SCIENCE ROBOTICS | REVIEW

BIOMIMETICS

Paleoinspired robotics as an experimental approach to the history of life

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Paleontologists must confront the challenge of studying the forms and functions of extinct species for which data from preserved fossils are extremely limited, yielding only a fragmented picture of life in deep time. In response to this hurdle, we describe the nascent field of paleoinspired robotics, an innovative method that builds upon established techniques in bioinspired robotics, enabling the exploration of the biology of ancient organisms and their evolutionary trajectories. This Review presents ways in which robotic platforms can fill gaps in existing research using the exemplars of notable transitions in vertebrate locomotion. We examine recent case studies in experimental paleontology, highlighting substantial contributions made by engineering and robotics techniques, and further assess how the efficient application of robotic technologies in close collaboration with paleontologists and biologists can offer additional insights into the study of evolution that were previously unattainable.

INTRODUCTION

Robotic platforms have taken a central role in the intersection of biology and engineering, a field known as bioinspired robotics. This area of robotics aims to tackle two main issues. First, it leverages the measurements of anatomical traits and locomotor behaviors of organisms that can lead to the development of improved robots (*1*, *2*). Bioinspired robotics posits that, when designing a robot to execute a specific function or task, a roboticist can take cues from living creatures that naturally perform similar tasks (*3*, *4*). This approach can draw from a variety of biological features, including physical structures, movement patterns, control mechanisms, and the integration and coordination of multiple systems, that are then adapted for robotic applications. Second, it explores ways in which robots can be used to understand biological phenomena and performance (*5*, *6*). Robots, when used as exploratory tools validated against living systems, have uncovered fundamental mechanical laws and advanced the understanding of physical rules underpinning natural phenomena.

Bioinspired robots as experimental platforms allow scientists to test the consequences of variations in specific morphological features on movement while maintaining constancy in the rest of the platform; such decoupling is impossible in live organisms. Full and Koditschek (*7*) have proposed that, when studying biological systems using robotic counterparts, researchers can use two categories of models: abstracted models of animals (“templates”) or elaborate models (“anchors”) that more closely replicate form and function than templates. A template allows exploration of general rules of animal form and function decoupled from the complexity of the whole animal, whereas an anchor enables causal explanations of neural and musculoskeletal systems by reproducing the specific joints and muscles of interest. Although Full and Koditschek specifically presented examples of templates and anchors of locomotor systems to which control mechanisms can then be applied, this paradigm can broadly be applied to other biological or engineered designs.

Webb (*8*), on the other hand, contended that, when developing robotic designs, a close adherence to biological anatomy is superior to a simplification of morphological features and that abstraction can be achieved instead by distilling complexity into simpler but accurate forms. Consequently, attaining broader complexity in these robotic models is achievable through an iterative process of adding features (*8*), but it is essential that movements must be understood and replicated under conditions encountered by living organisms in their natural habitats before testing alternative scenarios not observed in nature. Therefore, despite the extensive and historically successful trajectory of bioinspired robotics, its application has predominantly been confined to the analysis of extant species that could validate the data obtained with the robotic platform. This approach precludes a comprehensive understanding of form and function through time, given that mechanical constraints in extant species are inextricably linked to millions of years of evolutionary events. Robotic platforms offer an exciting avenue for the reconstruction and investigation of evolutionary pathways of multiple lineages of organisms, thereby contributing substantially to our understanding of the history of life through deep time.

In this Review, we propose “paleoinspired robotics,” an emerging research paradigm that combines the traditional bioinspired robotics framework with the study of evolutionary trajectories. Paleoinspired robotics markedly expands upon the conventional objectives and methodologies associated with bioinspired robotics (Fig. 1). Traditionally, bioinspired robotics research focuses on replicating and understanding certain features of a single extant animal. Conversely, paleoinspired robotics seeks to investigate the consequences of anatomical changes on the kinematics, biomechanics, and energetics of multiple species in different time periods, especially as applied to overarching evolutionary trajectories. Augmenting the field of paleontology with paleoinspired robotics enables the investigation of evolutionary feasibility of features, and the comparison between paleoinspired robotics and bioinspired robotics facilitates the study of artificial evolution (Fig. 1).

Physical robots give researchers the ability to change specific features of the animal-inspired design and to collect data about how the features of interest and the animal’s embodiment as a whole interacted with the surrounding world (*9*–*11*). Data generated by paleoinspired robots can be used to compare species both extant and extinct and to develop general models of the parameter space that can be extended to hypothetical past or future animals (*12*–*14*). By evaluating the effects of changes to the animal’s morphology on metrics of performance like

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locomotion speed or cost of transport, scientists can understand the progression of a feature through time as the evolutionary pressures on the animal and the environments available to the animal change.

Previous investigations into ancient organisms have used methodologies such as comparative studies with extant taxa (*15*, *16*), genetic and developmental tracing (*17*, *18*), and analysis of paleontological data (*19*, *20*), all aimed at testing hypotheses to elucidate evolutionary transitions. However, these methods cannot modulate physical variables within an experiment to properly evaluate the effects of changes in the feature of interest, which is a basic tenet of robotics research (*21*). Integrating robotics into the paleontological research process can provide experimental tests of biomechanical hypotheses and historical progressions of physical features, such as the potential selection processes that led to the evolution of vertebrae in ancient fish (*22*). The ability to manipulate or simulate evolutionary changes and transitions in a matter of days using robotic platforms allows for the examination of processes that unfolded over millions of years.

Moreover, paleoinspired robotics can interrogate the kinematics, biomechanics, and energetics of anatomical systems that are not necessarily analogous to those of known animals (*23*) by gathering physical data to test hypotheses about these unintuitive morphologies. Robotic platforms can be designed to test morphological characteristics and locomotor performance of organisms from the distant past that we cannot directly observe; conceivable future species subjected to as-yet undiscovered evolutionary pressures; or hypothetical forms that did not, do not, or cannot exist on the basis of physical or developmental constraints. This approach, therefore, holds the promise of offering insights into the actual and potential trajectories of life on Earth.

