.1%. Figure 4 shows a plot of the two largest PCs that best summarize the morphological variation present in the intermediate cuneiform among the monkeys (56.5% of the total variance). Overall, the PCA revealed substantial overlap among many taxa, but several groups occupied relatively distinct regions of morphospace. The most pronounced separation occurred along PC1, which differentiated atelids from colobus monkeys,

while PC2 and PC3 provided additional separation among several cercopithecid and cebid taxa.

PC1 explained 35.4% of the total variance and separated three broad distributions. Atelids (i.e., spider, woolly, and howler monkeys) plot to the positive extreme of this axis, colobus monkeys to the negative extreme, and the remaining species fall into a large cluster in the center of this axis. The position of atelids was associated with intermediate cuneiforms that were mediolaterally broad and dorsoplantarly short, whereas colobus monkeys were characterized by narrower and dorsoplantarly taller intermediate cuneiforms (Figure 5). In contrast, colobus monkeys cluster negatively along this axis because their intermediate cuneiforms are mediolaterally narrow and dorsoplantarly tall. One of the most apparent sources of variation is the second metatarsal articulation. In atelids, this surface has a very wide "T" shape. This contrasts with the ovoid, inverted teardrop shape in colobus monkeys. In other taxa, this surface displays a medial slant dorsally. In most taxa, the navicular articulation typically forms a "P" shape. However, the dorsoplantar height of this surface varies in that it is dorsoplantarly short in atelids but dorsoplantarly tall in other taxa.

PC2 explained 10.7% of the total variance and provided additional differentiation among several taxa (Figure 6). Crested mangabeys, macaques, and some howler monkeys occupied the positive portion of the axis, whereas northern plains gray langurs, capuchins, colobus monkeys, and some baboons occupied the negative portion. Variation along PC2 was primarily associated with overall dorsoplantar and mediolateral dimensions of the intermediate cuneiform and differences in the navicular and second metatarsal articular facets. For example, crested mangabeys had relatively broad and dorsoplantarly short intermediate cuneiforms, giving them a shorter and stouter appearance than the taller, more dorsoplantarly extended morphology of northern plains gray langurs. Crested mangabeys also exhibited a broad T-shaped second

metatarsal facet, although this configuration was less pronounced than in atelids. In northern plains gray langurs, the second metatarsal facet instead had an elongated plantar portion, while the navicular facet was more irregular and exhibited a pronounced medial projection in its dorsal region.

Along PC3 (10.0%) (Figure 7), capuchins, as well as some spider monkeys and mandrills, occupy the negative half of the axis, whereas baboons, howler, and colobus monkeys occupy the positive end of the axis, which mainly separates capuchins from baboons and colobus monkeys (Figure 8). In capuchins, both the navicular and second metatarsal articular facets have very similar shapes, which are somewhat wedge shaped and compact overall. In both, the dorsal portion of the bone is broad and rounded, while the plantar portion is narrower and more irregular. The medial side of these surfaces is more concave, while the lateral side is more convex, which contributes to the wedge-like shape. In contrast, the navicular and second metatarsal articular surfaces of baboon intermediate cuneiforms are more triangular rather than ovoid (as seen in capuchins), the distal end of the bone forms a rounded projection, giving it a slightly "pear" shaped appearance as viewed from the navicular articular surface. The plantar portion of the bone is narrower and more elongated, and tapers substantially. Additionally, along the navicular articular surface there appears to be a bulbous plantar projection.

Figure 9 shows a plot of the two largest PCs when specimens are grouped by locomotor category (i.e., arboreal and terrestrial quadrupeds) rather than taxonomy. There is substantial overlap between the arboreal and terrestrial quadrupedal taxa. Arboreal quadrupeds occupied a broad region of morphospace whereas terrestrial quadrupeds largely fell within one part of this distribution. The wide spread of arboreal quadrupeds is due mostly to atelids and colobus monkeys.

The Procrustes PERMANOVAs found that taxonomic group and locomotor category explain 47.3% and 9.4% of the total Procrustes shape variance. After sequential Bonferroni corrections, significant differences ($p < 0.001$) in intermediate cuneiform morphology (Table 3) remained primarily between atelids, cercopithecines, and cebids. Within the cercopithecids, significant pairwise differences were observed among baboons, macaques, mandrills, crested mangabeys, northern plains gray langurs, colobus monkeys, and proboscis monkeys. Cebids showed more limited but still notable differentiation between the atelids and some cercopithecids. Finally, atelids differed significantly from nearly all cercopithecids and cebids but not from each other. For locomotor categories, a significant difference in intermediate cuneiform morphology between arboreal and terrestrial quadrupedal taxa was also observed ($p = 0.0002$).

Hominoids

The first fifteen PCs collectively explain ~86% of the total variance observed, with PCs 1 to 3 explaining 54%. Figure 10 shows a plot of the two largest PCs that best summarize the morphological variation present in the intermediate cuneiform among extant hominoids and four fossil hominin specimens (44.5% of the total variance). Along PC1, gorillas plot toward the positive end, humans, orangutans, and hylobatids plot toward the negative end, and bonobos and chimpanzees plot more toward the center. Gorillas cluster positively along this axis because their intermediate cuneiforms are dorsoplantarly tall and mediolaterally narrow (Figure 11). In contrast, hylobatids plot towards the negative end because their intermediate cuneiforms are dorsoplantarly short and mediolaterally broad. Additional differences between the two extremes exist in the shape of the navicular and second metatarsal articular facets. In dwarf gibbons, the navicular articular facet is more triangular and is widest on the dorsal portion of the bone,

whereas in gorillas this facet is more “pear” shaped and tapers more distinctly inferiorly. Similarly, the second metatarsal articular facet of dwarf gibbons is rectangular in shape, appearing more “block-like” and robust, whereas in gorillas this facet is more “wedge” shaped.

On PC2, humans plot positively whereas bonobos plot negatively but several taxa (orangutans, chimpanzees, and hylobatids) span a relatively wide range (Figure 12). In bonobos, the second metatarsal articular facet is more irregular in shape and there is a slight narrowing towards the plantar region of the bone such that overall this surface is less squared and more asymmetrical. In humans, this facet is more symmetrical and compact as well as much broader in the dorsal region such that overall it is more squared off, with some tapering present towards the plantar region (but less pronounced than in bonobos). In bonobos, the navicular facet is more asymmetrical overall, with the dorsal portion of the bone being slightly irregular and less evenly rounded; additionally, it has stronger plantar tapering than in humans. In contrast, this facet in humans is more uniformly triangular, with a smoother dorsal margin, and is more evenly convex. Humans cluster near the center of Figure 10, overlapping mostly with orangutans. All four fossil hominin specimens plot just outside the modern human cluster.

On PC3, the only notable separation occurs between mountain and western lowland gorillas, which cluster negatively and positively, respectively (Figure 13). This separation is largely due to mountain gorillas having dorsoplantarly taller and mediolaterally narrower intermediate cuneiforms than western lowland gorillas (Figure 14). In addition, in mountain gorillas the navicular facet is triangular and is widest dorsally, tapering towards the plantar half of the bone. Western lowland gorillas, in contrast, have a broader navicular articular facet, which is more of a “T” shape rather than being triangular, and there is less dramatic tapering towards the plantar half of the bone. In mountain gorillas, the second metatarsal facet is wedge shaped

and is widest dorsally with tapering occurring towards the plantar portion of the bone, whereas in western lowland gorillas this facet is also wedge shaped but is more block-like or square than in other gorilla taxa.

Figure 15 shows a plot of the two largest PCs using the primary mode of locomotion of each taxon as the grouping variable (i.e., bipedal, suspensory (and brachiators), and knuckle-walking hominoids). All four categories overlap with each other, but the knuckle walkers do show slight differentiation from the other taxa, clustering towards the positive end of the axis, but this is mostly due to gorillas (see above).

The Procrustes PERMANOVA found that taxonomic group and locomotor category explained 44.3% and 24% of the total Procrustes shape variance. After sequential Bonferroni corrections (Table 4), significant differences in intermediate cuneiform morphology occurred between gorillas (grauer, mountain, and western lowland gorillas) and most other extant taxa. Humans differed significantly from all great ape taxa, but did not differ significantly from hoolok gibbons or siamangs. Additional significant differences were observed between orangutans and several African ape taxa. Note that the four fossil hominin individuals were not included in the PERMANOVA analysis for taxonomy because as single specimens (i.e., n=1), they unnecessarily inflate the number of comparisons and lower the statistical power of the test. For locomotor categories, differences occurred between all of the locomotor groups (Table 5).

All Species

The first fifteen PCs collectively explain ~87% of the total variance, with PCs 1 to 3 explaining 54.2%, and PCs 1 and 2 explaining 45.8% (Figure 16). Essentially the results of the two previous PCAs merge together such that along PC1 (34%), there are four clusters. Atelids cluster towards the negative end of the axis, followed by modern humans, Sumatran and Bornean

orangutans, cebids, and cercopithecids (except colobus monkeys). Clustering slightly more positively along PC1 are colobus monkeys, chimpanzees, and bonobos, followed by gorillas, which cluster furthest towards the positive end of the axis. As reported above, atelids cluster negatively along this axis because their intermediate cuneiforms are mediolaterally broad and dorsoplantarly short (Figure 17). In contrast, gorillas and also chimpanzees, bonobos, and colobus monkeys cluster positively along this axis because their intermediate cuneiforms are mediolaterally narrow and dorsoplantarly tall.

On PC2, the crested mangabey, white-eyelid mangabey, macaque, mandrill, howler, some capuchins, some baboons, and some mountain and grauer gorillas cluster on the positive end of the component. Rather than the negative end of the component being represented by specific groups, only a few individuals from a few species plot to this end of the component, including some grauer gorillas, some sumatran orangutans, and some humans. The remainder of the species from a relatively tight, overlapping cluster in the center to the positive half of this axis. For the purposes of this analysis, a crested mangabey was chosen as the representative specimen for the positive extreme, and a sumatran orangutan was chosen as the negative extreme. Variation along this axis is driven mainly by the morphology of the navicular and second metatarsal facets, as well as the overall dorsoplantar breadth of the intermediate cuneiform as a whole (Figure 18).

For example, in sumatran orangutans, the intermediate cuneiform is dorsoplantarly shorter than that of the crested mangabey, which is dorsoplantarly tall. Morphological differences on the articular facets are as follows: beginning with the navicular facet, in the sumatran orangutan it is triangular with rounded edges, and is widest dorsally, with some tapering towards the plantar half of the bone; it is overall broad and compact. In the crested mangabey, this surface is more “pear” shaped and slender; there is strong plantar tapering, giving the bone the

appearance of being elongated in a plantar direction. The second metatarsal articular facet in sumatran orangutans is rather broad and somewhat squared and is slightly trapezoidal in shape, with the dorsal margin forming the widest part of the surface. In the crested mangabey, this surface is narrower and more rounded, and has an inverted teardrop shape, which is the typical shape of this surface across primates, this surface tapers plantarly, and is widest along the dorsal half of the bone.

Figure 19 is a plot of PC3 against PC1 (42.4% of the total variance). Along PC3, the negative most specimen is a hoolock gibbon, there are only two specimens in this group, and the second hoolock gibbon plots close to the positive end of this axis, these two individuals span a large amount of the length of the axis. The other species that cluster to the negative end of this axis are a few individuals from the sumatran orangutan group, as well as two fossil hominins, LB 1 and KNM-ER 64062, and modern humans. While some sumatran orangutans plot towards the negative portion of this axis, the cluster as a whole is very central along the axis, thus this group will not be used as the negative most species for this analysis. Most of the species form a relatively tight cluster in the center of the positive half of this axis. Bonobos make up the positive most cluster along this axis. Thus, the variation on this axis occurs between modern humans and bonobos, with all other groups contributing to the overall variation very minimally. Variation along this axis reflects differences in the overall morphology of the intermediate cuneiform, with the second metatarsal articular facet contributing most strongly, and the navicular articular facet also contributing to the observed shape differences (Figure 20). Variation between these two taxa has already been reported in PC2 of the hominoids analysis (see above).

In PC1 and PC2, modern humans and fossil hominins cluster just to the negative side of the center of the axis. They do not contribute much to the variation in PC1, but contribute

slightly to the variation in PC2, as one individual plots close to the negative end. The hominin cluster overlaps strongly with the orangutan cluster, a pattern seen previously in the analysis of hominid species, as well as the siamang, gibbon, and baboon clusters. LB 1 plots to the negative half of the axis, just outside of the human cluster within the woolly and spider monkey clusters. OH 8 and StW 573 fall in the center of the human cluster. Finally, KNM-ER 64062 plots outside of the human cluster, closer to the center of the axis, overlapping with the chimpanzee and bonobo clusters close to the gorillas. With PC3, modern humans contribute very little to the variation along this axis. However, some fossil hominins plot towards the negative extreme of this axis, potentially contributing to the overall morphological variation in PC3. LB1 and KNM-ER 64062 plot outside of the human cluster and contribute to the overall variation in PC3. OH8 and StW573 plot just outside of the human cluster, towards the positive half of the axis, overlapping with the larger cluster of multiple primate species.

Figure 21 shows a plot of the two largest PCs using the primary mode of locomotion of each taxon as the grouping variable. There is minimal variation between these forms of locomotion among these species, with all the clusters overlapping. The terrestrial knuckle walkers do show slight differentiation from the other taxa, clustering towards the positive end of the axis, but this is due to the placement of the gorillas which was discussed earlier. The arboreal quadrupeds also cluster at the opposite end of the axis from the terrestrial knuckle walkers for the most part but the clusters do overlap near the center of the axis.

