

Biomechanics in anthropology

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Abstract

Biomechanics is the set of tools that explain organismal movement and mechanical behavior and links the organism to the physicality of the world. As such, biomechanics can relate behaviors and culture to the physicality of the organism. Scale is critical to biomechanical analyses, as the constitutive equations that matter differ depending on the scale of the question. Within anthropology, biomechanics has had a wide range of applications, from understanding how we and other primates evolved to understanding the effects of technologies, such as the atlatl, and the relationship between identity, society, culture, and medical interventions, such as prosthetics. Like any other model, there is great utility in biomechanical models, but models should be used primarily for hypothesis testing and not data generation except in the rare case where models can be robustly validated. The application of biomechanics within anthropology has been extensive, and holds great potential for the future.

KEYWORDS

anthroengineering, biomechanics, evolution, evolutionary anthropology, evolutionary biomechanics, four-field anthropology, four-field approach

1 | INTRODUCTION

Anthropology documents humanity: how we are similar, different, and have changed over time. It also asks why these similarities and differences exist and explores the processes that have contributed to our evolution. In doing so, it draws on methods and techniques from an array of other areas, including engineering.

The application of engineering to anthropology—or “anthroengineering”¹—is potentially very wide. For example, from a social anthropological perspective Abram² draws on her engineering training to examine the role of electricity in “connecting and disconnecting” individuals, places, and objects. Within evolutionary anthropology, tools from engineering, such as finite elements analysis, are rapidly becoming mainstream in biomechanical studies of morphology.³ Anthroengineering also has great promise in providing insights into topics as varied as spear throwing in the

Paleolithic^{4,5} and prosthetic limb design, manufacture, procurement, and repair.^{6–8} Some of these topics consider ultimate or evolutionary questions while others take a more proximate perspective. It is important to think about the proximate alongside the ultimate, as a major strength of biological anthropology is the integration of perspectives and evidence from multiple sources across multiple scales, considering ecology and behavior of modern populations alongside fossils and data from comparator groups such as non-human primates.

The four-field model of anthropology includes archaeology and linguistics as well as biological and sociocultural anthropology, and we take that broad definition here, although our examples are drawn mainly from biological and evolutionary anthropology and mechanical engineering. Given its prominence in these fields, we focus on biomechanics, but also draw on other aspects of anthroengineering as appropriate.

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1.1 | Phenotypic variation

Biological anthropologists often aim to explain why a phenotype or pattern of phenotypes exist. When sample(s) cover a short period or concern questions of microevolution, the role of behaviour, environment, and genetics in producing the observed phenotype is of primary concern.^{9–11} When sample(s) cover a long period or concern questions of macroevolution, the role of historical (i.e., phylogenetic), functional (e.g., adaptive), and structural (e.g., physical, exaptive) constraints are generally the focus (i.e., Gould's "aptive triangle," Figure 1).¹² In both cases, biomechanics can relate phenotypic diversity to underlying mechanisms and constraints. In other words, biomechanics can provide explanation about mechanism by identifying how behavioral, environmental, genetic, functional, and/or structural parameters relate to phenotypic diversity. Without biomechanical data to create the link between mechanisms and constraints, all we have is an untested hypothesis.

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1.2 | Objects and people

Investigation of the phenotype can also help inform questions of direct interest to archaeology, sociocultural, and linguistic anthropology. The ability to create artifacts and material culture—such as lithics, pottery, monuments, and homes—and language is biomechanically mediated. From a proximate perspective, investigating the biomechanical interactions between objects and people can give us clues about design constraints for particular artifacts and elements of material culture, or allow us to infer how such items might have been manipulated given phenotypic limitations. The atlatl, or spear throwing lever, would have

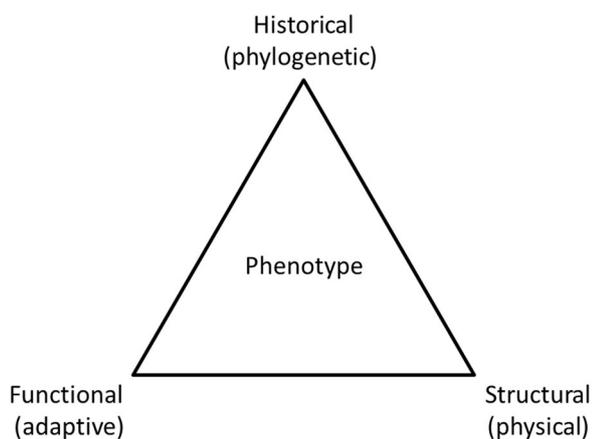


FIGURE 1 Gould's 'aptive triangle, depicting how observed phenotypes are a constrained by an organisms history, the structural/physicality of the world, and functional constraints, such as natural selection.

been designed with knowledge of the biomechanics (power and velocity of throw) of the human arm as well as the mechanics of the projectile being used.¹³ From an anthroengineering perspective, the form of the Schöningen spears can be explained through a rudimentary knowledge of mechanics—longer spears need a thicker cross-sectional area to prevent buckling under higher throwing forces.¹⁴ Additionally, the use of fire to treat many early spear tips can be explained by materials science, as this treatment made the spear tips harder, but potentially more brittle and easy to fracture.^{15,16} The anthropological aspect of these engineering problems relates to how the spear makers discovered these principles, presumably by observing successes and failures and iteratively refining designs, providing information about cognitive capabilities and cumulative culture.

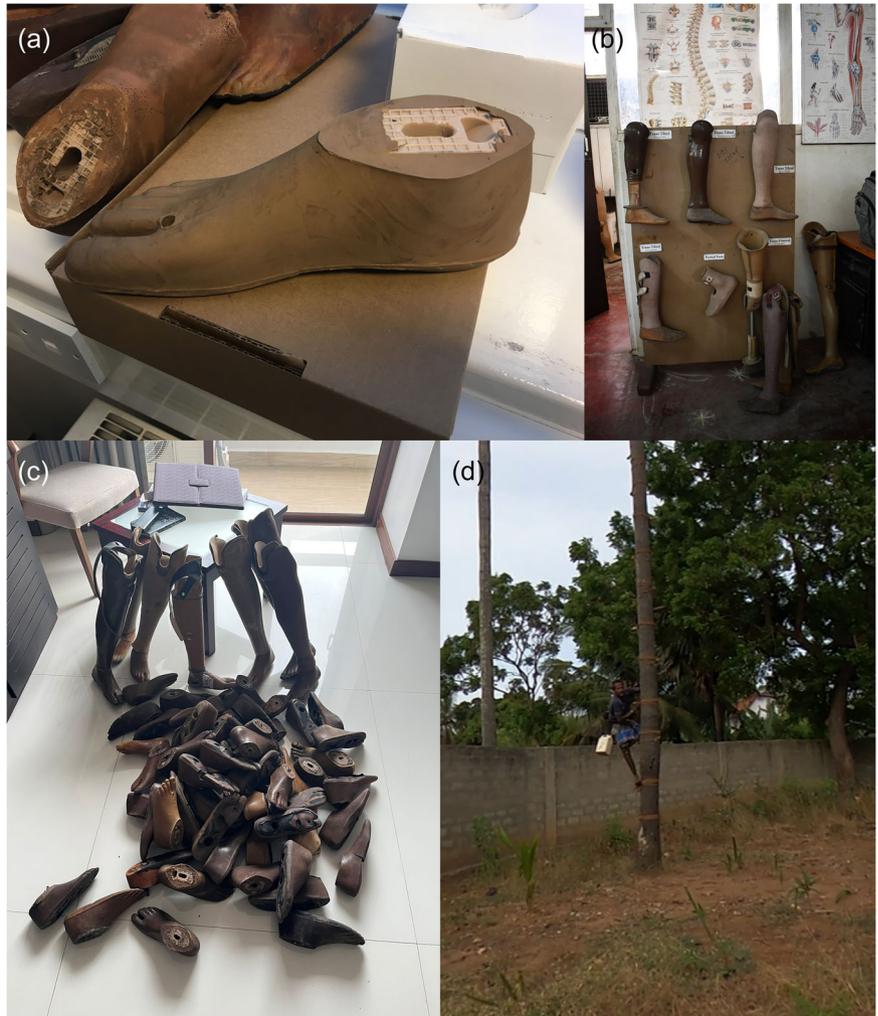
Biomechanics and anthroengineering principles can also tell us about the performance limitations of past populations and how these may have been overcome in certain circumstances using material culture. The standing stones at Stonehenge or building blocks of the great pyramids of Giza would have been much too large and heavy to be transported and raised by humans without mechanical aid, and that appreciation allows the formulation of hypotheses about the form that aid took, testing them with evidence from the archaeological record. This brings a wider aspect of anthroengineering into play: what mechanical challenges would have been solved and with what tools? At Stonehenge, the site constraints indicate that the large three-piece stones could not be raised by ropes, and extrapolation from ethnographic data from Rapa Nui suggests that they were more likely to have been raised by teams of people using levers and timbers to support and lift the structures.¹⁷ In Giza, the environmental constraints limit the resources that could have been used to move and lift the great 2 ton stones, and it has been suggested that an immense amount of person-power (~174 people) would have been needed to move the stones, which interestingly matches the 172 haulers depicted in the wall painting in the tomb of Djehuty-hotep.¹⁸

