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Perspective

Bio-inspiration unveiled: Dissecting nature's designs through the lens of the female locust's oviposition mechanism

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SUMMARY

Investigating nature's ingenious designs and systems has become a cornerstone of innovation, influencing fields from robotics, biomechanics, and physics to material sciences. Two key questions, however, regarding bio-inspired innovation are those of how and where does one find bio-inspiration? The perspective presented here is aimed at providing insights into the evolving landscape of bio-inspiration discovery. We present the unique case of the female locust's oviposition as a valuable example for researchers and engineers seeking to pursue multifaceted research, encompassing diverse aspects of biological and bio-inspired systems. The female locust lays her eggs underground to protect them and provide them with optimal conditions for survival and hatching. To this end, she uses a dedicated apparatus comprising two pairs of special digging valves to propagate underground, while remarkably extending her abdomen by 2- to 3-fold its original length. The unique digging mechanism, the subterranean steering ability, and the extreme elongation of the abdomen, including the reversible extension of the abdominal central nervous system, all spark a variety of questions regarding materials, morphology, mechanisms, and their interactions in this complex biological system. We present the cross-discipline efforts to elucidate these fascinating questions, and provide future directions for developing bio-inspired technological innovations based on this remarkable biological system.

INTRODUCTION

Nature has evolved over billions of years, resulting in intricate and efficient mechanisms and designs that have enabled organisms to adapt, survive, and thrive in diverse environments. By observing and understanding these natural solutions, researchers and engineers can create innovative technologies that mimic or are inspired by biological systems,[1–3] materials,[4–7] processes,[8–12] and structures.[13,14] Furthermore, they can establish fundamental guidelines and physical laws to explain specific structures, functions, and form-function relations.[15,16]

The field of bio-inspiration and biomimicry is a rapidly growing one.[1–3] However, while the potential benefits of this approach are undeniable, the challenges in finding and deciphering the distinct relevant biological phenomena and, moreover, translating these inspiring phenomena into practical solutions, are substantial and multifaceted.[17,18] In other words, biological information is by and large under-exploited.[19] Engineers possess essential knowledge and expertise in the development of mechanical systems, materials, and integrated frameworks that can bring bio-inspired concepts to realization. Most engineers, however, do not hold the necessary biological background and the basic knowledge that enables identifying, filtering, and understanding the biological solutions and applying them in technological innovations.[17,20] The crucial questions are, therefore, those of where to seek bio-inspiration and, once located, how to take advantage of it.

In the current short perspective, we seek to provide some insights into how to engage with the above challenges by presenting an example – a case study – of the journey: from an intriguing biological observation to bio-inspired innovations. We highlight the essential collaborative aspects of this endeavor, i.e., the interdisciplinary joint effort that encompasses the expert biologist on the one hand and the specialist engineer on the other. It should be noted that this is by no means a retrospective of past completed research. Some of the work we describe is ongoing, we present some new data, and we also suggest some future directions.

In the following, we first depict the biological observation (Section 1) – the specialized oviposition behavior of the female locust. The subsequent sections present different research directions, aimed at establishing an in-depth understanding of different aspects of this initial observation (Figure 1).

Section 2 engages with the investigation of the kinematics and dynamics of the female locust digging behavior. Section 3 presents a characterization of the properties of the oviposition

