

Impacted Bones: Can extant primates help identify tool-use in early hominins?

Rachel M. Hurwitz^{1*}, Katarina Almeida-Warren^{1,2,4}, Susana Carvalho^{2,3,4}, Thomas A. Püschel^{1*}

Affiliations:

¹ Institute of Human Sciences, School of Anthropology and Museum Ethnography,
University of Oxford, Oxford, UK

² Interdisciplinary Center for Archaeology and Evolution of Human Behaviour (ICArEHB)
FCHS, University of Algarve, Campus de Gambelas, Faro, Portugal

³ Department of Science, Gorongosa National Park, Mozambique

⁴ CIBIO-BIOPOLIS, Centro de Investigação em Biodiversidade e Recursos Genéticos,
Campus de Vairão, Portugal

**Corresponding authors: rachel.hurwitz@anthro.ox.ac.uk, thomas.puschel@anthro.ox.ac.uk*

Word Count: 8429

Abstract

Despite recent advances pushing back the earliest record of tool use, how and when it first emerged in the hominin lineage, and the extent to which it featured amongst the numerous co-existing hominin species, remain critical questions in palaeoanthropology. In addition to analysing extinct hominin fossils and lithic toolkits, tool-use in extant primates should be studied to help answer this question. Novel strides in understanding this phenomenon may be made by studying the skeletons of our closest living relatives, the great apes, as well as more distantly related tool-using primates and applying the resultant findings to the fossil record via predictive modelling methods. Thus, we review current methods of extrapolating tool use capabilities in extinct and extant taxa, and provide an innovative methodological framework to collect and analyse osteological remains for evidence of percussive tool use, using chimpanzees as a case study. We propose a shift in current methodological practice, wherein both sides of the body, rather than just one, must be routinely scanned (i.e. photogrammetry, structured light, computed tomography) to facilitate more insightful understanding of the effect percussive tool use on primate bone. Key species, including long-tailed macaques (*Macaca fascicularis* ssp.), robust and gracile capuchins (*Sapajus* and *Cebus* sp.) and western chimpanzees (*Pan troglodytes verus*), all of whom engage in lithic percussion, should be the work's focus. Due to bone's dynamic ability to respond to mechanical strain by preferential remodelling, percussive forms of tool-use, like nut-cracking, are expected to cause morphological changes to bone in the preferred hammering hands of these tool users as compared to their non-preferred hand, or the hands of individuals who do not utilize lithics. However, this potential 'damage signature' has not been examined or quantified. Thus, we propose a methodology for examining the effect of percussive tool use on primate bone by scanning skeletal remains bilaterally, analysing directional asymmetry, and using machine learning to discern patterns of variation. Long-term, our proposed methodology may be extrapolated to examine the lasting impact of tool-use on the hand bones of extinct hominins.

Keywords: percussive tool-use, lithic tool-use, primate tool use, chimpanzees, capuchins, macaques, bone morphology, nut-cracking, laterality, biological asymmetry

1. Introduction

Modern humans (*Homo sapiens sapiens*) are considered unique in numerous ways, including a propensity for tool-use, highly dexterous hands, strong degree of handedness, complex social structures, reliance on prosociality and social learning, high degree of encephalization, use of language, ability for cumulative cultural evolution and bipedal locomotion, among other evolutionary singularities ¹. While many of these anatomical and cognitive characteristics are present to varying degrees throughout the primate clade, humans seem to be at the extremes of these traits, and particularly in our tendency for strong (right) handedness ².

Human tool use is not unique in itself, as numerous other species utilize both lithic (stone) and organic implements to accomplish various tasks ³. While less than one percent of Earth's species are known to engage with tools, this still accounts for many species in distantly related clades, including corvids, parrots, various primates, aquatic mammals, elephants, and otters ³. Plentiful primate species in various families (Cercopithecidae, Cebidae, Hominidae) including capuchins (*Sapajus* sp. and *Cebus* sp.), macaques (*Macaca* sp.), chimpanzees (*Pan troglodytes* ssp.), and orangutans (*Pongo* sp.) all use tools frequently, with anecdotal evidence of other primate species such as baboons (*Papio ursinus*), gorillas (*Gorilla* sp.), and bonobos (*Pan paniscus*) using tools almost exclusively in captivity, most frequently to obtain food rewards or during experiments ^{3,4}. However, *Homo sapiens*' consistent construction of, reliance on, and functional requirement on tools for survival, is distinctive ^{1,4}.

When hominins began routinely making and using tools is a frequently debated topic in palaeoanthropology, with recent evidence implying that tool use began long before the emergence of the genus *Homo* over 3 million years ago ⁵⁻⁷. Debate surrounding this topic stems from the fact that lithic tools, although often in a similar geographic or temporal range, are rarely found contemporaneously alongside *in situ* preserved hominin fossils, and as a result, determining which hominin species created and used those tools becomes educated guesswork ⁸. Therefore, many studies have examined whether the morphological features of fossilized hominin hands would have allowed the degree of manual dexterity associated with the type of lithic tool-use seen in *Homo sapiens* ⁹. Additionally, organic (plant-based) tools, which likely comprised a significant portion of ancient toolkits, are not found in the archaeological record until 430 Ka ¹⁰, meaning there is even less concrete evidence for when or how hominins began employing these sorts of organic implements to aid in accomplishing

tasks ¹¹. While it is often stated that behaviours themselves cannot fossilize, physical traces may persist, a principle central to ichnology, the study of behavioural evidence preserved in the form of trace fossils. Such traces may include potential indicators of tool use, like cut marks on bone or teeth, scars on living plants from raw material extraction, fractured shells of cracked nuts, or the ashy remnants of a fire pit ^{12,13}.

Modern human's strong degree of cross-cultural rightward manual lateralization, something thought to be connected to our propensity for tool-use ¹⁴, has been linked to the development of skeletal asymmetries, particularly in cortical bone of the upper limbs, as early as nine years of age ¹⁵. Still, there is some debate regarding the extent and cause of upper limb directional asymmetries found ¹⁶. Directional asymmetry, as shown in Figure 1, refers to is the systematic and regular variance between two halves of a bilaterally symmetric organism, wherein one side develops larger or differently than the other in a predictable fashion ¹⁷. These asymmetries can be large, such as the additional lobe in the right lung compared to the left, or more subtle variations in the shape and size of structures ¹⁷. Although directional asymmetry is not solely a lasting physical result of manual lateralization in the upper limbs, it is often studied as a proxy for lateralization in humans-- yet this methodology has seldom been applied to non-human species ¹⁸⁻²¹.

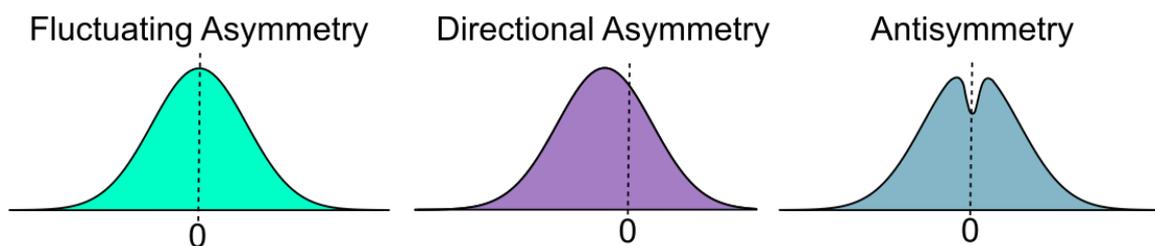


Figure 1. Main forms of biological asymmetry in bilaterally symmetric organisms. *Fluctuating asymmetry reflects levels of developmental stability and refers to minute, random deviations from the expected sameness in bilateral traits due to environmental, cellular, or genetic stressors. Directional symmetry is the systematic and regular variance between two halves of an organism in a predictable fashion within a population. Antisymmetry occurs between individuals of a population, with some displaying a significant left bias in a trait and others displaying a significant right bias, leading to a bimodal distribution.*

Because bone tissue is mechanosensitive and tends to remodel in response to the various strains it endures throughout the course of an individual's life, our highly lateralized behaviours can influence bone morphology ²². Importantly, aside from teeth, bone is the most frequently fossilized tissue, meaning the effects of manual lateralization may be visible in the fossil record. Thus, studying the upper limb, and particularly the hand and its skeletal scaffolding, is a critical area of primatology and palaeoanthropology, as it can provide insight not only into the various evolutionary pressures that shaped the bones of primate hands in diverse directions, but also the ways bone structure has been affected by habitual loads

unique to that species or individual, including potential manual preferences. Therefore, determining the level of directional asymmetry present in the bones of extant hominids may help us make inferences as to when and why hominins began to utilize tools, particularly percussive tools, and when our incredibly strong degree of manual lateralization evolved²³. Here, we review how tool use capabilities are typically studied in extinct taxa and provide an innovative methodological framework to collect and analyse extant and extinct osteological remains for potential tool use traces. Using chimpanzees as a case study, we aim to help clarify the relevance and applicability of this suggested methodology wherein bones from both hands of the same individual primates are compared for osteological changes that may reflect percussive tool-use behaviours.

