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SYMPOSIUM

The Comparative Approach to Bio-Inspired Design: Integrating Biodiversity and Biologists into the Design Process

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Synopsis Biodiversity provides a massive library of ideas for bio-inspired design, but the sheer number of species to consider can be daunting. Current approaches for sifting through biodiversity to identify relevant biological models include searching for champion adapters that are particularly adept at solving a specific design challenge. While the champion adapter approach has benefits, it tends to focus on a narrow set of popular models while neglecting the majority of species. An alternative approach to bio-inspired design is the comparative method, which leverages biodiversity by drawing inspiration across a broad range of species. This approach uses methods in phylogenetics to map traits across evolutionary trees and compare trait variation to infer structure–function relationships. Although comparative methods have not been widely used in bio-inspired design, they have led to breakthroughs in studies on gecko-inspired adhesives and multifunctionality of butterfly wing scales. Here we outline how comparative methods can be used to complement existing approaches to bio-inspired design, and we provide an example focused on bio-inspired lattices, including honeycomb, and glass sponges. We demonstrate how comparative methods can lead to breakthroughs in bio-inspired applications as well as answer major questions in biology, which can strengthen collaborations with biologists and produce deeper insights into biological function.

Introduction

Recent growth in the field of bio-inspired design, which includes biomimetics and biomimicry, has coincided with increased awareness about the importance of biodiversity (Wilson 1988; Lepora et al. 2013). While biodiversity is an important component of healthy ecosystems (Duffy 2009), it can also serve as a source for new medicines, products, and ideas (Bernstein and Ludwig 2008; Müller et al. 2018; Broeckhoven and du Plessis 2022). Current estimates for the total number of species on the Earth range from 5.3 million (Costello et al. 2013) to one trillion species (Locey and Lennon 2016), which represents a massive feedstock for potential innovations in bio-inspired design. This immense diversity can be both exhilarating and daunting for practitioners of bio-inspired design to consider when trying to select biological models. A major challenge going forward is to identify techniques that allow practitioners of bio-inspired design to leverage biodiversity without being overwhelmed by it.

One strategy that practitioners have used to parse biodiversity and select useful biological models is to identify champion adapters. Champion adapters are species whose strategies make them particularly adept at surviving in a given habitat or meeting a specific environmental challenge that coincides with a design problem (Baumeister et al. 2014). The use of champion adapters in bio-inspired design is similar to the use of model systems in much of the biology and has led to some of the most famous examples of bio-inspired

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design, such as the kingfisher-inspired Japanese bullet train. Initial designs of the bullet train caused pressure to build up when the train entered a tunnel, which produced a loud boom when the train exited the tunnel. The lead engineer on the project happened to be a bird watcher, and he knew that kingfishers could penetrate the surface of water with their beaks while barely making a splash. The kingfisher was the perfect match for the tunnel problem, as both the kingfisher and bullet train must reduce resistance as they transition from a low to high density medium, and this led to the design of a kingfisher-inspired nosecone that reduced drag, and solved the tunnel problem (McKeag 2012).

The champion adapter approach has been useful in helping design teams to narrow their search for biological models, but it does so by focusing on a small number of well-studied species. A recent analysis of species used in bio-inspired applications by (Ng et al. 2021) concluded that only a small fraction of biodiversity has been investigated. For example, 44 % of bio-inspired research articles on butterflies focused on a single genus, *Morpho*, which represents a tiny fraction of the more than 18,000 butterfly species described (Van Nieukerken et al. 2011). A similar pattern was observed in spiders, where 33 % focused on a single genus of orb-weaving spiders, *Trichonephila*, despite there being more than 4200 spider genera (Catalog 2022). Moreover, only 3–14 % of studies the authors analyzed, drew inspiration from more than one focal organism, which is in line with previous assessments (Snell-Rood 2016). These numbers demonstrate that current methods in bio-inspired design tend to limit the number of species investigated to focus on a small number of model species, while the potential for informing bio-inspired design has yet to be examined for the vast majority of species.