In the subsequent sections, we introduce a framework for paleoinspired robotics that combines experimental data from physical robots with observations of extant animals to make conclusions about extinct species and evolutionary transitions, such as those leading to a variety of vertebrate locomotion modes. We motivate the use of robots that integrate many features of a species into one experimental platform to understand how the animal's entire body affected its interactions with the environment and how this drove anatomical changes over time. We also present recent investigations in experimental paleontology that underscore the successes of using engineering techniques to analyze extinct organisms, and we argue that there is further untapped potential that can be unlocked with the use of paleoinspired robotics. We conclude with a discussion of the challenges, perspectives, and implications of using robots to test hypotheses about extinct and theoretical forms and how paleoinspired robotics can also push the boundaries of the general field of robotics.

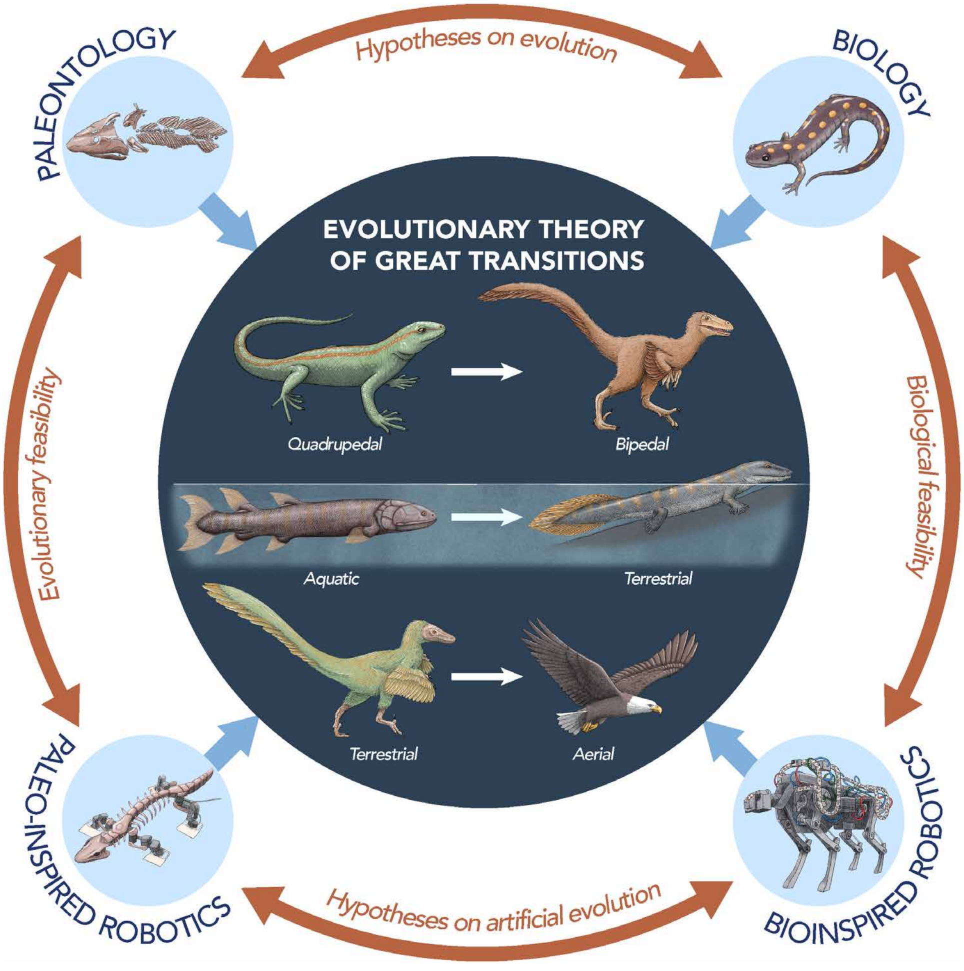

Fig. 1. Life–artificial life loop. The study of life (paleontology and biology) and the study of artificial life (bioinspired robotics and paleoinspired robotics) provide complementary knowledge about animal evolution. The interactions between biology and bioinspired robotics and between paleontology and paleoinspired robotics provide bidirectional information about feasibility of morphologies and motions. The dichotomy between biology and paleontology mirrors that of bioinspired robotics and paleoinspired robotics in which investigation of natural and artificial evolution, respectively, progresses through time.

MAJOR EVOLUTIONARY TRANSITIONS IN ANIMAL LOCOMOTION STUDIED VIA ROBOTICS

Paleoinspired robotics as a natural evolution of bioinspired robotics

Paleoinspired robotics can play an instrumental role in understanding the complex nature of evolutionary dynamics by filling in the gaps around the explanatory models generated by collaboration between paleontology and physiology (Fig. 2). To jump-start the field of paleoinspired robotics, we can build on the more established field of bioinspired robotics, which has already begun to tackle some of the challenges discussed in the previous section. Researchers can prescribe specific changes to individual features of the robot to directly investigate particular morphologies (*21*) and can leverage contemporary biological understanding of extant species to extend robotic models to hypothetical forms or behaviors, including those of paleontological interest (*23*).