1.3 | Public health and prosthetics

Anthropology has much to say about public health challenges. Prosthetic design is an overlooked topic in anthropology yet provides an excellent proximate example of how biomechanical and anthropological knowledge could be applied to improve public health outcomes. The Global Burden of Disease 2019 estimated there were 176 million amputees, worldwide.¹⁹ Prosthetics are used to replace amputated body parts, both in terms of looks (cosmesis) and function. The oldest known example is a prosthetic big toe found on the body of a mummified noblewoman (950 BC, Egypt).²⁰ As big toes play an important role in balance while standing and walking, this wood and leather toe likely had both cosmetic and functional purposes. The presence of prosthetics in past populations reveals information not only about culture, health systems, and the importance of cosmetic appearance, but also technologies, the ability to manipulate raw materials, and the ability to view the body as a mechanical system.

The Egyptian big toe, like many prosthetics used across the world today (Figure 2), was a passive device, lacking internal mechanisms for

FIGURE 2 Passive prosthetic devices used in northern Sri Lanka, today. (a) the JJCDR foot, modeled after the ICRC prosthetic foot, (b) range of lower-limb prosthetics available at the JJCDR, modeled after the ICRC prosthetic designs, (c) broken transtibial (back) prosthetics and prosthetic feet (front) manufactured at the JJCDR, (d) a transtibial amputee, using his transtibial lower-limb prosthetic to climb a palm tree to collect sap. These “toddy-tappers” use the sap to make products such as wine and ice cream. ICRC, International Committee of the Red Cross; JJCDR, Jaffna Jaipur Centre for Disability Rehabilitation.



generating force, such as an electric actuator or body-powered cable. Instead, force is applied externally, and the prosthetic reacts to this force by deforming, storing energy which is then later released. A modern example of this is the carbon fiber running blade, which is designed to store and return energy when running, reducing the energetic cost of locomotion. Advances in materials science have improved passive device design, and the ability to store and return energy more efficiently. Many of the prosthetic devices supplied to and used in low- or middle-income countries are passive and were designed by charities like the International Committee of the Red Cross (ICRC). These devices are easy to manufacture, produce, and maintain at a large scale. While the ICRC devices take some aspects of biological variation, like skin color and foot size, into account, they lack cultural specificity. For example, Hindu women in northern Sri Lanka wear toes rings on their third toe to signify marriage, but the fused second to fifth toes on the ICRC prosthetics prevent the wearing of these rings. Simply cutting the prosthetic toes compromises the structural integrity of the foot, and risks loss of the toe and ring.

Some ICRC devices, like the upper-limb mechanical claw, are active devices, using cables and pulleys to enable the prosthetic to function. In hot, humid climates, operating such devices can be problematic, as the metal components are prone to rust and seize. Active prosthetics, where

devices have motors and actuators in them to help them move, are common in high-income countries, like the United States and United Kingdom. Even more sophisticated bionic limbs establish an interface between the body and the electronic device, providing motor control to the prosthesis and sensitive feedback to the user. The three main categories of bionic limbs—nerve-transferred muscle interfacing (targeted muscular reinnervation), direct muscle interfacing, and direct nerve interfacing—create this interface in different manners, some of which are invasive, requiring intramuscular implants or an implantable peripheral neural interface to talk or interface directly with the nerves in the residual limb.²¹ The newest type of prosthetic devices, which are still being researched and developed, involve osseointegration, where a metal rod is inserted into the residual limb and sticks out of the skin. The prosthetic then attaches to this rod, creating a direct connection between the prosthetic and bone. There are some obvious issues with this technology that need investigation, including how to best handle bone breaks in the residual limbs. Whether the device is active, passive, or bionic, internal or external, designing culturally, ecologically, and biologically appropriate and sustainable prosthetics, in which the relationship between these factors, technology, and behaviour are understood deeply, would benefit enormously from a transdisciplinary anthropology and engineering perspective, improving design and thus quality of life.

1.4 | Tool form and phenotype

From an ultimate perspective, knowledge of tool form and human phenotype can be used to make inferences about selective pressures. For example, it appears that a strong selective pressure on human hand morphology was the use of hammerstones to produce flakes and extract marrow, because of the large load on the hand. The skill of the practitioner also has an influence on the load exerted.²² Many behavioral and cultural practices are dictated and shaped by not only the interaction between humans and the physically mediated forces of the world, but also the biomechanics and performance of the organisms with which we interact. Cracking bones to extract marrow is a case in point. Another is the endurance running hypothesis, in which Bramble and Lieberman¹⁹ argue that the human ability for endurance running is at least as good as that of cursorial animals (some of which may have been prey), and that endurance running may have been an influential factor in the evolution of morphological traits in *Homo*. Marrow extraction and endurance running relate to food procurement, and indeed the ways in which we produce and extra-orally process our foods are biomechanically mediated by either human biology or the biology of the organisms being consumed.

Within our bodies, food breakdown is a set of biomechanical processes at different scales (e.g., chewing, digestion, production of adenosine triphosphate). At the macro-scale, our muscles move our mandibles which in turn bring out teeth into occlusion. The teeth then transfer forces and energy to the food, breaking it into smaller pieces and increasing its surface area to volume ratio. Fluid dynamics then takes over as the base of the tongue retracts and the food bolus is driven across the oropharynx towards the esophagus where it is moved into the stomach and digestive system.²³ Chemical reactions and the gut microbiome work to physically break the food into smaller pieces, where nutrients are absorbed by the body through diffusive and transport mechanisms. Nutrients can be used as is, stored, or have energy added to them to create new compounds through nanolevel biomechanical processes.

1.5 | Language

Speech and language are cardinal human traits. Speech occurs when the diaphragm relaxes, increasing air pressure in the lungs. The pressure differential between the lungs and the atmosphere pushes air up the trachea and through the larynx, causing the vocal cords to vibrate and create sound. Muscular forces cause the vocal cords, soft palate, tongue, and lips to change shape and size, shaping the sound. Applying muscular forces at differential velocities and accelerations, within the capabilities and biological limits of the soft tissue, creates speech. The expanded thoracic vertebral canal in modern humans and Neanderthals is probably correlated with innervation that allows fine breath control via the intercostal and abdominal muscles, facilitating linguistically essential sounds.²⁴ Just as important as sound production is

sound capture. Sound is initially captured by the pina (outer ear), which directs the sound down the ear canal to the tympanic membrane. The sound waves cause the tympanic membrane to vibrate, vibrating the bones in the middle ear. The vibrating bone causes the fluid in the cochlea (inner ear) to move. Hair cells within the cochlea move and convert the motion into electrical signal that is sent to the brain. The relationship between vibrations and motion in the ear are controlled by the laws of physics. Biomechanics can not only help explain why certain tones, pitches, sounds, and word frequencies are used, but also why others are avoided. As many biological systems prefer to move at their natural frequencies, biomechanics can also help explain why different speech patterns are preferred at different times (e.g., a soothing voice).

The examples above demonstrate the value of interdisciplinary work involving anthropological and biomechanical perspectives, whether they be from the proximate perspective of prosthetic limb design or understanding selective pressures during human evolution. Biomechanics is taught only patchily in anthropology programs, so one important step in increasing interdisciplinary interaction is to increase understanding of basic biomechanical principles among anthropologists. In this review, we provide an overview of the basic principles of biomechanics, considering among other things, data, models, standards, and scales. We then suggest ways in which comparative evolutionary models can be integrated into biomechanical studies.

2 | WHAT IS BIOMECHANICS?

Biomechanics is the set of tools that explain organismal movement and mechanical behavior.²⁵ Every movement in the universe, from atomic attraction to cosmic repulsion, is mediated by forces pulling matter together or pushing matter apart. Because biomechanics relates biology to the physically mediated forces of the world, biomechanics can help explain nearly every biological, and thereby anthropological, phenomena, from how muscular contractions affect bone shape and how changes in gene expression occur to why adults can stand on 2 feet, but babies cannot.