The Procrustes PERMANOVA found that taxonomy explains ~50% of the total Procrustes shape variance and locomotor category explains ~28% of total shape variation. These results indicate strong differentiation in intermediate cuneiform morphology among groups, as half of the observed shape variation is separated by taxonomic classification. After sequential

Bonferroni correction, (Table 6) significant differences in intermediate cuneiform morphology remained among most major primate clades. Significant differences were observed between *Gorilla* and all other clades. Hominins also differed significantly from all clades, while *Pan* and *Pongo* showed significant differences from atelids, cercopithecids, *Gorilla*, hominins, and each other. Cebids had more limited differentiation, differing significantly only from *Gorilla*, hominins, and *Pongo*, while hylobatids differed significantly from atelids, cercopithecids, *Gorilla*, hominins, and *Pan*, but not from cebids or *Pongo*. After sequential Bonferroni correction, all locomotor groups remained significantly different from one another in intermediate cuneiform morphology (Table 7).

Discussion

The main aim of this study was to quantify shape variation in the intermediate cuneiform among anthropoid primates and to examine how this variation relates to taxonomy, phylogeny, and locomotor behaviour. Across the three analyses, the results demonstrate that intermediate cuneiform morphology does not correspond neatly with broad locomotor categories. Taxa with broadly similar locomotor repertoires can occupy very different regions of the morphospace, while distantly related taxa with substantially different locomotor behaviours can exhibit similar intermediate cuneiform morphologies. Atelids and gorillas for instance, represent particularly distinctive morphologies, while colobus monkeys overlap with gorillas despite their predominantly arboreal locomotion. Modern humans and the included fossil hominins also do not form a distinct functional group; instead, despite the distinctive biomechanical demands of habitual bipedalism, they overlap with orangutans, cebids, and cercopithecids along the major axes of variation, particularly PC1. At the same time, the strong clustering of closely related taxa and the results of the Procrustes PERMANOVA indicate that taxonomy accounts for a

substantial component of intermediate cuneiform shape variation. Together, these results suggest that intermediate cuneiform morphology is structured by a combination of taxonomic history and functional or structural constraints rather than being primarily determined by broad locomotor behaviour alone.

The following discussion considers five questions raised by these findings: (1) what aspects of intermediate cuneiform morphology vary among anthropoids; (2) how well does this variation correspond with locomotor behaviour; (3) how much of the observed variation corresponds with taxonomy and phylogeny; (4) what do these results suggest about the distinctive human condition and the evolution of bipedalism; and (5) what can and cannot presently be inferred from the fossil hominins.

Variation in intermediate cuneiform morphology among anthropoids

The analyses demonstrate substantial variation in intermediate cuneiform morphology among anthropoids, with several taxonomic groups occupying distinctive regions of the morphospace. Atelids consistently form a lineage-specific cluster and occupy one extreme of the observed variation. In the all-species analysis, the spider and woolly monkeys, in particular, appear as the inverse of gorillas and colobus monkeys along PC1, reflecting major differences in overall intermediate cuneiform morphology. Initially it was predicted that atelid intermediate cuneiform morphology, like the morphology of other tarsal bones, would reflect locomotor behaviour (arboreal quadrupedalism and suspension). However, atelids plot directly opposite along PC1 from colobine monkeys, despite similarities in their broad arboreal locomotor repertoires.

Across the PCAs, spider monkeys (*Ateles*), woolly monkeys (*Lagothrix*), and howler monkeys (*Alouatta*) consistently form a lineage-specific cluster, with a uniquely mediolaterally

broad and dorsoplantarly short intermediate cuneiforms when compared to the taller and narrower morphologies observed in all other anthropoid species (Figure 21). The second metatarsal facet is especially distinctive, taking on an atypical broad, flattened "T"-like shape, rather than the more common oval, inverted teardrop, or "P" shaped surface seen in other anthropoids. Additionally, the two facets that articulate with the medial and lateral cuneiforms, are much wider mediolaterally, than any other species, and are a true square shape rather than the more rectangular, elongated shape seen in the same surface in other species. The consistency of these features across the sampled atelids indicates that their morphology represents a distinctive structural pattern shared across the lineage.

Gorillas and colobus monkeys represent another distinctive region of the morphospace. Both gorillas and colobus monkeys are characterized by having a relatively dorsoplantarly tall and mediolaterally narrow intermediate cuneiform, in contrast to the atelids, which occupy the opposite extreme of this axis and have a comparatively dorsoplantarly short and mediolaterally broad intermediate cuneiform. All other species in this analysis have an intermediate cuneiform that is dorsoplantarly tall and mediolaterally narrow relative to the atelids, but not to the degree of gorillas and colobus monkeys. Thus, these two taxa follow a generalized anthropoid intermediate cuneiform shape but to an extreme degree.

The consistency of the gorilla morphology is also apparent within the genus. In the hominoid PCA, the eastern gorilla specimens show substantial overlap with one another across the major axes, while western gorillas overlap with eastern gorillas to a somewhat lesser extent. This within-genus similarity contrasts with the broader separation observed between gorillas and several other hominoids and supports the interpretation that the distinctive gorilla morphology

represents a consistent taxonomic pattern rather than variation attributable to individual specimens alone.

Figure 22 compares the average colobus monkey to an average gorilla specimen (mountain gorilla). The purpose of this comparison is to illustrate the similarities that exist between these two individuals despite their substantial differences in locomotor behaviour and phylogeny. It is immediately apparent that the intermediate cuneiform morphology of these two individuals, and thus the two taxonomic groups, is very similar, with only minor differences appearing in the overall shape of the bone. Additionally, the facets of this bone that articulate with the navicular and second metatarsal are very similar across both taxa. The facet that articulates with the navicular in both primates is shaped like an inverted teardrop combined with the letter "P", with a slight protrusion on the medial half of the dorsal portion of the bone. Likewise, the facet articulating with the second metatarsal is similarly shaped as an inverted teardrop in both species. Although this surface is marginally shorter and stouter in the mountain gorilla relative to the colobus monkey, this difference is subtle. The articular surfaces for the medial and lateral cuneiforms are essentially identical in shape across both species; however, in the mountain gorilla, these surfaces appear slightly more mediolaterally narrower. These shape similarities suggest similar articulation points with the other cuneiform bones. These similarities indicate that the same broad intermediate cuneiform configuration can occur in taxa with very different locomotor repertoires.

These patterns demonstrate that intermediate cuneiform morphology varies meaningfully among anthropids, but the distribution of this variation does not correspond to a single functional gradient. Instead, several lineages exhibit distinctive morphologies while substantial overlap occurs among many of the remaining taxa. This combination of differentiation and overlap is

important for interpreting the functional significance of the intermediate cuneiform.

Relationships between intermediate cuneiform morphology and locomotor behaviour

Originally, this thesis predicted that intermediate cuneiform morphology would be influenced by locomotor behaviour and the associated functional demands. However, the results do not support a simple relationship between locomotor behaviour and intermediate cuneiform shape. Species with broadly similar locomotor repertoires often occupy very different positions in the morphospace. Most notably, atelids and colobus monkeys are both highly arboreal, yet they occur at opposite extremes along PC1 in both the monkeys, and all species analyses. Similarly, gorillas are among the most distinctive taxa despite sharing terrestrial knuckle-walking behaviour with chimpanzees and bonobos, humans also do not form a distinct functional cluster despite being the only obligate bipeds included in the study, instead they overlap with orangutans and plot near several monkey taxa.

The adelaide-colobus comparison provides particularly strong evidence that similar locomotor repertoires do not necessarily produce similarly intermediate cuneiform morphology. Despite both groups being highly arboreal and frequently engaging in behaviours that require similar midfoot functions their intermediate cuneiform morphologies are markedly different. If locomotor behaviour were the primary driver of intermediate cuneiform shape, species with broadly similar locomotor repertoires would be expected to converge morphologically and occupy similar regions of the morphospace. Atelids and colobus monkeys exhibit convergence in several aspects of their locomotor skeleton, including features associated with arboreal mobility, climbing, grasping, and suspension (Fleagle, 2013). Despite this clear pattern of convergence across multiple regions of the locomotor skeleton, the intermediate cuneiform does not follow

the same pattern of functional similarity between the atelids and colobus monkeys. Instead, atelids possess short, broad and robust intermediate cuneiforms whereas colobus monkeys have a comparatively taller, and narrower morphology that are more similar in shape to that of gorillas. The presence of markedly different intermediate cuneiform morphologies in these taxa that otherwise have broad functional similarities in their locomotor skeleton suggests that intermediate cuneiform morphology is not primarily influenced by locomotor behaviour. Instead, it suggests that other factors, likely phylogenetic history and lineage-specific constraints played a stronger role in shaping variation in this bone.

This contrast is important because it demonstrates that locomotor behaviour cannot be assumed to exert the same morphological influence across all elements of the foot. Other tarsal elements, including the talus and calcaneus, have been shown to exhibit stronger relationships with locomotor behaviour and functional adaptation (Harper et al., 2020; Knigge et al., 2015; Monclús-Gonzalo et al., 2025; Nozaki et al., 2021a; Parr et al., 2014; Tocheri et al., 2011). In contrast, the extensive overlap among locomotor groups in the present study suggests that the intermediate cuneiform is comparatively conservative. This difference between pedal elements may be important for understanding how the primate foot responds to different functional demands. Rather than all elements of the foot recording locomotor adaptation in the same way, individual bones may have different degrees of functional responsiveness.

The anatomical position of the intermediate cuneiform provides one possible explanation for this pattern. The bone articulates proximally with the navicular, distally with the second metatarsal, and medially and laterally with the adjacent cuneiforms. The bone sits directly within pathways responsible for transferring loads throughout the midfoot, and pathways that are responsible for balance and stability (Asghar and Naaz, 2022; Chauhan and Taqi, 2022; McNutt

et al., 2018; Suzuki et al., 2020). Its position within the middle of the midfoot means that changes in its morphology occur within a network of closely integrated articular surfaces. Thus, substantial modifications to the morphology of this bone would likely have consequences for multiple neighboring bones and overall foot mechanics. The intermediate cuneiform may therefore have a relatively limited range of variable configurations that can maintain appropriate articulation with the surrounding bones.

This possibility provides a useful hypothesis for future research, but it should not be considered demonstrated by the present analyses. The current results show that intermediate cuneiform shape is relatively conservative across many locomotor groups; they do not directly test the developmental or functional mechanisms responsible for this pattern. Nevertheless, the extensive overlap among locomotor categories is consistent with the possibility that functional adaptations can occur elsewhere in the foot while the intermediate cuneiform remains comparatively constrained by its position in the midfoot.

Taxonomy and Phylogeny

At the beginning of this thesis it was predicted that intermediate cuneiform morphology would be influenced by locomotor behaviour and the associated functional demands. However, the results do not support a simple relationship between locomotor behaviour and intermediate cuneiform shape in anthropoids. Taxonomy appears to explain a substantial portion of the observed shape differences. Species with broadly similar locomotor repertoires often occupy very different positions in the morphospace (atelids vs colobus monkeys, and gorillas vs chimpanzees and bonobos). The Procrustes PERMANOVA for all the species found that taxonomy explained 47.3% of the observed variation in intermediate cuneiform shape. Nearly half the total shape variation is explained by taxonomic grouping, suggesting shared evolutionary

history structures intermediate cuneiform morphology. Significant differences remained primarily between most taxa following Bonferroni correction (Table 6). In combination with the repeated clustering of closely related taxa across the PCAs, these results indicate that taxonomic affinity is an important component of intermediate cuneiform variation.

The distinctive atelid morphology provides the clearest example of this pattern. Spider, woolly, and howler monkeys consistently cluster together despite differences in their ecology, substrate use, and locomotor repertoires. This consistency is more likely supported by a shared ancestral condition inherited from the last common ancestor of Atelidae rather than independent convergence within each genus. Morphological traits in primates often exhibit strong phylogenetic signals, meaning that closely related species resemble each other due to common ancestry and not similar ecological pressures (Blomberg et al., 2003). The results therefore support the interpretation that atelid intermediate cuneiform morphology has a strong phylogenetic component. Locomotor behaviour may contribute to variation within the lineage, but the broader pattern appears to be associated with shared ancestry.

The results do not demonstrate that phylogeny is the sole determinant of intermediate cuneiform morphology. The overlap between gorillas and colobus monkeys provides an important example. These taxa are phylogenetically distant but occupy similar regions of morphospace, demonstrating that taxonomic history alone cannot account for every aspect of intermediate cuneiform variation. Their similarity may reflect functional requirements shared across different locomotor contexts, structural constraints imposed by the surrounding bones of the midfoot, or some combination of these factors.

The results therefore suggest that intermediate cuneiform morphology is best understood as reflecting the interaction of phylogenetic history with functional and structural constraints.

Rather than assuming that one mechanism explains the entire distribution of intermediate cuneiform shape, the observed pattern suggests that phylogenetic history may establish much of the baseline variation among lineages, while functional and structural factors may contribute to similarities or differences among particular taxa. The intermediate cuneiform appears to retain a relatively conserved anthropoid morphology. Locomotor adaptations influence foot function and morphology, but these adaptations occur in other regions of the foot, while the intermediate cuneiform has a generalized morphology that works with diverse locomotor behaviours. Taxonomy provides an important framework for the distribution of morphology, while the presence of similarities among distantly related taxa indicates that vastly different evolutionary histories can produce similar intermediate cuneiform configurations.

The human intermediate cuneiform and the evolution of bipedalism

One of the most unexpected findings of this study is that modern humans are not particularly distinct in intermediate cuneiform shape despite the highly derived biomechanical demands of habitual bipedalism. Before analysis, it was predicted that the human intermediate cuneiform would be significantly different from that of nonhuman primates. Instead, humans occupy a relatively central position in morphospace and overlap with orangutans, cebids, and many cercopithecids along the major axes of variation. The fossil hominins included in the study also occur near or within the modern human distribution.