2. Defining Non-Human Tool-use

While tool-use is relatively rare in the animal kingdom, it been observed to some extent in numerous non-human primate species, including in all of the extant great apes (*Hominidae*), capuchins (*Cebus sp.* and *Sapajus sp.*), macaques (*Macaca sp.*) and baboons (*Papio*), as well as non-primates including some aquatic mammals like bottle-nose dolphins and otters, and birds like corvids and parrots³. Many definitions for, and categories of, what constitutes tool-use in non-human species exist, but most succinctly, tool-use entails the dynamic manipulation of an object which is not part of the animal's body in order to help it achieve a particular goal³. The tool may or may not be modified before use, but it typically adds some functionality to the animal's body and aids in completing the task in some way³. For example, if a chimpanzee has a goal of eating termites hidden in a mound, they could hold a stick in their hand, insert that stick into the termite nest, wait for the termites to bite the stick, extract the stick with the insects, and eat said insects. By using the stick, the chimpanzee can access the nutritional resource (in the form of termites) when its finger likely would not fit into the nest holes, and it is able to do so without less risk of being bitten by defensive termites. This constitutes extractive foraging, which is when an animal removes a nutritional resource that is 'hidden' in some way, such as encased within a shell or concealed underground²⁴. For primates, tool use can be grouped into broad contextual categories, which tend to be related to feeding, hygiene, communication or social interactions, and protection²⁵. The utilization of sticks in the aforementioned termite example, and the use of stones to crack open nuts, would fall under the tool-assisted foraging category²⁶. Examples

of tool use in the other categories include using moss or leaves for fluid transportation (feeding), using an object to groom (which can fall into either the social or hygienic category), manipulating large leaves to act as umbrellas (for protection from the elements), throwing stones as weapons (combative social interactions), and assistance in manoeuvring or climbing^{3,25}. There is debate regarding whether behaviours such as nest-building or communicative gestures using non-body objects should be included as forms of tool use, which is based on the 'objective' of the task and the observer's interpretation of how and why the item is being utilized³.

In order to reconstruct the evolution of hominin tool-use, combined with analysing skeletal morphology, observation of modern primate toolkits and the ways they manipulate, grasp, and engage with lithic or organic tools can serve as proxies into the potential abilities of extinct hominins^{27,28}. For this reason, studies of extant primates from different clades can complement evidence for tool-use from the paleoanthropological record. Due to their close evolutionary proximity to both modern humans and extinct hominins, the great apes, and particularly the genus *Pan*, often serve as the main models for inferring the behavioural capabilities of extinct hominins^{8,29}. However, other, more distantly related primates can also serve as varied models for early forms of hominin tool use⁴, providing new ways to interpret paleoanthropological remains. This is the case for capuchins, who accidentally create flakes that resemble early knapped technology³⁰; macaques, who use lithic tools in coastal environments³¹; and orangutans who use tools in arboreal contexts³². The primate genera who have been documented engaging in percussive lithic tool use, both in the wild and in captivity, are summarized in Figure 2. While all of these primates are evolved to, and specialized for, their own ecological niches which are inherently different from those of the first hominin tool-users, they can still provide insight into the potential behavioural mechanics of tool-use by extinct hominins^{7,30}.

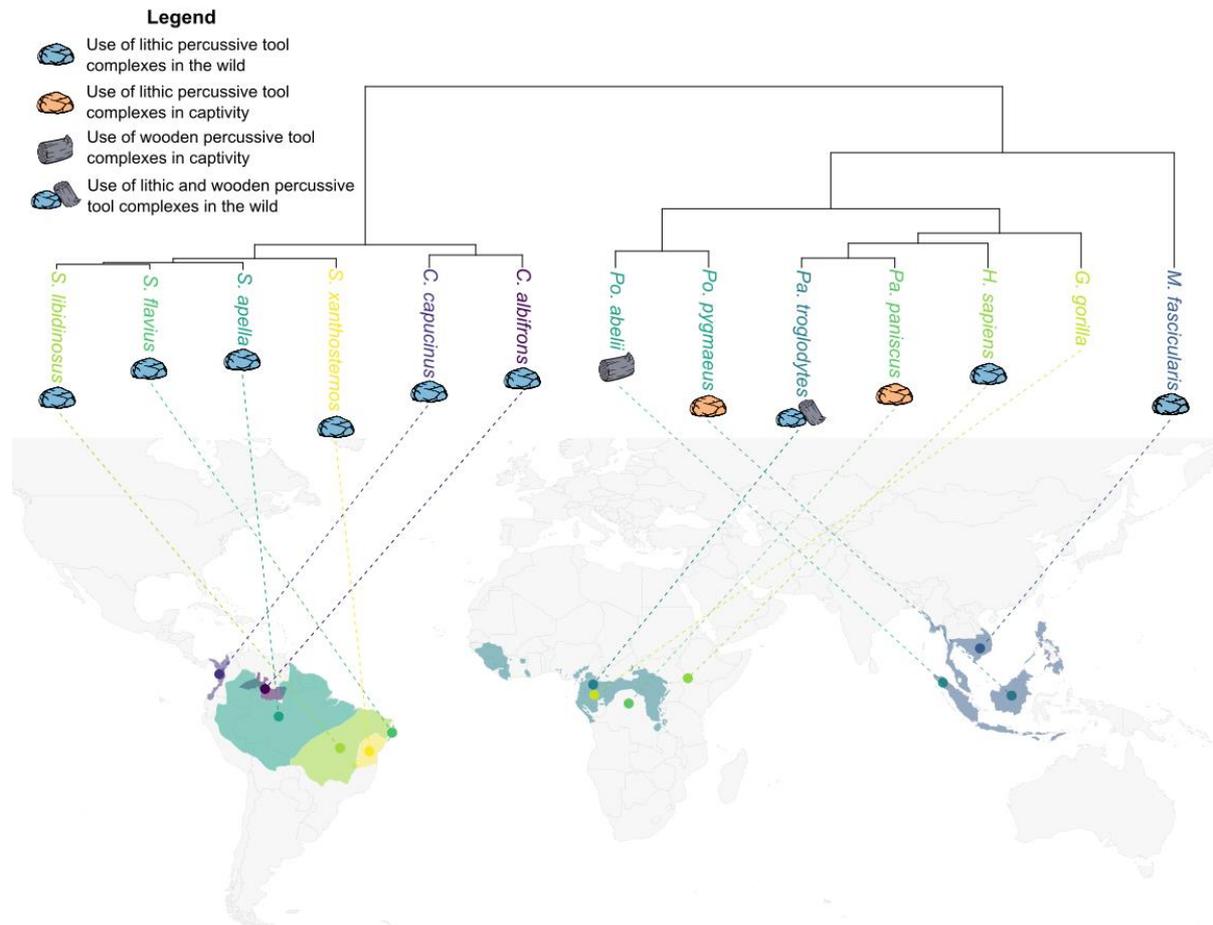


Figure 2. Phylogenetic Distribution of percussive tool use among anthropoid genera. This includes lithic on lithic, or lithic on wood tool complexes. Use of stone as projectiles are not included in this phylogeny, nor are cracking behaviours wherein only an anvil is used (i.e. hitting a coconut on a rock to fracture its shell). Range data from IUCN Red List 2024. The IUCN Red List of Threatened Species. Version 3.1. <https://www.iucnredlist.org>. Downloaded on 05-03-2026³³. The coordinates for *Homo sapiens* reference the earliest site of the most widely accepted human remains from the Omo-Kibish Formation³⁴. References for lithic percussive use for each genera are as follows: **Pongo**; Bandini, E., Grossmann, J., Funk, M., Albiach-Serrano, A., Tennie, C., 2021. Naïve orangutans (*Pongo abelli* and *Pongo pygmaeus*) individually acquire nut-cracking using hammer tools. *American Journal of Primatology*. 83, e23304.; Motes-Rodrigo A et al. 2022.; *Experimental investigation of orangutans' lithic percussive and sharp stone tool behaviours*. *PLoS One* 17:e0263343.; **Pan paniscus**, Neufuss J, Humle T, Cremaschi A, and Kivell TL. Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency. *Am J Primatol*. 2017; 79:e22589. doi:10.1002/ajp.22589.; **Pan troglodytes**: Luncz LV et al. 2019. Cultural diversity of nut-cracking behaviour between two populations of wild chimpanzees (*Pan troglodytes verus*) in the Côte d'Ivoire. In: Boesch C, Wittig R, editors. *The Chimpanzees of the Tai Forest: 40 Years of Research*. Cambridge: Cambridge University Press. p 194–220.; **Macaca fascicularis**: Gumert, M.D., Malaivijitnond, S., 2012. Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *American Journal of Physical Anthropology*. 149, 447–457. **Cebus capucinus**, Barrett BJ et al. 2018. Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *Royal Society Open Science Royal Society*. 5:181002. **Cebus albifrons**, Araujo P et al. 2022. First record of tool use by a wild population of *Cebus albifrons* (Humboldt, 1812) (Primates, Cebidae) in Puerto Misahuallí, Napo, Ecuador. *Boletín Técnico/Technical Bulletin* 15:59.; **Sapajus apella**, Struhsaker TT, Leland L. 1977. Palm-Nut Smashing by *Cebus a. apella* in Colombia. *Biotropica* [Association for Tropical Biology and Conservation, Wiley]. 9:124–126.; **Sapajus flavius**, Lima GCB et al. 2024. A new addition to the toolbox: stone tool use in blonde capuchin monkeys (*Sapajus flavius*). *Primates Springer Nature Singapore*. 65:383–389.; **Sapajus libidinosus**, Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. g., Andrade, F. r. d., 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology*. 132, 426–444.; **Sapajus xanthosternus**, Mainette RD et al. 2025. Characterization of Stone Tool Use in Wild Groups of Critically Endangered Yellow-Breasted Capuchin Monkeys (*Sapajus xanthosternus*). *American Journal of Biological Anthropology* 186:e70002.