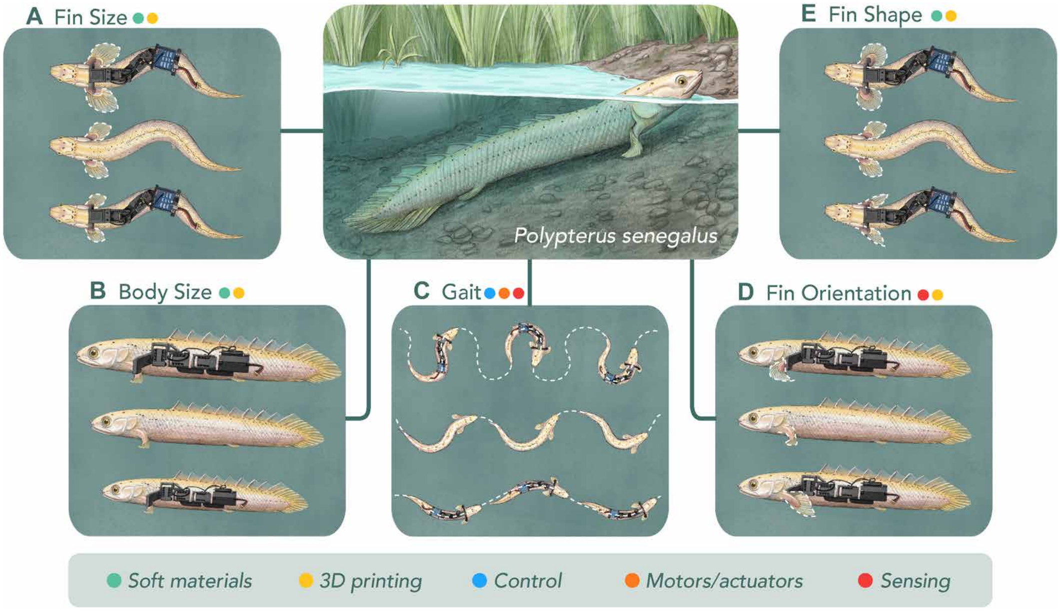

Fig. 2. Hypothetical experiments leveraging robots as models of animals. Conceptual demonstration of experiments varying form and function that can be performed using a robot but not an animal, using the exemplar of studying the water-to-land transition of tetrapods. Experiments elucidating the effects of varying (**A**) fin size, (**B**) body size, (**C**) walking gait, (**D**) fin orientation, and (**E**) fin shape can be accomplished using robotics techniques like soft material casting (blue); 3D printing structures (yellow); control engineering and machine learning (green); servo motors, fluidic actuators, or smart materials (orange); and bioinspired or soft sensing (red).

Many broad bioinspired templates explaining biological phenomena, like muscle contraction (*24*), dynamic legged locomotion (*25*), and swimming (*26*), have been developed and validated with experiments on extant animals and can be applied to extinct species or extended to additional environments. Using an octopus-inspired robot as an experimental platform, researchers extended the spring-loaded inverted pendulum model of dynamic legged locomotion to the underwater environment by adding the effects of additional fluid forces to the model (*27*, *28*). Robots have been used to evaluate the hypothesis that evolution preserved asynchronous wingbeat actuation alongside synchronous actuation capability in many insect species by demonstrating a bioinspired flapping robot capable of transitioning between both modes of actuation via a single muscle interpolation factor in the controller (*29*). The combination of well-studied neural circuit elements, like coupled oscillators and leaky-integrator neurons, can be used to generate gaits in a variety of animal (*30*, *31*) and robotic models (*32*, *33*) and can generate complex behavior like an automatic transition between walking and swimming gaits of a salamander-inspired robot (*34*).

Furthermore, knowledge gained in the development of multimodal mobile robotics can be applied to paleoinspired robotics research on changes in locomotion during transitions between different media. Snakes use body undulation in both aquatic and terrestrial environments and are an appendage-less counterpoint to tetrapod locomotion (*35*, *36*). Amphibious robots demonstrate additional principles of underwater and in-air locomotion, such as the importance of walking appendages with large surface areas to improve swimming via paddling (*37*) or variable stiffness materials for operating under different buoyancy conditions (*38*). In addition, the water-air interface has been explored in the context of robots inspired by animals that live in both aquatic and aerial environments (*39*, *40*).

These techniques developed for bioinspired robotics to analyze biological systems can be applied to experimental paleontology. Computational fluid dynamics simulations used to analyze fins of extant fish (*41*) can be applied to reconstructed morphologies of extinct swimmers (*42*), principles of legged stability can apply to both lizards and ancient tetrapods (*12*), and evolutionary algorithms can be used to develop the gaits of dog-like robots (*43*) and bipedal dinosaur models alike (*44*). Further examples of the intersection between engineering methods and paleontology are included in Table 1. These techniques have provided information about single features, but limiting analysis to a narrowly defined system and abstracting away a real environment complicates the process of drawing conclusions about the effects on an entire animal.

Many of the previous studies in experimental paleontology using physical instantiations of an extinct animal have investigated narrow research questions about an individual species and limited the recreation of the animal's embodiment to one feature that performs a behavior of interest. It is important to expand these constrained representations to study the effects of morphology on performance, which necessarily involves examining the interactions between the entire body of the animal and a real environment. Performance then has an effect on fitness and selection, which drive the evolutionary trend through time (*45*). For example, we know that analyzing the kinematics of animal propulsors in a vacuum removes the context of forces on the body through the interaction with the environment, which determines important components of locomotion, such as balance, stability, and energetics (*46*, *47*). Likewise, the recreation of a single appendage might not accurately represent complex systems, such as multiple moving fins each generating flow that interacts with the vortices off of the other fins and body (*48*, *49*). Thus, paleoinspired robotics is the natural next step in the collaboration between engineering and paleontology: creating a robot from morphology observed in fossils capable of intelligent and diverse motions to elucidate how the effects of interaction with the physical world shape morphology and motion over time.

Table 1. Examples of previous paleontology research leveraging interdisciplinary techniques. We group the previous work into four categories: using biological observations of extant animals to support paleontological hypotheses (*12*, *52*, *86*, *126*), applying computational methods to analyze form and/or function of extinct animals without a physical model (*42*, *44*, *83*, *84*, *94*, *127*–*133*), creating a physical model of one element of an extinct animal on the basis of paleontological data to investigate a narrow hypothesis (*9*, *10*, *63*, *64*, *134*, *135*), and paleoinspired robotics coupling data from fossils and a robot that moves and interacts with its environment to evaluate hypotheses about extinct animals (*13*, *14*, *23*).