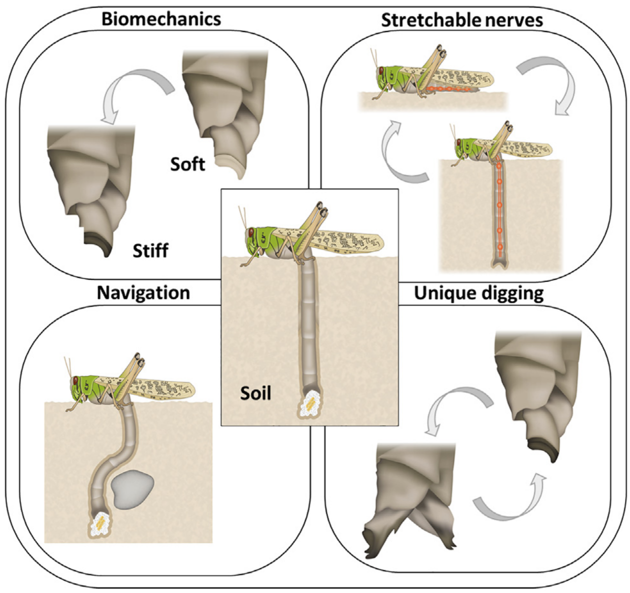

Figure 1. Finding bioinspiration in the female locust's oviposition
The female extends her abdomen, digs, propagates and navigates underground using two pairs of valves and various sensory modalities.

valves in terms of materials and mechanical response; and Section 4 presents a study of the ultra-stretchable nervous system of the female locust, allowing the abdomen to stretch up to 3-fold during oviposition. These seemingly unrelated aspects of this successful mechanism demonstrate the complexity of the biological system and its multi-faceted nature. We then move on to offer a perspective of the development of a locust-inspired digging robot with the ability to interact with its environment (Section 5), and a short summary.

The female locust's oviposition behavior

Egg-laying constitutes a pivotal element in the reproductive biology of all insects. The strategic deposition of eggs in a meticulously chosen location, on or within a carefully selected substrate, constitutes a significant decision and a critical action undertaken by the female insect to secure the survival of her offspring. Locusts (Orthoptera: Acrididae), notoriously recognized for their capacity to undergo drastic population explosions, transforming from solitary individuals to formidable swarms, impose a profound negative impact on crops and ecosystems.[21] The oviposition behavior of female locusts assumes a central role in their population upsurge and outbreak.[22] The female lays her eggs deep underground, in order to protect them from predators and to provide them with optimal conditions for hatching (Figure 2). This behavior involves various physiological adaptations and challenges related to negotiating the subterranean environment.

Accordingly, evolution has developed a highly specialized structure — the ovipositor: the principal apparatus that enables burrowing into the ground. It comprises two dedicated pairs of sclerotized oviposition valves – a ventral and a dorsal pair, extending beyond the distal end of the female's abdomen[23,24] (Figure 1: Unique digging; Figure 3). These external structures are aided by a prominent pair of internal apodemes (a ridge-like ingrowth of the exoskeleton), hinges, and large supporting muscles.

The oviposition behavior marks the culmination of the egg maturation cycle, occurring approximately every 7–10 days. The female carefully chooses the site where her offspring will develop. This should have optimal conditions in terms of temperature, salinity, and humidity.[22,25] Hence the ovipositor is equipped with a sophisticated sensing ability by means of ample sensory hairs and other sensory receptors.[26,27] Females possess the ability to postpone egg-laying for several days when no appropriate site is available. The female may also decide to retract her abdomen after initiating the burrowing without laying the eggs. Thus, the decision-making process, coupled with the mechanisms governing oviposition behavior, indicates the intricate and dynamic interplay between the female locust's internal physiological state and her adaptive responses to the environmental cues that are crucial for an optimal reproductive outcome.

The kinematics and dynamics of female locust digging

As noted, the initial phase of oviposition behavior in grasshoppers and locusts entails digging a deep hole in the ground. What sets them apart from many other insects is their distinctive ovipositor valves, which operate through precise opening and closing motions rather than simply sliding over one another. To initiate this process, the female generates sweeping movements of the digging valves, while pressing the tip of her abdomen into the substrate. Once the ovipositor is firmly embedded in the soil, the female maintains her position on the surface while the ovipositor delves beneath her. The cyclical movements of the valves include opening, closing, retraction, and protraction movements (Figure 3), which are produced by the contractions of ten pairs of muscles innervated by a central pattern generator network in the terminal abdominal ganglion.[28–30] While this two-dimensional analysis has led the investigation and discussion in many previous studies, we emphasize here that in order to achieve a thorough understanding of the digging mechanism, and for the ability to mimic its kinematics using robotic systems, a detailed three-dimensional analysis is crucial.