3. Current Methodologies for Examining Tool Use Skills in Extinct Hominins

As a result of morphological studies, many scholars agree that various australopiths, such as *A. afarensis*, *A. sediba*, and *A. africanus*, as well as members of the *Paranthropus* clade were able to make and use tools in some capacity^{6,36}. Yet, studies often provide contradictory results in regard to the frequency and ease with which these tools could have been produced and used. Some scholars argue that morphological evidence suggests some australopiths could create and use knapped lithics in a similar manner modern humans^{6,37,38}, while others use similar analyses and evidence to suggest the exact opposite^{39,40}. For example, recent analysis of newly discovered fossils of *Paranthropus boisei*'s hand have revealed morphology convergence with gorillas, except feature a more human-like pollex (thumb) to finger ratio, that is unlike modern gorillas³⁶. The authors conclude that *P. boisei* would have moved arboreally in a manner similar to gorillas, and would have been capable of strong grip strength for the processing rough foods, and further suggest it would have been able to engage tool use similar to that of modern humans³⁶.

When examining morphological features of extinct hominins, studies oftentimes examine the external features of bone, including apomorphic (evolutionarily 'new' or derived) features like broad apical tufts (the flared distal end of a distal phalangeal bone in primates)⁵ or compare morphology to the known effects of various forms of manual labour on the entheses (muscle attachment sites)⁴¹, as well as the distribution of stress that would be expected during lithic tool-use in extant non-human primates and extinct hominins⁴². For example, Kunze et al, 2022 used three entheses on the 1st metacarpal (MC1) to reconstruct muscle recruitment patterns in modern humans, extant hominids, and some extinct hominins. They found that the resultant muscle recruitment patterns differed between modern humans and extant hominids, but was similar to modern humans in all extinct hominins (except *A. africanus*) studied⁶. Similarly, studies of external morphology typically focus on the degree of curvature of the phalanges, shape of muscle insertion sites (such as flexor sheath ridges), or the length of the pollex relative to the other digits, as proxies for how much the hand was used in (likely arboreal) locomotion or how human-like it was, and thus whether it could complete delicate, precise, manipulation, or they use biomechanical methods to model potential dexterity^{5,6,43}. It is rare for fossils from both sides of body of the same individual to be found⁵, making bimanual studies understandably scarce, however, even when looking at extant primates, research seldom compares bones from both sides of the same individual.

Importantly though, asymmetric variation has been observed using various methods in the few studies which have investigated this in both humans and apes. For example, in a study of human humeri from various geographic origins found right-sided asymmetry in terms of length, weight, and mid-shaft circumference, but more variable patterns of asymmetry in terms of the angle of torsion ⁴⁴. Another study examining human humeri and second metacarpals (MC2), found entheses were more likely to be asymmetric on both bones, although they did not report a trend in directionality of the asymmetries found ⁴⁵. Studies examining total subperiosteal area in the midshaft of human and chimpanzee humeri and MC2 found that all human populations studied demonstrated a right-bias in both bones, whereas chimpanzees tended toward left-lateralization in the humerus but right-lateralization in the MC2 ^{18,46}. Directional asymmetries have also been identified in an ontogenetic series in captive old world monkey (*Macaca mulatta*)²⁰ and in adult new world monkey, the cotton-top tamarin (*Saguinus oedipus*), albeit only in the lower limb in the latter ⁴⁷.

Unilateral studies examining the internal, trabecular structure of bones, which is particularly reactive to mechanical strain and therefore may be uniquely suited to help infer behavioural capabilities of fossil hominins, are rare as well, likely due to the logistical challenges and cost of acquiring microCT scans, though they do exist ^{9,22,38,48}. Similarly few studies have looked at potential asymmetries present in internal bone microarchitecture in humans bilaterally, and only one small study has done so in any of the extant great apes, which found the MC1 reflected rightward directional asymmetries in humans but leftward ones in chimpanzees ^{19,43}. Alternatively, however, it has been suggested trabecular analyses may be less adept at capturing directional asymmetries as a result of lateralization in the carpals and metacarpals in modern humans ⁴⁹. Limited work has used Finite Element Analysis (FEA) - a virtual computational technique that simulates how complex structures withstand physical loads by breaking them down into smaller, simpler 'elements'-- to model the potential stress distribution patterns of hammerstone use on the proximal pollical phalanx in humans, neanderthals, and extant apes unilaterally ⁴².

While several studies have investigated use-wear from percussion on both organic anvils and lithic hammers and anvils themselves, used by both humans and primates, uncovering specific microwear signatures ^{29,50-52}, the effects on the tool user themselves are not examined. The tools discussed are often limited to human-knapped, manufactured tools, like those used for hunting or butchering carcasses. Organic tools, or unmodified lithics, such as those used to crack open nuts by modern primates and in the archaeological past⁵¹, are less frequently analysed, even though the latter of which can unintentionally create flakes that are

morphologically similar to early purposefully knapped technologies³⁰. It is recognized that the variation in individual skill is reflected in tool use, such as how the technique and skill of capuchins affects unintentional flaking of stones when nut-cracking^{50,52}, and that chimpanzees in the same community consistency crack at differing efficiencies^{53,54}. Ultimately, this lack of study into directional asymmetries leaves a gap in our understanding of the effect of tool-use on primate bone, particularly those who engage in lithic percussive tool use.

4. Percussive Tool-use in Primates

Lithic percussive tool-use in non-human primates has been defined as “pounding, using a hammer and/or a hammer-and-anvil technique in order to crack open foodstuffs,” with the known exception of Kanzi, a captive bonobo who was taught to flaking stone tools similar to Oldowan instruments⁵⁵. While other primate species use various plant-based tools, the only primates with long-term evidence of percussive lithic tool use in the wild are capuchins, macaques, and chimpanzees⁴. In all these species, stone tools, occasionally used in combination with organic ones, are utilized for extractive foraging purposes, most frequently to remove the kernel from varied species of nut-producing plants, or to acquire other nutritional resources as shown in Figure 3⁵².



Figure 32. Primates engaging in lithic tool use. *A.* A group of Bossou Chimpanzees (*Pan troglodytes verus*) using a lithic hammer and anvil to crack nuts in the outdoor laboratory, Photo Credit: Cyril Ruoso. *B.* A female long-tailed macaque (*Macaca fascicularis*) using a lithic hammer and anvil to break open a mollusc, Photo Credit: Cyril Ruoso. *C.* A male bearded capuchin (*Sapajus libidinosus*) cracking a piassava palm nut at Fazenda Boa Vista, Photo Credit: Luca Antonio Marino.

4.1 *Macaca*

Of the old-world monkeys, multiple species of macaque such as *Macaca silenus*, *M. radiata*, and *M. fuscata*, and subspecies of long-tailed macaque (*Macaca fascicularis fascicularis*, *M. f. umbrosus*, *M. f. aurea*) have been documented engaging in extractive foraging and food preparation behaviors, such as washing sweet potatoes, rubbing off bitter pulp using tree bark, or processing coconuts⁵⁶. However only *Macaca fascicularis* ssp. Have been documented engaging in lithic percussion. In intertidal habitats in Thailand, *M. f. aurea* has been documented conducting extractive foraging using stone hammers to crack open the shells of nearly 50 marine species, primarily of aquatic molluscs, oysters, as well as some crustaceans, and plants such as sea almonds (*Terminalia catappa*)^{31,57}. Regarded as a generalist species, it seems unsurprising that these macaques opportunistically exploit such a wide variety of prey species, even though a few species are processed and eaten at much higher rates (such as the rock oyster, *Saccostrea cucullata*; chameleon nerite, *Nerita chamaeleon*; drill rock shell snail, *Thais bitubercularis*; tooth-lipped snail, *Monodonta labio*). When engaging in lithic percussion to open shelled aquatic species, macaques may utilize

one or both hands to hold the hammerstone⁵⁸. Whether one or both hands are used varies based on the size of the hammerstone, which tend to be smaller ‘axe’ hammers for cracking sessile oysters cemented to coastal rocks, or larger ‘pound’ hammers for cracking sea almonds^{31,58}. In inland forest habitats of another island in Thailand, *M. fascicularis* have begun to crack non-native oil palm nuts (*Elaeis guineensis*), the same variety which chimpanzees have been documented cracking for decades, recently introduced to the island by human farmers^{59,60}. Similarly, anvil and hammerstone re-use is common, with macaques transporting tools and prey⁶¹, leading to large amounts of macro and microwear including flake removals, pitting, and flattening of the surface^{57,60}. Importantly, the accidental production of sharp-edged flakes through this extractive foraging can result in objects which could easily be misinterpreted as purposeful and anthropogenic in nature, making them hard to distinguish from the human archaeological record⁶².

4.2 *Sapajus* and *Cebus*

Although there are limited reports of other new world monkeys using organic tools, capuchin monkeys of both genera (*Sapajus* and *Cebus*) are the most well-documented tool-using new world monkey in the wild^{13,25}. Even though robust capuchins (*Sapajus* sp.) are thought to be more adapted to extractive foraging than gracile capuchins (*Cebus* sp.) due to the ecological availability of nutritional resources in their environments, species from both genera have been reported engaging lithic tool use to some degree in the wild⁶³.