Data suitable for biomechanical analysis can be gathered experimentally—on material culture or live or dead (parts of) organisms for example—or through computer simulations (Figure 3). Data gained from experiments using living organisms/material are termed *in situ* (original place), *in vivo* (whole organism), or *in vitro* (outside the body, in a test tube for example), depending on how the experiment is conducted. Data gained from experiments on dead organisms/material is termed *ex vivo*. Experimental data can be collected directly, or it can be calculated (e.g., on a computer, or *in silico*). Direct measurements are often preferred, but this is not always possible due to physical/size constraints, ethical considerations, and/or because the biomechanical metric of interest cannot be measured (e.g., stress). Biomechanical data are often discussed as continuous, but can be discrete (e.g., number of steps), nominal (e.g.,

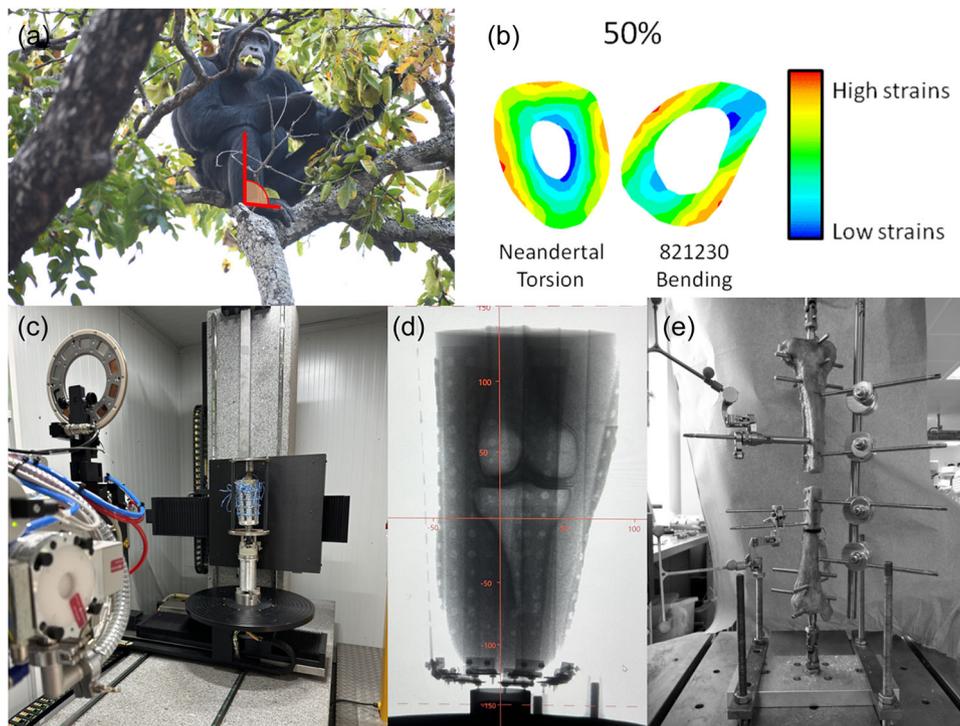


FIGURE 3 Examples of different types of biomechanical data. (a) In vivo, in situ biomechanical data showing the ankle angle of a chimpanzee sitting in a tree, consuming mkulungu (*Pterocarpus tinctorius*) seeds, (b) von Mises strain plot at the 50% cross-section of in silico, finite elements analysis models of a Neandertal and modern human humerus, loaded with forces to mimic spear throwing,⁴ (c, d) in exemplum (stand-ins for biological materials, such as fake bones or flesh) biomechanical experiment investigating interfragmentary motion of a residual limb replica (from a transtibial amputee),²⁶ imaged in Diondo d5 system at the national X-ray computed tomography facility. (e) Ex vivo testing of a human tibia, for preclinical testing of a newly designed external fixator, codesigned with orthopedic surgeons and technicians in Sri Lanka to account for cultural variability in medical practices, supplies, and local production skills (<https://www.imperial.ac.uk/external-fixator/>).²⁷ The locally manufacturable device entered clinical trials in Sri Lanka and was used in Ukraine at the beginning of the Russo-Ukrainian War.

running, walking, stumbling), ordinal (e.g., walk, trot, gallop), or binary (e.g., fall/not fall).

Biomechanics operates on a wide range of length scales, from nano- to kilometer. At the nanoscale, biomechanics has been used to help understand phenomena such as how changes in histone shape can provide or withhold access to certain genes, thus playing a significant role in gene expression,²⁸ and how the perfect misalignment of dental enamel crystallites between enamel prisms and the interprismatic matrix can help prevent fracture propagation.²⁹ At the microscale, biomechanics has been used to examine the effect of sickle cells on blood's rheological properties and explain why sickle cells are detrimental to health,³⁰ construct models cellular injection operations,³¹ and understand how shark scale microstructures reduces friction drag between the scales and the fluid flowing over them.³² Most readers are more familiar with biomechanical models at the centimeter, meter or kilometer scale, where biomechanics has been used to understand a wide range of phenomena, such as how orangutans can engineer safe nests with tree branches,³³ how birds like the kingfisher can efficiently dive through water,³⁴ and—the example readers are all probably most familiar with—how we, as humans, can run and walk effectively while standing upright on 2 feet.^{35–37}

It is well-known in biological and evolutionary anthropology that scale matters.^{38–41} Considering scale in biomechanical studies is

important because the “non-macro” levels are often disregarded, yet depending on the scale, different forces are differentially influential (Box 1). At the macro scale, inertial forces due to mass and acceleration dominate when traveling through air. As scale decreases, inertial forces diminish relative to the viscous forces generated by the biological structure traveling through a viscous fluid (e.g., water, cytoplasm, air) become increasingly important. Eventually, viscous forces similarly become unimportant and atomic forces dominate.

Conceptually, viscosity can be thought of as the resistance of a liquid when it is forced to flow over a surface. Viscous liquids flow slowly, while nonviscous liquids flow fast, and the magnitude of viscous forces can be estimated using Stokes' law. It is possible to use the dimensionless Reynolds number to determine when inertial (or indeed, viscous) forces are important, as it describes the ratio of inertial to viscous forces.⁴³ High Reynolds numbers indicate that inertial forces are relatively important (turbulence), and viscous forces can be ignored, while the opposite is true for low Reynolds numbers.

We live in a physical world which adheres to the laws of physics. Organisms, like inanimate objects, must operate within these constraints: humans and other primates are no exception. The laws of physics are scientific generalizations based on empirical observations of the physical behavior of objects and/or materials when

BOX 1 Common definitions for biomechanical phenomena

Particle model	Mechanical models where all boundary conditions are acting on a single, finite point.
Rigid body model	Mechanical models where boundary conditions are acting on a geometry, but the geometry cannot deform.
Flexural model	Mechanical models where boundary conditions are acting on a geometry, and the geometry can deform.
Biology	The study of living organisms.
Mechanics	The branch of applied mathematics dealing with motion and forces producing motion.
Biomechanics	1) The study of how physical forces interact with living systems. 2) The set of tools that explain organismal movement and mechanical behavior.
Newton's laws of motion	A set of laws which describe the motion of objects subjected to inertial forces.
Stoke's law	A law which describes the motion of a spherical object moving through a viscous fluid.
Boyle's law	A law which states the volume and pressure of a gas are inversely related.
Kepler's laws	A set of laws which describe the motion of planets around a single star.
Mechanical property ^a	Characteristics of a material that describe how it behaves under a load.
Geometry	The shape, size, and arrangements of parts of an object.
Boundary condition	An input to a set of differential conditions. For the conditions to be solved, they must be satisfied at all or part of the boundary of a region. Examples in biomechanics are force, displacement, and velocity.
Constraint	A boundary condition which describes the effects of forces.
Concentrated force	A force acting on a singular, exact point in space.
Distributed force	A force acting over a surface and not just on a singular point.

Constitutive equations	Relationship between two or more physical quantities that approximates the response of the object to stimuli.
First principles	A basic proposition or assumption that is in its most reduced form, and cannot be deduced by any other proposition or function.
Homogeneous ^a	Mechanical properties that are uniform throughout a material.
Heterogeneous ^a	Mechanical properties that change throughout a material.
Isotropic ^a	Mechanical properties that are directionally independent, having equivalent magnitudes in every direction.
Transversely isotropic ^a	Mechanical properties that are isotropic in a plane and nonisotropic along an axis running orthogonal to that plane.
Orthotropic ^a	Mechanical properties that are directionally dependent and defined by three orthogonal axes.
Anisotropic ^a	Mechanical properties that are directionally dependent along random axes.
Tensile load ^a	A load which pulls atoms apart from one another, causing their atomic bonds to lengthen.
Compressive load ^a	A load which pushes atoms closer to one another, causing their atomic bonds to shorten.
Shear load ^a	A load which causes atoms to slide past one another.
Bending load ^a	A load which causes a flat or slightly curved surface to become significantly curved.
Linear relationship ^a	A relationship where one variable can be described in terms of another variable times a constant (the slope), plus another constant (the intercept).
Nonlinear relationship ^a	A relationship where one variable cannot be described in terms of another variable times a constant (the slope), plus another constant (the intercept). Examples include quadratic, cubic, and exponential relationships.
Viscoelasticity ^a	A form of deformation which exhibits elastic and viscous characteristics.
Bulk properties	Mechanical properties that arise from one or more substance bonded together to form a solid.