In order to monitor the three-dimensional trajectory of the digging valves, it is useful to induce their rhythmic motion in air (out of the soil; Figure 3). This can be achived by severing the ventral neural connectives anterior to the abdomen and releasing the motor program from descending inhibition.[30] Figure 3 shows the digging valves throughout their movement cycle, including projections of their three-dimensional tracks from three perspectives. The projections demonstrate several vital points: the dorsal valves perform much larger longitudinal motion in comparison to the ventral valves, supporting their postulated major role in the digging (soil shoveling), while the ventral valves mostly act as anchors. When the valves open, the gap between the ventral valves expands in order to grip the sides of the tunnel, while the gap between the dorsal valves contracts in order to better compress the soil and dig more efficiently. When closing, the ventral valves draw close together, as there is no longer a need to grip the ground, and the dorsal valves move apart from each other to allow the ventral valves to rest between

Figure 2. Time lapse of oviposition process

A female locust extending her abdomen deep into the substrate (snapshots from a video sequence captured through a glass wall). Bars on the left (i) indicate centimeters. White arrows (i-iv) indicate the ovipositor digging valves and the yellow dashed line in (iv) shows the egg pod left in the burrow as the female retracts her abdomen.

them. Finally, the right and the left dorsal and ventral valves move in a coordinated way: namely, each pair of valves operates in synchrony.

The oviposition behavior also involves the hyperextension of the female's abdomen, as detailed below. In addition, the abdomen is able to rotate around its long axis to enable the valves to compress the displaced granular matter to the sides of the burrow. Video monitoring of the oviposition digging (same sequence as shown in Figure 2) revealed a rotation of at least 90° to the left and to the right (overall rotation of ca. 180°; Ayali and Pinchasik, unpublished). A further important ability of the female is that of circumventing obstacles by bending and steering her abdomen underground. As recently investigated and well documented by Klechevski et al.,[31] upon encountering an obstacle in their path, the digging valves are steered away taking a new route (even perpendicular to the original route), and returning to vertical digging once clear of the obstacle (Figure 1: Navigation).

The properties of the locust's oviposition valves

The female locust's oviposition valves demonstrate very well-adapted functional, morphological and structural properties. From a developmental perspective (ontogeny), the transformation of the female locust ovipositor valves is particularly intriguing. These valves originate from embryonic, paired, ventral appendages, which are serially homologous to structures like legs and wings.[32] In newly hatched females, the valves appear as paired outgrowths at the posterior margins of the last abdominal segments (A8 and A9). They undergo a series of growth and differentiation steps across five larval stages, achieving the adult ventral/dorsal orientation by the third instar. During the fourth and fifth larval stages, the valves continue to grow with each molt, extending beyond the abdomen's tip upon reaching adulthood. Over the course of two to three weeks, these initially soft valves undergo further enhancement and become densely sclerotized as the animal matures sexually.[24]

While the two pairs of valves are morphologically similar in principle, their size and shape are specifically adapted to their respective functions. This was recently reaffirmed using a geometrical model and finite element methods.[33] Interestingly, it is postulated that the unique geometrical adaptations of the valves have evolved to enhance their digging capabilities rather than solely to maximize the mechanical bearing of their digging forces.

In order to gain insights into the functionality of the specialized oviposition apparatus and provide mechanical guidelines for the design of bio-inspired digging mechanisms,[2] it is crucial to quantify various biomechanical factors.[24] These include the physiological force range, force-deformation behavior, yield strength, ultimate strength, flexibility and adaptability to difference surfaces,[34] and the directional dependence of mechanical responses to applied forces.

Recently Das et al.[24] quantified and analyzed the direction-dependent biomechanics of the locust female's dorsal digging valves under forces within the physiological range and beyond, considering the hydration level as well as the female's sexual maturation state. The responses of the valves to compression forces in the digging and propagation directions, and the valves' stiffness were found to change upon sexual maturation. In the case of insect cuticles, the hydration state is also a key factor influencing their mechanical properties. Hydration was found to reduce stiffness, but increase resilience against failure.