Bearded capuchin monkeys (*Sapajus libidinosus*, formerly *Cebus libidinosus*) are well-studied for their percussive tool use. In savannah habitats, they use stones to crack various species of nuts and seeds, and in dry forest and woodland habitats, they use them to break down tubers, or small vertebrate prey^{64,65}. They also engage in stone-on-stone percussion for aggressive or sexual displays, often licking at the stone’s fracture point afterward, possibly to ingest the pulverized rock or lichens^{66,67}. Interestingly, and like with long-tailed macaques, this behavior can create flakes which are morphologically similar to intentionally flaked hominin tools in the archeological record⁶⁶. Golden-bellied capuchins (*Sapajus xanthosternos*) in Northern Brazil have been recorded using lithic hammers to open the enclosed fruits of three species (*Acrocomia aculeata*, *Cnidosculus pubescens*, and *Syagrus oleracea*) during the dry season only⁶⁸. Blond capuchins (*Sapajus flavius*) have recently been reported using hammerstones in the Caatinga dry forest, although it is unclear which plant species they processed, or which individuals in the group were engaging with the

tools⁶⁹. While the manipulative and cognitive abilities of tufted capuchins (*Sapajus apella*, formerly *Cebus apella*) with tools have long been studied in captivity there are fewer examples of them using lithics in the wild^{63,70}. Most reports of this species engaging in nut-cracking in the wild do not involve any lithics, as they instead hit tough fruit on tree branches, with lithic-based nut-cracking reported only in semi-captive groups^{71,72}. Similarly, crested capuchin monkeys (*Sapajus robustus*) crack open nuts using stones and other hard objects, however this has only been reported in captivity, and not all of the individuals who were reported to attempt this behavior were successful⁷³.

Gracile capuchins have far more limited evidence of lithic percussion in the wild, although a few species have been documented using lithics for extractive foraging. Much like macaques in tidal habitats, some groups of Panamanian white-faced capuchins (*Cebus capucinus imitator*) use lithic tools to crack open mollusks such as snails, as well as crabs, and *Terminalia catappa* seeds^{24,74}. Their engagement with this behavior varies with the fluctuation in the tides and has only been documented in males. There is limited documentation of male Trinidad white-fronted capuchins (*Cebus albifrons trinitaris*) using stones to open almond tree fruits (*Terminalia catappa*) in an anthropically modified environment in the Ecuadorian Amazon as well⁷⁵.

4.3 Pan

Chimpanzees (*Pan troglodytes*) are the most adept extant non-human tool-user, with a complex repertoire of tool-using behaviours which are found to some extent in all studied wild communities^{76,77}. Their tool-use is also culturally-specific with certain groups using tools in ways that are absent in other communities, even if the same tool substrate, or nutritional resource is available in both ecologies^{35,77}. For example, some groups in Bossou in Guinea, West Africa, and across the border into Liberia in Kpala, engage in pestle-pounding, which entails using a young oil palm (*Elaeis guineensis*) frond to pound the top of the palm tree and access the fibrous palm heart inside, a behaviour which is not documented in other communities with oil palm trees⁷⁸.

The most common form of percussive lithic tool-use in chimpanzees is a type of percussive hammering aptly named nut-cracking, wherein rocks (or in some communities, tree roots) are used to break open the shells of nuts so the kernel inside can be consumed⁷⁹. Nut-cracking involves a chimpanzee placing a nut on a stone or wooden anvil, which may or may not be mobile, then hitting it with a stone or wooden hammer^{35,79}. While chimpanzees

live in numerous communities throughout western and central Africa, this behaviour is only observed in some of the chimpanzee groups of West Africa, with the sites of Taï and Bossou being particularly well-studied ⁷⁷. Similarly, even in communities of the same subspecies of chimpanzees (*Pan troglodytes verus*) that all engage in nut-cracking, there is still diversity in the types of nuts they crack and the tool material they chose for the task. Chimpanzees from Taï in the Ivory Coast, use immobile anvils in the form of tree roots or rock patches in combination with stone or wooden hammers, and vary their hammer type based upon the hardness of the nut they are attempting to crack, which include numerous species such as *Coula edulis*, *Parinari excelsa*, *Panda oleosa* and *Detarium senegalensis* ^{35,80}. Conversely, the Bossou chimpanzees from Guinea exclusively use movable stone anvils and hammers, which are often transported short distances specifically to be used for nut-cracking and they primarily crack oil palm (*Elaeis guineensis*) nuts ^{79,81}.

The cultural diversity within chimpanzee subspecies and neighbouring groups is particularly striking when comparing them to their sister species and only other extant member of the genus *Pan*, the bonobo (*Pan paniscus*) ²⁸. While bonobos are capable of complex tool manufacture and use in captivity, they have infrequently been documented using tools, particularly in extractive foraging contexts, in the wild ⁸². Their use of tools in the wild primarily involves the use organic materials like sticks and leaves as part of communicative displays, to cover themselves from rain, or in grooming/cleaning contexts, with some cultural diversity in how habitual these behaviours ^{83,84}. The drastic difference in documented wild tool-use between chimpanzees and bonobos may be due to fewer research teams studying them ^{76,85}. It has also been suggested, however, that the rationale for tool-use differs inherently between the two species. This distinction is thought to be the result of a disparity in the ecologies of the species, particularly in relation to nutritional resources, as bonobos tend to have fewer environmental barriers to nutritional success, resulting in their decreased intrinsic motivation for tool-use ⁸³. On the whole, bonobos seem to have smaller tool repertoires than chimpanzees⁸², a difference that is particularly interesting given that the two only diverged from each other around 1 Ma ⁸⁵.

5. Defining Laterality

Many vertebrates express some form of behavioural lateralization, however, modern humans are an evolutionary singularity in the primate order due to the strong cross-cultural

bias for right-handedness we display ². Up to 96% of humans use their right hand for skilled manipulation of objects ¹⁴. Individual chimpanzees tend to have a manual preference when engaging in complex tasks such as tool use, which is similar, but not identical to the handedness seen in modern human populations ⁸⁶. An individual chimpanzee may change which hand is preferred based on whether it is employing a tool, and what sort of tool is being used to accomplish the given task, something which is rare in humans ⁸⁶. It has been hypothesized that the switching of preferred hand during different types of tool-use may stem from the varied cognitive and motor demands of the task, such that a chimpanzee prefers one hand for more delicate, dextrous movements like termite-fishing, but prefers the other for more forceful behaviours like nut-cracking ⁸⁷. In terms of percussive tool use, while young chimpanzees begin nut-cracking ambidextrously, they show a 100% hand preference by the time they are ‘experts’ at the skill, something not demonstrated in other sorts of manual behaviours ⁷⁹. When engaging in percussive behaviours, macaques may use one or both hands depending on what they are attempting to open, whereas capuchins typically use both forelimbs to lift and throw hammerstones on the object ⁵². Similarly, capuchins and macaques often demonstrate individual preference for one hand in standardized bimanual tasks ^{63,88}.

Comparisons between primate’s percussive tool-using behaviours have been proposed as a step towards, and compared to the origins of knapping in the hominin clade ^{30,51,89,90}. The relevance of laterality to this work stems from the fact that in humans, handedness is known to lead to asymmetric variation in the skeleton ^{14,15}. Therefore, when individual chimpanzees and macaques use one hand more frequently for certain repetitive tasks such as percussive hammering, it would be expected to cause small, yet quantifiable changes in osseous tissue of long bones of this preferred hammering hand compared to the less-used hand, whereas in capuchins who engage in bimanual cracking, less directional asymmetries would be expected.

6. Relevance of Bone Morphology

Both cortical and trabecular bone can break while experiencing excessive loads, but are relatively resistant to routine stress and strain, helping to prevent breakage in normal use scenarios, as they can be fatal in the wild. The types and degree of strain varies between individuals due to their lifestyles, such that those experienced by athletes who throw with one arm at high speeds, or individuals who partake in certain types of manual labour, meaning their bone remodels to reflect the repetitive strains they personally experience ⁴¹. The

minimum effective strain (MES) constitutes the minimum amount of force needed to cause the mechanical force to be transmitted as a nervous signal ⁹¹. Forces significantly surpassing the MES will cause microscopic damage to the osteon, the basic functional unit of bone, which then begins a modelling or remodelling process ⁹¹. This process is commonly referred to as Wolff's Law (or bone's functional adaptation), which describes bone's ability to remodel in response to the mechanical loads it regularly experiences ^{22,91}. Thus, recurrent biomechanical loading, such as during frequently lateralized behaviours like percussive tool use, will cause bone cells to preferentially resorb bone in areas that are not experiencing much strain, and deposit bone in areas enduring higher rates of strain ^{19,22}.