Citation	Animal	Description
	Animal observation applied to paleontology	
Libby *et al.* (*12*)	Lizard	Showed that tail motion stabilizes lizard body motion through experiments with a robot and applied the model to the body morphology of a velociraptor
Standen *et al.* (*52*)	*P. senegalus*	Compared the skeletal structure of *Polypterus* specimens raised on land with those raised in water; found similar structures as in early tetrapods
Falkingham and Horner (*86*)	Lungfish	Imaged tracks of extant lungfish to compare with fossilized trackways
McInroe *et al.* (*126*)	Mudskipper	Tested tail usage in walking over granular media on a robot with locomotion based on extant mudskippers to hypothesize about tetrapod locomotion
	Computational analysis without physical model	
Gutarra *et al.* (*42*)	Plesiosaur	Used computational fluid dynamics modeling to determine effects of body size and neck length on hydrodynamics
Sellers and Manning (*44*)	Bipedal dinosaurs	Used an evolutionary algorithm to generate muscle activation and gaits
Esteve and Rubio (*83*)	Trilobite	3D models and imprints reveal different gaits in trilobites
Cooper *et al.* (*84*)	*Otodus megalodon*	Used fossil remains and extant species to build a 3D model of an extinct shark and infer speed and diet
Wintrich *et al.* (*94*)	Plesiosaur	Performed finite element analysis to estimate the range of motion of the neck using a multimaterial vertebrae model
Kogan *et al.* (*127*)	*Saurichthys* (actinopterygian)	Used computational fluid dynamics to evaluate fluid disturbances caused by the extinct fish and compared these with extant fish
Falkingham and Gatesy (*128*)	*Corvipes lacertoideus*	Created a model of impact in granular material applied to analysis of fossilized tracks
Hutchinson *et al.* (*129*)	*T. rex*	Analyzed moment arms of limb muscles to estimate posture for walking
van Bijlert *et al.* (*130*)	*T. rex*	Simulated the natural frequency of a dinosaur model to estimate tail motion parameters
Manning *et al.* (*131*)	Dromaeosaurid (theropod)	Used finite element analysis of claws with material properties from extant bird claws; determined that claws were strong in longitudinal plane for forces during climbing
Bishop *et al.* (*132*)	*Coelophysis* (theropod)	Solved optimal control problems on a simulated dinosaur musculoskeletal model; found active tail lateroflexion increased locomotory efficiency
Henderson (*133*)	Sauropod	Computer models to assess location of center of mass based on trackways, inferences from extant elephants
	Physical model and experiments	
Muscutt *et al.* (*9*)	Plesiosaur	Built flipper pairs to image vortex interactions
White *et al.* (*10*)	*Australovenator*	Used a soft, deformable foot to identify theropod tracks

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Citation	Animal	Description
Peterson *et al.* (*63*)	*Archaeopteryx*/early avian forms	Built a hybrid robot capable of both running and flapping to investigate whether flapping wings improved legged robot before flying capabilities were developed
Talori *et al.* (*64*)	Oviraptorosaur	Measured forces at the wing joints of a 3D printed model under airflow
Huynh *et al.* (*134*)	Blastoid echinoderm	3D printed fluid channels and imaged flow mixing through the channels
Fukuoka and Akama (*135*)	*Compsognathus* (theropod)	Applied a CPG to create locomotion in a dinosaur-shaped bipedal robot
	Robot-fossil motion pair	
Peterman and Ritterbush (*13*)	Cephalopods	Simulated and experimentally tested stability and maneuverability of a jetting robot with different shell morphologies based on fossils
Nyakatura *et al.* (*14*)	*Orobates* (stem amniote)	Applied sprawling locomotion CPG to a simulation and a physical fossil replicate to match trackway
Desatnik *et al.* (*23*)	Rhombifera (pleurocystitids/echinoderm)	Tested different locomotion gaits of soft appendages designed on the basis of fossils and hypothesized muscle location

Using robotics to study paleontological questions about locomotory transitions

There are a vast number of unsolved paleontological questions surrounding the major locomotor transitions in evolutionary history. These transitions include, but are not limited to, the invasion of land by aquatic vertebrates, the progression from quadrupedal to bipedal walking, and the development of multimodal locomotion (for example, flight) that enabled traversal of various environments. However, data on the function and physiology of the species of interest are limited because these animals have been extinct for hundreds of millions of years.

Comparisons of these locomotor transitions aim to elucidate the broader principles underlying evolutionary shifts in locomotion and the physical and mechanical constraints that might render certain evolutionary trajectories infeasible. Understanding these principles not only informs our comprehension of life's evolutionary potential but also expands our projections for future biological and synthetic life forms under varying environmental conditions. Biomechanical and physiological studies provide critical data and insights into locomotor diversity (*50*) and energetics (*46*, *51*), and developmental manipulations yield information that can explain mechanisms driving the evolutionary transition from aquatic to terrestrial habitats (*52*, *53*). Extrapolations based on these studies allow for the generation of hypotheses regarding the soft tissue structures, kinematic patterns, and behavioral repertoires of extinct taxa (*54*).

However, the use of comparative methods and genetic manipulations in biological research is often hindered by the impossibility of adhering to what is known as the "ceteris paribus" assumption, which is that, aside from the trait being investigated, all other traits remain unchanged. It is not feasible to induce radical morphological changes in extant animals in a controlled manner, nor is it possible to isolate and modify a single anatomical feature without causing compensatory changes in other characteristics (*21*). These constraints inherently limit the direct application of findings from living species to their extinct counterparts. The utility of inferences drawn from modern species when applied to their extinct relatives presupposes a degree of morphological and physiological congruence that requires further empirical substantiation. Integrative evidence that juxtaposes attributes of both extant and extinct species would substantiate these comparisons, grounding such extrapolations in a more tangible biological framework.

Paleoinspired robotics expands on bioinspired robotics to include evolutionary conjectures that bridge the temporal span, facilitating what could be described as testing "millions of years of evolution in a single day." To apply this paradigm to a variety of evolutionary hypotheses, researchers must be able to compare different morphologies and their associated motions throughout history. The interactions between the particular features of interest and the environment are essential elements of the pressures on the animal that drive evolution (for example, the shape of a foot affects contact with the terrain, which influences locomotion speed and efficiency). This motivates the use of physical robots capable of generating these interactions with the real world spanning the parameter spaces of interest.

Bipedalism evolved separately from quadrupedalism in reptiles (for example, archosaurs) (*55*) and mammals (for example, hominids) (*56*) and likely in response to different evolutionary pressures. Bipedalism is strongly correlated with cursoriality in archosaurs but not in mammals (*57*). One potential explanation is that, unlike in mammals, the hindlimbs of archosaurs support a higher percentage of their body weight because of their large tails; this particular mass distribution could have contributed to the development of larger and stronger hindlimbs that lend themselves to bipedalism (*18*). Whereas bipedalism and quadrupedalism are closely related forms of locomotion, the well-established fields of bipedal (*58*, *59*) and quadrupedal robotics (*60*, *61*) have largely existed independently of each other. Although these two subfields of legged robotics have coalesced around different research questions and applications, connecting them can help researchers understand the crucial sensing and morphological adaptations necessary to enable quadrupedal animals to walk on two legs.