This result should not necessarily be interpreted as evidence that the human intermediate cuneiform is simply “generalized”. The comparison between human and orangutan specimens demonstrates that the two taxa are anatomically distinct despite their overlap in the morphospace. At first glance, the overlap between humans and orangutans along the most significant axes in both the hominoid and all-species analyses suggests the possibility that both taxa either retain or

have secondarily converged on the primitive condition for great apes. Figure 23 compares an average modern human specimen with that of an orangutan. This comparison demonstrates that the two taxa are anatomically distinct despite their overlap in morphospace. Humans and orangutans are functionally and structurally distinct particularly in their articulations with the navicular proximally and the second metatarsal distally. However, the two clades share one similarity, both humans and orangutans exhibit a slanted intermediate cuneiform, but, the facet that this slant occurs on differs substantially. In humans, the 2nd metatarsal facet slants toward the side of the foot on which it occurs (likely a bipedal adaptation) whereas in orangutans it is the navicular surface that slants towards the side of the foot on which it occurs (Figure 24). Cebids and cercopithecids also exhibit a slanted navicular surface on the intermediate cuneiform, demonstrating that the orangutan condition is shared among several anthropoids. Because Procrustes analysis emphasizes overall shape rather than functional context, taxa sharing this aspect of morphology plot in similar regions of the morphospace despite vast differences in locomotor behaviour, phylogenetic relationships, and overall foot function.

The human intermediate cuneiform shape may therefore provide insights into the role of this bone in the evolution of the bipedal foot. The absence of strong differentiation in this element suggests that the transition to habitual bipedalism did not require the same degree of morphological specialization in the intermediate cuneiform as may have occurred in other parts of the foot. This is particularly interesting when considered alongside studies of other pedal elements that show clearer relationships with locomotor behaviour. If other elements underwent substantial functional modification during hominin evolution while the intermediate cuneiform remained comparatively conservative, the contrast suggests that different components of the foot may have contributed to the evolution of bipedalism in different ways.

Two evolutionary scenarios are hypothesized for explaining the similarity between humans and orangutans. One possibility is that humans retain an intermediate cuneiform morphology that is relatively primitive for great apes, while African apes subsequently evolved more derived morphologies. In this scenario, the last common ancestor of African apes and humans had an intermediate cuneiform morphology that is more similar to what is seen in orangutans. Orangutans would thus represent the retention of this ancestral condition, which was while the African apes independently evolved a more derived morphology, with changes driven by increased body size, greater terrestriality, and/or adaptations associated with knuckle walking. Alternatively, the last common ancestor of humans and African apes may have possessed a more African-ape-like morphology, with humans subsequently evolving toward a morphology that resembles the condition observed in orangutans and some monkeys. In this case, the last common ancestor of humans and African apes had an intermediate cuneiform shape that fell within the chimpanzee-gorilla range, with the African apes retaining this condition while early hominins returned to a morphology resembling what is seen near the divergence of orangutans and African apes. The present data cannot distinguish between these alternatives. The similarity of humans and orangutans in morphospace is therefore best treated as a starting point for future investigation rather than evidence supporting one evolutionary scenario over the other.

Importantly, the results do not demonstrate that the human intermediate cuneiform is unaffected by bipedalism. Instead, they suggest that any functional modifications associated with habitual bipedalism are not sufficiently pronounced in overall intermediate cuneiform shape to produce a distinct position in the morphospace. This distinction is important because a lack of clear differentiation does not necessarily mean a lack of functional significance.

Fossil hominins

The included fossil hominins provide an important opportunity to examine intermediate cuneiform morphology in an evolutionary context, but their interpretation should remain minimal as the fossil sample consists of only four specimens. Their positions within the extant morphospace provides useful observations about how individual fossil intermediate cuneiform compare with living anthropoids, but the sample is too small to reconstruct broader patterns of morphological evolution within the hominin lineage. The close proximity of the fossil hominins to modern humans across much of the morphospace is notable. It suggests that the specimens examined here possess intermediate cuneiform that fall within or near the range of modern human variation. However, this interpretation cannot be interpreted as evidence that the human-like intermediate cuneiform morphology was established at a particular point in hominin evolution, nor does it demonstrate that subsequent changes in the bone were minor across the hominin lineage. A larger fossil sample representing more specimens and different points in the hominin evolutionary timeline would be necessary to evaluate those possibilities.

Instead, the primary contribution of the fossil sample is to establish a comparative framework. The extant sample demonstrates the range of intermediate cuneiform variation across anthropoids, allowing fossil specimens to be evaluated in relation to the broader morphological context. As additional fossil intermediate cuneiforms are recovered and incorporated into comparative datasets, this framework can be used to assess whether particular fossil morphologies fall within existing extant patterns or represent new ones.

Implications for the evolution of the anthropoid foot

Taken together, the results suggest that intermediate cuneiform morphology records aspects of anthropoid evolutionary history differently from some other elements of the foot. The intermediate cuneiform varies substantially among taxa, but broad locomotor categories alone do

not predict the distribution of this variation. Instead, taxonomic patterns are prominent, while similarities among distantly related taxa indicate that structural and functional constraints may also contribute.

This finding has important implications for interpreting the primate foot as a functional system. The intermediate cuneiform's position between several articulating bones may limit the extent to which its overall shape can change while maintaining relationships with the surrounding midfoot. Overall, intermediate cuneiform morphology appears to reflect a combination of taxonomic history and constraints associated with its position within the midfoot, with locomotor behaviour providing a less direct explanation for broad patterns of variation. The distinctive morphologies of atelids and gorillas demonstrate that substantial differentiation can occur, but the extensive overlap among most locomotor categories indicates that these differences cannot be reduced to a simple explanation such as locomotor behaviour or phylogeny alone. Importantly, the results demonstrate that the intermediate cuneiform should be considered independently when evaluating functional adaptation in the anthropoid foot rather than assuming that patterns observed in other pedal elements apply equally to this bone.

Conclusion

This study provides a broad 3DGM comparison of intermediate cuneiform morphology across anthropoid primates and demonstrates substantial variation among taxa. The most important finding is that this variation does not correspond neatly with broad locomotor categories. Taxa with similar locomotor repertoires can possess markedly different intermediate cuneiform morphologies, as demonstrated by the contrast between atelids and colobus monkeys, while distantly related taxa with different locomotor behaviours, such as gorillas and colobus monkeys, can occupy similar regions of morphospace.

Taxonomic affiliation accounts for a substantial component of the observed variation, and the repeated clustering of closely related taxa suggest that phylogenetic history is an important influence on intermediate cuneiform morphology. However, phylogeny alone does not explain the observed patterns, indicating that structural and functional constraints may also contribute to the limited range of morphologies observed across many anthropoids.

The human intermediate cuneiform is particularly informative in this regard. Despite the distinctive biomechanical demands of habitual bipedalism, humans do not form a distinct functional cluster. Instead, they overlap with several nonhuman anthropoids, suggesting that the intermediate cuneiform may have remained comparatively conservative during the evolution of the bipedal foot. This raises the possibility that different pedal elements contribute to locomotor adaptations in different ways, with some elements undergoing greater functional modification than others. Fossil hominins further demonstrate the value of placing individual fossil intermediate cuneiforms within a broad comparative morphospace, but the small fossil sample prevents reconstruction of broader evolutionary changes within the hominin lineage. Future research incorporating additional fossil specimens, other tarsal elements, and more detailed behavioural and ecological data will be important for determining whether the patterns identified here are specific to the intermediate cuneiform or reflect broader patterns of morphological evolution across the anthropoid foot.

Overall, this study demonstrates that intermediate cuneiform morphology provides meaningful information about anthropoid evolutionary history, but that its variation cannot be interpreted solely through locomotor behaviour. Instead, the results point towards an interaction between phylogenetic history, locomotor behaviour, and the structural and functional characteristics of the intermediate cuneiform.

Tables

Table 1: Comparative locomotor classifications and supporting references for the taxa included in this study. (back to text)

Common Name	Primary Locomotor Behaviour	Reference
Howler Monkey	Arboreal Quadrupedalism	(Fleagle, 2013; Schön Ybarra, 1998; Youlantos and Meldrum, 2011)
Spider Monkey	Arboreal Quadrupedalism	(Cant, 1986; Cant et al., 2003; Fleagle, 2013).
Woolly Monkey	Arboreal Quadrupedalism	(Cant, 1986; Cant et al., 2003; Fleagle, 2013).
Capuchin	Arboreal Quadrupedalism	(Fleagle, 2013; Gebo, 1992, Wright et al., 2019)
Baboon	Terrestrial Quadrupedalism	(Aerts, et al., 2023; Fleagle, 2013; Hunt, 1991; Schmitt, 1994)
Mandrill	Terrestrial Quadrupedalism	(Fleagle, 2013; Leischner et al., 2018)
Macaque	Arboreal or Terrestrial Quadrupedalism (depends on the species)	(Fleagle, 2013; Hunt, 2016; Weinstein, 2011)
Common Patas	Terrestrial Quadrupedalism	(Fleagle, 2013;Leischner et al., 2018)
White-Eyelid Mangabey	Terrestrial Quadrupedalism	(McGraw, 2017; Nakatsukasa, 1996)
Crested Mangabey	Arboreal Quadrupedalism	(McGraw, 2017; Nakatsukasa, 1996)
Colobus	Arboreal Quadrupedalism	(Gebo and Chapman, 1995; Fleagle, 2013)
Northern Plains Gray Langur	Arboreal or Terrestrial Quadrupedalism	(Ripley, 1967; Sugiyama, 1976)
Proboscis	Arboreal Quadrupedalism	(Harding, 2015; Rachma Jadi et al., 2020)
Gibbon	Suspensory (Brachiation)	(Fleagle, 1974; Fleagle, 2013; Michilsens et al., 2009)

Siamang	Suspensory (Brachiation)	(Fleagle, 1974; Fleagle, 2013; Michilsens et al., 2009)
Orangutan	Suspensory	(Cant, 1987; Fleagle, 2013; Manduell et al., 2011; Thorpe et al., 2007b)
Gorilla	Terrestrial Quadrupedalism (knuckle walking)	Fleagle, 2013; Leischner et al., 2018; Simpson et al., 2018)
Chimpanzee	Terrestrial Quadrupedalism (knuckle walking)	Fleagle, 2013; Leischner et al., 2018; Simpson, 2018)

Table 2: Taxonomic composition and sample sizes of the intermediate cuneiform dataset, including taxonomic affiliation, scientific name, common name, and number of specimens analyzed for each taxon. (back to text)

Taxonomic Affiliation	Scientific Name	Common Name	Sample Size
Atelids	*Alouatta*	Howler Monkey	7
Atelids	*Ateles*	Spider Monkey	10
Atelids	*Lagothrix*	Woolly Monkey	5
Cebids	*Cebus*	Capuchin	4
Cercopithecids	*Papio*	Baboon	27
Cercopithecids	*Theropithecus gelada*	Gelada Baboon	10
Cercopithecids	*Mandrillus sphinx*	Mandrill	15
Cercopithecids	Macaca	Macaque	12
Cercopithecids	*Erythrocebus patas*	Common Patas	1
Cercopithecids	*Cercocebus*	White-Eyelid Mangabey	3
Cercopithecids	*Lophocebus*	Crested Mangabey	4
Cercopithecids	*Colobus*	Colobus	4
Cercopithecids	*Semnopithecus entellus*	Northern Plains Gray Langur	7
Cercopithecids	*Nasalis larvatus*	Proboscis	4
Lesser Apes	*Hylobates klossii*	Dwarf Gibbon	17

Lesser Apes	*Hoolock hoolock*	Hoolock Gibbon	2
Lesser Apes	*Symphalangus syndactylus*	Siamang	8
Great Apes	*Pongo abelii*	Sumatran Orangutan	7
Great Apes	Pongo pygmaeus	Bornean Orangutan	19
Great Apes	*Gorilla beringei graueri*	Grauer Gorilla	30
Great Apes	*Gorilla gorilla gorilla*	Mountain Gorilla	28
Great Apes	*Gorilla beringei beringei*	Western Lowland Gorilla	28
Great Apes	*Pan paniscus*	Bonobo	27
Great Apes	*Pan troglodytes*	Chimpanzee	41
Hominins	*Homo sapiens*	Human	77
Hominins	*Homo floresiensis*	LB 1	1
Hominins	*Homo habilis*	OH 8	1
Hominins	*Homo erectus*	KNM-ER 64062	1
Hominins	*Australopithecus*	StW 573	1

Table 3: Significant pairwise Procrustes comparisons of intermediate cuneiform shape between monkey taxa following sequential Bonferroni correction for multiple comparisons. Only statistically significant comparisons ($p < 0.05$) are shown. (back to text)

Locomotor Category	Biped	Brachiator	Knuckle Walker	Suspension
Biped	—	0.0012	0.001	0.0008
Brachiator	0.0012	—	0.0006	0.0068
Knuckle Walker	0.001	0.0006	—	0.0004
Suspension	0.0008	0.0068	0.0004	—