Resolution	The level of detail in an image or scan.
Precision	How close two or more measurements are to each other.
Accuracy	How close a measurement is to a given value, being treated as the ground truth. This value could be a standard.
Phylogenetic comparative methods	A set of statistical methods which use information about the phylogenetic relatedness of species to test hypotheses.
Optical tweezers	Instruments which use lasers to trap, hold, and move (sub)-microscopic particles.
Atomic force microscopy	Also known as scanning force microscopy, a high-resolution type of scanning probe (tactile) microscopy with nanometer resolution.

^aDefinitions taken verbatim from Berthume (2016).⁴²

subjected to loads, displacement, and/or energy during scientific experimentation. After years of repeated experiments have yielded consistent conclusions, these generalizations become universally accepted within the scientific community, at which point they become laws. Some of these laws may be familiar, such as Newton's laws of motion, while others, which are arguably equally important in anthropology, such as Stoke's or Boyle's laws, may be less familiar because their use in evolutionary anthropology is limited (Box 2).

We live in a physical world which adheres to the laws of physics. Organisms, like inanimate objects, must operate within these constraints: humans and other primates are no exception.

Not all laws are relevant to all research questions, and their relevance depends on the desired performance metric and length scale of the question. For example, Kepler's laws, which describe planetary motion, are relevant when describing motion at the Giga- but not the microscale (the Earth is 149.6 Gm from the sun), and Stoke's law, which describe the motion of a spherical object through a viscous fluid, is relevant for an object moving through a fluid, like air or water, but not a vacuum. In the field of biomechanics, these laws become the first principles and constitutive equations that govern how organisms mechanically respond to an applied force or displacement.

2.1 | Biomechanical models

2.1.1 | Types of biomechanical data

The role of biomechanics in anthropology is largely determined by the type of data that can be gathered.^{59,10,36,45–47} Biomechanical data can be gathered experimentally—on live or dead (parts of) organisms—or through

computer simulations (Figure 3). Data gained from experiments on living organisms/material are termed *in situ*, *in vivo*, or *in vitro*, depending on how the experiment is conducted, while data gained from experiments on dead organisms/material is termed *ex vivo*. Experimental data can be gathered directly or calculated.⁴⁸ Direct measurements are often preferred, but this is not always possible due to physical/size constraints, ethical considerations, and/or because the biomechanical metric of interest cannot be measured (e.g., stress).^{3,49}

2.1.2 | Why use biomechanical models?

Anthropologists are mostly experimentalists, using data from the field or museums to address research questions and statistical, mathematical models to gain confidence in these results.³⁶ When interpreting fossil, archaeological, or ichnological data, researchers often use extant or modern analogs as models to interpret extinct or artifactual data.^{50,51} Despite confidence in non-biomechanical models, many anthropologists are skeptical about the *in silico* data gathered from biomechanical models.⁴³ This is generally because of a lack of understanding of the model and its assumptions or a lack of confidence in the modeling assumptions, validation, and/or interpretation.

Biomechanical models have many benefits, the biggest being that they enable the collection of data that are very difficult or impossible to gather experimentally. Data could be difficult to gather because the organism is difficult, dangerous, or impossible to work with or because of ethical concerns. In these situations, biomechanical models can provide information not otherwise obtainable.^{51,52} For example, it may not be possible to conduct experiments on animals which are rare and/or endangered, or organisms which can cause grievous harm if not handled or stored properly. While not all ethical concerns (e.g., the use of illegally or unethically gathered skeletal material) can be alleviated by using biomechanical models, some, such as the conduction of invasive or debilitating procedures, can be.

Biomechanical models also enable researchers to gather data that cannot be measured experimentally.⁴⁸ For example, a three-dimensional (3D) strain map on a skull during biting, the creation and analysis of extinct or hypothetical organisms such as a gracile *Australopithecus* with robust features or an intersex macaque, or scenarios that have not yet been observed in nature.^{53,54} This is done commonly in bioengineering during preclinical trials to test orthopedic products, and in anthropology could be done to predict the effect of certain interventions, for example, for conservation.⁵⁵ The construction of hypothetical or composite organisms allows individual or suites of characters to be altered, and the effect of these characters to be quantified.^{54,56,57} This can aid substantially in understanding the evolution of these characters, and whether or not biomechanics played a role in this evolution.

2.1.3 | Types of biomechanical models

There are three basic categories of biomechanical models (Box 3).⁵⁸ Particle models assume the object being studied is of negligible size

BOX 2 Scales of biomechanics**Nanobiomechanics**

DNA lies at the core of most life. In humans, proteins pack the 2+m of DNA into cell nuclei by wrapping DNA around histones to create spool-like structures which resemble beads on a string. "Strings" are connected by histone linkers to create chromatin fibers, and gene expression is highly dependent on the method of packing in the chromatin fiber. Changes in packing and packing malfunctions often lead to changes in gene expression. At this scale, inertial forces can safely be ignored, and it can be assumed viscous and atomic forces dominate.⁴³

Using lasers (optical tweezers), researchers trapped the two ends of DNA and used these "optical tweezers" and unzipped the DNA and to investigate how linker histones interacted with and bound to DNA. The interactions were dynamic, exhibiting rapid binding and dissociation which created forces and used energy. This dynamic information is crucial for determining the symmetry of the spool-like structure.²⁸ An improved understanding of linker histone–DNA dynamics is crucial for understanding and modeling the packing and unpacking of DNA. This could, in turn, help us better understand the role of environment in shaping human biology.

Cellular biomechanics

As cell size can vary dramatically, with the biggest cells being ostrich eggs (approximately 15 cm wide, 1.4 kg), inertial forces cannot always be ignored in cellular biomechanics. Depending on the size, many of the tools used for cellular biomechanics are the same as those used for nano- and macro-biomechanics. Cellular material is generally too large and heavy for methods like laser tweezers, but atomic force microscopy (AFM) is often used to address questions like:

- How is it that cells, filled with organelles floating in cytoplasm, derive their strength and rigidity from cell walls and extracellular matrices?
- How do cells adhere to the extracellular matrix and remain attached in response to external loads? How do organelles move about the cell?
- How is it that some nerve cells in the human body—with single axons that can grow up to 1 m long and have aspect ratios of 5×10^6 —do not snap or break when subjected to the relatively extreme external loads brought on by joint flexion/extension?

Within anthropology, AFM has been used to investigate the role of dietary abrasives, such as phytoliths and grit, on enamel wear.⁴⁴

Macro-biomechanics

Often, "biomechanics" is used to explicitly describe macro-level biomechanics because of historic reasons. The first known written account of biomechanics is by Aristotle in the 4th century BC, where he wrote a series of essays discussing the general principles of animal locomotion. In the following centuries, anatomists documented how bones and joints moved and hypothesized how muscles caused these movements. After World War 1, there was a large population of young amputees requiring prosthetics in the United States. As this was not a medical emergency, medical doctors took the time to work with professors in mechanical engineering to create limbs which moved and functioned like the limbs they were replacing. This marriage of macro-level anatomy, physiology, physics, and mathematics led to the first university programs in the United States to be referred to as "biomechanics" programs. Thus, biomechanics became synonymous with macro-level mechanical analyses. Macro-level biomechanics has many applications, especially in prosthetics, health, athletics, and evolution.

and shape and can be modeled as a single point in space (Table 1). Exercise trackers do this when they report on the number of steps you walk each day; they do not care how many arms or legs you have and treat your body as a single point in space. Rigid body models assume an object's shape and size are important, but shape and size do not change under loading. Flexural models assume the object's size and shape change under loading. Additionally, mixed models (Box 3) combine two or more of the aforementioned models.

Beyond typical research considerations (e.g., question, time-frame, sample size, budget), many linked factors determine biomechanical model choice and construction, including scale and constraints brought on by ethical and practical concerns surrounding the gathering of data. Often, more than one model is appropriate, which can make choosing model type and modeling assumptions challenging. It is common to identify models in the literature that have been used to answer similar questions and use the same protocol, or to use a model/method because it is new and interesting. However, biomechanical models and their construction should be driven by the research question, not by common practice or method.