Researchers have hypothesized that one trajectory from legged to aerial locomotion began with the development of wing-like appendages on bipedal terrestrial species. A bipedal dinosaur such as *Archaeopteryx* flapping its wing-like appendages could theoretically generate lift to increase its running speed; with sufficient runup and acceleration, the lift forces could exceed its body weight, enabling takeoff (*62*). Testing these ideas on robots revealed that flapping wings could increase the maximum running speed of a small hexapodal robot (*63*); however, a robotic implementation of the bipedal *Caudipteryx* indicated that the lift and drag generated by the wings were measurable but not sufficient to achieve takeoff (*11*, *64*). Nevertheless, these results suggest that the development of wings could aid terrestrial-legged locomotion and indicate pathways along which animals' morphologies needed further optimization to achieve flight.

By studying how animals evolve to take advantage of different environments, we can learn the basic principles of locomotion, how multifunctional features are developed, and why they may or may not become optimized for a specific environment. This can help explain the history of evolutionary transitions and the basis for predictions about what future transitions are possible.

Paleoinspired robotics in the study of the water-to-land transition

The transition of vertebrates from an aquatic to a terrestrial environment is a critical juncture in evolutionary history (*65*). This water-to-land transition necessitated substantial morphological and physiological transformations to counteract gravitational forces, permit respiration from air instead of water, enable feeding in a substantially less viscous fluid environment, and develop diverse sensory reception systems and complex neural processing of sensorial information (*19*, *66*, *67*). Central to these questions is the understanding of biomechanics and energetics in species throughout the development of terrestrial locomotor modalities. Paleontological evidence suggests that many elements necessary for terrestrial locomotion, such as the evolution of robust limbs, enhanced musculoskeletal structures, and augmented load-bearing capacity, predated the terrestrial colonization by ancestral taxa, which implies that these traits may have had a function in an aquatic environment (*65*).

To explore the evolution of these traits, researchers can investigate the development of underwater walking, which arose multiple times independently in bony (lobe-finned and ray-finned) and cartilaginous fishes. This has resulted in extant fishes with substantial anatomical differences, such as compositions of their internal skeletons (for example, bone versus cartilage) (*68*), shapes of their bodies and propulsors (*69*, *70*), and mechanisms for control of their buoyancy (for example, swim bladder versus liver) (*71*) to walk underwater. Researchers can use data from extant species that exhibit a variety of walking behaviors, such as the "crutching" of mudskippers (*72*), the "forward walking" of flatfishes (*73*), and the "punting" of skates (*74*), to synthesize underlying principles of underwater walking.

However, comparing walking patterns across different fish species is nontrivial because underwater walking includes a variety of behaviors where propulsors and the body are in contact with the substratum (*75*–*77*). Therefore, there are many ways to walk and many morphologies by which to achieve this task. One way to tackle this issue is to customize robots to mimic features of different fish species while standardizing parameters such as their sizes or shapes. Robots inspired by the morphology of a fish species can be programmed to move using patterns observed in another species. This approach allows scientists to pinpoint the contribution of morphology and kinematics on locomotor strategies, providing insights into the efficacy and efficiency of motion.

This framework, once validated by the observed motions of extant fishes, can be used to study the relationship between form and function in extinct benthic fishes where only partial morphology is known (for example, *Tiktaalik roseae*) or to hypothetical forms whose remains may have yet to be found in the fossil record. For instance, current hypotheses on the water-land transition hold that adaptations for a more efficient walking gait include the rotation of the glenoid joint and appendage from caudally facing to laterally facing (*78*), a corresponding change in orientation of the scars on the humerus that are assumed to have held the pectoral muscles (*20*, *79*), and the increased flexion of the elbow of the fin (*19*). Researchers can investigate how gradually changing a single element of the system (for example, limb orientation or natural position of a joint) as it might progress in evolutionary time can affect stride length, power, and energetic efficiency. Designing a reconfigurable paleoinspired robot and measuring its interactions with the dirt, rocks, water, and air around it can quantify the ways a changing environment (for example, fully aquatic walking over rocks in a stream, partially submerged walking on a muddy riverbank, and fully terrestrial walking) can affect the evolutionary pressures on a fish (Fig. 2).

Paleoinspired robotic platforms can generate experimental data on dynamic system-environment interactions to link energetics, morphological characteristics, and movement. Changing features of the robot in isolation can be used to investigate specific causal relationships, whereas changing features in combination can test larger hypotheses of anatomical change and function on the scale of entire organisms. Advanced rapid prototyping and robotics techniques allow experiments with an array of structural and mechanical variations as analogs for unseen extinct species. Furthermore, the ability to create robots with properties not observed in extant or fossilized fishes can help discover which morphologies are fundamentally improbable or impossible. These discoveries can provide additional hypotheses, such as potential missing links in the evolutionary tree. Furthermore, this paleoinspired robotics approach spanning the study of extinct to extant organisms not only can focus on individual species of interest but also can validate evolutionary trajectories and postulates as a whole.

CASE STUDIES

As described above, paleontologists have previously used many engineering methods to advance the understanding of biological evolution (*80*–*84*). To understand how lineages evolved, though, researchers need to understand the interactions between these animals and their environments that created the pressures that drove evolution. The use of physical systems and experiments is thus critical in understanding evolutionary pressures; here, we detail recent research relevant to paleontology, plasticity, and robotics that draw conclusions about ancient organisms from physical models.

Exploring plastic responses in extant amphibious fish as an analog to water-to-land evolution

One method of investigating the water-to-land transition is to examine existing organisms that have similarities to the early fishes of interest because the bodies of extant fishes can be compared with fossilized structures (*85*) and locomotory patterns can be compared with ancient trackways (*86*) of extinct animals. Researchers have identified the bichir *Polypterus senegalus*, a fish native to African swamps, as a target for research on the water-to-land transition because it is phylogenetically similar to the common ancestor of ray-finned fishes and tetrapods (*87*), it has pectoral fins located ventrolaterally that can support its body mass on land, and it has lungs so it can be raised under terrestrial conditions (*52*).

The body and fin motions of *P. senegalus* are specific to the environment in which it is moving. Although terrestrial walking is driven by undulatory motion, contact with the substrate and decreased buoyancy constrain the amount of motion exhibited by the body. As *P. senegalus* transitions from fully aquatic to semiterrestrial environments, its pectoral fins switch from in-phase to antiphase motion (*88*). Its fin muscles also increase the stiffness of propulsors to support the body mass on one fin while the other fin moves forward (*89*).