Table 4: Significant pairwise Procrustes comparisons of intermediate cuneiform shape between hominoid taxa following sequential Bonferroni correction for multiple comparisons. Only statistically significant comparisons ($p < 0.05$) are shown. (back to text)

	dwarf gibbon	hoolok gibbon	siamang	sumatran orangutan	bornean orangutan	western lowland gorilla	mountain gorilla	grauer gorilla	bonobo	chimpanzee	human
dwarf gibbon	—	—	—	—	—	0.0078	0.008	0.008	—	0.021	0.01
hoolok gibbon	—	—	—	—	—	—	0.024	0.014	—	—	—
siamang	—	—	—	—	—	0.0058	0.0064	0.007		—	—
sumatran orangutan	—	—	—	—	—	0.0056	0.0062	0.007	0.0104	0.0204	0.046
bornean orangutan	—	—	—	—	—	0.0092	0.0094	0.01	0.0011	0.01	0.01
western lowland gorilla	0.008	—	0.0058	0.0056	0.0092	—	0.006	0.007	0.0102	0.0084	0.007
mountain gorilla	0.008	0.024	0.0064	0.0062	0.0094	0.006	—	0.018	0.0106	0.0086	0.007
grauer gorilla	0.008	0.014	0.0074	0.0072	0.0098	0.007	0.0176	—	0.011	0.009	0.008
bonobo	—	—	—	0.0104	0.00108	0.0102	0.0106	0.011	—	0.0144	0.011
chimpanzee	0.021	—	—	0.0104	0.02	0.0084	0.0086	0.009	0.0144	—	0.009
human	0.01	—	—	0.0456	0.0096	0.0066	0.0068	0.008	1.0108	0.0088	—

Table 5: Significant pairwise Procrustes comparisons of intermediate cuneiform shape between hominoid taxa based on locomotor behaviour following sequential Bonferroni correction for multiple comparisons. Only statistically significant comparisons ($p < 0.05$) are shown. (back to text)

Locomotor Category	Biped	Brachiatior	Knuckle Walker	Suspension
Biped	—	0.0012	0.001	0.0008
Brachiatior	0.0012	—	0.0006	0.0068
Knuckle Walker	0.001	0.0006	—	0.0004
Suspension	0.0008	0.0068	0.0004	—

Table 6: Significant pairwise Procrustes comparisons of intermediate cuneiform shape between all primate clades in this analysis following sequential Bonferroni correction for multiple comparisons. Only statistically significant comparisons ($p < 0.05$) are shown. (back to text)

	Atelid	Cebid	Cercopithecid	*Gorilla*	Hominin	Hylobatid	*Pan*	*Pongo*
Atelid	—	—	0.0056	0.0054	0.0052	0.005	0.0048	0.0046
Cebid	—	—	—	0.0044	0.0456	—	—	0.036
Cercopithecid	0.0056	—	—	0.0042	0.004	0.0038	0.0036	0.0034
Gorilla	0.0054	0.0044	0.0042	—	0.0032	0.003	0.0028	0.0026
Hominin	0.0052	0.0456	0.004	0.0032	—	0.0024	0.0022	0.002
Hylobatid	0.005	—	0.0038	0.003	0.0024	—	0.0018	0.0408
Pan	0.0048	—	0.0036	0.0028	0.0022	0.0018	—	0.0016
Pongo	0.0046	0.036	0.0034	0.0026	0.002	0.0408	0.0016	—

Table 7: Significant pairwise Procrustes comparisons of intermediate cuneiform shape between all species in this analysis based on locomotor behaviour following sequential Bonferroni correction for multiple comparisons. Only statistically significant comparisons ($p < 0.05$) are shown. (back to text)

Locomotor Category	Arboreal Quadruped	Biped	Brachiator	Knuckle Walker	Suspension	Terrestrial Quadruped
Arboreal Quadruped	—	0.003	0.004	0.0028	0.0026	0.0024
Biped	0.003	—	0.0022	0.002	0.0018	0.0016
Brachiator	0.004	0.0022	—	0.0014	0.0068	0.0012
Knuckle Walker	0.0028	0.002	0.0014	—	0.001	0.0008
Suspension	0.0026	0.0018	0.0068	0.001	—	0.0006
Terrestrial Quadruped	0.0024	0.0016	0.0012	0.0008	0.0006	—

Figures

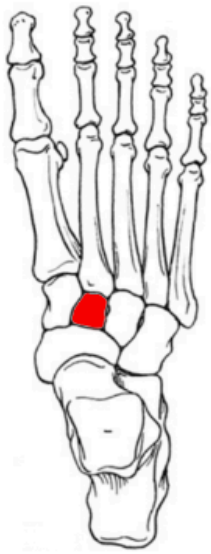

Figure 1: Dorsal view of the foot skeleton of extant humans with the intermediate cuneiform indicated in red (modified from Schultz, 1963). (back to text)

Figure 2: The human intermediate cuneiform shown from the right side (with the dorsal surface toward the top of the page), from left to right, in four anatomical views (proximal, distal, medial, and lateral). (back to text)

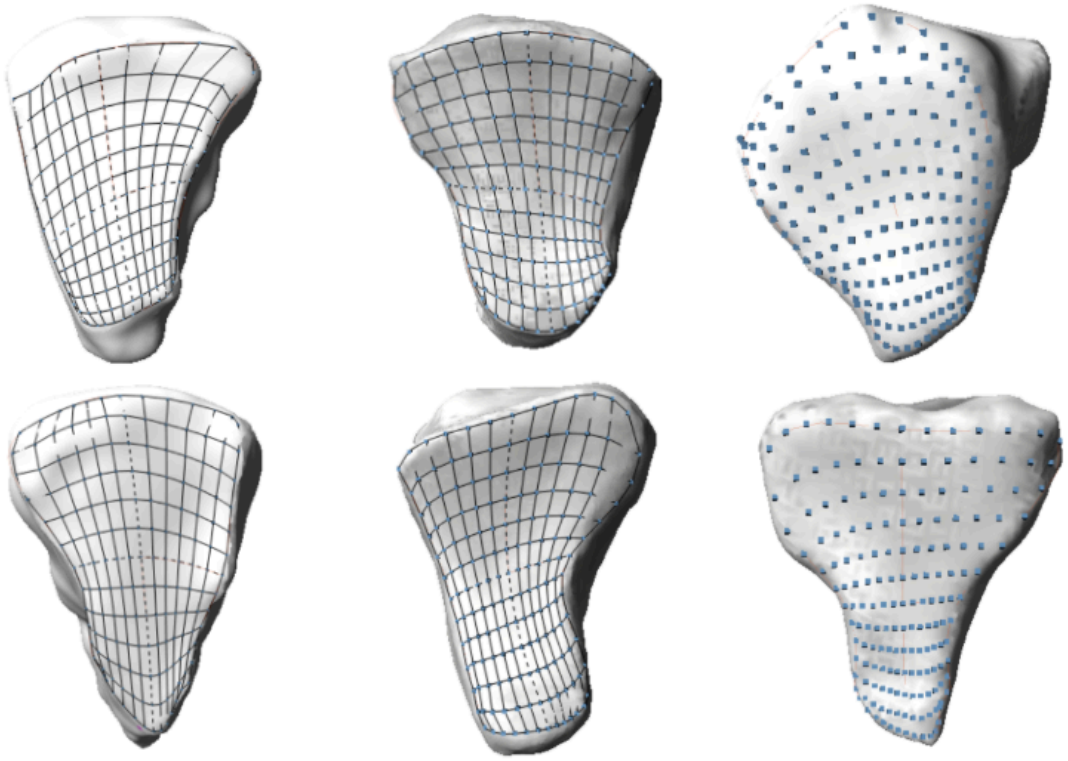

Figure 3: Landmark configurations on representative intermediate cuneiform specimens. Three specimens representing the placement of each landmark patch on different specimens, shown from left to right: human, grauer gorilla, and spider monkey. The top row shows the landmark configurations on the navicular articular surface and the bottom row shows the landmark configurations on the second metatarsal articular surface. Landmarks are depicted on each specimen to illustrate their placement across differing morphologies. (back to text)

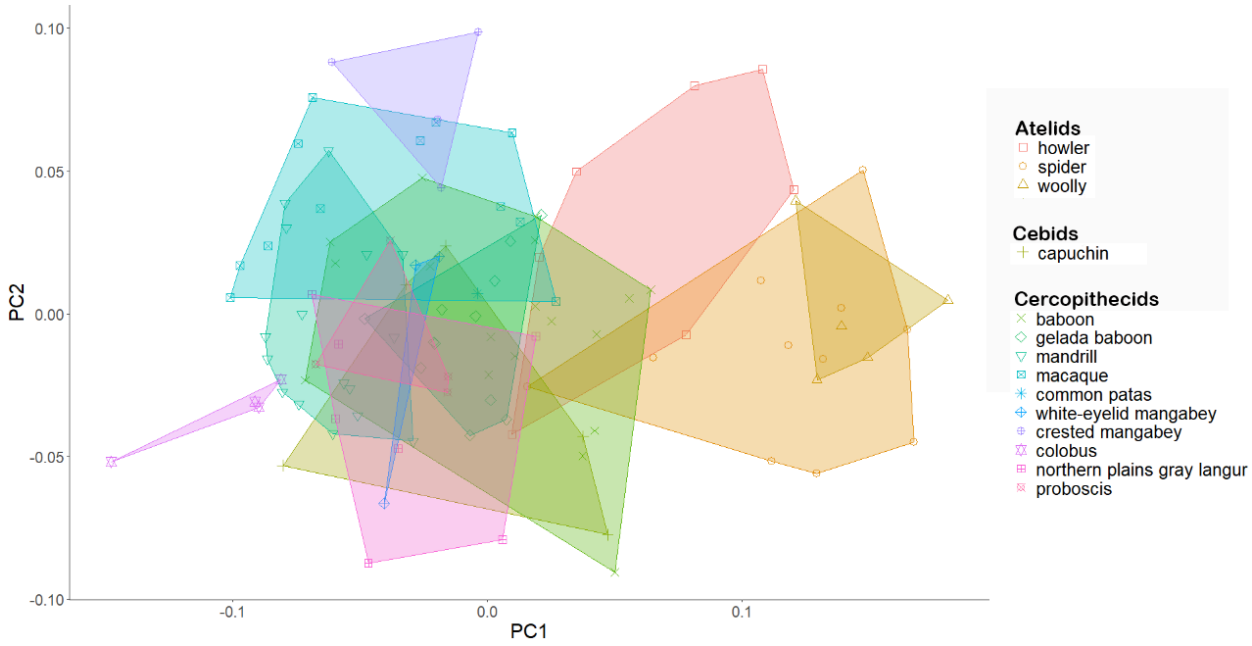

Figure 4: Plot of the first (PC1) and second (PC2) principal components that explain 35.4% and 10.7% of the total variance in intermediate cuneiform shape among monkeys. (back to text)

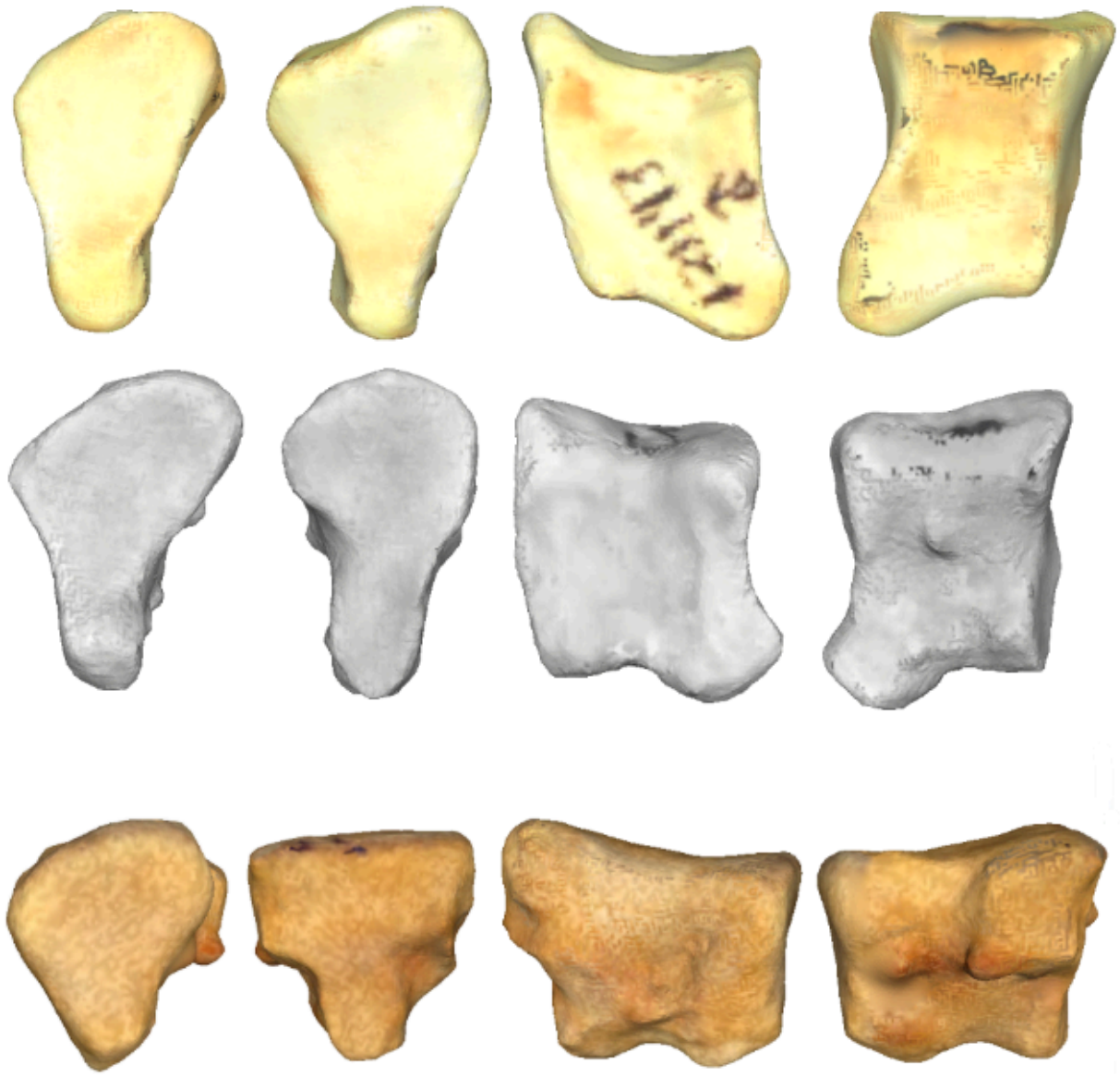

Figure 5: Comparison of extreme intermediate cuneiform morphology along PC1 among monkeys. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a colobus monkey (negative extreme), bottom row is a woolly monkey (positive extreme), and a gelada is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline (back to text)

