Integrative and Comparative Biology

Integrative and Comparative Biology, volume 59, number 6, pp. 1629–1635
doi:10.1093/icb/icz134

Society for Integrative and Comparative Biology

SYMPOSIUM INTRODUCTION

Adaptation and Evolution of Biological Materials

Robert A. Campbell[1,*] and Mason N. Dean[2,†]

*Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-son, Okinawa 904-0495, Japan; †Max Planck Institute of Colloids and Interfaces, Department Biomaterials, Am Muehlenberg 1, Potsdam 14424, Germany

The authors contributed equally to this work.

From the symposium "Adaptation and Evolution of Biological Materials" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2019 at Tampa, Florida.

[1]E-mail: robert.campbell@oist.jp

[2]E-mail: mason.dean@mpikg.mpg.de

Synopsis Research into biological materials often centers on the impressive material properties produced in Nature. In the process, however, this research often neglects the ecologies of the materials, the organismal contexts relating to how a biological material is actually used. In biology, materials are vital to organismal interactions with their environment and their physiology, and also provide records of their phylogenetic relationships and the selective pressures that drive biological novelties. With the papers in this symposium, we provide a view on cutting-edge work in biological materials science. The collected research delivers new perspectives on fundamental materials concepts, offering surprising insights into biological innovations and challenging the boundaries of materials' characterization techniques. The topics, systems, and disciplines covered offer a glimpse into the wide range of contemporary biological materials work. They also demonstrate the need for progressive "whole organism thinking" when characterizing biological materials, and the importance of framing biological materials research in relevant, biological contexts.

Introduction

As biologists, we are interested in materials in context. The materials that organisms build and use are not the result of sudden *de novo* inspiration, they are the product of an accumulated history of interactions among organism, environment, and phylogeny (Knoll 2003; Fig. 1). Unlike engineered materials, biological materials are constrained to a far more limited palette of pre-existing ingredients, and yet they attain incredible ranges of functionality, mediating relationships between organism and environment, fitness and survival (Wegst and Ashby 2004; Fratzl and Barth 2009). There is significant interest in bio-inspired materials design, but pursuits in this direction still struggle to replicate biological tissues and processes (Holland et al. 2012; Eder et al. 2018). At the core of this challenge is an issue of scale: materials characterization often demands approaches that restrict attention to very fine resolutions, making it easy to lose track of the organism making the materials. While decades of research in biophysics, biomechanics, and biochemistry have proven the utility of bringing different disciplines to bear on biological topics, sometimes these fields forget what biology has to offer in return.

The papers in this symposium volume are a call for a more organismal perspective on biological materials research, one that considers not only the biology, but also the ecology and phylogeny of materials of interest. To quote Fratzl and Barth (2009, 422), "there is no biomimetic materials research without proper biological research, including a thorough analysis of what a material is made for under the conditions of the organism's species-specific behaviour and ecological situation." Although materials perspectives in organismal biology are still comparatively rare, characterization techniques that were mostly known only to materials scientists a decade ago (e.g., synchrotron microCT, Raman spectroscopy, nanoindentation, FIB-SEM, and cryo-TEM)