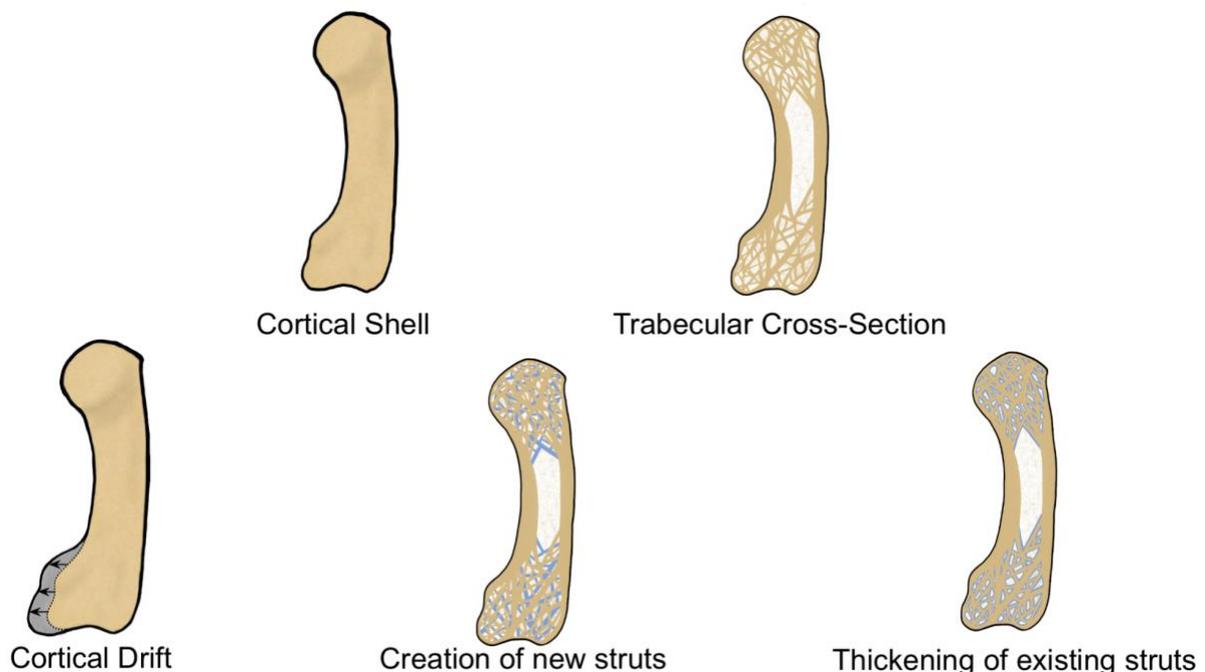


Figure 4. Bone Remodelling. *Depicting the bone remodelling can change the internal and external structure of a bone, in this case, a metacarpal. For illustrative purposes only.*

Over time, remodelling can cause cortical drift, thickening of existing trabecular struts, changes to the direction of struts, or creation new struts entirely, as seen in Figure 4, so the bone can better withstand the repeated type of loads it has been enduring ^{9,22,91}. Infrequent tool-use, and other sporadic actions which may result in significant, but inconsistent, forces are unlikely to cause significant changes to bone. By contrast, actions which repeatedly surpass the MES, such as pitching by elite baseball or cricket athletes, can cause significant changes to the macro- and microstructure of the bone, though there is some debate as to the differences in how trabecular bone may remodel between species and body regions ^{22,92,93}.

Due to factors like cortical drift, the external features of long bones, such as the entheses' (muscle attachment sites) size and shape, or density of bone tissue can vary

between species, as well as individuals of the same species^{9,91}. Since bone reacts to these repeated mechanical loads in quantifiable ways, studying morphological variation can provide insights into the locomotor patterns and functional abilities, and potential tool use behaviours, that extinct hominins may have engaged in^{48,94}. This methodology of examining external bone morphology has been used for many decades, as it only requires evaluating the physical features of the bone's surface, rather than any additional analyses which may require cutting, drilling or otherwise damaging the specimen, while still providing numerous ways to examine bones of the upper limb of the same individual for asymmetries^{23,44,95,96}. For example, numerous studies have examined how various physical actions particularly associated with lateralized sports like tennis, cricket, or baseball can affect the micro- and macrostructures of the long bones of the extremities asymmetrically^{92,93}. However, when examining fossil specimens for asymmetries, recognizing potential impacts of taphonomic distortion because of fossilization, pathological or age related changes, and burial is crucial⁹⁷.

7. Proposed Case Study: Nut-cracking in chimpanzees

As discussed in previous sections, multiple wild primate species engage in use of lithic tool complexes, however, the most long-term studies of this phenomenon have occurred in nut-cracking chimpanzees. For this reason, they can serve as a valuable starting point for research into the effect of manual lateralization and potential resultant asymmetries in primate bone. Chimpanzees have a complex understanding of the mechanical properties of the tools they utilize and there is individual variation in the efficiency with which they crack these nuts^{7,52,53}. Similar evidence of tool selection and material property knowledge has been demonstrated in capuchins⁹⁸. Nut-cracking is one of the most complex tool-use practices observed in non-human animals, and as a result, it takes many years for young chimpanzees to master through observational social learning and practice^{35,53,54}.

Nut-cracking is estimated to have been transmitted across 200 generations of chimpanzees, as lithic assemblages have been discovered in the home of the Taï chimpanzees, Côte d'Ivoire, dating back 4,300 years, and both lithic and organic remnants of these behaviours can be found in the archaeological record^{99,100}. For the Taï chimpanzees, tool-use is thought to be a daily occurrence⁸⁰. The Taï chimpanzees start learning to crack nuts around 3-4 years old and primarily crack nuts during the four-month 'coula season,' which coincides with the dry season, making the nuts an important component of the

chimpanzee's diet ⁸⁰. The other most-studied nut-crackers are the chimpanzees of Bossou, located in Guinea ⁷⁹. The Bossou chimpanzees begin learning to crack nuts between the ages of 3-4 years old with a critical period from 3-7 years, which, if missed, means the chimpanzee is unlikely to ever acquire the skill (¹⁰⁰ but see ⁵¹). Both the anvils and hammers are movable stones, typically made of granite, quartz, or diorite, and are often transported short distances specifically to be used for nut-cracking ^{79,81}. Nut-cracking occurs year-round in Bossou, with oil palm (*Elaeis guineensis*) being the most frequently cracked nut ⁷⁹.

Due the differences in the ways the Tai and Bossou nut-cracking communities employ and choose their tools, along with evidence that the behaviour cannot be individually reinvented, nut-cracking is considered to be culturally specific to the groups that practice it and is passed on via a type of cultural transmission ¹⁰². Importantly, because of modern chimpanzees' close evolutionary relationship with humans, use of tools, and their culturally varied implementation of percussive instruments, they are an incredibly useful proxy for the study of the evolution of percussive tool-use in potential human ancestors ^{12,76}. By comparing the ways humans and chimpanzees create and interact with tools, we can learn about which traits might be plesiomorphic (i.e., ancestral and inherited from the last common ancestor (LCA) of the two species). Additionally, by connecting actions with resulting morphological traits, it can help us infer behaviour when similar morphology is described in extinct species.

Nut-cracking has also been suggested as a potential precursor to early stone-flaking in the hominin lineage ^{8,29,50,89,90,100}. The action requires a significant amount of power to crack the shell, but not so much that the kernel inside is shattered, which creates meaningful forces on the hand holding the hammerstone ⁹⁰. This should cause enough mechanical strain to active bone's dynamic remodelling, thus causing morphological changes in the bones of nut-crackers. Furthermore, as chimpanzees are fully lateralized once they have mastered nut-cracking, there could be a quantifiable bilateral asymmetry, or an osteological signature caused by nut-cracking behaviours, particularly in the communities that engage in nut-cracking year round ^{45,53,79}. Quantifying what the potential 'damage signature' left by the repetitive, forceful act of nut-cracking has on the hand bones of chimpanzees, has not yet been done. While some research has investigated and compared the bone microarchitecture of the metacarpals and carpals in bonobos, chimpanzees, orangutans, gorillas, and modern *Homo sapiens*, these studies have often focused on a single bone, on a single side, and they have not analysed these specimens in the context of tool-using behaviours ^{40,103}. Thus, examining bones of both hands of nut-cracking chimpanzees and comparing them to non-nut-

crackers can help answer the question of when do repeated, forceful actions, such as nut-cracking, cause quantifiable, morphological change to bone in non-human primates ¹⁰⁴?

Importantly, this sort of research is inherently comparative in nature; to determine whether one hand is impacted by percussive tool-use behaviours, both hands of the same individual must be studied. However, scanning both sides of the same individual is not current practice in the field. A key example of this issue is present in a new dataset meant for comparative morphology in hominoid and anthropoid primates, which collected a massive amount of data from over 386 individuals from 47 genera ¹⁰⁵. While this is an incredible collection, it lacks bones from both sides of the body of most individuals, essentially limiting these scans from being used in any asymmetry studies until, or unless the other sides of those individuals are scanned. Current scanning and analysis practices essentially ignore any potential for directional or fluctuating asymmetries in the primate order, inherently assuming a lack of asymmetry. However, limited previous work has shown that while humans are more strongly lateralized both in terms of strength and direction than any other primates, directional asymmetry can be quantified in bones of the upper limbs of other species, such as chimpanzees, so it can likely be identified in species who have not yet been examined in this manner ^{18,44,45}.