Figure 4 presents maximum intensity projection auto-fluorescence high-resolution laser scanning confocal micrographs (LSCM) of the female locust's dorsal valves at different stages of life. We used excitation lasers in wavelength of 543 and 633 nm. One week after molting (Figure 4A), the tip of the valve is sharp, the cuticle is covered with several sensilla and the valve surface emits photons mostly in the green region of the light spectrum, indicating cuticle structural materials that are less densely sclerotized.[35] In a four-week-old adult female with oviposition history, the image appears very different (Figure 4B). Namely, the tip is worn and rounded with visible abrasion exhibited by grooves in the direction of digging. The sensilla are less distinct, probably due to the significant mechanical shear forces during oviposition and digging underground. While a significant region is dominated by red color, indicating a higher density of sclerotized chitinous exoskeleton material, the tip seems

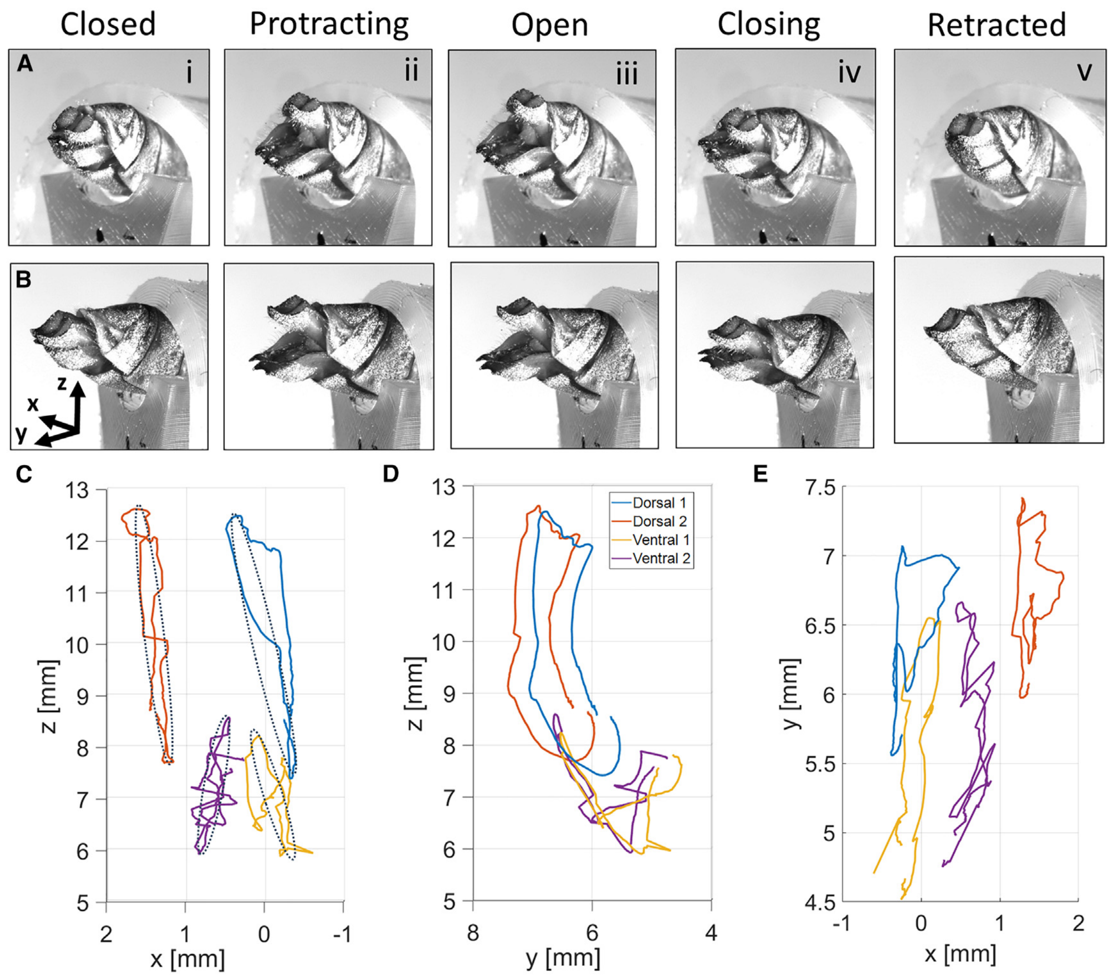

Figure 3. Three-dimensional imaging of the digging motion

(A) The valves open and close cyclically.