Advance Access publication July 31, 2019

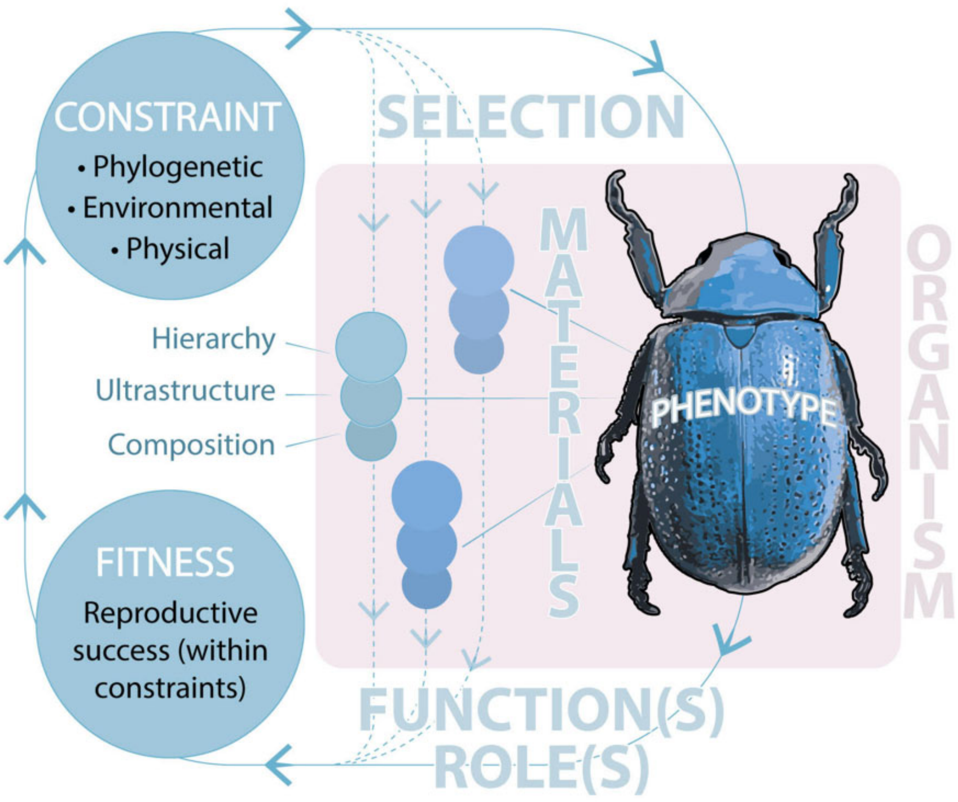

Fig. 1 Schematic of factors influencing evolution and adaptation in biological materials, underlining the need for "whole organism thinking" in biological materials research. (The explanation moves in a clockwise fashion from the top left, with terms used in the figure written in bold. For color version of figure, see online PDF.)

Biological materials face a variety of *constraints* that shape their evolution and adaptation. These can, in a general sense, be:

Phylogenetic: aspects of evolutionary history that limit future evolutionary pathways.

Environmental: for example, abiotic factors like resource availability, humidity, or temperature associated with the organism's environment (biotic factors like population-level pressures also fall into this category).

Physical: for example, constructional limits associated with material scaling laws or performance.

These factors interact with an organism's genotype, thereby shaping and imposing *selection* pressures on an organism's *phenotype*.

Understanding the action of the various constraints on a specific biological material is complex because organismal phenotypes are comprised of a huge number of interacting components (e.g., *materials*). The organization of these materials—their *composition*, *ultrastructure*, *structural hierarchy*—can all be influenced through the mentioned constraints. Organizational aspects of a biological material can also be shaped by interactions with the other materials in the organism and by interactions among levels of organization within a material. For example, the environmental availability of a chemical might affect a biological material's chemical composition, which in turn influences the structure of the tissue it is part of.

All of these interactions influence a biological material's *function* or performance (e.g., the stiffness of a beetle carapace or its ability to produce a structural color), which then dictates how well that material can perform a certain organismal *role* (e.g., the protection of soft internal components, the ability to camouflage). The interaction of an organism's many functional materials may impose a further constraint on material performance, such that the *organismal* performance optima of a material may be different from the performance maximum of the bulk material. As a hypothetical example, if the structural aspects dictating stiffness and color are at odds to some degree and selective pressure for good camouflage is strong, a beetle carapace may be less stiff than is possible, given its constituent materials. In fact, a multi-role optimum may be more ecologically relevant, where the material's stiffness and color performance may each be "sub-optimal," but together allow the carapace to be simultaneously protective and camouflaging.

How an organism and its materials perform relative to the rest of the population and in the context of the given constraints will determine its reproductive success (*fitness*). In these ways, the organism, its materials, and its constraints are filters for population-level variation, shaping, for example, which heritable material features become established, altered, and culled through evolution (even if not all of those features are necessarily advantageous).

are increasingly available to and sought out by biologists. The overlapping interest in characterization techniques and biological study systems creates ready platforms for cross-disciplinary interaction among life- and physical-science disciplines.