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More complex models are often more time intensive and expensive, and therefore have smaller samples. Picking samples can be difficult, and often mediated by accessibility or assumed relationships between morphology and biomechanical performance.^{52,62} When picking samples, researchers should recall that, with rare

BOX 3 Types of biomechanical models**Particle**

Particle models assume an object can be modeled as a single point, with negligible geometry and mechanical properties. They assume an object's mass is acting at a single point, and that all forces, displacements, and other boundary conditions are similarly acting on this point.⁵⁸ Boundary conditions are constraints needed to solve a boundary problem. The velocity a particle is moving and the spatial limits the particle can move in are examples of boundary conditions for particle models (Figure 4). Solutions can be numerical (e.g., a scalar, vector, or matrix) or a function. An example of a vector solution would be a person's maximum velocity while foraging, while an example of a functional solution might be foraging velocity plotted against time. Boundary conditions are usually explicitly stated but some are implicitly assumed, such as ambient temperature or air pressure during foraging.

Particle models can be simple, involving a single dimension or complex involving two or more dimensions. These models are often dynamic, including time as a parameter, and consequently solutions often involve "rates of change." While many equations and calculations are done in Cartesian coordinate systems, it is sometimes useful to use other coordinate systems, such as cylindrical or spherical coordinate systems, particularly when rotational motion is being analyzed (Figure 5). Rotational motion is often of importance in locomotion, such as when modeling brachiation as a pendulum. Linear motion is measured in meters or feet, whereas rotational motion is measured in radians or degrees.

Within anthropology, boundary conditions for particle models can be gathered using equipment such as handheld GPS for humans, GPS collars for primates, and accelerometers or inertial measurement units (IMUs). IMUs measure acceleration plus rotational changes in orientation, informing on what direction an object is moving in and with what inertial force. GPS data can reveal distances organisms have traveled, velocities, accelerations, and, when combined with IMUs, orientations. Two-dimensional (2D) latitude and longitude information may be appropriate to answer research questions, but often with primate studies, the third dimension is important, not only when climbing trees/cliffs is involved, but also when climbing on mountainous landscapes.

Particle models can answer such questions as the force required for the red ruffed lemur (*Varecia rubra*), to leap between branches, the group dynamics of different groups of ring-tailed lemurs, (*Lemur catta*), with overlapping home ranges, and the behaviors of chacma baboons (*Papio ursinus*) when they are not being directly observed. Particle

models have many limitations. When handheld GPS is used, the resolution and accuracy of the data can be poor and the third dimension is often lost. There are many problems associated with GPS collar data, including anesthetization and the weight/size of the collar relative to the animal may inhibit its movements. Finally, particle models have many underlying assumptions (discussed above) which limit their utility and ability to address research questions related to biological diversity.

Rigid body

Rigid body models assume an object's geometry matters, but as the object does not change shape/size significantly under loading. Boundary conditions can be concentrated, acting as a single point (as in particle models), or distributed over a curve or surface. Solutions can be scalar but are often vector or matrix, producing sets of outputs that are spatially and/or temporally distributed. Models can also be static or quasistatic, having boundary conditions that are (essentially) independent of time, or dynamic, having boundary conditions that are dependent on time. As the geometry of an organism is being modeled, boundary conditions can also be external, originating from the external environment, or internal, originating from within the organism, itself (Figure 6).

The methods used for data collection for rigid body models often differ from those used for particle models, as the relative motion of individual body segments is often of interest. A nonexhaustive list for rigid body boundary conditions and common methods of data collection includes motion capture and IMUs for motion data, force plates, (implanted) load cells, and electromyography for force data, and pressure mats for pressure data.

Geometries can be 2D or 3D, involving measurements from the actual organism or digital representations of the organism. When data are acquired from the actual organism, for example, using a set of calipers, measuring tape, osteometric board, or microscribe to take measurements off cadavers or museum collections, geometry must be reconstructed using mathematical equations and/or computer-aided design to create a visual representation. Digital representations such as photographs, surface scans, and those derived from magnetic resonance imaging, (micro)computed tomography scanning, and ultrasound can be processed to directly create a geometric representation of the organism. Internal geometry (e.g., trabecular bone, enamel microstructure) generally does not matter for rigid body models, but some internal geometries (e.g., bones inside a living human) are important for modeling. The line between geometry acquisition and creation is often blurred when geometries are captured digitally and processed later.

Rigid body models have a large variety of applications, the most common being to address musculoskeletal questions, where it is assumed bone deformation is minimal compared to the motion to be considered in the analysis, such as during gait or mastication. When combined with evolutionary theory, these models can address evolutionary biomechanical questions, such as the energetics of bipedality.³⁵ While less common in anthropology, rigid bodies have extensive applications when considering the movement of a body through a fluid, such as when walking or swimming through water. They can also be used to test structural devices meant to interact with an organism's body before they are used in the field, as is done in medicine for preclinical trials of orthopedic devices.

The limitations of rigid body models can vary widely depending on the size and complexity of the models. Larger, more complex models can sometimes take months to construct and years to validate, and many more models remain unvalidated or validated for purposes other than the ones they are currently being used. Validation can become increasingly difficult, as it is not always possible to gather the desired (resolution of) experimental data for model validation. Because models can represent large investments of time, they often do not consider biological variation in a meaningful manner, instead creating "average" models. This can be problematic, as average inputs often do not yield average biomechanical outputs (i.e., the Generic Modeling Fallacy⁵⁹), particularly when nonlinear constitutive equations are being used (as is the case with modeling muscles). Reproducibility can be difficult as researchers may make different modeling assumptions when gathering or processing boundary condition or geometry data. Finally, these models lack the ability to answer classes of questions related to how certain biomechanical forces may affect an organism, as they assume the shape and size of the organism will remain constant under loading.

Flexural

Flexural models assume an object's geometry matters, and its shape/size change significantly under loading. Solutions are almost exclusively vector or matrix. As with rigid body models, boundary conditions can be concentrated or distributed, static, quasistatic, or dynamic, and external or internal. Data collection for boundary conditions and geometry is similar as with rigid body models, except internal geometry matters more for flexural models as the body is deforming, meaning internal structural support (or lack thereof) can have a significant effect on the solutions.

Mechanical properties are characteristics of a material that describe how it behaves under a load. They can vary with location throughout a material (homogeneous vs. heterogeneous), with direction (isotropic vs. transversely isotropic vs. orthotropic vs. anisotropic), and with load

(tension vs. compression vs. shear vs. bending). Mechanical properties can also be linearly or nonlinearly correlated with displacement, and independent of or dependent on time (e.g., viscoelastic). Finally, mechanical properties can dictate changes in shape and/or size in response to an applied load which are permanent (plastic) or reversible (elastic), meaning the object will rebound to its original shape/size when the load is removed.

Because loads applied are often reversible and of difficulty in obtaining spatial, directional, time-dependent resolution in mechanical properties, materials like bone are often modeled as linearly elastic, homogeneous, and isotropic when it is actually nonlinear, heterogeneous and orthotropic/anisotropic. To build an accurate mechanical property model of bone would require a highly accurate distribution of bone type, composition, age, and hydroxyapatite crystal organization. As this information is impossible to obtain in the timeframe of flexural body model construction, validation, and interpretation and would be needed for each bone being modeled, researchers use "bulk" properties, measured on the scale of the research question.

Mechanical properties are intensive, and therefore independent of size. This means small samples can be used to calculate the mechanical properties of large objects. Universal testers are machines with large, rigid frames which can apply loads to materials. Depending on the setup and capabilities of the tester (e.g., load cell capability), mechanical properties can be tested under any type of load, and both time-dependent and plastic mechanical properties can be gathered. Many International Organization for Standardization and American Society for Testing and Materials (ASTM) protocols exist for the gathering of mechanical properties, and they should be followed carefully.

As every object deforms, changing shape and/or size when a load is applied, flexural models are by far the most applicable to anthropology and the world. While linear, elastic models used to answer questions on functional morphology are by far the most popular in anthropology, this is because of the ease with which they can be constructed and analyzed, not because they are the most appropriate. Some less common but highly appropriate models in anthropology include nonlinear contact models to investigate tooth-tooth or tooth-food item contact, fracture mechanics models to investigate bone and/or enamel mechanical failure, and viscoelastic models to investigate the effect of the periodontal ligament on cranial or mandibular stresses/strains during mastication.

Most biomechanical flexural models in anthropology deal with solid materials, particularly hard solid materials that experience small deformations when loaded, such as bone and teeth. But flexural body models can also be used to address questions of soft solids (like muscle) and fluid

dynamics. Soft solids rarely deform in a linear manner, and therefore operate under a different set of constitutive equations compared to linear models, so the same equations that describe how bone deforms under a load cannot describe how a muscle deforms under the same load. Questions related to fluid dynamics are common in anthropology, for example, when answering questions related to heat conservation/dissipation, the circulatory system, and digestion. However, these models remain rare.