Numerous studies have analysed each of the metacarpals when attempting to determine extinct hominin's manual capabilities, so examining the effect of percussive tool-use on the metacarpals in primates is in line with current morphological practice ^{39,40,42}. Particular attention should be given to the pollical metacarpal as it plays a critical role in primates' grasping abilities and is a focus of research into potential tool-use abilities in extinct hominins ^{19,40,43}. Prior studies have rarely identified handedness-related directional asymmetries in the carpals' trabecular and cortical structure in humans, so these bones likely do not need to be the focus of this research ^{49,91}. To be used for quantification of variation in both the internal trabecular and external cortical morphology, high-resolution microcomputed tomography (microCT) scan from both hands of adult chimpanzees should be acquired. While scans of lower resolution may be used for analysing cortical morphology, having trabecular metrics may provide more insight into the potential implications of percussive tool-use on chimpanzee bone, due to its faster turnover rate, and the ability to measure the degree of and direction of anisotropy. Other scanning methodologies, like photogrammetry or structured light scanners can be used to quantify external, cortical asymmetries, such as enthesal shape and size, which can be affected by differential muscle use ⁴⁵.

Scans of chimpanzees from communities like Taï and Bossou, will be a critical dataset for this research, as they have well-documented life history information such as preferred hand during various forms of tool use, are prolific nut-crackers in the wild, and for whom skeletal collections exist¹⁰⁴. Results could then be compared to the scans of individuals who come from similarly long-studied communities, but who do not engage in nut-cracking like Budongo, or Ngogo. An alternative comparative dataset could come from museum collections or captive environments like zoos and research centres. However, the former would likely have less life history data on individuals and as such, their nut-cracking history would be an unknown and thus uncontrolled variable. The results from the known nut-cracking chimpanzees can be used to create a scale nut-cracking ‘damage,’ which scans of unknown history can be compared to. As demonstrated in Figure 5, numerous types of analyses can be used to investigate potential asymmetries in the bones of nut-crackers.

Osseous Scan Analyses



Figure 5. Summary of potential osteological analyses to analyse asymmetries related to percussive tool-use. All images for illustrative purposes only, and do not depict actual analyses. Chimpanzee photo credit to T. Matsuzawa/Kyoto University Primate Research Institute. Metacarpal photo taken by K. Almeida-Warren. For further methods on basic geometry refer to: Sarringhaus L a. et al. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). *American Journal of Physical Anthropology* 128:840–845. For further information on geometric morphometrics: Morley J et al. 2022. Characterizing the body morphology of the first metacarpal in the Homininae using 3D geometric morphometrics. *American Journal of Biological Anthropology* 177:748–759. For further methods on enthesal morphology: Karakostis FA, Hotz G. 2022. Reflections of manual labor in the hand entheses of early industrial women workers with extensively documented life histories. *American Journal of Biological Anthropology* 2022:1–15. For further methods on Finite Element Analysis: Bucchi A et al. 2020. Finite element analysis of the proximal phalanx of the thumb in Hominoidea during simulated stone tool use. *Comptes Rendus Palevol* 19:16. For further methods on beam theory: I van Lenthe GH et al. 2008. Tissue modulus calculated from beam theory is biased by bone size and geometry: Implications for the use of three-point bending tests to determine bone tissue modulus. *Bone* 43:717–723. For further methods on examining internal

Chimpanzees, like humans, are typically somatically mature by the time they begin reproducing, which is often in their early- to mid-teens⁸⁵. In female chimpanzees, this corresponds with the time they disperse from their natal group⁸⁵. Immature bone is more disorganized than adult bone and has not yet experienced enough remodelling for trabecular struts and haversian canals to be aligned in response to the typical forces²². Thus, to ensure only skeletally mature individuals are included in the dataset, individuals who are under the age of 15 should be excluded. Similarly, older chimpanzees may begin to show degeneration of their bone, or osteopenia (decreased bone density) as bone tissue is resorbed faster than it is deposited¹⁰⁶. In females the risk of this increases during menopause, a life history milestone which has recently been demonstrated in chimpanzees¹⁰⁷. However, these individuals should not be excluded unless the bone mineral density and bone mineral content measures are outside the standard deviation of the other scans.

While chimpanzees are a strong candidate for initial research into the effects of tool use, specifically of a percussive nature on primate bone, the relevance of this research can only be improved by applying it to multiple different primate species. By extending this research to include other percussive tool-using species like macaques and capuchins, as well as extant hominids not known to engage in percussive tool-use, a broader understanding of how manual abilities affect, or are reflective of directional asymmetries can be elucidated. Importantly, by quantifying whether and what type of asymmetry is present in various primate species, predictive models can be created, which can then be applied to fossil remains. Thus, by understanding the degree of bilateral asymmetry in the hand bones of our closest living relatives, and particularly whether it occurs to a higher degree in chimpanzees who engage in a percussive tool-use behaviour like nut-cracking, could add another method for examining tool use behaviour in the archaeological record.

8. Applicability to the Fossil Record via Machine Learning

Critically, once the morphological impact of percussive tool-use has been quantified in numerous individuals of different primate species, including those who were and were not known percussive tool users, powerful approaches such as machine learning (ML) classification techniques can be used to categorise other specimens, such as hominin fossils, as being tool-users v. non-tool users. This could be done in a variety of ways, as ML approaches can be applied to multiple tool use proxies extracted from geometric

morphometric data, such as shape or size asymmetries. Using the results of how lithic tool use affects primate bone in different clades to train machine learning models could likely increase the accuracy with which the models can predict whether various fossil hominins show potential osteological evidence of tool use. Alternatively, the results could help train models to predict the extent of microdamage caused by percussive hammering that must be present in different species to be detected in the fossil record. Essentially, these data could be used as predictors in either ML regression or classification tasks and thus can help improve our understanding of lithic tool use in fossil species. This sort of machine-learning based classification methodology has been used previously to identify damaged vs. undamaged areas on wooden tools caused by wild chimpanzees during nut-cracking from 3D models with 96.3% +/-1.4% accuracy¹². This study then used models to create ‘heat maps’ of surface damage, which helped to delineate between regions of wear on the tools¹².

Similar methodology has previously been used to help discriminate the most likely locomotor repertoire of fossil primates¹⁰⁸. By training models with both the tool-holding and non-tool holding hand of known percussive tool-users, as well as non-percussive tool users of various species, there is a lower likelihood of overfitting^{12,109}. Numerous ML classification algorithms should be employed and then the performance of classification of tool user type can be compared for accuracy via cross-validation¹⁰⁹. Furthermore, if behavioural data is integrated with the osseous effects of tool-use in the various primate species known to use percussive tools (e.g., capuchins, macaques, chimpanzees), phylogenetic comparative methods can be used to extrapolate the likelihood of percussive tool-use in extinct hominins, more broadly, hominid taxa, while accounting for the phylogenetic non-independence of these species¹¹⁰. Thus, having examples from varied primate species and infraorders can allow phylogeny to be accounted for in these models. Examinations into these features in the hands of both modern and ancient *Homo sapiens*, as well as other hominins, may also allow us to determine when the cross-cultural right handedness bias evolved as well^{2,14}.

9. Conclusions

While researchers have extensively studied the behaviour of percussive tool use in several primate species and have investigated the physical effects of these behaviours on the tools used^{12,50,100}, studying the hand bones of percussive tool-users themselves to determine whether lasting changes to bone morphology occur as a result of this behaviour would be

novel¹⁰⁴. Analysing the bones of both hands of individual primates who engaged in percussive tool-use, as well as individuals lacking this cultural skill, can provide critical insight into the interplay between manual behaviours and hand morphology. Furthermore, this sort of investigation would fill the void in the current literature as the first to examine asymmetries in the hammering versus non-hammering hand for the effects of percussive tool-use in primates. Both the bones of non-percussive tool-using chimpanzees, and the non-hammering hands of percussive tool users can serve as controls in this sort of study. Creating a better understanding of the effects that percussive tool-use has on the hands of primates, who may use tools in ways similar to extinct hominins, means this research provides insight into the degree and range of percussive tool-use evolution in the hominin clade.

By comparing the morphology from both upper limbs of the same chimpanzees, this sort of study could help determine whether the degree of lateralized behaviours demonstrated by individual chimpanzees causes asymmetrical variation at the skeletal level. If the expected long-term remodelling from behaviours like-nut cracking is found asymmetrically, this can affirm current evidence that wild chimpanzees show an individual-level manual lateralization, or population-level directional asymmetries could support broader concepts of handedness⁸⁷.

Even if no significant changes are found in the preferred hand versus the non-preferred hand of percussive tool-users, this will still be an important result. This could mean that even though highly lateralized behaviours can induce morphological change in human bone, it may not in other primates. This could be because the MES in chimpanzee bone is higher than in human bone, meaning that percussive hammering may not affect their internal bone morphology in the same way it does in humans and as a result, signatures of remodelling may not be apparent at all. Alternatively, the level of MES in humans could be a derived trait, which resulted from our bipedality. Because we do not bear weight on our hands like knuckle-walking chimpanzees do while ambulating, the routine loads our hands endure is likely lower than that of chimpanzees. Knowing this would also be important for extrapolation to the paleoanthropological record, as it could mean that other obligate bipeds may show more evidence of tool-use than more occasional bipeds in the bones of their hands even if they engaged in the same amount of percussive tool-use. Ultimately, by providing a better understanding of the effects that tool-use has on the hands of primates, this research potentially provides insight into the degree and range of percussive tool-use in human clade.