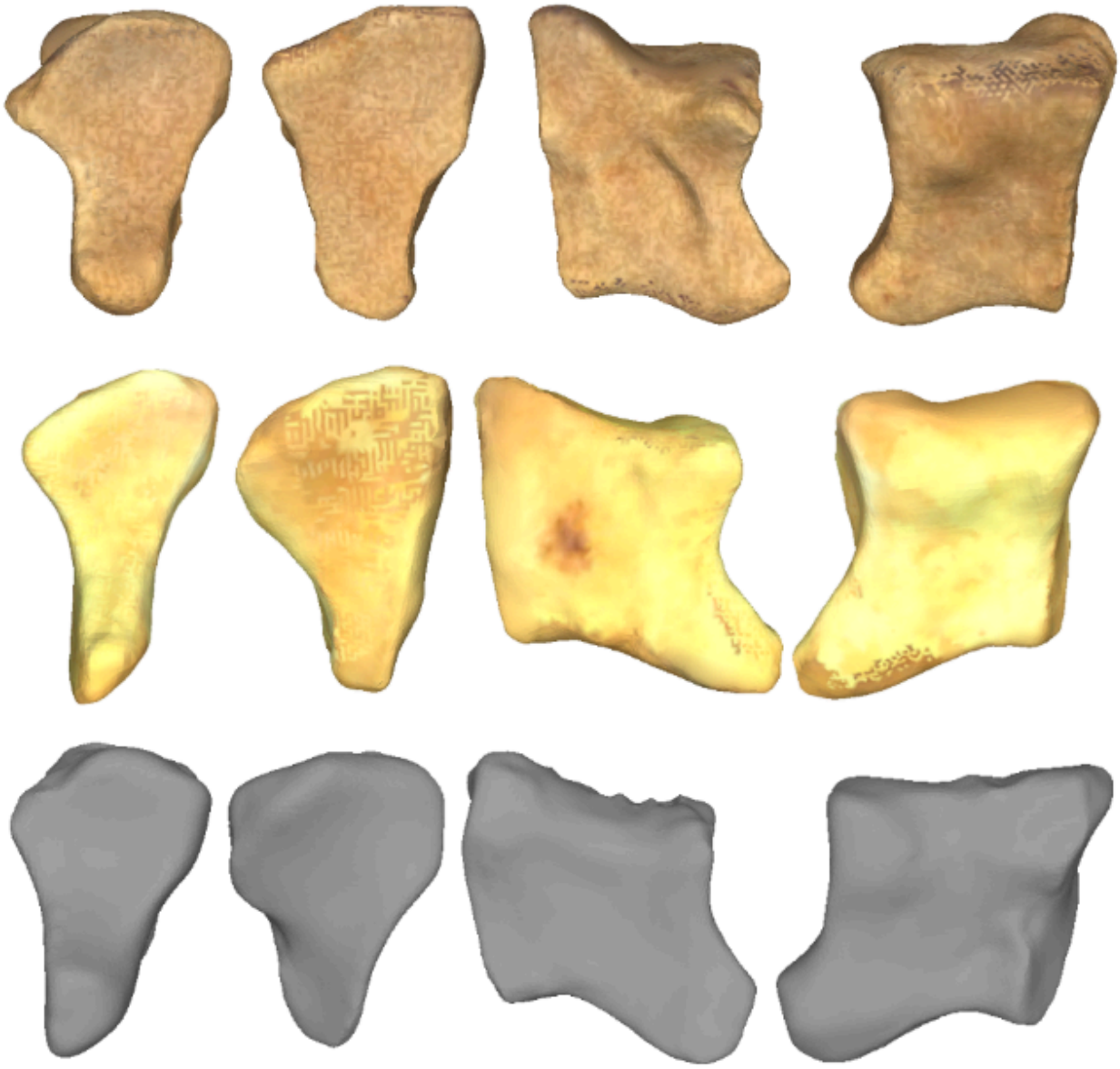

Figure 6: Comparison of extreme intermediate cuneiform morphology along PC2 among monkeys. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a northern plains gray langur (negative extreme), bottom row is a crested mangabey (positive extreme), and a macaque is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of

the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline . (back to text)

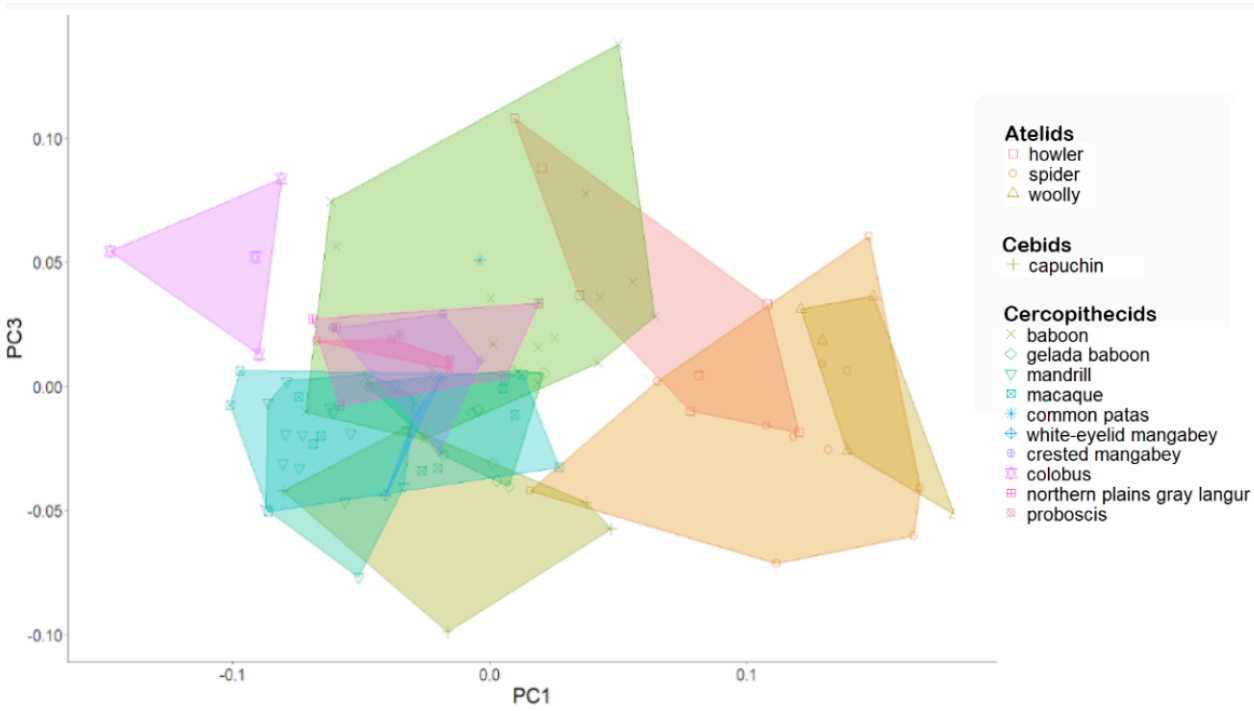

Figure 7: Plot of the first (PC1) and third (PC3) principal components that explain 35.4% and 10.0% of the total variance in intermediate cuneiform shape among monkeys. (back to text)

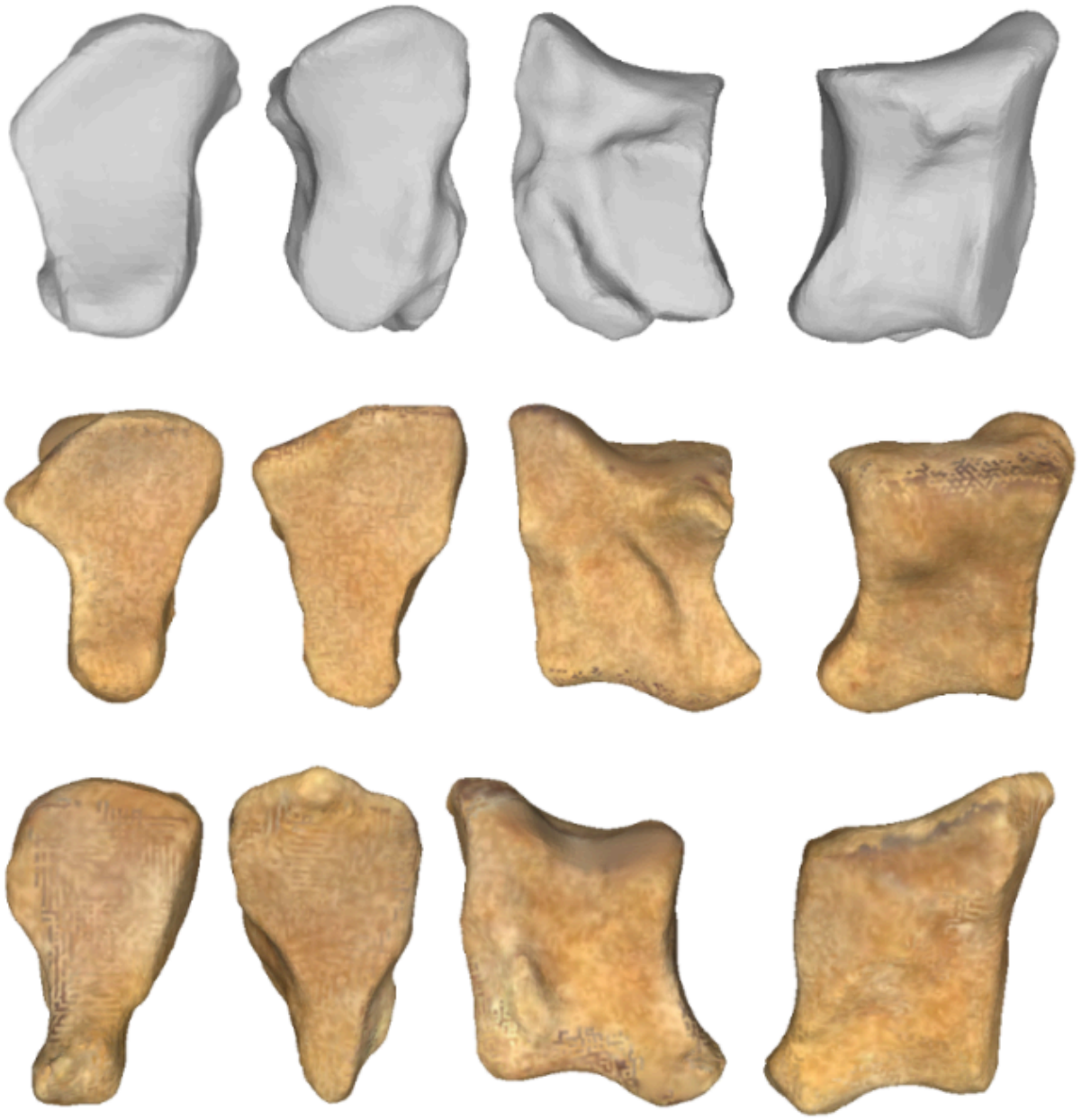

Figure 8: Comparison of extreme intermediate cuneiform morphology along PC3 among monkeys. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a capuchin (negative extreme), bottom row is a baboon (positive extreme), and a northern plains gray langur is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from

the midline. (back to text)

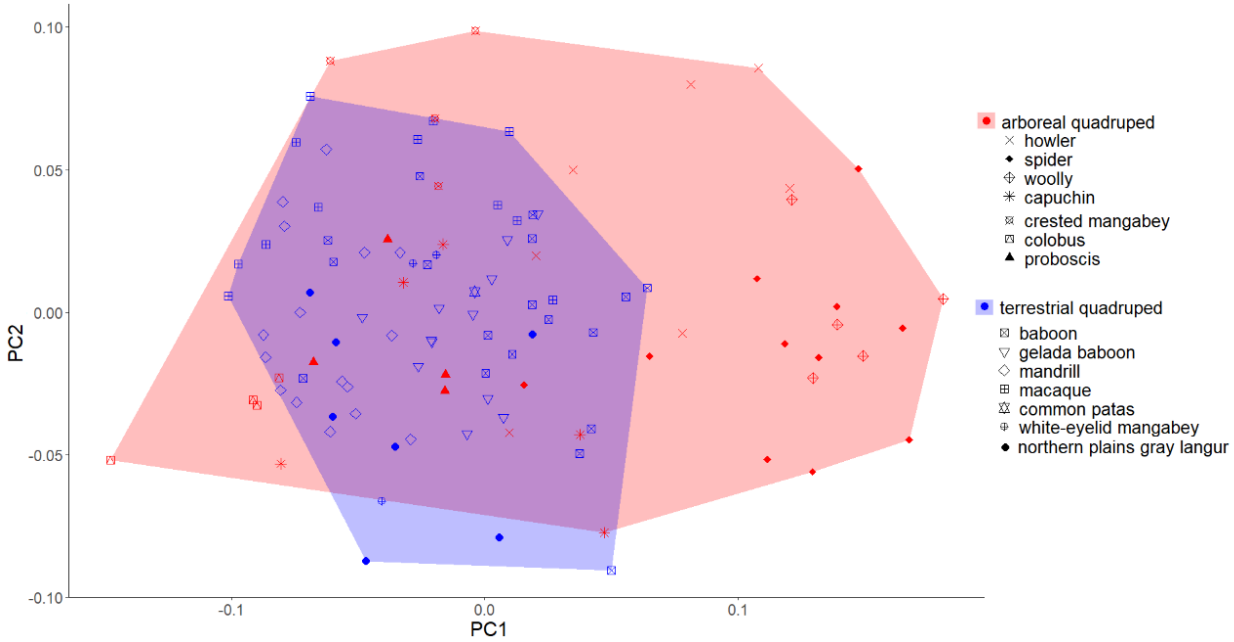

Figure 9: Plot of the first (PC1) and second (PC2) principal components that explain 35.4% and 10.7% of the total variance in intermediate cuneiform shape among monkeys, species sorted by locomotor behaviour. (back to text)