The studies herein focus on a diversity of systems and themes at a variety of organizational scales: from skeletal and shell form–function evolution to material-mediated vibration sensing, light transmission and load-damping behaviors, structural color to plant and animal anchoring tools. Authors hail from a variety of disciplinary backgrounds—including evolutionary biology, morphology, biochemistry, materials, computer, and engineering sciences—demonstrating the breadth of modern materials research. In this introduction, we present three thematic areas that offer opportunities for deeper integration between organismal biology and materials science: structural hierarchies, whole organism thinking, and adaptation and evolution. It is our hope that the work collected in this issue will help introduce biologists to new lenses for viewing their work, while culturing materials-minded researchers to consider how materials adapt and evolve with organisms (Fig. 1). These reciprocal approaches can advance understanding of biological material innovations in biological contexts, while also contributing to effective methods for biomimetic engineering.

Structural hierarchies

The highly limited range of substances available for building biological tissues means that Nature, unlike engineering, typically plays more with structure than composition to attain different functions (Wegst and Ashby 2004; Dunlop et al. 2011; Eder et al. 2018). A common natural design strategy involves the use of structural hierarchy, where distinct structural and morphological features exist at multiple size scales (Lakes 1993; Wegst and Ashby 2004). In this way, structural arrangements at very small scales (e.g., crystal and/or fiber arrangements) can contribute to bulk properties at much larger scales (e.g., the tissue- or organ-level). Bone (Reznikov et al. 2018), enamel (van Casteren and Crofts 2019), mollusc nacre (mother-of-pearl) (Baum et al. 2019), and silk (Sponner et al. 2007) are all well known biological examples of hierarchical materials, structured in a way that achieves extremely high toughness. Hierarchical structures can also achieve other functions individually or in combination, such as color (Saranathan et al. 2015), transparency (Bagge et al. 2019), adhesion (Brodoceanu et al. 2016), and/or self-cleaning (Barthlott et al. 2016).

At the core of understanding the function(s) of a given structural hierarchy is the need to bridge a huge range of size scales, from molecule to meter (Cranford and Buehler 2010). This makes biological materials problems both challenging and ideal for interdisciplinary collaboration within and outside the comparative biology community. Biologists are cultured to think about hierarchical problems, relating different levels of evolutionary pressure, organismal anatomy, and community ecology into an integrated biological picture. The availability of magnetic resonance (Hesse et al. 2019), x-ray (Knötel et al. 2017), and electron (Weber et al. 2014) imaging techniques in modern morphological research has pushed the morphologist's toolkit to finer and finer scales, while in the process increasing the amount of detail and information available for description. To manage the deluge of data, analysis and modeling tools are increasingly automated, making multi-scale, high-throughput analyses attainable on a scale previously impossible. Baum et al. (2019), for example, show that the application of a single data transform method to microCT datasets can allow rapid and semi-automatic analysis of huge numbers of morphological features, even across very different types of anatomical data. Although such modern visual data analysis techniques draw heavily on computer science (e.g., machine learning approaches), they will always require biological expertise (e.g., to distinguish between relevant and irrelevant material in segmentation; Baum et al. 2019), making organismal knowledge a vital input for guiding and constraining data evaluation.

Perhaps less appreciated in organismal biology disciplines is that structural design concepts also play roles in driving seemingly complex tissue assembly at chemical levels. For example, several animals that make slime or threads (spiders, mussels, hagfish, velvet worms) store the necessary precursor biomolecules in a highly concentrated fluid state, which can be surprisingly rapidly converted into a solid (e.g., fiber) through specific triggers (e.g., mechanical shear, pH change, salt concentration, and water loss; Holland et al. 2012; Kurut et al. 2015; Baer et al. 2019a). This triggered self-assembly is programmed into the biochemical structure of the protein building blocks and their higher-order organization. The specifics of the self-assembly processes differ across taxa, but their commonalities offer the potential to identify universal material design principles for sustainable manufacturing (e.g., of polymers, biomedical scaffolds). Many of the physical and chemical features of assembly also find analogies at much larger length scales, where groups of organisms form entangled systems, as in worm blobs (Aydin et al. 2019), fire ant rafts or towers

(Phonekeo et al. 2017), and fly larvae fountains (Shishkov et al. 2019b). These systems mimic molecular assembly and soft matter physics to solve population-level problems, such as overcoming physical obstacles (Phonekeo et al. 2017) or increasing individuals' access to resources during feeding activity (Shishkov et al. 2019a).