Prolonged exposure to terrestrial environments can induce a shift in the locomotor behavior of *P. senegalus* that is accompanied by a morphological change to better support its weight out of water and to increase the mobility and efficacy of the walking fins (*52*). Bichirs raised under terrestrial conditions exhibit fewer unnecessary movements, and prolonged exercise on land possibly affected skeletal and muscle growth (*90*, *91*). The plastic responses to training resemble the changes observed in fossils of early stem tetrapods, suggesting that plasticity may have facilitated the emergence of traits involved in the transition from water to land (Fig. 3A) (*52*). Robots could be used to further quantify how these shifts in morphology and kinematics affect ground reaction forces and loads on joints, which can then be applied to paleoinspired robots.

Combining computational and experimental fluid dynamics to analyze the unique body plan of plesiosaurs

Plesiosaurs have been a popular case study in both paleontological and engineering research because of their unusual body morphology. Their morphology (long necks, large bodies, and two identical pairs of flippers) is so different from other animals (*92*) that research on plesiosaur morphology is a useful example of the ways engineering methods and paleoinspired robotics can be integrated to study extinct organisms.

Many researchers have contributed to the extensive analysis of plesiosaurs and their interactions with the surrounding aquatic environment. Models using computational fluid dynamics have shown that further elongation of the neck of the plesiosaur did not noticeably affect the drag for thicker neck diameters (*93*) and that the effects of substantially elongated necks were mitigated by increasing the thickness of the entire trunk (*42*). Bending of the neck increases the surface area in contact with the flow during swimming, thus increasing drag, but a finite element analysis of the neck structure predicted a small range of motion and increased stiffness against bending (*94*). This suggests that hydrodynamic effects were not a notably negative evolutionary pressure on the length of the neck but did incentivize a thicker neck, which partially explains how this unique morphology could develop.

Researchers have also performed computational analysis on the unusual identical pairs of flippers, showing that the length and slenderness of identical pairs of foils affect the vortices from the fore fins that interact with the rear fins (*95*). By imaging physical foils in a tank, researchers found that the relationship between the amplitude of the flapping for generic identical pairs of foils can either act constructively to increase the thrust of the rear foils or create destructive interactions that decrease the thrust of the hind foils (*96*). A similar type of experiment was performed using flippers specifically fabricated to mimic plesiosaur morphology and indicated that the phase difference between the fore and hind flippers affected the efficiency of the rear flippers (Fig. 3B) (*9*).

These techniques allow the examination of dynamic phenomena that would, otherwise, be lost to deep time. Engineering analyses demonstrated that the unusual morphologies of plesiosaurs were evolutionarily neutral from a fluid mechanics standpoint, contradicting the previous consensus. Researchers were also able to extract general scientific principles from abstracted designs (for example, identical pairs of generic flippers) that can be extended to physical models based on fossilized animals, adding to the domain knowledge across fields. Furthermore, paleoinspired robotics could be used to evaluate how the animal's swimming speed and maneuverability changes with gradual morphological changes between the pairs of flippers, linking the fluid dynamics and vorticity analysis directly to performance and to explore why two distinct pairs of flippers evolved in other species.

Studying animal-ground interactions during locomotion using a soft model of a theropod foot

Physical models can be extremely helpful for examining potential interactions between an extinct organism and its environment. However, analysis of fossils and biomechanical simulations often give incomplete pictures of an animal's existence, especially with respect to the soft tissues that are rarely preserved in the fossil record (*97*). A common technique used by paleontologists is to apply some assumptions on the basis of the organization of the tissues of extant animals to the missing tissue around the preserved remains (*98*, *99*).

These details are important for studying interactions with the environment because soft tissue can deform noticeably when forces are applied during locomotion. Researchers reproduced fossilized *Australovenator* foot morphology by casting soft silicone in a three-dimensional (3D) printed mold, and tracks made by the soft model in sediment matched an unidentified fossilized trackway, allowing researchers to conclude that the trackway was likely created by a theropod. The softness of the artificial foot was necessary to reproduce specific features in the fossilized tracks caused by the deformation of the soft tissue between the foot bones as the foot impacted the sediment (Fig. 3C) (*10*).

Understanding the differences between underwater and in-air environments is vital for understanding the water-to-land transition because the fluid forces on the same system are often vastly different in different environments (*100*). For example, the way an animal supports its weight in terrestrial existence (low-buoyancy environment) is hugely different than the way it does so in aquatic life. Depending on whether the system was aquatic or terrestrial, evolutionary algorithms pushed the design of soft mobile robots toward different stiffnesses and morphologies of locomotory structures even when starting from similar initial conditions (*101*). The differences in environment can result in strong pressures on an