Flexural models are by far the most complicated of the biomechanical models, meaning they are most prone to providing inaccurate results; models are limited by the inputs provided by and abilities of the user.

Mixed models

The combination of more than one category of biomechanical model can be used to address questions more efficiently. In these cases, it is easier to integrate simpler models into more complex ones. During gait analysis, participants are often asked to walk across a force plate where the reaction forces of their feet pressing down are the force plate are determined. These reaction forces are combined with kinematic data in musculoskeletal models to determine locomotor kinetics via inverse dynamic simulations. The force plate models the person as a particle, while the musculoskeletal models model the skeleton as a rigid body.

Recently, Hatala et al.⁶⁰ combined rigid body and flexural models to investigate the relationship between foot kinematics and footprint formation in different substrates. In these simulations, the foot was treated as a rigid body and the substrates were modeled as flexural bodies using particle dynamic simulations. In Berthaume et al.,⁶¹ the role of hominin occlusal tooth shape during hard food item fracture was investigated using finite element analysis, where the teeth were treated as rigid bodies and the food item was treated as a flexural body. In both these studies, treating one object as a rigid body greatly simplified the models and sped up computational time. It additionally allowed the researchers to avoid potentially incorrect assumptions about the inner anatomy of the participant's foot/hominin's teeth.

exception, average morphology does not mean average biomechanical performance. In biomechanics, this is referred to as the "Generic Modelling Fallacy."⁵⁹

2.1.4 | Standards

It is common in engineering and mechanics for methods of data acquisition, processing, and reporting to follow international standards. This allows for standardization, replication, and comparability between

TABLE 1 Inputs required for particle, rigid body, and flexural models.

	Boundary conditions	Geometry	Mechanical properties
Particle	X	O	O
Rigid body	X	X	O
Flexural	X	X	X

studies, improving study longevity. Two of the main governing bodies for standardization are the ASTM and the International Organization for Standardization (ISO). There are thousands of standards, many of which would be directly applicable to anthropology. For example, ISO/TC 159/SC 3 is the "Standardization in the field of ergonomics/human factors for anthropometry and biomechanics..." and includes "measurement methods for the human body." Recognized and agreed upon standards are uncommon in anthropology, but their adoption would not only aid the rigor and replication of research but also data sharing, their perpetuity and the confident use of published data even if the original material was not available for verification.

2.1.5 | Simplifications: Everything is relative

Boundary conditions are conceptually complicated. Mathematically they are the conditions necessary for the constitutive equations to be solved and must hold true over the boundary of the region (Box 1). In biomechanics, conceptually, they are the required inputs which are not geometry or mechanical properties. Whereas geometries and mechanical properties are predominantly genetically and environmentally mediated, boundary conditions are predominantly behaviorally mediated, and limited by genetics and environment.

In biomechanics, boundary conditions (Box 3) can be concentrated or distributed and (in)dependent of time. In reality, all boundary conditions are distributed and dependent on time—even a nail with a tip the diameter of a single atom would be distributing the force of the hammer over the surface area of the atom. But, for modeling purposes, it is sometimes acceptable to model boundary conditions as concentrated and time independent because everything in life is relative. If investigating results near the boundary conditions, then it is important to model the boundary conditions as accurately as possible. But if investigating results far away from the boundary conditions, then modeling boundary conditions correctly becomes less important: this is known as Saint Venant's principle. Scale must also be considered when investigating boundary conditions. For example, when investigating the evolution of bipedal gait, displacement is measured on the scale of meters, meaning it is acceptable to ignore the micrometer-to-millimeter level bone deformations that occur as the bone is loaded and treat bones as rigid bodies.³⁶

Similarly, sacrifices can be made in terms of geometry accuracy, resolution, and sometimes even precision if the effect of these simplifications on the output are relatively small or, in comparative

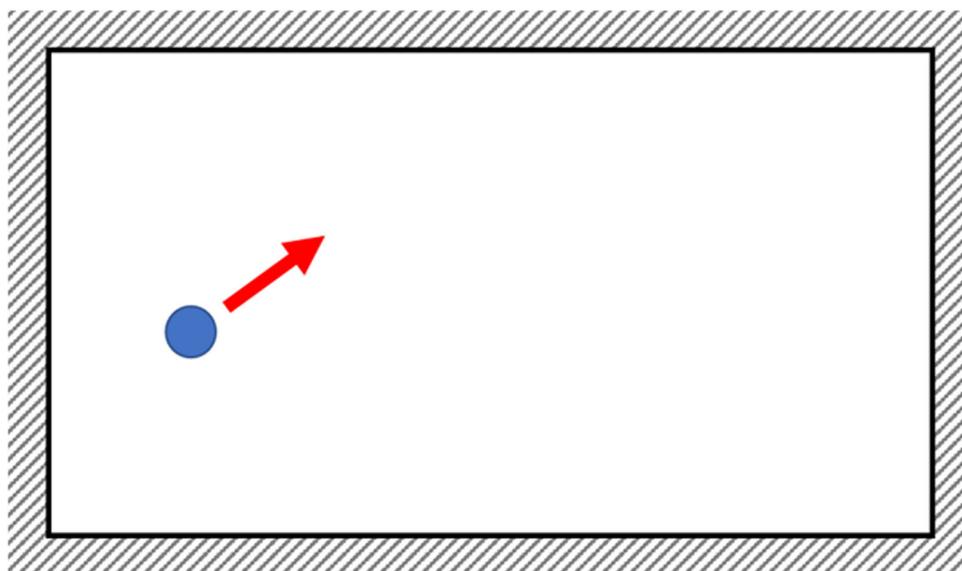
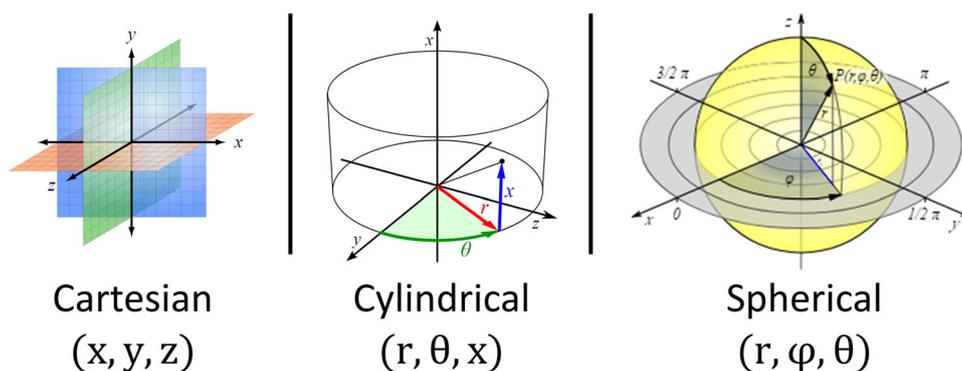


FIGURE 4 Particle model with two sets of boundary conditions, a velocity (red arrow) and constraints to prevent the particle from moving past the upper, lower, left and right borders (gray hashed lines).



Cartesian
(x, y, z)

Cylindrical
(r, θ, x)

Spherical
(r, φ, θ)

FIGURE 5 Examples of Cartesian, cylindrical, and spherical coordinate systems. Cartesian coordinate systems measure distance linearly, while spherical coordinate systems measure distances angularly, and cylindrical combine the two. Images reproduced with the creative commons license.

studies, if geometric simplifications are smaller than the differences between groups. In Berthaume et al.,⁶¹ high-resolution casts of fossils were used, potentially compromising accuracy, resolution, and precision, but it was assumed any differences between the casts and the fossils would be less than the differences between robust and gracile *Australopithecus*. Similarly, it is common to standardize surfaces for geometric morphometric analyses by downsampling them to the same number of triangles. This decreases the resolution and potentially accuracy and precision of the surfaces. The same simplifications can be made in mechanical properties.^{49,63}

2.1.6 | Mechanical properties

Beyond simplifications in accuracy, precision, and resolution, there are many assumptions made about how mechanical properties are

quantified and subsequently modeled. Similar assumptions have been made with geometry (e.g., the human body can be modeled as a cylinder with a diameter equal to bi-iliac width),⁶⁴ but such assumptions are becoming rarer with the advent of advanced scanning technologies.

Mechanical properties are often, and almost exclusively, modeled as bulk, linear, isotropic, homogeneous, and independent of time: none of these assumptions are true for biological systems.^{65–67} This can have significant effects on the results, particularly when metrics such as stress, strain, and strain energy density are being considered.⁴⁹ However, it is also nearly impossible to gather this information on extant taxa, and completely impossible to gather this data on extinct taxa.