10. References

- 1 Hill K et al. 2009. The emergence of human uniqueness: Characters underlying behavioral modernity. *Evol Anthropol Issues News Rev* 18:187–200.
- 2 Püschel TA et al. 2025. Phylogenetic meta-analysis implicates large brains and our unusual posture in human handedness. *bioRxiv Cold Spring Harbor Laboratory*. :2025.06.17.660131.
- 3 Shumaker RW et al. 2024. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. JHU Press.
- 4 Bandini E et al. 2022. Examining the suitability of extant primates as models of hominin stone tool culture. *Humanit Soc Sci Commun Palgrave*. 9:74.
- 5 Kivell TL. 2015. Evidence in hand: recent discoveries and the early evolution of human manual manipulation. *Philos Trans R Soc B Biol Sci* 370:20150105.
- 6 Kunze J et al. 2022. Enthesal Patterns Suggest Habitual Tool Use in Early Hominins. *PaleoAnthropology* 2022.
- 7 Braun DR et al. 2025. Stone selection by wild chimpanzees shares patterns with Oldowan hominins. *J Hum Evol* 199:103625.
- 8 Carvalho S et al. 2009. Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim Cogn* 12:103–114.
- 9 Dunmore CJ et al. 2023. Tool use and the hand. In: Hirst CS et al., editors. *Behav. Our Bones*. Elsevier. p 135–171.
- 10 Milks A et al. 2026. Evidence for the earliest hominin use of wooden handheld tools found at Marathousa 1 (Greece). *Proc Natl Acad Sci Proceedings of the National Academy of Sciences*. 123:e2515479123.
- 11 Pascual-Garrido A, Almeida-Warren K. 2021. *Archaeology of the Perishable: Ecological Constraints and Cultural Variants in Chimpanzee Termite Fishing*. Curr Anthropol The University of Chicago Press. 62:333–362.
- 12 Luncz LV et al. 2022. Chimpanzee wooden tool analysis advances the identification of percussive technology. *iScience* 25:105315.
- 13 Pascual-Garrido A et al. 2024. Primate archaeology 3.0. *Am J Biol Anthropol* 183:e24835.
- 14 Uomini NT. 2009. The prehistory of handedness: Archaeological data and comparative ethology. *J Hum Evol* 57:411–419.
- 15 Blackburn A. 2011. Bilateral asymmetry of the humerus during growth and development. *Am J Phys Anthropol* 145:639–646.

- 16** Danforth ME, Thompson A. 2008. An Evaluation of Determination of Handedness Using Standard Osteological Measurements*. *J Forensic Sci* 53:777–781.
- 17** Klingenberg CP. 2015. Analyzing Fluctuating Asymmetry with Geometric Morphometrics: Concepts, Methods, and Applications. *Symmetry Multidisciplinary Digital Publishing Institute*. 7:843–934.
- 18** Stock JT et al. 2013. Skeletal evidence for variable patterns of handedness in chimpanzees, human hunter–gatherers, and recent British populations. *Ann N Y Acad Sci* 1288:86–99.
- 19** Stephens NB et al. 2016. Trabecular architecture in the thumb of Pan and Homo: implications for investigating hand use, loading, and hand preference in the fossil record. *Am J Phys Anthropol* 161:603–619.
- 20** Hallgrímsson B. 1999. Ontogenetic Patterning of Skeletal Fluctuating Asymmetry in Rhesus Macaques and Humans: Evolutionary and Developmental Implications. *Int J Primatol* 20:121–151.
- 21** Morbeck ME et al. 1994. Skeletal asymmetry and hand preference during termite fishing by gombe chimpanzees. *Primates* 35:99–103.
- 22** Kivell TL. 2016. A review of trabecular bone functional adaptation: what have we learned from trabecular analyses in extant hominoids and what can we apply to fossils? *J Anat* 228:569–594.
- 23** Zelazny KG et al. 2021. Bilateral asymmetry and developmental plasticity of the humerus in modern humans. *Am J Phys Anthropol* 174:418–433.
- 24** Barrett BJ et al. 2018. Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *R Soc Open Sci Royal Society*. 5:181002.
- 25** Pal A, Sinha A. 2022. Beyond food for thought: tool use and manufacture by wild nonhuman primates in nonforaging contexts. *Curr Opin Behav Sci* 47:101201.
- 26** Silva FJ, Silva KM. 2021. Primate Tool Use. In: Shackelford TK, Weekes-Shackelford VA, editors. *Encycl. Evol. Psychol. Sci*. Cham: Springer International Publishing. p 6235–6241.
- 27** Marzke MW. 1997. Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102:91–110.
- 28** Neufuss J et al. 2017. Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency. *Am J Primatol* 79:e22589.
- 29** Arroyo A et al. 2016. Nut Cracking Tools Used by Captive Chimpanzees (*Pan troglodytes*) and Their Comparison with Early Stone Age Percussive Artefacts from Olduvai Gorge. *PLOS ONE Public Library of Science*. 11:e0166788.
- 30** Luncz LV et al. 2022. A primate model for the origin of flake technology. *J Hum Evol* 171:103250.

- 31** Gumert MD, Malaivijitnond S. 2012. Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *Am J Phys Anthropol* 149:447–457.
- 32** Bandini E et al. 2021. Naïve orangutans (*Pongo abelii* and *Pongo pygmaeus*) individually acquire nut-cracking using hammer tools. *Am J Primatol* 83:e23304.
- 33** 2024. IUCN Red List.
- 34** Vidal CM et al. 2022. Age of the oldest known *Homo sapiens* from eastern Africa. *Nature* Nature Publishing Group. 601:579–583.
- 35** Luncz LV et al. 2019. Cultural diversity of nut-cracking behaviour between two populations of wild chimpanzees (*Pan troglodytes verus*) in the Côte d’Ivoire. In: Boesch C, Wittig R, editors. *Chimpanzees Tai For. 40 Years Res.* Cambridge: Cambridge University Press. p 194–220.
- 36** Mongle CS et al. 2025. New fossils reveal the hand of *Paranthropus boisei*. *Nature* Nature Publishing Group. 647:944–951.
- 37** Kivell TL et al. 2011. *Australopithecus sediba* Hand Demonstrates Mosaic Evolution of Locomotor and Manipulative Abilities. *Science American Association for the Advancement of Science*. 333:1411–1417.
- 38** Skinner MM et al. 2015. Human-like hand use in *Australopithecus africanus*. *Science* 347:395–399.
- 39** Domalain M et al. 2017. Was *Australopithecus afarensis* able to make the Lomekwian stone tools? Towards a realistic biomechanical simulation of hand force capability in fossil hominins and new insights on the role of the fifth digit. *Comptes Rendus Palevol* 16:572–584.
- 40** Galletta L et al. 2019. Three-dimensional geometric morphometric analysis of the first metacarpal distal articular surface in humans, great apes and fossil hominins. *J Hum Evol* 132:119–136.
- 41** Karakostis FA, Hotz G. 2022. Reflections of manual labor in the hand entheses of early industrial women workers with extensively documented life histories. *Am J Biol Anthropol* 2022:1–15.
- 42** Bucchi A et al. 2020. Finite element analysis of the proximal phalanx of the thumb in Hominoidea during simulated stone tool use. *Comptes Rendus Palevol* 19:16.
- 43** Karakostis FA et al. 2021. Biomechanics of the human thumb and the evolution of dexterity. *Curr Biol* 31:1317-1325.e8.
- 44** Dare SS et al. 2019. Evaluation of Bilateral Asymmetry in the Humerus of Human Skeletal Specimen. *BioMed Res Int* 2019:3194912.
- 45** Deschênes V, Drapeau MSM. 2025. A New Method for Whole Bone Analysis of Bilateral Asymmetry. *Am J Biol Anthropol* 186:e70004.

- 46** Sarringhaus LA et al. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). *Am J Phys Anthropol* 128:840–845.
- 47** Reeves NM et al. 2016. Fluctuating and directional asymmetry in the long bones of captive cotton-top tamarins (*Saguinus oedipus*). *Am J Phys Anthropol* 160:41–51.
- 48** Tsegai ZJ et al. 2013. Trabecular Bone Structure Correlates with Hand Posture and Use in Hominoids. Bondioli L, editor. *PLoS ONE* 8:e78781.
- 49** Reina N et al. 2017. Laterality and grip strength influence hand bone micro-architecture in modern humans, an HRpQCT study. *J Anat* 230:796–804.
- 50** Proffitt T et al. 2021. Three-dimensional surface morphometry differentiates behaviour on primate percussive stone tools. *J R Soc Interface* 18:20210576.
- 51** Goren-Inbar N et al. 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya‘aqov, Israel. *Proc Natl Acad Sci Proceedings of the National Academy of Sciences*. 99:2455–2460.
- 52** Luncz LV et al. 2024. Tool skill impacts the archaeological evidence across technological primates. *Sci Rep Nature Publishing Group*. 14:16556.
- 53** Berdugo S et al. 2024. Reliable long-term individual variation in wild chimpanzee technological efficiency. *Nat Hum Behav Nature Publishing Group*. :1–9.
- 54** Howard-Spink E et al. 2025. Old age variably impacts chimpanzee engagement and efficiency in stone tool use. *eLife eLife Sciences Publications Limited*. 14.
- 55** Toth N et al. 1993. Pan the Tool-Maker: Investigations into the Stone Tool-Making and Tool-Using Capabilities of a Bonobo (*Pan paniscus*). *J Archaeol Sci* 20:81–91.
- 56** Pal A et al. 2018. Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). *Primates Springer Japan*. 59:173–183.
- 57** Falótico T et al. 2017. Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *Am J Primatol* 79:e22629.
- 58** Tan A et al. 2015. There Is More than One Way to Crack an Oyster: Identifying Variation in Burmese Long-Tailed Macaque (*Macaca fascicularis aurea*) Stone-Tool Use. Petraglia MD, editor. *PLOS ONE* 10:e0124733.
- 59** Luncz LV et al. 2017. Technological Response of Wild Macaques (*Macaca fascicularis*) to Anthropogenic Change. *Int J Primatol* 38:872–880.
- 60** Proffitt T et al. 2018. Analysis of wild macaque stone tools used to crack oil palm nuts. *R Soc Open Sci Royal Society*. 5:171904.
- 61** Haslam M et al. 2016. Stone tool transport by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *J Archaeol Sci Rep* 7:408–413.
- 62** Proffitt T et al. 2023. Wild macaques challenge the origin of intentional tool production. *Sci Adv* 9:eade8159.