(B) During this opening and closing, the valves protract or retract from the abdominal cuticle.

(C–E) Graphs demonstarte the 3-D trajectory of the two pairs of valves; projections from three perspectives. Different colores depict the different valves; see insert in (D).

green, indicating removal of the exoskeletal layer. Recently, we have extended this example and conducted a detailed mechanical and nano-mechanical analyses of the locust valves.[36] There remain, however, important open questions regarding the presence of structural and material gradients in the locust oviposition valves, and the role of these in the digging mechanism and in resistance against wear. Our understanding of the effects of friction forces acting on the locust valves in different granular media is also very limited to date.

The biomechanics of the ultra-stretchable nervous system of the female locust

To enable the abdominal elongation during digging, the soft cuticle between several abdominal segments and the intersegmental muscles are modified, permitting about a 10-fold length change without damage.[23,37] It was, however, unclear until recently whether the nervous system stretches during oviposition or simply comprises undulated nerves that unfold reversibly, as known in other animals in which the nerves can extremely elongate.[38,39] In our recent study, we showed that the abdominal nervous system (ANS) of mature female locusts exhibits a remarkable ability to elongate, stretching to approximately 250% of its original length (Figure 5).[40] This exceptional hyper-extension ability is exclusive to sexually mature females, as pre-mature females and males show significantly smaller elongation capacity. Moreover, this extraordinary stretchiness is fully reversible within the physiological range of extension rates and can be repeated multiple times throughout the lifetime of mature female locusts. Specifically, sexually mature females display only minimal nerve fiber undulation, which cannot account for the ANS tissue's remarkable hyper-extension.

Based on the afore-mentioned discoveries, it is crucial to delve deeper into characterizing the biomechanics of the distinctive hyperextension observed in the ANS of sexually mature female locusts. Understanding and emulating the reversible

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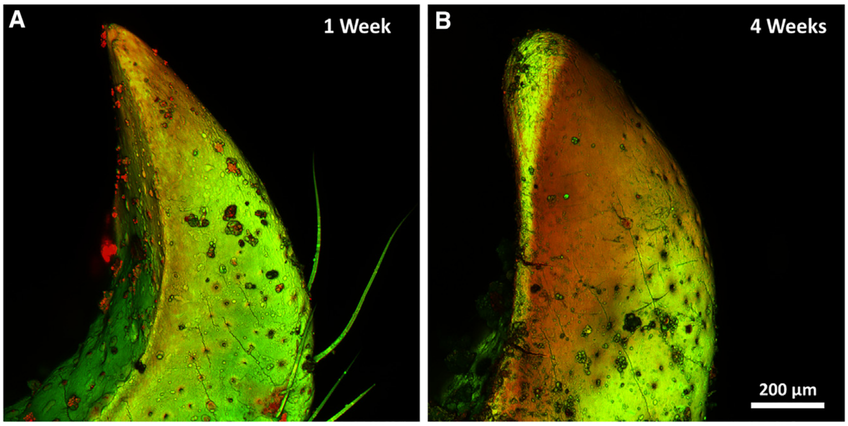

Figure 4. Material gradients in the female locust's digging valves

(A) A laser scanning confocal microscopy image of a dorsal digging valve of a female one week after adult emergence, showing mostly green region fluorescence, indicating less densely sclerotized cuticle structural materials.

(B) A similar image of the dorsal valve of a one-month-old adult female with oviposition history. The digging surface is dominated by red colors, indicating higher density of sclerotized chitinous exoskeleton material. Note the worn tip (see text for details, and see[36]).

stretching mechanism of locust nerves may pave the way for producing new models of tissue regeneration and repair. Furthermore, this insight can contribute to the structural design and development of soft robotic systems characterized by significant stretchability and multiple degrees of freedom.