Comparative methods in biology offer an alternative approach to bio-inspired design that harness biodiversity by drawing inferences from a broad spectrum of species. Unlike the champion adapter approach, which typically focuses on a single species from which to draw inspiration, the comparative approach investigates trait variation among multiple species, preferably more than two (Garland Jr and Adolph 1994). This can involve broad comparisons among distantly related taxa (e.g., differences in body shape and swimming biomechanics of fish and mammals (Fish and Lauder 2006) or detailed comparisons among closely related species (e.g., differences in pectoral fin shape and swimming performance among members of a single fish family (Kane and Higham 2012)). In either case, the goal is to use these multi-species comparisons to understand trait evolution and clarify structure–function relationships, the latter of which is also a primary goal of bio-inspired design. Practitioners of bio-inspired design have already used the comparative approach with success (Higham et al. 2019; Tan et al. 2019; Tsai et al. 2020; Yu et al. 2020), though the relative lack of species diversity in bio-inspired research and applications described above suggests the comparative approach could be expanded. Here we outline how comparative methods can be used to complement existing approaches to bio-inspired design, including the champion adapter approach, and we detail how our team has used this approach with regard to bio-inspired lattice design.

Comparative methods in biology

Comparative methods in biology rely heavily on phylogenetics, or the creation of evolutionary trees, to determine the evolutionary underpinnings of trait variation (Garamszegi 2014). Morphological, physiological, behavioral, or social traits can be mapped onto evolutionary trees to investigate how traits vary among species, and with respect to their evolutionary history. Most commonly, these methods are used to control for confounding effects of shared evolutionary history on trait variation to infer functional relationships (Garland Jr et al. 2005). Some functional traits may be widespread, such as the articulated exoskeletons of arthropods, but these traits are products of shared evolutionary history rather than cases of independent evolution among related lineages. Functional relationships can also be supported by examples where traits have been lost or evolved through convergent evolution, which occurs when similar traits evolve independently in distantly related species in response to shared environmental challenges. Examples of trait losses and convergence provide some of the strongest evidence for structure–function relationships and can also help elucidate environmental factors that select for specific trait values. More subtle changes in trait values can also be mapped onto phylogenies to examine how trait variation may correlate with fine-scale environmental differences as well as scale with changes in body size or other morphological factors. What all of these methods have in common is that they use multi-species comparisons to identify patterns in trait evolution that can be used to infer structure–function relationships and later be tested using experimental manipulations.

Comparative methods in bio-inspired design

Just as biologists use comparative methods to infer structure–function relationships, researchers in bio-inspired design have used these methods to identify traits that can be abstracted into biological design principles regarding morphology and behavior (Pavlic and Pratt 2013; Snell-Rood 2016; Ng et al. 2021). Although comparative methods have not been widely used in

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bio-inspired design, they have been used with success in the three most commonly studied organisms—geckos, spiders, and butterflies (Snell-Rood 2016; Ng et al. 2021). Comparative studies on the adhesive toe pads of geckos, for example, have identified numerous instances of evolutionary losses and convergence (Gamble et al. 2012). While the external morphology of toe pads remains remarkably similar across species that evolved attachment mechanisms independently, there are lineage-specific differences that could relate to variation in the environment that species inhabit or their ability to attach to smooth versus rough surfaces (Niewiarowski et al. 2016). A major advance in research on dry adhesion emerged from another example of convergent evolution discovered in *Anolis* lizards (Garner et al. 2019). *Anolis* lizards evolved structures similar the microsetae found on gecko toes to facilitate dry adhesion, but *Anolis* setae are simpler and easier to mimic using current manufacturing techniques, which has obvious applications in the design of dry adhesives (Garneret et al. 2021).

Another major challenge in bio-inspired design is identifying how functional traits scale, which can be important when trying to match biological models with their intended application. This is relevant to the development of gecko-inspired adhesives, as adhesive properties scale in relation to weight they must hold. A multispecies comparison of lizard adhesion in relation to body size identified a common scaling coefficient related to toe pad area, though large lizards appeared to be using additional mechanisms to compensate for increases in size (Irschick et al. 1996), and a more recent comparison investigating a broader set of species came to a similar conclusion (Labonte and Federle 2015). The underlying mechanisms that species use to compensate for increased body size remain unclear, and further research of adhesive mechanisms among diverse lineages is likely to identify solutions that have relevance to the design of dry adhesives. Similar comparative studies regarding the scaling properties of spider silk are likely to have applications in bio-inspired material design. The majority of research on spider silk has focused on only a single genus of orb-weaving spiders, but studies of other spider species have identified silks that vary significantly in toughness and resilience (Agnarsson et al. 2010; Haynl et al. 2020). Broader comparisons of spider silk across species could help identify properties that scale to fit diverse functions.