- 63** de Andrade AC, de Sousa AB. 2018. Hand preferences and differences in extractive foraging in seven capuchin monkey species. *Am J Primatol* 80:e22901.
- 64** de A. Moura AC, Lee PC. 2004. Capuchin Stone Tool Use in Caatinga Dry Forest. *Science American Association for the Advancement of Science*. 306:1909–1909.
- 65** Falótico T et al. 2022. Stone tools differences across three capuchin monkey populations: food's physical properties, ecology, and culture. *Sci Rep Nature Publishing Group*. 12:1–14.
- 66** Proffitt T et al. 2016. Wild monkeys flake stone tools. *Nature Nature Publishing Group*. 539:85–88.
- 67** Falótico T, Ottoni EB. 2016. The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behaviour Brill*. 153:421–442.
- 68** Mainette RD et al. 2025. Characterization of Stone Tool Use in Wild Groups of Critically Endangered Yellow-Breasted Capuchin Monkeys (*Sapajus xanthosternos*). *Am J Biol Anthropol* 186:e70002.
- 69** Lima GCB et al. 2024. A new addition to the toolbox: stone tool use in blonde capuchin monkeys (*Sapajus flavius*). *Primates Springer Nature Singapore*. 65:383–389.
- 70** Westergaard GC, Suomi SJ. 1997. Capuchin monkey (*Cebus apella*) grips for the use of stone tools. *Am J Phys Anthropol* 103:131–135.
- 71** Izawa K, Mizuno A. 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates* 18:773–792.
- 72** Ottoni EB, Mannu M. 2001. Semifree-ranging Tufted Capuchins (*Cebus apella*) Spontaneously Use Tools to Crack Open Nuts. *Int J Primatol* 22:347–358.
- 73** Steinberg DL et al. 2022. A robust tool kit: First report of tool use in captive crested capuchin monkeys (*Sapajus robustus*). *Am J Primatol* 84:e23428.
- 74** Goldsborough Z et al. 2023. Coupling of coastal activity with tidal cycles is stronger in tool-using capuchins (*Cebus capucinus imitator*). *R Soc Open Sci* 10:230355.
- 75** Araujo P et al. 2022. First record of tool use by a wild population of *Cebus albifrons* (Humboldt, 1812) (Primates, Cebidae) in Puerto Misahuallí, Napo, Ecuador. *Boletin Tec Bull* 15:59.
- 76** Rolian C, Carvalho S. 2017. Tool Use and Manufacture in the Last Common Ancestor of Pan and Homo. In: Muller MN et al., editors. *Chimpanzees Hum. Evol.* Harvard University Press. p 602–644.
- 77** Whiten A et al. 1999. Cultures in chimpanzees. *Nature Nature Publishing Group*. 399:682–685.
- 78** Ohashi G. 2015. Pestle-pounding and nut-cracking by wild chimpanzees at Kpala, Liberia. *Primates J Primatol* 56:113–117.

- 79** Matsuzawa T. 2011. Stone Tools for Nut-Cracking. Chimpanzees Bossou Nimba. Tokyo: Springer Japan. p 73–84.
- 80** Boesch C, Boesch H. 2000. Tool-use in Wild Chimpanzees. Chimpanzees Taï For. Oxford University Press. p 191–224.
- 81** Carvalho S et al. 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J Hum Evol* 55:148–163.
- 82** Furuichi T et al. 2015. Why do wild bonobos not use tools like chimpanzees do? *Behaviour Brill*. 152:425–460.
- 83** Koops K et al. 2015. Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Sci Rep Nature Publishing Group*. 5:11356.
- 84** Samuni L et al. 2022. Tool use behavior in three wild bonobo communities at Kokolopori. *Am J Primatol* 84:e23342.
- 85** Gruber T, Clay Z. 2016. A Comparison Between Bonobos and Chimpanzees: A Review and Update. *Evol Anthropol Issues News Rev* 25:239–252.
- 86** Marchant LF, McGrew WC. 2013. Handedness is more than laterality: lessons from chimpanzees: Handedness is not laterality. *Ann N Y Acad Sci* 1288:1–8.
- 87** Lonsdorf EV, Hopkins WD. 2005. Wild chimpanzees show population-level handedness for tool use. *Proc Natl Acad Sci Proceedings of the National Academy of Sciences*. 102:12634–12638.
- 88** Caspar KR et al. 2022. The evolution and biological correlates of hand preferences in anthropoid primates. Tung J et al., editors. *eLife eLife Sciences Publications, Ltd*. 11:e77875.
- 89** Davidson I, McGrew WC. 2005. Stone Tools and the Uniqueness of Human Culture. *J R Anthropol Inst* 11:793–817.
- 90** Bril B et al. 2015. How similar are nut-cracking and stone-flaking? A functional approach to percussive technology. *Philos Trans R Soc B Biol Sci* 370:20140355.
- 91** DeMars LJD et al. 2023. Bone biology and microscopic changes in response to behaviour. *Behav. Our Bones*. Elsevier. p 7–38.
- 92** Hong AR, Kim SW. 2018. Effects of Resistance Exercise on Bone Health. *Endocrinol Metab* 33:435–444.
- 93** Sada K et al. 2020. Bone Mineral Density and Microstructure of the Elbow in Baseball Pitchers: An Analysis by Second-Generation HR-pQCT. *J Clin Densitom Off J Int Soc Clin Densitom* 23:322–328.
- 94** Kivell TL et al. 2011. Methodological considerations for analyzing trabecular architecture: an example from the primate hand: Quantifying trabecular architecture in primate hands. *J Anat* 218:209–225.

- 95** Steele J. 2000. Handedness in past human populations: Skeletal markers. *Laterality* Routledge. 5:193–220.
- 96** Trinkaus E et al. 1994. Postcranial robusticity in Homo. II: Humeral bilateral asymmetry and bone plasticity. *Am J Phys Anthropol* 93:1–34.
- 97** Hedrick BP et al. 2018. The effects of skeletal asymmetry on interpreting biologic variation and taphonomy in the fossil record. *Paleobiology* The Paleontological Society. 45:154–166.
- 98** Luncz LV et al. 2016. Wild capuchin monkeys adjust stone tools according to changing nut properties. *Sci Rep* Nature Publishing Group. 6:33089.
- 99** Mercader J et al. 2007. 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *Proc Natl Acad Sci Proceedings of the National Academy of Sciences*. 104:3043–3048.
- 100** Proffitt T et al. 2024. The archaeological visibility of chimpanzee (*Pan troglodytes*) nut-cracking. *J Hum Evol* 195:103582.
- 101** Biro D et al. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223.
- 102** Koops K et al. 2022. Field experiments find no evidence that chimpanzee nut cracking can be independently innovated. *Nat Hum Behav* 6:487–494.
- 103** Zeininger A et al. 2011. Metacarpal head biomechanics: A comparative backscattered electron image analysis of trabecular bone mineral density in *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens*. *J Hum Evol* 60:703–710.
- 104** Matsuzawa T. 2018. Chimpanzee Velu: the wild chimpanzee who passed away at the estimated age of 58. *Primates* 59:107–111.
- 105** Alméjija S et al. 2024. Primate Phenotypes: A Multi-Institution Collection of 3D Morphological Data Housed in MorphoSource. *Sci Data* Nature Publishing Group. 11:1391.
- 106** Lowenstine LJ et al. 2016. Comparative Pathology of Aging Great Apes: Bonobos, Chimpanzees, Gorillas, and Orangutans. *Vet Pathol* SAGE Publications Inc. 53:250–276.
- 107** Wood BM et al. 2023. Demographic and hormonal evidence for menopause in wild chimpanzees. *Science* American Association for the Advancement of Science. 382:eadd5473.
- 108** Püschel TA et al. 2018. Inferring locomotor behaviours in Miocene New World monkeys using finite element analysis, geometric morphometrics and machine-learning classification techniques applied to talar morphology. *J R Soc Interface* Royal Society. 15:20180520.
- 109** Kuhn M, Johnson K. 2013. Measuring Performance in Classification Models. In: Kuhn M, Johnson K, editors. *Appl. Predict. Model*. New York, NY: Springer. p 247–273.
- 110** Nunn CL, Barton RA. 2001. Comparative methods for studying primate adaptation and allometry. *Evol Anthropol Issues News Rev* 10:81–98.