Whole organism thinking

As in physiological and organism-level systems, biological materials are subject to functional balancing acts. Bones are mechanical devices and calcium stores, fish scales offer protection and influence hydrodynamics. The features of a biological material, therefore, often cannot be understood outside of the material's ecology, its specific role in the organism's interaction with its environment (Fig. 1). For example, silk has historically been studied primarily as a structural material, but it also serves important vibrational sensing functions. This multifunctionality helps to explain, on the one hand, the diversity of silk types in webs and web shape (Mortimer et al. 2016), and on the other hand, the sensitivity range of the built-in vibration sensors in web-spinning spiders' legs (Mortimer et al. 2019). Organismal context is also important for understanding the function of nanofibrous spider silks, which interact with insect cuticle waxes to achieve higher adhesion on prey (Bott et al. 2017). Similarly, the mechanical drawing necessary for rapidly converting the fluid capture slime of velvet worms into stiff, adhesive threads is put in context when the slime-spraying behavior of the worm and struggling of the prey are considered (Baer et al. 2019b). Such functional context-dependence can make it very difficult to predict specific functions from material structure alone. Joel and Weissbach (2019) describe how different types of surface structure—microchannels or repeating pillars or capillary networks—are used in a wide variety of ecological roles in animals, including water collection in deserts, oil transport for defensive secretions, self-cleaning surfaces that reduce pathogens, and air-retention for diving. These structural features offer ambiguous clues to their function in the organism, making their biological roles easily falsely interpreted and underlining the importance of integrating ecological and behavioral research into biological materials' study.

Just as loading history is important to understanding a manmade material's potential for mechanical failure (e.g., from high-cycle fatigue), an organism's life history provides important context for a biological material's performance over time and use. For example, although mammalian enamel and shark enameloid are compositionally similar, the former covers teeth that typically last a lifetime (van Casteren and Crofts 2019), whereas the latter covers teeth that are constantly replaced (Corn et al. 2016). The attachment threads of mussels (byssal threads) are long-lasting, whereas the capture slime threads of velvet worms are constantly recycled and regenerated, although both are protein-based materials with beta sheet structural motifs (the difference is in the cross linking: covalent in the former, non-covalent in the latter) (Baer et al. 2019b). Additionally, the functional properties of a given material can change with specific triggers, as in the hydration-dependent, reversible unfolding of ice plant seed capsules (actuated by a swellable cellulose layer) (Harrington et al. 2011) and the opening of *Banksia* seed pods after repeated exposure to fire (Huss et al. 2018). Methods for testing biological materials in such active contexts are increasingly available. For example, faster imaging and more customizable laboratory devices now make it possible to perform "4D" (time-resolved) MRI and microCT incorporating *in situ* mechanical testing stages, allowing characterization of how morphology responds to load (e.g., Gustafsson et al. 2018; Hesse et al. 2019). Such technological advancements are expanding our abilities to ask quantifiable questions in states closer to physiological conditions.

Contextualizing adaptation and evolution

Biology is not static and therefore biological materials must also adapt to different situations and environments and can evolve over time. A new frontier in materials engineering is to push beyond static material states to characterize adaptable, active states of materials over different time scales (Burla et al. 2019; de Pablo et al. 2019). Shorter-term adaptation in active material properties can be dynamic, as in the ability of fire ant swarms to modulate a wide range of flow and viscoelastic properties (Vernerey et al. 2018), or more passive, as in fluid transport that increases silk adhesion during prey capture (Bott et al. 2017). Material responsiveness can also be biologically constraining, like the sudden opacity of transparent-bodied shrimp when physiologically stressed, making them visible to predators (Bagge et al. 2017). Over longer timescales (e.g., relating to organismal growth), alterations in structure can dictate more efficient uses of space in skeletal tissues (Baum et al. 2019) and better load-bearing capacity, as in the adaptive alteration of vascular architecture in dragon tree branches (Hesse et al. 2016).