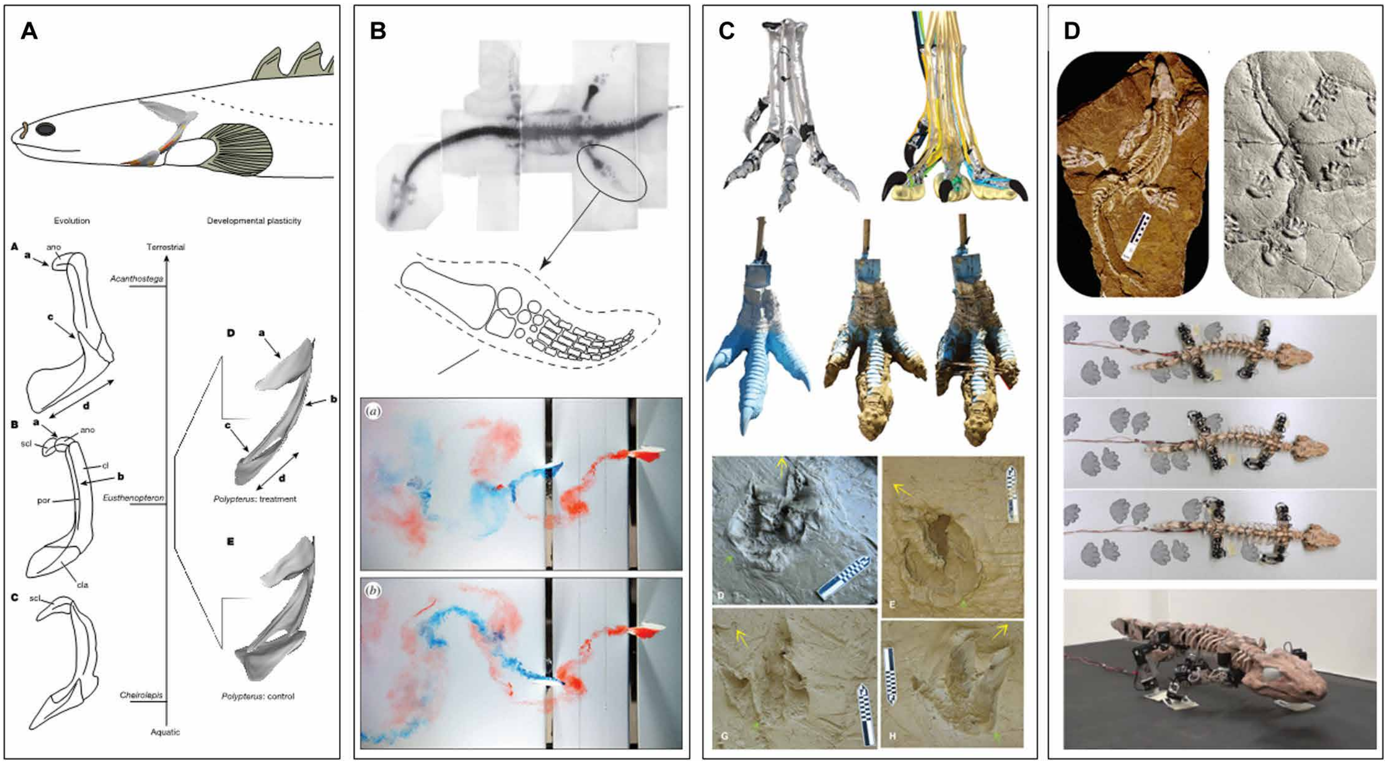

Fig. 3. Examples of research combining paleontology, biology, and robotics. (**A**) An example of using observations of extant animals to hypothesize about the evolutionary development of extinct species. *P. senegalus* specimens raised in a terrestrial environment exhibited morphological changes to enable both fin mobility and load bearing during land locomotion, adaptations similar to those found in early tetrapod fossils (*52*). (**B**) An example of using experimental fluid dynamics techniques on a replicated appendage from an extinct species. Constructive interactions between the vortices shed by the plesiosaur flippers could increase the efficiency of the hind flippers by up to 40% (*9*). (**C**) An example of using a physical model to mimic soft tissue of an extinct animal. Researchers used soft material in a foot model to replicate deformation during contact with the ground to match a fossilized trackway of a theropod (*10*). (**D**) An example of applying a neurological model developed from extant animals to match the structure of an extinct tetrapod to a fossilized trackway. CPG-driven locomotion derived from salamanders was prescribed to a robot replicating the skeleton of a stem amniote and the footfall pattern of the robot matched observed prints (*14*).

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animal in both the evolutionary time scale [for example, the development of laterally facing fins from caudally facing ones (*65*)] and the individual time scale [for example, additional ossification of bones in terrestrially raised *Polypterus* specimens compared with aquatically raised ones (*52*)]. These studies motivate the use of a paleoinspired robotic model that can move and interact with the physical world so that researchers can measure the effects of morphological changes on locomotory performance rather than limiting the analysis to the matching of a single type of static trackway.

Applying a neurological paradigm to an extinct stem amniote and its trackway

Robotic models and simulations can be used to contextualize observations from fossils with similar features and behaviors in extant animals. An analysis of *Orobates pabsti*, an extinct stem amniote (*102*), indicated a body plan conducive to sprawling locomotion in which the legs of the animal protrude from the sides of the body rather than the underside of the body. To develop models for sprawling gait walking, researchers investigated the locomotion kinematics, energetics, and neuroactivation of animals like the salamander.

The development of a neurological model underpinning locomotion of vertebrates in both terrestrial and aquatic environments allows researchers to investigate the transition between the two environments and the mechanisms that govern coordination of appendage and body movements induced by neural activity (*34*). A set of central pattern generators (CPGs) drives motion of the body and of the legs separately, and coordination between the two is possible because the CPG of the appendages can override the natural frequency of the body CPG. An automatic transition between walking and swimming gaits is achieved by modulating the frequency of the input because saturation of the appendage oscillators occurs at sufficiently high drive frequencies. The relationships between these oscillator dynamics were further explored in a robot with limbs and body segments driven by two CPGs, verifying that the velocity, direction, and type of gait could be governed by modulating the frequencies of these two inputs to the robot.

To further anchor robotic models of sprawling locomotion, more detailed robots were created to study interaction with the physical world. An amphibious salamander-inspired robot explored the effects of parameters, such as input frequency and amplitude, tail morphology, and limb posture, on both swimming and walking motions (*103*). The model was extended even further to replicate the morphology and kinematics of the Iberian ribbed newt, *Pleurodeles waltl*. Using computed tomography imaging of the animal's body structure and visual tracking of the range of motion of its limbs, a robot could closely reproduce the locomotion of this animal so that experiments modifying actuation parameters could be tested in the physical world (*104*).

Then, to generalize these findings to other quadrupedal animals, extensive observations of several extant species were used to identify a set of parameters and performance metrics that define a class of locomotory behaviors called the sprawling gait space. The large sprawling gait space was narrowed down via anatomically detailed simulations first to feasible gaits through kinematic constraints (for example, avoiding self-collisions within the skeleton) and then to likely gaits via performance metrics (for example, power expenditure and accuracy of foot placement within trackways). Researchers evaluated this framework by simulating existing animals and comparing the generated gaits to the kinematics observed from the animals. Last, this framework for modeling tetrapod locomotion was applied to *O. pabsti*, an extinct organism for which both intact skeletons and fossilized trackways have been discovered, and a paleoinspired robot, OroBot (Fig. 3D). The generated gaits suggested that the gait of *O. pabsti* occupied a similar position in the sprawling gait space as caimans and that it exhibited locomotory properties previously thought to have evolved later in the amniote lineage (*14*).