Concluding remarks and outlook: A digging robotic device inspired by the female locust oviposition

In the above short perspective, we have presented several recent research projects, focusing on different, yet related aspects of the female locust oviposition; from behavior and physiology, to biomechanics and material science. These were meant to exemplify a principal research approach, or even a way of thinking that we consider essential for any successful attempt of harnessing nature's ingenuity to technological innovation. Namely, the constant interdisciplinary exchange of data, insights and ideas. Including engineers in the early, basic-research phases of the research, as well as having the biologists accompany the later, applied engineering phases of the process, will mitigate and facilitate the successful transfer of the biological knowledge to the engineering solution. A joint, cross-disciplinary effort is required to decipher and fully appreciate bio-inspired innovation.

Given the above-noted aspects of the female locust oviposition, we have highlighted some of the different characteristics that need to be addressed when approaching the development of a female locust-inspired digging robot: namely, the shape of the valves and their mechanical stability, the dynamics of digging, stretchable materials (alternatively, soft robotics), sensing, energy consumption and, finally, control and decision making in response to external cues. Maybe even more important, however, we have identified some general principles, fundamental to the (evolutionary) processes that shape natural mechanisms and designs, that must be considered. These include (but are not limited to) nature's "good enough" principle,[36] and to the multiple and interacting facets of biological systems.

Nature's "good enough" principle suggests that natural materials and mechanisms answer specific needs without the unnecessary improvements and enhancements known as "over-engineering" in man-made systems. Robotic systems, in conjunction with additive manufacturing, offer the possibility to determine whether the natural solution is indeed the optimal one (e.g., in terms of digging efficiency and energy consumption), or can it be further improved using alternative designs,[41] motion planning,[42–44] and reinforcement learning.[45,46] For

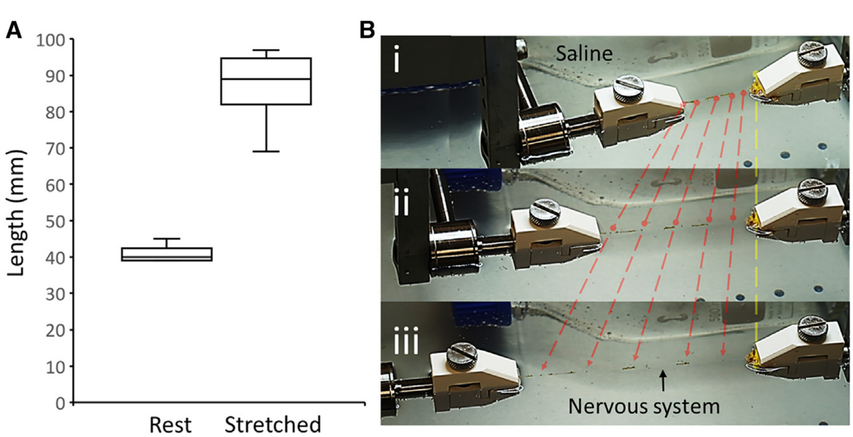

Figure 5. The biomechanics of the female locust nervous system

(A) The abdominal nervous system of a sexually mature female locust before and after manual stretching, demonstrating a ca. 220% extension. Error bars correspond to the data range.

(B) The nervous system was clamped and stretched in a controlled manner while its length and the exerted forces were monitored. Bullets and dashed red lines denote the location of the five abdominal ganglia along the nerve cord. Figure modified from Das et al. 2022.[40]

these reasons, brushless motors are used in many robots, which offer efficiency, reliability and high energy density.[47–49] In addition, the mechanical design can be engineered and modified in order to adjust the robots to different environments, including granular matter of varying densities, mechanical properties, and dispersity.