On evolutionary timescales, knowing the phylogenetic distribution of a material is vital for understanding the pressures that shaped its structure and function. Identifying similar materials across biology is a start, and contextualizing materials' diversity in the context of evolutionary relationships can provide more biological information about convergence vs. homology and the co-opting of existing tools for new functions. Biology offers myriad chances for such materials meta-analyses, due to the extremely widespread nature of important tissue base components (e.g., calcium carbonate, keratin) and structural motifs (e.g., twisted plywood architectures, trabeculation) (Knoll 2003; Eder et al. 2018). Broad material surveys are already offering insight into the biological features that guide bird egg shape (Stoddard et al. 2017), the evolutionary origin of 3D photonic crystals (Seago et al. 2019) and the relationship between enamel variation and dietary ecology (Lucas et al. 2016). In the same way that high-throughput sequencing revolutionized broad phylogenetic studies, now high-throughput imaging and analysis tools, along with shared online data repositories (e.g., oVert, MorphoMuseum, iDigBio, MorphoSource), are facilitating investigations of functional morphology on larger, more phylogenetically-relevant scales (Wipfler et al. 2016).

Toward understanding innovations

The works presented in this issue are a small sample of the advanced approaches and multidisciplinary topics that characterize the growing field of integrative biological materials research. The symposium and this volume bring together a variety of different systems, disciplines, and perspectives in the shared pursuit of understanding biological materials in their organismal frames of reference. Biological materials science is pushing into an exciting phase, moving beyond imaging and characterization of static materials and into the study of more active, adaptable systems. At this threshold, organismal biologists stand to offer deep perspectives on the biological context of material structure and function, while at the same time, having unprecedented access to tools and collaborations relevant to expansive questions. Is material performance evolutionarily selected? How do abiotic factors limit or enhance biomaterial function? How do these materials adapt and evolve with organisms across environments? From morphological structural hierarchies, to wider organismal and behavioral contexts, to adaptation and evolution of functional properties on multiple size- and timescales, there are many exciting areas where whole organism perspectives on biological materials can reciprocally inform our understanding of both biological and material systems.

Acknowledgments

The organizers would like to thank the symposium speakers and workshop leaders, whose presentations both engaged and inspired the SICB audience. It was a pleasure working with all of you. We would also like to thank Shahrouz Amini, Júlia Chaumel, John Dunlop, Matthew Harrington, and Ronald Seidel for helpful comments on the manuscript.

Funding

This work was contributed in association with the "Adaptation and Evolution of Biological Materials" symposium at the Society for Integrative and Comparative Biology 2019, and was generously supported by the numerous Society for Integrative and Comparative divisions (DCB, DCPB, DEE, DIZ, and DVM), the American Microscopy Society, the Company of Biologists, the journal Bioinspiration and Biomimetics, Micro Photonics Inc., Overleaf, and Thermo Fisher Scientific.

References

Aydin YO, Culver J, Tennenbaum M, Goldman D, Bhamla MS. 2019. Dynamics of a worm blob [abstract]. In: The Society for Integrative and Comparative Biology 2019 annual meeting. Tampa, McLean (VA): The Society for Integrative and Comparative Biology. p. S4–5.

Baer A, Horbelt N, Nijemeisland M, Garcia SJ, Fratzl P, Schmidt S, Mayer G, Harrington MJ. 2019a. Shear-induced β-crystallite unfolding in condensed phase nanodroplets promotes fiber formation in a biological adhesive. ACS Nano 13:4992.

Baer A, Schmidt S, Mayer G, Harrington MJ. 2019b. Fibers on the fly: multiscale mechanisms of fiber formation in the capture slime of velvet worms. Integr Comp Biol published online (https://doi.org/10.1093/icb/icz048).