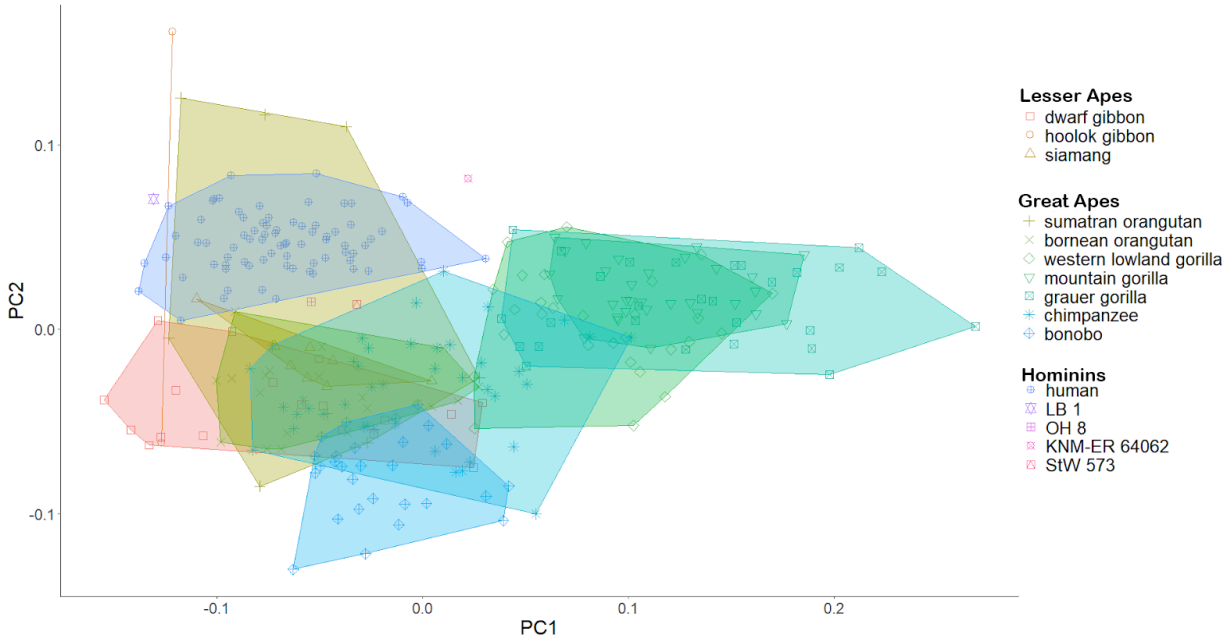

Figure 10: Plot of the first (PC1) and second (PC2) principal components that explain 34.0% and 10.5% of the total variance in intermediate cuneiform shape among hominoids. (back to text)

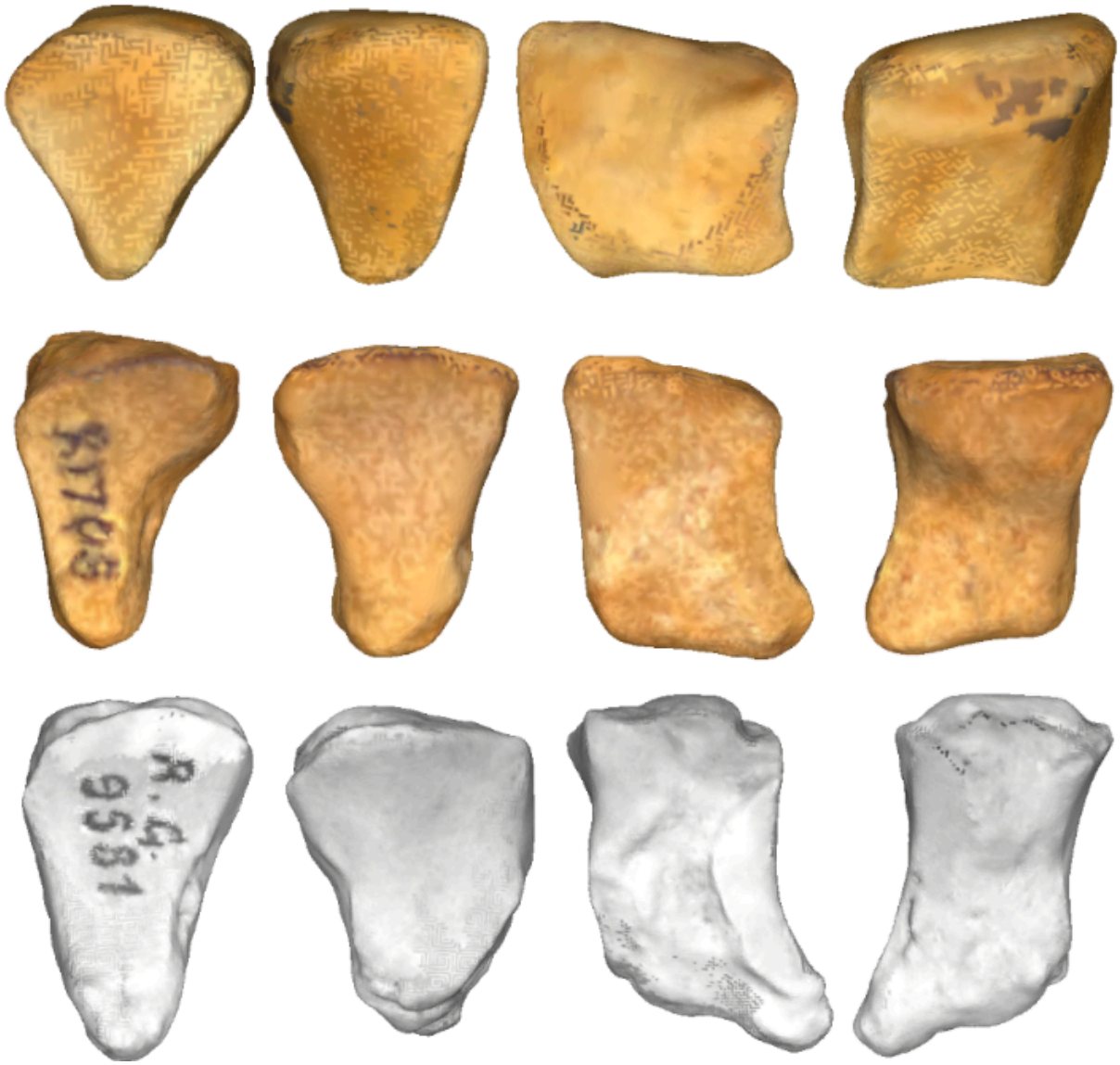

Figure 11: Comparison of extreme intermediate cuneiform morphology along PC1 among hominoids. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a dwarf gibbon (negative extreme), bottom row is a grauer gorilla (positive extreme), and a bonobo is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to text)

Figure 12: Comparison of extreme intermediate cuneiform morphology along PC2 among hominoids. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a bonobo (negative extreme), bottom row is a human (positive extreme), and a chimpanzee is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline . (back to

text)

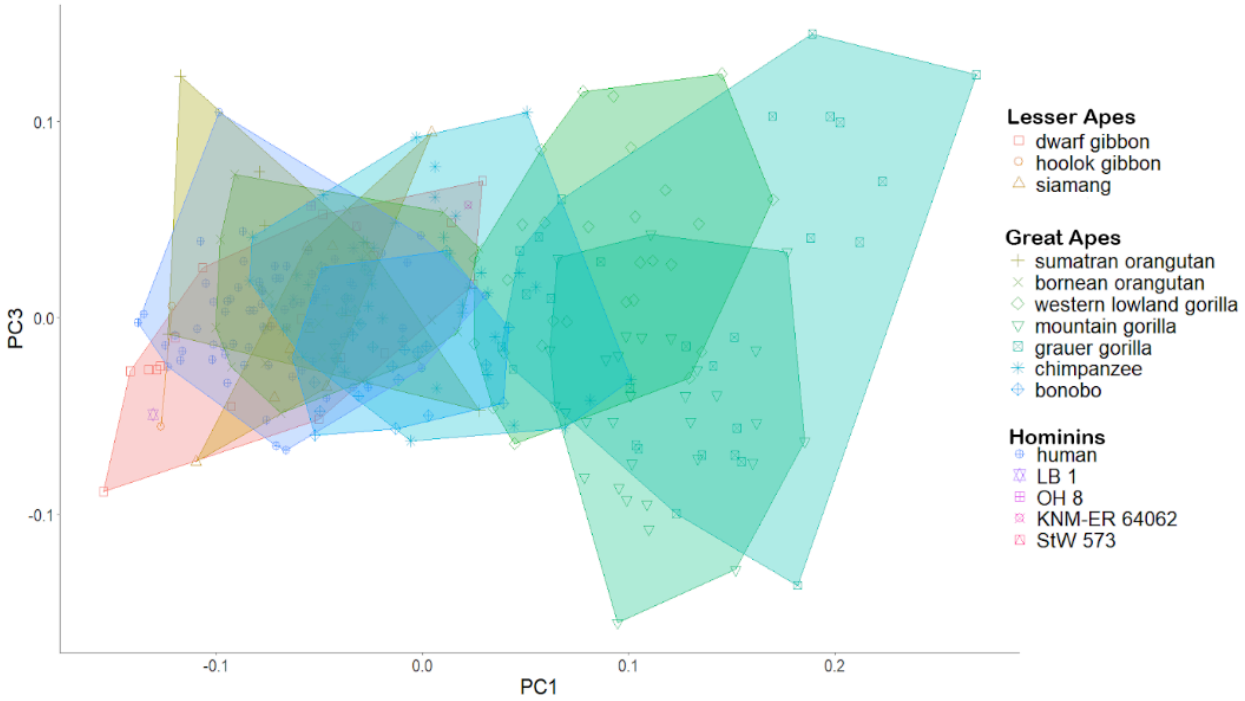

Figure 13: Plot of the first (PC1) and third (PC3) principal components that explain 34.0% and 9.47% of the total variance in intermediate cuneiform shape among hominoids. (back to text)

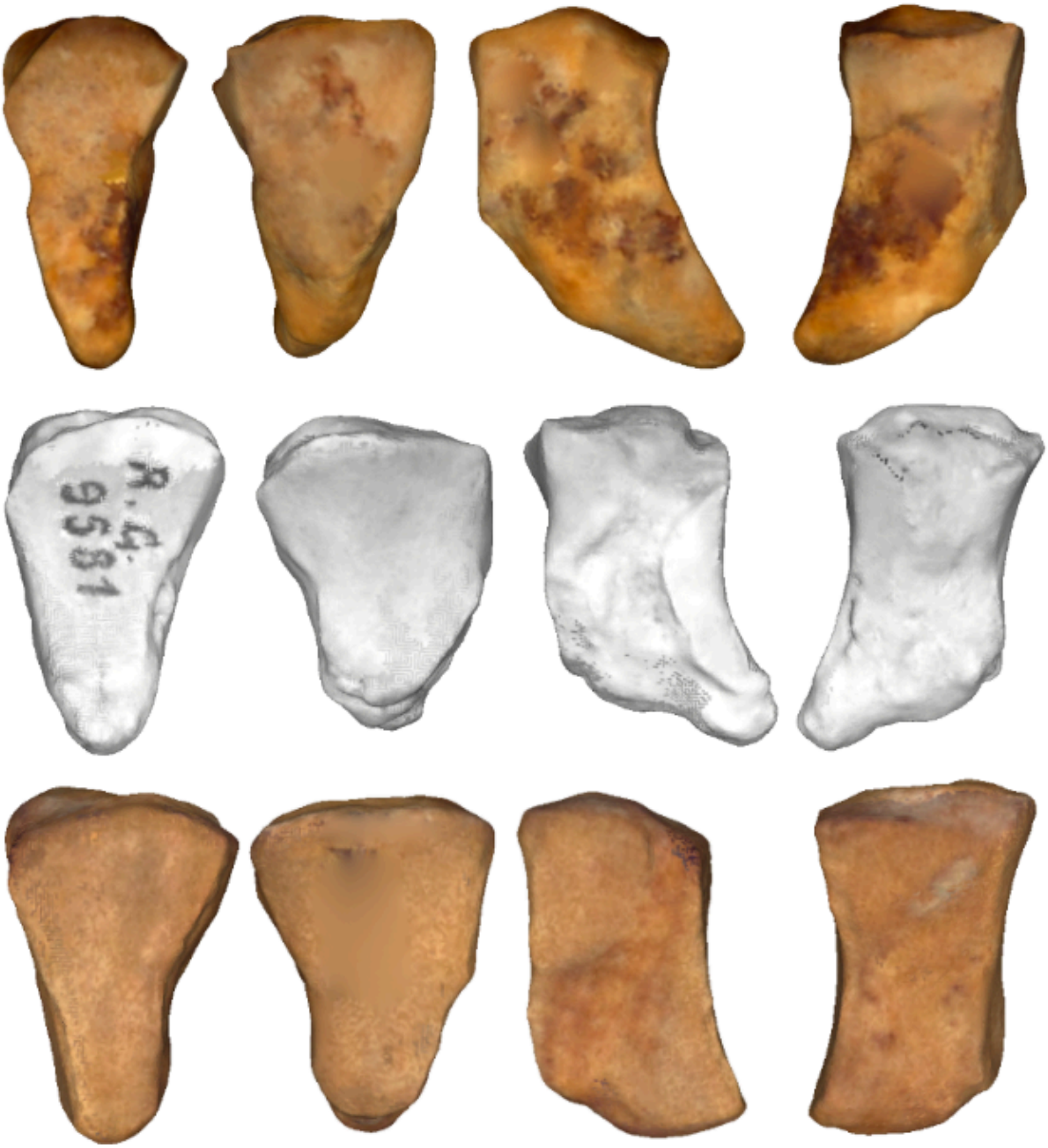

Figure 14: Comparison of extreme intermediate cuneiform morphology along PC3 among hominoids. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a mountain gorilla (negative extreme), bottom row is a western lowland gorilla (positive extreme), and a grauer gorilla is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone,

medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to text)