What should be done? Sensitivity analyses can be run to see if error due to modeling assumptions is less than difference between samples.^{68–73} If this is true, the conclusions of the study are likely

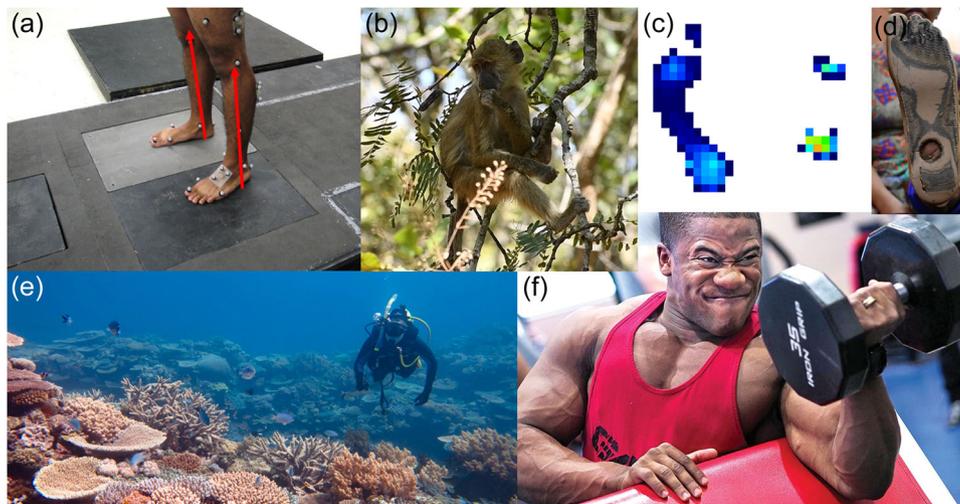


FIGURE 6 Examples of boundary conditions that are internal and external to the individual's body. (a) External: ground reaction force or a person standing on two force plates, (b) compliant branch pushing up on a juvenile yellow baboon (external), while it is using its muscles to bite down (internal) on a hard seed pod, (c) external: foot pressure distribution of a prosthetic foot when standing on a pressure mat, (d) bottom of the same prosthetic foot, showing wear patterns from external forces that correspond with foot pressure distribution (c), (e) external: water pressure pressing hydrostatically on a diver's body, (f) bodybuilding flexing their muscles (internal) to lift a weight (external). Images (a), (e), and (f) reproduced with the creative commons license.

robust. If not, measurement error is too large, and the results should be ignored. Unfortunately, sensitivity studies have shown the error associated with mechanical modeling assumptions is often larger than differences in the magnitudes of biomechanical performance. However, it appears some biomechanical metrics, such as stress/strain/strain energy density patterns and the mode of deformation are robust against these modeling assumptions.⁶³ As with all modeling assumptions, there are some general patterns in the literature that can be used to form hypotheses for future modeling assumptions, but modeling assumptions should be tested for every model, individually, to prove the robustness of the results.

2.1.7 | Trade-offs

Trade-offs in gathering and analyzing boundary conditions, geometry, and mechanical properties data exist because of time, costs, and accessibility constraints. Time and money are always limited, which can lead to trade-offs with accuracy, precision, and resolution of the data and answer to the research question. For example, musculoskeletal, rigid body models which are used to address questions like how humans, chimpanzees, and our ancestors walk bipedally are usually constructed using a single/few or average set of cadaveric musculoskeletal data.^{36,51} These cadavers are usually older and have begun to show signs of degeneration, and do not encompass species-level biological variation. In the case of humans this often means leaving out small, occasionally present sesamoid and accessory bones and variations in muscle origins, insertions, force production potential, and even the number of heads (e.g., double-headed popliteus muscles).^{74,75}

Accessibility constraints prevent access to subjects, specimens, material, equipment, and knowledge, which may influence accuracy,

precision, and resolution.⁷⁶ There are, and continue to be, ethical concerns over access to data and precious, rare, (sub)fossil material.^{76,77} In the past, this would have been limited to just the actual (sub)fossils, themselves, but today, this includes, for example, the isotopic, proteomic, and ancient genomic data generated from these (sub)fossils as well. Trade-offs must be considered within the context of the research question being asked and within the future of the data after the study is complete, especially when destructive sampling is concerned.

2.1.8 | Dimensionality

Primate movement is 3D (forwards–backwards, up–down, left–right; sensu the inverted pendulum⁷⁸) but is often simplified to one or 2D. Decreasing the dimensionality of the problem can drastically simplify the calculations, reducing the chance of human error, but this often comes at the cost of information loss. Local instead of global coordinate systems, and use of non-Cartesian coordinate systems (Figure 5), could be employed to reduce dimensionality without losing information. Non-Cartesian coordinate systems are particularly useful when describing nonlinear motion and can both simplify the mathematics and dimensionality of a problem. For example, cylindrical or spherical coordinate systems can be used to describe motion of a body segment about a joint, where angular motion is occurring. Instead of using trigonometry and a complex set of coordinates to model the movement, it can instead be modeled as a change in angle. Similarly, the question of dimensionality is crucial in geometrical construction of biomechanical models. Simpler 1D and 2D models were more common but are becoming rarer with advances in technology and modeling techniques. A recent finite element study

has demonstrated that incorrect results can be obtained by creating 2D instead of 3D models.⁷⁹

2.2 | Comparative biomechanics: The future

2.2.1 | Constructing models

When constructing biomechanical models for comparative analyses, parameters such as mechanical properties are often held constant between models, so the effect of differences in boundary conditions (e.g., changes in muscle force) or geometries can be assessed. These comparisons could be used to investigate the effects of orthognathism in cranial stresses or strains during hard food item biting, for example.⁸⁰ But it should be remembered that these models assume that intertaxon differences in mechanical properties do not affect the results, which is not true: while a taxon with an orthognathic skull may experience lower strains than a taxon with a prognathic skull, it may have more compliant mechanical properties which make the magnitude of strains comparable between taxa. *In short, there may be biological trade-offs between mechanical properties and geometry.*⁸¹ Therefore, by holding mechanical properties constant, what is being observed in the solutions may not be intertaxon differences in strains. Similarly, particle models assume that differences in geometry do not matter, and differences in rigid body models assume that differences in mechanical properties do not matter. Instead of assuming these differences do not matter, the effect of these assumptions on the results should be considered.

In short, there may be biological trade-offs between mechanical properties and geometry.

2.2.2 | Analyzing data

In comparative methods, taxa are treated as datapoints. Phylogenetic comparative methods (PCMs) recognize that, because of evolutionary relatedness, these datapoints are not completely independent of each other, and taxa are hierarchically related to each other based on the time since divergence.^{82,83} PCMs have been developed as a way of statistically “normalizing” for phylogenetic relatedness. In comparative analyses, researchers often assume that morphology is determined by taxonomy and that intertaxonomic morphological variability is predominantly genetically controlled.⁸⁴ Therefore, the underlying assumption is that there is some sort of phylogenetic structure in the morphological data, and this is why the data must be phylogenetically corrected. First principles dictate that biomechanical performance is at least somewhat a product of morphology (geometry). There must, therefore, be some sort of phylogenetic structure to the biomechanical data—the only way there would not be is if biomechanics was independent of morphology, morphology was independent of phylogeny, or phylogeny was independent of genetic relatedness.⁸⁵ Yet, researchers often do not phylogenetically

correct their data and assume any differences in biomechanical performance are instead a product of selective pressures: this adaptationist viewpoint ignores the potential role of genetic drift and other nonselective evolutionary models.

Current phylogenetic methods may or may not be appropriate for analyzing biomechanical data. There is a many-to-one relationship between genotype and phenotype, and a many-to-one relationship between phenotype and biomechanical performance, meaning there is a many-to-many-to-one relationship between genotype and biomechanical performance. It is, therefore possible that whatever genetic structure would have been present in the biomechanical data has been lost. Taking phylogeny into account using PCMs is therefore likely important, but as most current methods take phylogeny into account by including the phylogenetic tree in statistical analyses (which is based on genotypic/molecular/phenotypic data), current methods may need to be altered. The authors are currently investigating whether current PCMs are appropriate for analyzing biomechanical data, and if not, how they might be altered to do so.⁸⁶

2.3 | The known, the unknown, and the unknowable

Some biomechanical data will be easy to collect and calculate, but some can only be estimated; this is particularly true when reconstructing the biomechanics of dead organisms or when using discretizing methods, like digital surface models in finite element analysis or rigid body dynamics. Most biomechanical data are ill-posed, meaning there is a many-to-one relationship (where many elements of one group map onto one element of another group) between boundary conditions, geometry, and/or mechanical properties and biomechanical performance. Biological systems have redundancy built in to prevent failure of the system if one of its components fails to perform. This is crucial for organism survival, but challenging in biomechanical analyses where researchers are conducting complex inverse problems to try and reconstruct biomechanics based on aspects of, for example, the organism's morphology or bone modeling pattern.