Bagge LE, Kinsey ST, Gladman J, Johnsen S. 2017. Transparent anemone shrimp (*Ancylomenes pedersoni*) become opaque after exercise and physiological stress in correlation with increased hemolymph perfusion. J Exp Biol 220:4225–33.

Bagge LE. 2019. Not as clear as it may appear: challenges associated with transparent camouflage in the ocean. Integr Comp Biol published online (doi: 10.1093/icb/icz066).

Barthlott W, Mail M, Neinhuis C. 2016. Superhydrophobic hierarchically structured surfaces in biology: evolution, structural principles and biomimetic applications. Philos Trans A Math Phys Eng Sci 374:20160191.

Baum D, Weaver JC, Zlotnikov I, Knötel D, Tomholt L, Dean MN. 2019. High-throughput segmentation of tiled biological structures using random walk distance transforms.

Integr Comp Biol published online (doi: 10.1093/icb/icz117).

Bott RA, Baumgartner W, Bräunig P, Menzel F, Joel A-C. 2017. Adhesion enhancement of cribellate capture threads by epicuticular waxes of the insect prey sheds new light on spider web evolution. Proc R Soc B 284:20170363.

Brodoceanu D, Bauer CT, Kroner E, Arzt E, Kraus T. 2016. Hierarchical bioinspired adhesive surfaces-a review. Bioinspir Biomim 11:051001.

Burla F, Mulla Y, Vos BE, Aufderhorst-Roberts A, Koenderink GH. 2019. From mechanical resilience to active material properties in biopolymer networks. Nat Rev Phys 1:249–63.

Corn KA, Farina SC, Brash J, Summers AP. 2016. Modelling tooth–prey interactions in sharks: the importance of dynamic testing. R Soc Open Sci 3:160141–6.

Cranford S, Buehler MJ. 2010. Materiomics: biological protein materials, from nano to macro. Nanotechnol Sci Appl 3:127–48.

de Pablo JJ, Jackson NE, Webb MA, Chen L-Q, Moore JE, Morgan D, Jacobs R, Pollock T, Schlom DG, Toberer ES, et al. 2019. New frontiers for the materials genome initiative. npj Comput Mater 5:41.

Dunlop JWC, Weinkamer R, Fratzl P. 2011. Artful interfaces within biological materials. Mater Today 14:70–8.

Eder M, Amini S, Fratzl P. 2018. Biological composites—complex structures for functional diversity. Science 362:543–7.

Fratzl P, Barth FG. 2009. Biomaterial systems for mechanosensing and actuation. Nature 462:442–8.

Gustafsson A, Mathavan N, Turunen MJ, Engqvist J, Khayyeri H, Hall SA, Isaksson H. 2018. Linking multiscale deformation to microstructure in cortical bone using in situ loading, digital image correlation and synchrotron X-ray scattering. Acta Biomater 69:323–31.

Harrington MJ, Razghandi K, Ditsch F, Guiducci L, Rueggeberg M, Dunlop JWC, Fratzl P, Neinhuis C, Burgert I. 2011. Origami-like unfolding of hydro-actuated ice plant seed capsules. Nat Commun 2:337.

Hesse L, Masselter T, Leupold J, Spengler N, Speck T, Korvink JG. 2016. Magnetic resonance imaging reveals functional anatomy and biomechanics of a living dragon tree. Sci Rep 6:32685.

Hesse L, Leupold J, Poppinga S, Wick M, Strobel K, Masselter T, Speck T. 2019. Resolving form–structure–function relationships in plants with MRI for biomimetic transfer. Integr Comp Biol published online (doi: https://doi.org/10.1093/icb/icz051).

Holland C, Vollrath F, Ryan AJ, Mykhaylyk OO. 2012. Silk and synthetic polymers: reconciling 100 degrees of separation. Adv Mater 24:105–9.

Huss JC, Schoeppler V, Merritt DJ, Best C, Maire E, Adrien J, Spaeker O, Janssen N, Gladisch J, Gierlinger N, et al. 2018. Climate-dependent heat-triggered opening mechanism of *Banksia* seed pods. Adv Sci 5:1700572.