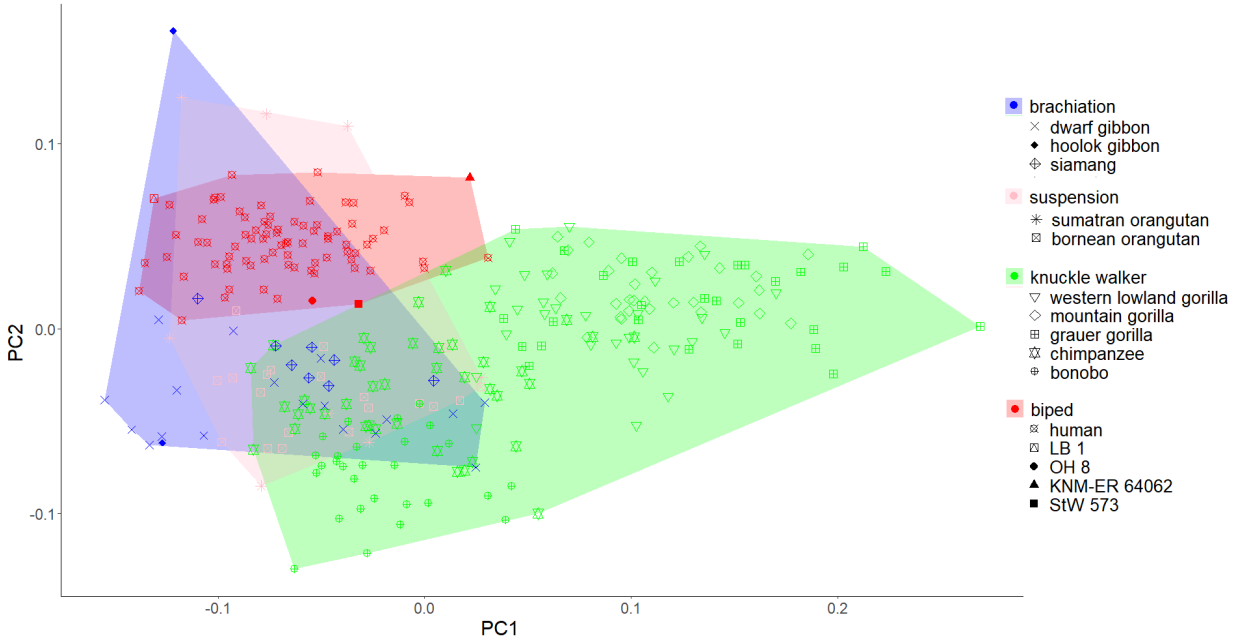

Figure 15: Plot of the first (PC1) and second (PC2) principal components that explain 34.0% and 10.5% of the total variance in intermediate cuneiform shape among hominoids, species sorted by locomotor behaviour. (back to text)

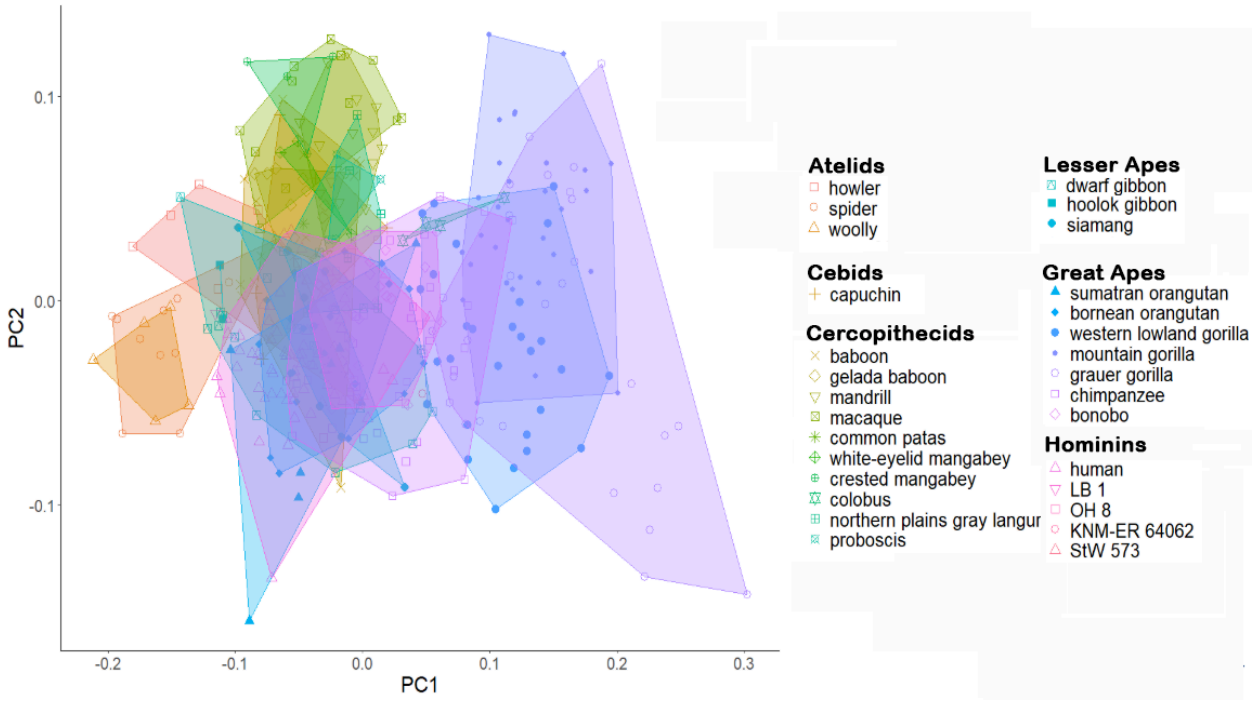

Figure 16: Plot of the first (PC1) and second (PC2) principal components that explain 34.0% and 11.8 % of the total variance in intermediate cuneiform shape among primates. (back to text)

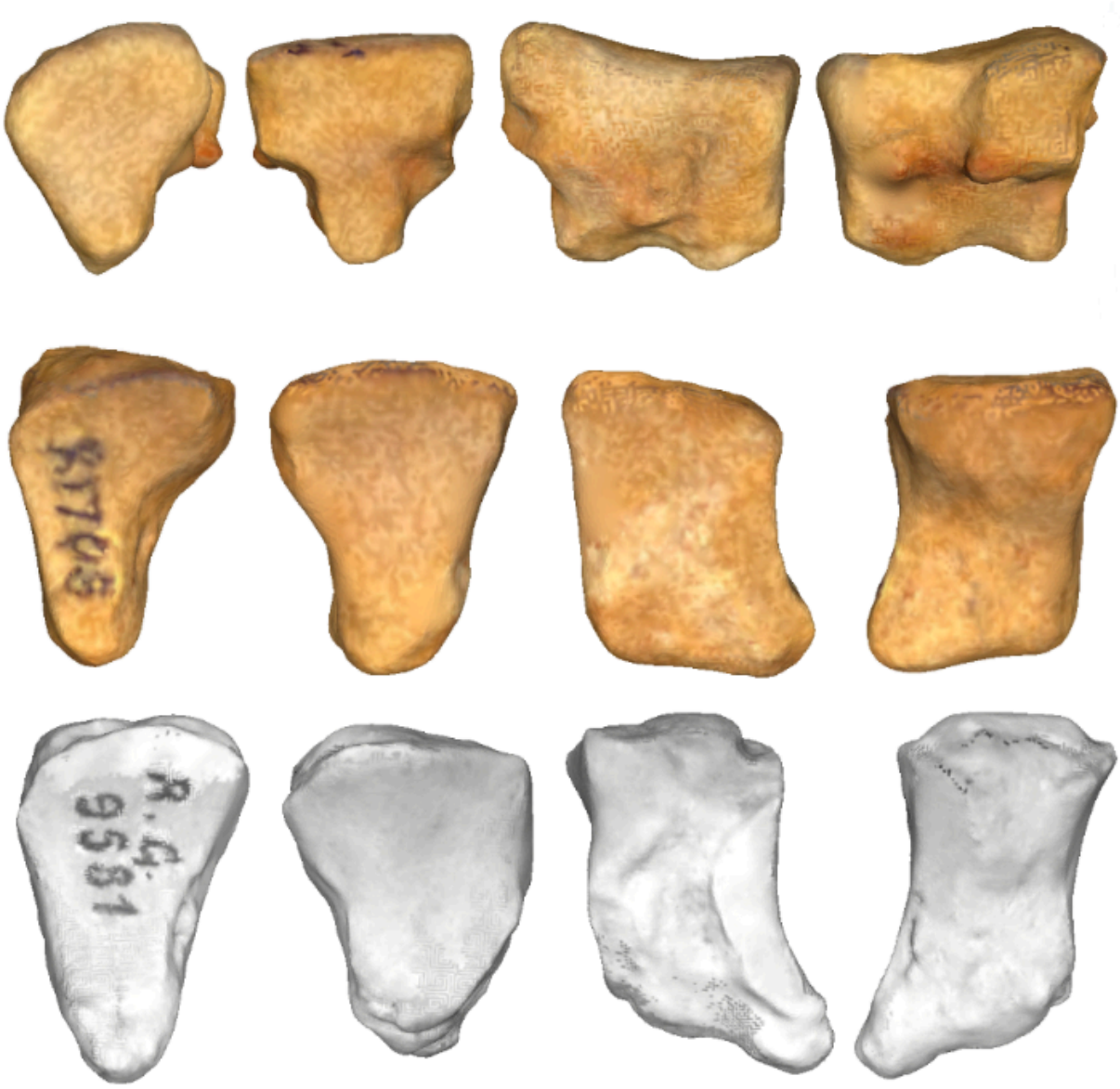

Figure 17: Comparison of extreme intermediate cuneiform morphology along PC1 among primates. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a woolly monkey (negative extreme), bottom row is a grauer gorilla (positive extreme), and a chimpanzee is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to text)

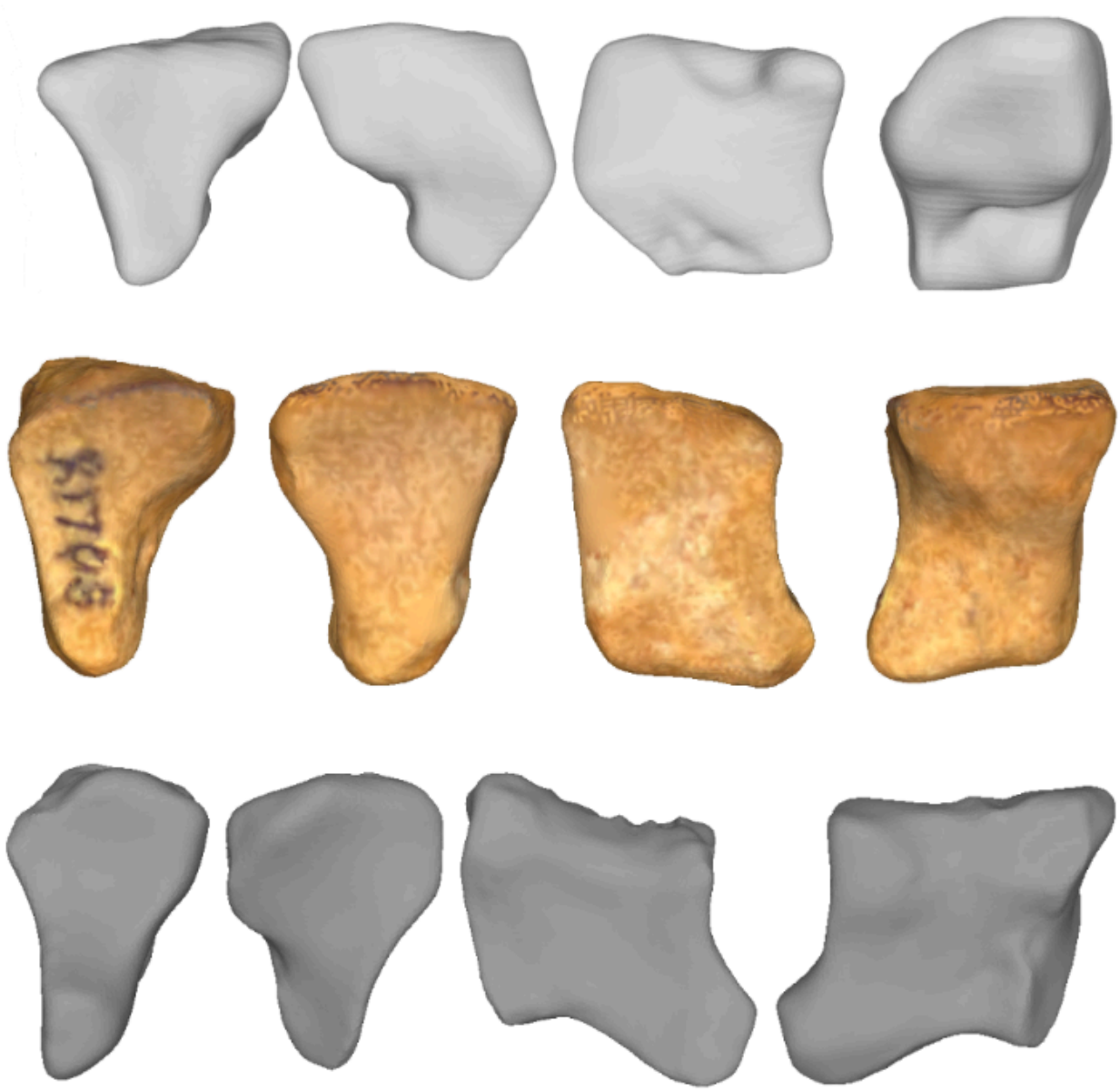

Figure 18: Comparison of extreme intermediate cuneiform morphology along PC2 among primates. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a sumatran orangutan (negative extreme), bottom row is a crested mangabey (positive extreme), and a chimpanzee is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away

from the midline. (back to text)