Finally, traits in biology rarely serve only one function, and multispecies comparisons can be useful for elucidating multifunctional aspects of trait variation. For example, butterflies have long served as models to study structural coloration, and comparative studies of wing scale nanostructures have been used to identify structural and pigmentary effects that tune wings to reflect different colors (Wilts et al. 2015). A recent investigation of wing scale nanostructures among non-canonical species found that these same nanostructures can serve to dissipate heat and aid in thermoregulation (Tsai et al. 2020). Similarly, a comparison of structural coloration in beetles found some species that produce structural colors are unlikely to use them for visual functions (Seago et al. 2009). Instead, (Seago et al. 2009) presented evidence from water beetles and burrowing snakes that these nanostructures might be used for water repellency or friction reduction. It is through multispecies comparisons like those described above that the alternative functions of well-studied traits became evident and can then be studied in further detail.

Collaborating with biologists

An indirect benefit of using comparative methods in bio-inspired design is the potential to increase engagement with biologists. The paradox of bio-inspired design is that while biology is used to advance technological innovations, biologists are rarely involved (Snell-Rood 2016; Graeff et al. 2019, 2020). For example, a comparison of nearly 300 studies in bio-inspired design found that less than 8 % included a biologist in the author list (Snell-Rood 2016). This lack of engagement from biologists has been cited as a primary reason for why so few species have been investigated for their biomimetic potential (Snell-Rood 2016; Ng et al. 2021). In addition, biologists may be able to offer more nuanced insight into the processes of evolution and limitations when abstracting biological principles (Ng et al. 2021). Despite the lack of engagement from biologists in bio-inspired design to date, there is general consensus among practitioners that increasing participation from biologists would help address current difficulties in analyzing and understanding biological systems to achieve successful outcomes (Rovalo et al. 2020).

Typically, the role of biologists in bio-inspired design has been limited to the early stages of the design process —identifying biological models—and abstracting design principles (Fayemi et al. 2017; Graeff et al. 2020). Incorporating comparative methods into bio-inspired design creates an opportunity to make these stages more iterative to increase engagement with biologists and leverage their technical skills. Bio-inspired design is inherently multidisciplinary, but major advances have typically come from the application of novel tools or methodologies from fields outside of biology (Liu and Jiang 2011; Roberts et al. 2014; Kumar et al. 2019). In contrast, comparative methods rely heavily on advanced analytical skills of biologists (Goolsby 2015), which can shift the involvement of biologists from superficial to critical in the design process. Outcomes of

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phylogenetic comparisons can also provide answers to major questions in biology, such as understanding how complex traits evolve. Biologists benefit from these collaborations by having access to new funding sources, technological tools outside the scope of what is typically in a biology lab, and increased exchange of ideas among fields that are adjacent to biology that may offer new insights into deep biological questions (Snell-Rood 2016; Hashemi Farzaneh 2020; Ng et al. 2021). Taken together, increasing engagement with biologists throughout the design process can create better alignment between the goals of biologists and other members of the design team to enhance interdisciplinary collaboration (Boix Mansilla et al. 2016).