Joel AC, Weissbach M. 2019. Same principles but different purposes: passive fluid handling throughout the animal kingdom. Integr Comp Biol published online (https://doi.org/10.1093/icb/icz018).

Knoll AH. 2003. Biomineralization and evolutionary history. Rev Mineral Geochem 54:329–56.

Knötel D, Seidel R, Prohaska S, Dean MN, Baum D. 2017. Automated segmentation of complex patterns in biological tissues: lessons from stingray tessellated cartilage. PLoS One 12:e0188018.

Kurut A, Dicko C, Lund M. 2015. Dimerization of terminal domains in spiders silk proteins is controlled by electrostatic anisotropy and modulated by hydrophobic patches. ACS Biomater Sci Eng 1:363–71.

Lakes R. 1993. Materials with structural hierarchy. Nature 361:511–5.

Lucas PW, Philip SM, Al-Qeoud D, Al-Draihim N, Saji S, van Casteren A. 2016. Structure and scale of the mechanics of mammalian dental enamel viewed from an evolutionary perspective. Evol Dev 18:54–61.

Mortimer B, Soler A, Siviour CR, Zaera R, Vollrath F. 2016. Tuning the instrument: sonic properties in the spider's web. J R Soc Interface 13.

Mortimer B, et al. 2019. A spider's vibration landscape: adaptations to promote vibrational information transfer in orb webs. Integr Comp Biol published online (doi: 10.1093/icb/icz043).

Phonekeo S, Mlot N, Monaenkova D, Hu DL, Tovey C. 2017. Fire ants perpetually rebuild sinking towers. R Soc Open Sci 4:170475.

Reznikov N, Bilton M, Lari L, Stevens MM, Kröger R. 2018. Fractal-like hierarchical organization of bone begins at the nanoscale. Science 360:eaao2189.

Saranathan V, Seago AE, Sandy A, Narayanan S, Mochrie SGJ, Dufresne ER, Cao H, Osuji CO, Prum RO. 2015. Structural diversity of arthropod biophotonic nanostructures spans amphiphilic phase-space. Nano Lett 15:3735–42.

Seago AE, Oberprieler R, Saranathan V. 2019. Evolution of insect iridescence: origins of three-dimensional photonic crystals in weevils (Coleoptera: Curculionoidea). Integr Comp Biol published online (https://doi.org/10.1093/icb/icz040).

Shishkov O, Hu M, Johnson C, Hu DL. 2019a. Black soldier fly larvae feed by forming a fountain around food. J R Soc Interface 16:20180735.

Shishkov O, Trebuchon J, Yunker PJ, Franklin S, Hu DL. 2019b. Black soldier fly larvae rearrange under compression. Integr Comp Biol. published online (doi: 10.1093/icb/icz133).

Sponner A, Vater W, Monajembashi S, Unger E, Grosse F, Weisshart K. 2007. Composition and hierarchical organisation of a spider silk. PLoS One 2:e998.

Stoddard MC, Yong EH, Akkaynak D, Sheard C, Tobias JA, Mahadevan L. 2017. Avian egg shape: form, function, and evolution. Science 356:1249–54.

van Casteren A, Crofts S. 2019. The materials of mastication: material science of the humble tooth. Integr Comp Biol published online (https://doi.org/10.1093/icb/icz129).

Vernerey FJ, Shen T, Sridhar SL, Wagner RJ. 2018. How do fire ants control the rheology of their aggregations? A statistical mechanics approach. J R Soc Interface 15: 20180642.

Weber B, Tranfield EM, Höög JL, Baum D, Antony C, Hyman T, Verbavatz J-M, Prohaska S. 2014. Automated stitching of microtubule centerlines across serial electron tomograms. PLOS One 9:e113222.

Wegst UGK, Ashby MF. 2004. The mechanical efficiency of natural materials. Philos Mag 84:2167–86.

Wipfler B, Pohl H, Yavorskaya MI, Beutel RG. 2016. A review of methods for analysing insect structures—the role of morphology in the age of phylogenomics. Curr Opin Insect Sci 18:60–8.