This is a promising example of the whole paleoinspired robotics framework: using observations of extant animals (caimans, salamanders, and others) to elucidate general principles of a physical phenomenon (sprawling legged locomotion) that can then be applied to extinct animals whose behaviors cannot be observed (*O. pabsti*) via a physical robot (OroBot). This combination of paleoinspired robotics and engineering-driven analysis of biological systems is crucial for generating physical data to close the loop between environment and morphology in experimental paleontology. Because paleontologists are often unable to directly observe features of interest (for example, structures made of soft tissue and the time-series motions of joints during locomotion), researchers must find other methods to anchor models in measurable mechanical data. Clearly defined quantitative metrics for comparing extant and extinct animals establish a pathway for validating conclusions from a paleontological model using present-day biological data. Identifying parameter spaces in which similar species' morphologies and motions exist can increase the generality of the model to broadly study the evolution of a feature. Researchers might even be able to hypothesize about the likelihood of specific features or behaviors in a species that may have existed but for which no fossils have yet been found on the basis of where the traits of other species fall within the models' parameter spaces.

FUTURE DIRECTIONS FOR PALEOINSPIRED ROBOTICS

This Review discussed the inclusion of an evolutionary dimension in bioinspired robotics to create the emerging paradigm of paleoinspired robotics. Understanding the major discrete stages of the history of life, such as water-to-land transitions, is a fundamental scientific challenge that can advance our understanding of how biodiversity, habitats, and evolutionary adaptations are related to each other. To investigate the evolutionary lineage of extinct animals whose complete morphologies and behaviors can no longer be observed, we can use analogous robotic models to fill gaps in the fossil record and explore other potential intermediate forms. Like bioinspired robots, paleoinspired robots can create repeatable experiments without the variation between specimens inherent in real animals and can take specific, prescribed morphologies and behaviors to investigate features of interest. As such, robots enable the closing of the iterative feedback loop in both paleontological and biological research because researchers can refine their hypotheses as new experimental data are generated from the robot.

Roboticists are sensitive to the "sim2real gap," which refers to the differences between a real system and a simulated system that is fundamentally made with simplifications in elements such as the environment, material models, or general resolution (*105*). Although paleoinspired robotics avoids some of these traditional sim2real drawbacks by operating in the physical world, there are analogous discrepancies and uncertainties that arise from the intrinsic differences between animals and robots. Thus, conclusions reached from data collected on a robotic platform cannot automatically be accepted without some analysis of whether the robot is a realistic representation of all of the pertinent aspects of the animal. It is difficult to use the paleoinspired robotics framework with an unobservable, extinct species without biological analysis and bioinspired robots that anchor new robots in data from extant animals (for example, energetics and kinematics). If roboticists can justify that their bioinspired robot acceptably replicates the relevant features of a living organism, then they can have more confidence in extending the method to replicating an extinct organism. For example, if the motor control strategy of a fishlike robot can create an undulation motion like that of the bichir, then it is reasonable to think that similar motor control on a robot with morphology inspired by *T. roseae* can create an undulating motion representative of that extinct animal.

The expansion of the field of paleoinspired robotics can be substantially accelerated today because of the extensive development of robotics technologies such as 3D scanning and printing, soft material actuation and fabrication, computational optimization and design, and machine learning. The case studies introduced here demonstrate the power of these technologies to advance scientific understanding of evolution and ancient organisms and habitats. Three-dimensional scanning and printing can produce complex, realistic internal structures like bones or joints on demand (*106*). Soft materials can make life-like models, create realistic interactions with the ground or surrounding fluid, and enable experiments about hypothetical soft tissues, like skin and ligaments, that cannot be done with traditional rigid materials (*107*). Control engineering and machine learning techniques can also be used to understand how adaptive actuator control can evolve along with morphological evolution (*108*).

However, to study physical evolution in robots, roboticists need to address the large time and effort costs of building new generations of robots (*109*) and push the boundaries of evolvable hardware to create a robotic analog to structural growth (*110*). Although there have been previous approaches to shape-changing robots, they cannot exhibit the large degree of morphological changes necessary for true evolution of physical robots. Shape-morphing robots are often only able to change between predetermined states (*111*), and self-healing and regenerative robots can only reform parts of their structures to restore functionality and cannot create completely new features (*112*, *113*). Everting vine robots can extend in length, but their overall topologies remain constant (*114*, *115*), and growing robots that leverage additive manufacturing cannot alter their existing structures (*116*). Biohybrid robots that couple mechanical and electrical hardware to living cells can produce robots that can grow and evolve (*117*–*120*), but the presence of living cells reduces the experimenter's control of the resulting system.

Despite these challenges of creating evolvable hardware, imitating evolution using physical robots is a critical element of studying how morphological optimization mechanisms dictate an animal's progression through a sequence of forms and how successive adaptations are affected by evolutionary pressures. Although this article focuses on the benefits of applying robotics to paleontological research, it is important to mention that paleoinspired robotics research can also advance evolutionary robotic technologies and applications. There has been much progress in the simulated evolution of robots (*121*, *122*) but few advances in the evolution of real-world robots (*123*, *124*). Traditional evolutionary robotics involves a substantial amount of stochastic search that, when applied to physical robots, can result in wasted time and material through the fabrication of infeasible configurations. Instead, roboticists can use processes informed by the principles of natural evolution that incrementally modify elements of a design over time, such as selection gradient analysis that quantifies the direction and magnitude that specific traits of interest change in successive generations or morphospace walks that account for the interplay between morphological forms and traits in an n-dimensional feature space (*125*). With a design process drawn from paleontology and evolutionary biology, the system-environment interaction generates an intentional, directional search for solutions instead of a random search.

We envision a future where paleontologists, biologists, and roboticists work closely to study the link between form and function across the evolutionary history of groups of organisms from different angles. Much as the field of bioinspired robotics has driven roboticists to study biological mechanisms and biologists to learn engineering techniques, including paleontology in the partnership will further enhance the training of early-career researchers in interdisciplinary thinking and problem-solving. Not only does collaboration produce more conclusive paleontological and biological theories, it also creates new paradigms for physical evolution of higher-performance robots. Understanding evolution from the sparse information remaining from deep time will require the fusion of fossil evidence, observations of and experiments with extant animals, and robotic models with soft materials and intricate rigid structures that can both perceive and act within the physical, natural environment. Examining life in the past will help scientists of all disciplines understand more about the world as it is today and how our ever-changing environment may possibly influence form and function in the future.

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