Application: bio-inspired lattices

In the following sections, we describe how our team has applied the comparative approach to select biological models and to improve the structural performance of bio-inspired lattices. Lattices, also referred to as cellular materials, are structures composed of repeating unit cells that divide space, and provide structural support (Ashby and Gibson 1997). In nature, lattices can be found in the honeycomb of bees and wasps, the skeletons of glass sponges and cacti, as well as the complex three-dimensional structures of corals, plant parenchyma, and trabecular bone (Bhate et al. 2019; Fig. 1). Lattices have several advantages over solid materials in relation to weight reduction, the ability to locally tune structural properties, and to add multifunctionality (Schaedler and Carter 2016). For these reasons, lattices have been used in a wide range of engineering applications, especially in the aerospace industry where weight reduction and thermal management are essential (Goss et al. 2022). Interest in lattice materials has greatly expanded with the advent of new technologies in additive manufacturing and Computer Aided Design (CAD) that have made it easier to produce complex geometries that were previously cost prohibitive or simply infeasible to produce, including those found in nature (Yang et al. 2018; Du Plessis et al. 2019).

There is a long history of looking to natural models to inspire structural design, which goes back to the work of Roman scholar Marcus Terentius Varro on honey bees in 37 BC. Varro proposed what is now known as the honeycomb conjecture, in which he postulated that bees build their nests using hexagonal cells because the hexagon is the most efficient shape for dividing space into equal parts (Varro 37BC). This conjecture was based on the idea that bees should maximize the amount of space to store honey and pollen while using the least amount of wax, which they secrete from wax glands on the underside of their abdomens, and

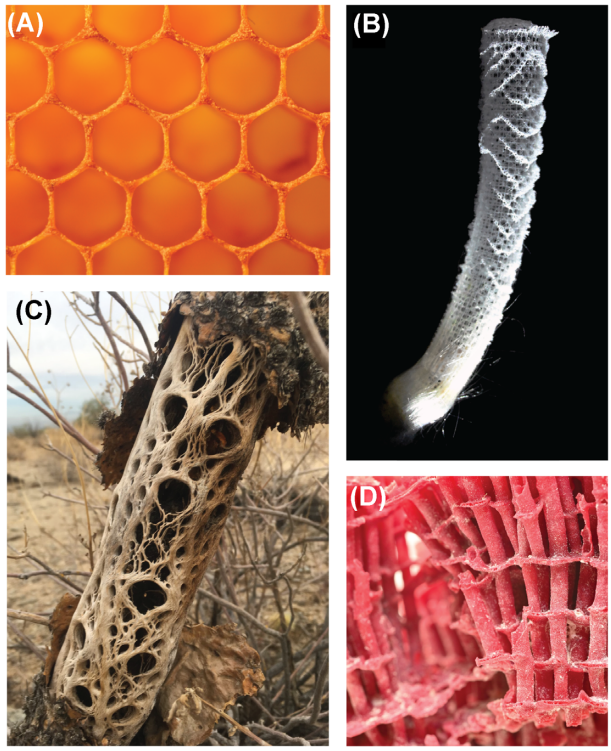

Fig. 1 Natural lattices used as models for bio-inspired design. **(A)** Honey bee honeycomb, **(B)** venus flower basket glass sponge, **(C)** cholla cactus skeleton, and **(D)** organ pipe coral.

is metabolically expensive to produce (Winston 1987). Nearly 2000 years later, mathematician Thomas Hales proved Varro's conjecture (Hales 2001), and honeycomb has inspired a wide range of engineering applications where material conservation is a priority (Bitzer 1997). Engineers have since found ways to mimic a broad spectrum of natural lattices ranging from the skeletal structure of the Venus flower basket glass sponge (Aizenberg et al. 2005) to the micro architecture of cellular patterns inside porcupine quills (Tee et al. 2021).

Selecting biological models

No matter what approach is taken, the process of selecting a biological model typically begins by considering a wide range of species. It can be a challenge to select an appropriate biological model from among millions of options, so practitioners have developed a range of tools and techniques to help narrow the search (Wanieck et al. 2017). Perhaps the best-known example is AskNature.org, which is an online catalogue of 1700 biological strategies and applications compiled by the Biomimicry Institute and translated for non-biologists (Deldin and Schuknecht 2014). AskNature is helpful during the initial search for biological models, though it still only captures a small fraction of biodiversity. It is at this stage of the design process that research teams often work

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Table 1 Description of natural lattices and their proposed functions.