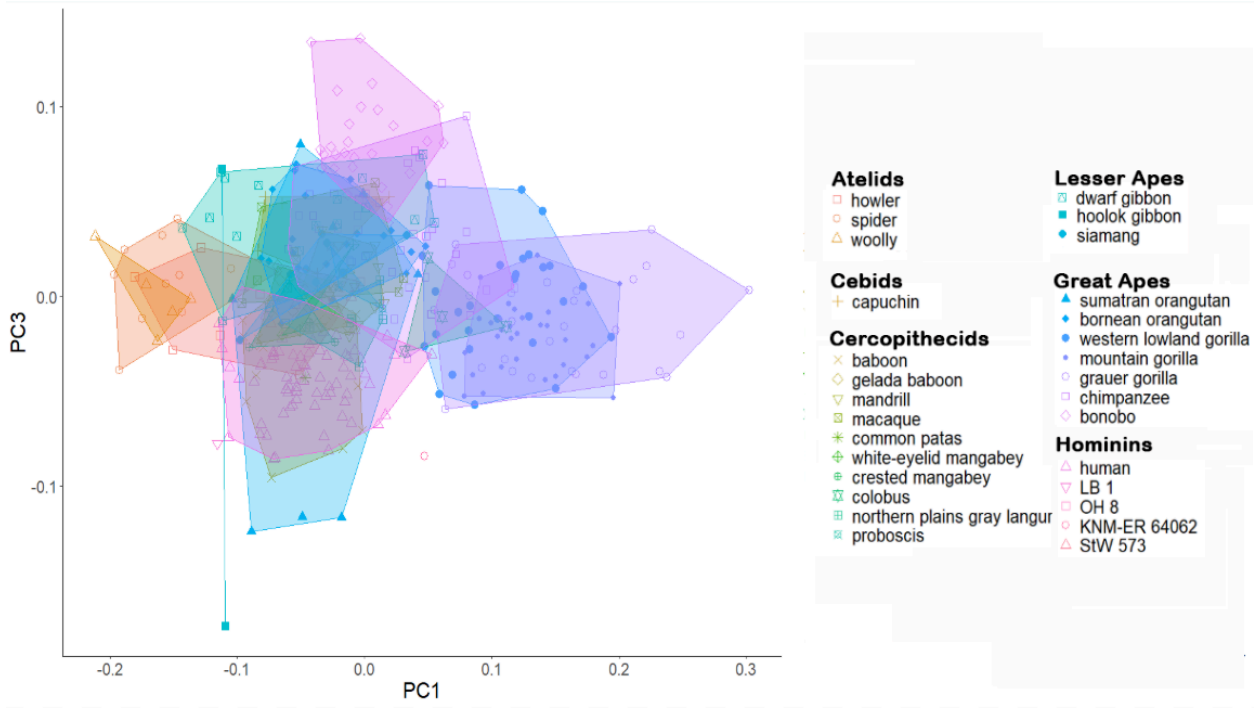

Figure 19: Plot of the first (PC1) and third (PC3) principal components that explain 34.0% and 8.4% of the total variance in intermediate cuneiform shape among primates. (back to text)

Figure 20: Comparison of extreme intermediate cuneiform morphology along PC3 among primates. Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Top row is a human (negative extreme), bottom row is a bonobo (positive extreme), and a chimpanzee is shown in the middle row for comparison. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to

text)

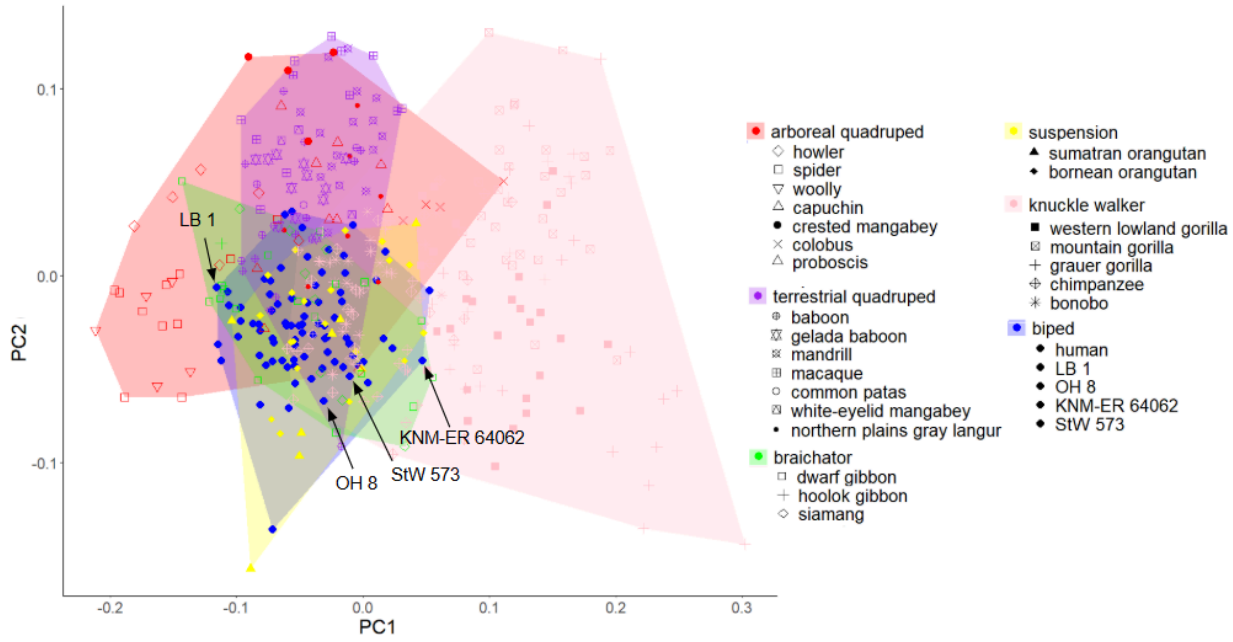

Figure 21: Plot of the first (PC1) and second (PC2) principal components that explain 34.0% and 11.8% of the total variance in intermediate cuneiform shape among primates, species sorted by locomotor behaviour. (back to text)

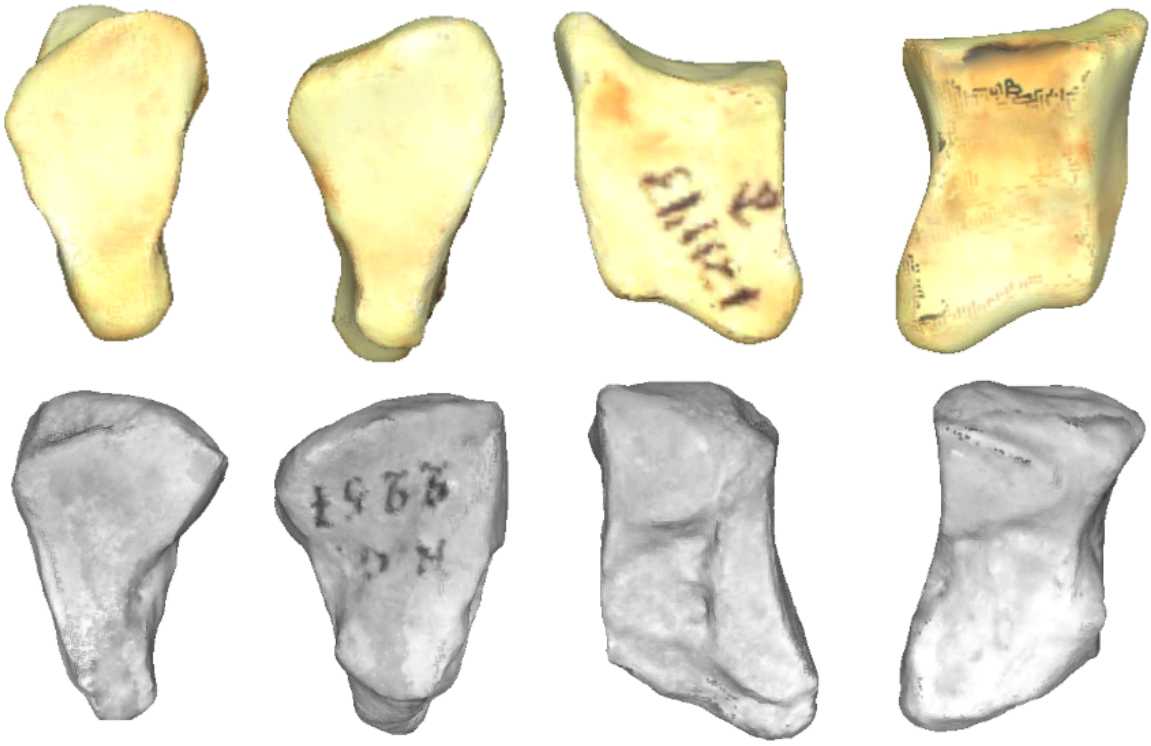

Figure 22: Comparison of the intermediate cuneiforms representing an average colobus monkey (top) versus an average mountain gorilla (bottom). From left to right, this image depicts the articulating facets of the intermediate cuneiform for the navicular, second metatarsal, medial cuneiform, and lateral cuneiform. Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to text)

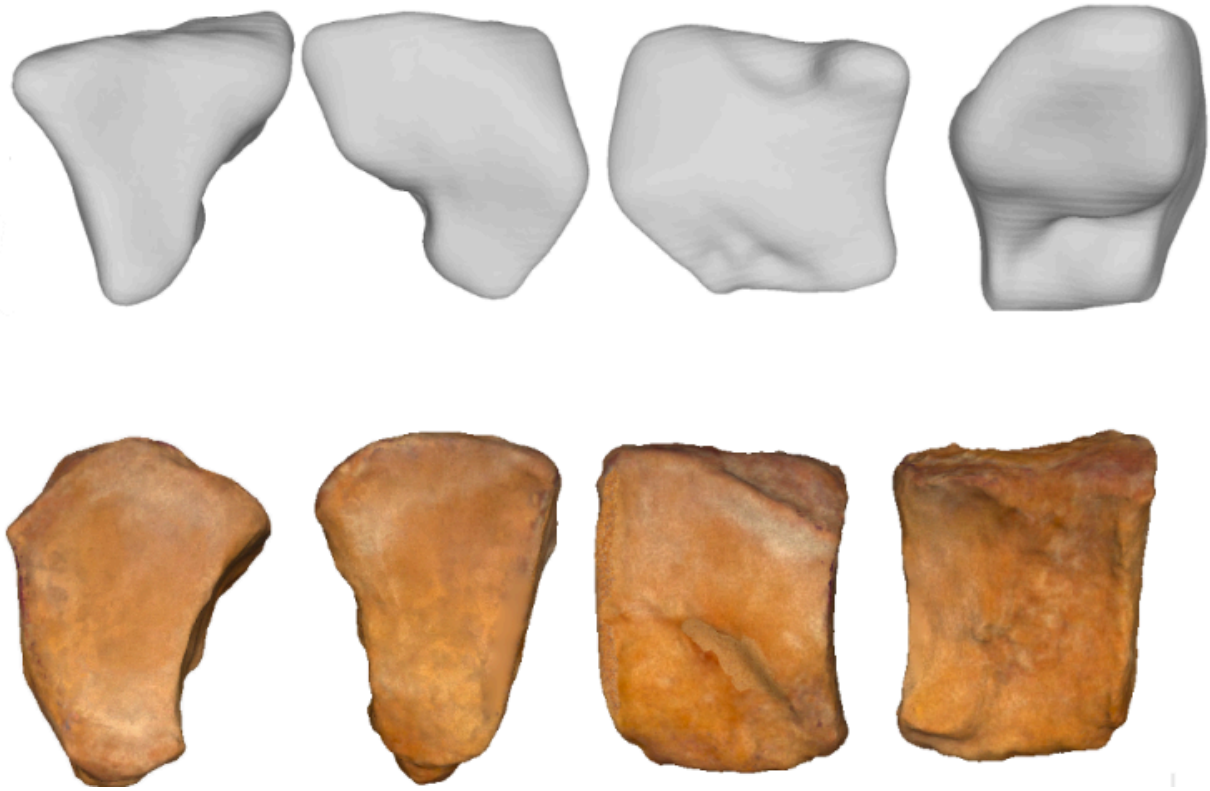

Figure 23: Comparison of an average sumatran orangutan intermediate cuneiform (top) versus an average human intermediate cuneiform (bottom). Each intermediate cuneiform is shown, from left to right, in four anatomical views (proximal, distal, medial, and lateral). Dorsal refers to the top of the bone, plantar refers to the bottom of the bone, medial refers to the side of the bone that is closest to the midline of the body, and lateral is away from the midline. (back to text)

Figure 24: Comparison of the intermediate cuneiform representing a human (left) versus the intermediate cuneiform representing an orangutan (right), showcasing the slants along the lateral metatarsal base and medial navicular base. The distal side of the bone is up. (back to text)

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