We can certainly use living organisms to estimate the limits of boundary conditions and derive relationships between morphology and boundary conditions, or morphology and mechanical performance, but the error associated with these relationships must be carried through biomechanical analyses. This method also suffers from the fatal assumption that all possible variation in dead organisms is captured by live ones today, which is simply not true. Not only are there extinct organisms for which there is no modern analog, such as the thick enameled, orthognathic, sedge-eating *Paranthropus boisei*,^{87,88} but wild-caught, dead, extant animals in collections lived in very different environments than their living relatives today, due to, for example, global warming and the extensive deposition of plastics around the world. Conclusions from modern experiments or models based on modern data to derive relationships between organisms and biomechanics, therefore have

limited utility, and this should be considered and brought through as error in biomechanical measurements.⁸⁹ In these situations, sensitivity analyses are vital for understanding the cloud of error that exists around biomechanical performance data. Biomechanical data should be dealt with in a more probabilistic, and less deterministic, fashion.⁶³

Like all other models, biomechanical models are just that: models. This does not lessen their utility or validity, but, as with any other type of model, biomechanical models must be relevant, encompassing, and validated. A criticism of many biomechanical models is that because it is a model, it is inferior to experimental or observed data. But it should be remembered that experimental and observed data similarly suffer from simplifications and assumptions in data collection, and so can also be imperfect. Models can provide information not possible to gather through experiments or observations. When living organisms are concerned, experimental/observed data should be used in concert with biomechanical data. In this way, behavior and actions can be related to the physical effects of those behaviors and actions on the organism.

2.4 | Evolutionary biomechanics

Phenotypes evolve through a complex interaction of historical, structural, and functional constraints that can be modeled using Gould's 'aptive triangle' (Figure 1).^{12,85} Evolutionary biomechanics can help explain how these constraints interact with each other to produce the observed phenotypes. Historical constraints are those imposed by phylogeny, genetics, and inherited patterns of gene expression (epigenetics). Structural constraints have to do with the physicality of the system, such as the fact that no two solid objects can exist in the same space, and spandrels can form because of the evolution of other structures.^{12,90} Finally, functional constraints are those brought on by processes like adaptation. Animals must be able to operate within their environments, and many of those functional parameters, such as locomotor, foraging, and masticatory force production and speed, are biomechanical. The physical and mathematical framework of biomechanics provides a formal framework for analyzing the interaction between these constraints (vertices in the 'aptive triangle') and also provides a pathway to describe *how* the observed phenotypes evolved.

Within anthropology, evolutionary biomechanics has played a significant role in understanding many of the physical changes to the musculoskeletal system, for example, because of changes in locomotion and diet. An important addition to many of these studies is biomechanical data, as many studies make conclusions about biomechanics based solely on morphological data. Problems with wrong measurements, ill-posedness, vagueness and morphological independence, and incongruence with mechanical theories of bone modeling, biomechanical conclusions should not be drawn solely from morphological data alone. Doing so could, for example, lead to an incorrect understanding of how locomotion or feeding evolved, locomotor/feeding reconstructions, and/or which extinct hominins used lithics and how.

2.5 | When do differences in biomechanical performance matter?

The discipline of mechanics concerns motion and the forces that cause motion.⁵⁸ Based on this, speed, force, energy, acceleration, and displacement are the biomechanical performance metrics we think are most useful to consider in an evolutionary anthropological context. It is common in comparative contexts to quantify biomechanical performance in two or more individuals or models and ask whether observed differences in biomechanical performance matter.^{57,80,91} This is true not only for evolutionary contexts, but others as well as, for example, comparing populations before and after the introduction of technologies, like the atlatl, or the introduction of new hunting strategies, such as spear thrusting versus spear throwing, or interventions, like new rehabilitation regimens or medical devices.

In anthropology, athletes are often used as models to understand how the body reacts to biomechanical loads. This information can be used to interpret when changes in morphology reflect changes in behavior. For example, athletes who participate in sports that asymmetrically load their limbs (e.g., tennis, cricket) have asymmetrically formed bones, presumably because the asymmetric loads lead to asymmetric bone modeling. Conversely, athletes who participate in sports that bilaterally load their limbs (e.g., swimming, rowing) have symmetrically formed bones.^{92,93} Energetic studies also draw on modern athletic performance.⁹⁴ These data help to construct and inform evolutionary biomechanical models.

Obvious consideration must be given to the accuracy, precision, and resolution of the data. Any difference in biomechanical performance, as long as it is larger than measurement or model error, has the potential for being significant in the context of the question being asked. At the nano- and micro-level, this depends on, for example, whether the DNA, proteins, and cells can fulfill their function. Any changes in speed at which these functions are carried out must be analyzed using a systems approach and considered at higher level(s). For example, an increased consumption of energy at the cellular level can be beneficial or detrimental, depending on the metabolism and metabolic needs of the cells and the organism and rate at which energy can be provided to the cells.

Within evolutionary biomechanics, it is necessary to understand the relationship between biomechanical performance and evolutionary fitness to determine if changes in biomechanical performance are important. The use of athletes is a potentially untapped model to understand when biomechanical changes are biologically/evolutionarily meaningful. In clinical biomechanics, a small improvement in biomechanical performance is generally considered unimportant. But in athletics, a miniscule improvement in biomechanical performance can be the difference between victory and defeat. Determining whether a change in biomechanical performance is important or not depends less on the magnitude of change and more on the environment in which that change is operating.³⁷ Where sections of the biomechanics-fitness curve are steep, small changes in biomechanics would cause relatively large changes in fitness, and, therefore will matter greatly from an evolutionary perspective. A flatter section of the curve indicates that large changes in biomechanics would cause relatively small changes in fitness, and

therefore may not matter from an evolutionary perspective. Evolutionarily, a 10% reduction in locomotor energetics might be unimportant when dietary competition is low or dietary resources are plentiful, meaning selection may not act in favor of this change. But a 0.1% change in locomotor energetics may be important when dietary competition is high or dietary resources are rare. This is the basic premise of why the evolutionary pressures brought on by the consumption fallback foods would be greater than those brought on by preferred diet. This is why it has been hypothesized fallback foods may play a significant role in primate evolution.⁹⁵⁻⁹⁷ Comparing athletes at different abilities and levels of performance to each other, for example, may help create a framework for understanding when changes in biomechanical performance are evolutionarily important.

Commonly in evolutionary biomechanics studies, and as we assume above, it is taken for granted that there is a correlation between biomechanical performance and fitness. By extension, it is assumed that biomechanical performance can be used as a surrogate for fitness. To our knowledge, the shape of the relationship between biomechanical performance and fitness (i.e., the biomechanics-fitness curve) remains largely unexplored, both with real and theoretical data.

For example, reduction in locomotor energetics during persistence hunting is hypothesized to be a driver behind obligate bipedalism in hominins. Energy expenditure for a given task is normally assumed to be negatively correlated with fitness.⁹⁸ However, there is a point at which a reduction in energy expenditure related to persistence hunting leads to decreases in fitness, for example, if energy use was reduced to the point where the hominin was unable to follow the animal efficiently, or even move. The relationship between energetics and fitness would no longer be linear. Indeed, the relationship between biomechanical performance and fitness might be best considered as a bell-shaped (although not necessarily symmetrical) distribution, where there is one or more optimal points where biomechanical performance has the best effect on fitness. This is similar to the Yerkes-Dodson law in psychology, which describes the relationship between anxiety and performance: too much and too little anxiety are both deleterious.⁹⁹ Lessons can be learned from curves relating other functional metrics to fitness. However, other functional metrics should not be used as proxies for biomechanical performance, for many of the same reasons that morphology should not be used as a proxies for biomechanical performance. Functional morphospaces, like those described by Simpson¹⁰⁰ which build upon Wright's adaptive landscapes,¹⁰¹ can be used to relate biomechanical performance to phenotypic changes, such as palate length and width relate to mechanical advantage or cranial stresses when feeding in bats.¹⁰²

3 | CONCLUDING THOUGHTS

Biomechanics has played a formative role in anthropology, providing explanations for cultural and biological changes in humans and non-human primates. With advances in computers and computational modeling, it has the potential to provide a more complete understanding of how we evolved, and the effects of technological, behavioral, and environmental changes on primate culture, biology,

and evolution in the years, decades, and centuries to come. Experimental biomechanical data play a vital role but is limited in the data they can provide. When combined with validated and well-constructed biomechanical models, much more information can be gleaned. As with any other line of data, biomechanical data are most powerful when combined with other lines of evidence and has the potential to link social and behavioral decisions to the physicality of the organism. Moving forward, it is important biomechanical data are collected and analyzed in frameworks consistent with current disciplinary theories, including modern evolutionary models.

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No data were used in this manuscript.

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