Structure	Classification	Description	Habitat	Functional benefits
Bee/wasp honeycomb	**Kingdom:** Animalia **Phylum:** Arthropoda **Class:** Insecta **Order:** Hymenoptera **Family:** Apidae, Vespidae	Flattened panel nests composed of hexagonal cells constructed from wax, paper/carton, mud, or a combination.	Terrestrial, global distribution excluding arctic	Storage of honey and pollen, space for brood rearing, support for adult colony members, damage protection
Glass sponge	**Kingdom:** Animalia **Phylum:** Porifera **Class:** Hexactinellida	Hollow cylindrical skeletons composed of silaceous spicules.	Marine, global distribution with high abundance in arctic waters and deep oceans	Support for filter feeding, damage protection from fish and predators
Cactus skeleton	**Kingdom:** Plantae **Phylum:** Magnoliophyta **Order:** Caryophyllales **Family:** Cactaceae **Subfamily:** Opuntioideae	Hollow cylindrical (*Cylindropuntia*) and flattened (*Opuntia*) skeletons composed of cellulose and lignin.	Terrestrial, arid, and semi-arid habitats in the nearctic and neotropical bioregions	Support for photosynthesizing cells and internal water storage, material conservation to prevent strain on branch points
Sea fan	**Kingdom:** Animalia **Phylum:** Cnidaria **Class:** Anthozoa **Order:** Hymenoptera **Suborder:** Holaxonia, Scleraxonia, Stolonifera	Flattened (Holaxonia, Scleraxonia) and three-dimensional (Stolonifera) colonial skeletons of soft coral composed of gorgonin, and/or calcium carbonate.	Marine, global distribution in shallow warm waters and coral reefs	Support for filter feeding, damage protection from fish and predators

with biologists to conduct a deeper survey that goes beyond the most popular models. This process can involve reviewing scientific literature, visiting museum collections, and brainstorming to identify the most relevant models.

We used the methods described above to survey potential biological models for lattice design, and we compiled a list of roughly 30 examples that fit into broad categories. We then classified each example using a system developed to describe both engineered and natural lattices (Bhate et al. 2019). This system follows a decision tree to classify materials using three aspects: tessellation (unit cell shape and periodicity), elements (the use of beams or surfaces to construct unit cells), and connectivity (how unit cells are arranged and connect to each other). We narrowed our focus primarily to periodic structures that repeat the same unit cell in two or three dimensions. In the end, we selected four biological models (Fig. 1) that included a prismatic, surface-based lattice (honeycomb), two examples of beam-based lattices organized into cylinders (glass sponge and cactus skeleton), and a three-dimensional, beam-based lattice (organ pipe coral). We deliberately chose models that represented a variety of materials (wax, silica, cellulose/lignin, and calcium carbonate) and environmental constraints (terrestrial, aquatic, etc.) that could lead to novel insights into lattice optimization (Table 1).

Assessing biological context

For each biological model we selected, we conducted background research into their biology and the proposed function of their lattice structure (summarized in Table 1). Honeycomb is unique among the structures we considered in that it does not grow as part of the organism, but represents an extended phenotype that emerges from selection on the behavior of comb-building bees (Dawkins 1999). Bees and wasps build comb to rear brood, provide nest structure, and—in the case of honey bees—store pollen and honey. Because the primary purpose of comb is to rear brood that will grow into similarly sized adults, bees and wasps build comb using a periodic structure composed of regularly shaped hexagons (but see Smith et al.). Honeycomb must be strong enough to support its own weight and the weight of the colony and cell contents, which can be substantial (a honey-filled frame in a commercial beehive holds 2–4 kg of honey). The comb must also be able to resist damage from falling debris or intruders, which is important for bees and wasps that nest in the open. There has likely been selection on bees to use the least amount of material when building new comb because wax is metabolically expensive to produce—it takes roughly 8 kg of honey for bees to produce 1 kg of wax (Whitcomb 1946). While wasps do not secrete nest materials, they must also invest substantial effort in collecting and processing wood pulp and mud; for this reason, bees and wasps face similar selection pressures associated with the conservation of material when building new comb.