Somewhat related to the above, it is important to look at biological systems as a whole and acknowledge the multiple, parallel mechanisms that allow each function to exist. In the case of the female locust oviposition, this is reflected, among others, in her ability to dig in a specific area using a unique digging apparatus, to develop the strengthened materials that can bear the mechanical loads during digging, extensively stretch the abdomen and nervous system to enable it to reach the proper depth, and more. It is crucial to realize that all these aspects have evolved in conjunction. An effort to understand a particular biological solution to a specific technical challenge should always take into account the wider natural context. Understanding the large assembly and interaction between the systems allows us to focus on the required functionality and accordingly simplify the mechanisms. We do not have the ability to produce everything on any scale; therefore, part of the simplification of the mechanisms contributes to reducing the degrees of freedom and reducing the volume and complexity of the system.[2,50–52]

A female locust oviposition-inspired robotic device should be able to demonstrate some, if not all the capabilities that allow the locust to successfully negotiate granular substrate and deliver substance to (or alternatively sample substance from) the subterranean environment at varying depths. These abilities comprise (but should not necessarily be limited to): digging capacity by way of shifting and compressing granular matter; swiveling and rotation to allow the burrow construction and maintenance; extension and bending to achieve the underground progress and also steering capacity (including obstacle negotiation). The leading digging mechanism can follow that of the locust digging valves but can also be improved by changing its overall size, macro and microstructure and materials composition. Energy efficiency comparable (in order of magnitude) to the biological system should be desired, though it is most probably a non-realistic goal. In contrast, resistance to wear and life expectancy of the artificial device should exceed that of the biological system. The rest of the system (beyond the leading mechanism) will probably much divert from the biological model due to our current largely insufficient ability to construct artificial muscles and connective tissues with characteristics comparable to natural ones.

Here may be a good point to stress the foremost important principle of bio-inspired technological innovation – namely, the fact that it is not merely *biomimicry* that we are pursuing, but rather *bio-inspiration*. The locust oviposition-inspired robot may and probably should look very different from the female locust, in every aspect – size, materials, and even mechanisms. It is the principles and ideas that we seek in a bio-inspired design process. Those that were developed and repeatedly tested over millions of years of evolution. It is for us to then selectively adopt, adapt and improve these to suite the specific technological challenge on hand. The animal kingdom exhibits immense biological diversity, ranging from microorganisms to giant whales. Bio-inspiration can be drawn from life forms of all sizes, where scale plays a critical role. Physical phenomena vary across different scales, meaning that in some cases, scaling the mechanisms under investigation is feasible, but not always straightforward.[48,53–56] As these systems interact with their environment, altering the system's scale requires adjusting the environmental context as well. However, this scaling is often imprecise, introducing complexities inherent to real-world environments.[2,57–60]

Developing and constructing a digging robot inspired by the locust oviposition will be applicative to a variety of different fields, from subterranean exploration all the way to a model system for brain surgery.[61–63] These different tentative applications have some major common demands. First, the need for the induction of minimal interference and damage to the substrate. Unlike traditional digging technologies that are primarily based on removing and transferring excavated material, the envisioned bio-inspired device rather "pushes its way" through the substrate, implicating relatively minimal damage. A second and much related point is that of minimalizing the "external or future signature" of the digging procedure. This is most easily demonstrated by or contrasted with the huge pile of dirt left behind after any common digging-for-construction endeavor. These aspects are relevant both on Earth and in extraterrestrial environments, such as Mars.[64–66] Adopting or following basic features and principles of the digging mechanism of the locust will ensure the above demands are addressed.

Last, recent years have witnessed the emergence of robotics-assisted biology, which utilizes robots as a way to create dynamically-controlled conditions, enabling the testing of various biology hypotheses that could otherwise not be tested (e.g.,[67–70]). While we develop the bioinspired device, it will also facilitate an in-depth understanding of the biological nature, function, and evolution of the biological digging organs, offering answers to questions such as whether the shape of the ovipositor valves is indeed the most efficient for soil removal, and what are the relations between the digging kinematics, soil removal, and the consequent energy consumption? These and other questions can be directly investigated and quantified in a locust-inspired digging robot, whereas they are practically impossible to study in the locust itself. Hence, bio-inspired robotics goes hand-in-hand with robotics-assisted biology.

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DECLARATION OF INTERESTS

The authors declare no competing financial interest.

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