Glass sponges and organ pipe coral are both marine filter feeders that require support to stand in the water column to feed. To meet these requirements, the

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skeleton of the Venus flower basket consists of a regular square lattice with diagonal elements passing through every second square to provide mechanical stability while maximizing open space for water to pass through (Aizenberg et al. 2005). Stability is further enhanced by external ridges that extend perpendicular to the surface of the cylinder as well as nanostructural elements of individual spicules (Aizenberg et al. 2005; Morankar et al. 2022). The structure of organ pipe coral is less complex than the Venus flower basket at the macroscale and consists of upright tubes connected by transverse platforms composed of calcium carbonate spicules (Spiro 1971). The full structure is produced by a colony of living polyps that extend feather-like tentacles from the top of each tube to feed. Under magnification, the walls of the organ pipe coral are perforated and allow for the exchange of water and waste with the environment (Spiro 1971). In addition to providing support for filter feeding, the skeletons of glass sponges and organ pipe coral provide protection against predation and damage from accidental impacts from passing fish or other large vertebrates. The protective feature may be particularly important for glass sponges, which primarily inhabit deep arctic waters where temperatures are cool and growth rates are slow (Leys et al. 2007). Thus, it may be difficult for glass sponges to recover from significant damage.

Cacti are relatively unique among plants in that they evolved skeleton-like structures. Woody skeletons have evolved independently in a range of stem-succulent plants, but they exhibit the highest diversity in cacti (Gibson 1978). Early lineages of cacti feature cylindrical skeletons that are relatively solid and do not provide much space for water storage. In large columnar cacti, such as saguaros, skeletons evolved to form distinct ribs that allow cacti to expand and contract in accordance with seasonal patterns of water availability (Altesor and Ezcurra 2003). While the skeletons of all cacti provide support structure to accommodate water storage, the most complex skeletons evolved in cholla (*Cylindropuntia*) and prickly pear (*Opuntia*) (Hernández-Hernández et al. 2011; Fig. 2B). Both feature complex lattice structures arranged into cylinders in cholla and as flattened pads in prickly pear. One explanation for why cholla and prickly pear evolved lattice-like skeletons is that they have a modular growth form with pads connected to each other at weak joints. For this reason, there may be a greater need for weight reduction in modular cacti to reduce strain at the joints compared with columnar cacti, though this remains to be tested.

Phylogenetic comparisons and ontogeny

To understand the evolution of lattice structures in our biological models, we traced their lineages within higher-order phylogenies (Fig. 2). This process allowed us to compare closely related species that lack similar lattices as well as identify cases of convergent evolution. An additional benefit of mapping functional traits onto a phylogeny is that it can be useful in identifying related species where similar traits evolved. The majority of research on honeycomb has focused on the European honey bee, *Apis mellifera*, but thousands of other bee and wasp species build honeycomb nests that share similar characteristics and could be used to inspire design applications (Jeanne 1975; Wongsiri et al. 1997; Roubik 2006; Fig. 2A). Likewise, the Venus flower basket, *Euplectella aspergillum*, has served as the primary model for functional comparisons of glass sponge anatomy (Aizenberg et al. 2005), but there are >600 described species of glass sponges in the class Hexactinellida that also display lattice-like skeletons but face different environmental challenges and vary in structure and material qualities (Dohrmann et al. 2017; Fig. 2B). The phylogenies of cacti and sea fans also reveal cases of multiple lineages where lattice structures have evolved that could be useful in comparative studies (Fig. 2C, D).

Another aspect we considered was the growth and development of lattices through an organism's lifetime. Honey bees initially build comb with extremely thin walls topped by a thickened edge of coping (Zhang et al. 2010). The function of this coping has not been established, although it does provide some benefit to structural properties in three-point bending tests (Goss et al. 2020). Over time, bees gradually increase the thickness of the cell walls and incorporate silk from used pupal cocoons into the wax, which does significantly enhance structural integrity (Zhang et al. 2010). It is likely that functional aspects of honeycomb construction differ over the course of nest development, with some structures adding support during the initial construction phase, while others play important roles at the mature stage. Understanding how a structure changes over the course of development can also be used to identify structural elements that might appear functional but have been left over from the early construction phase and no longer serve a functional purpose. Venus flower baskets similarly exhibit a stereotypical developmental pattern transitioning from a flexible phase to a rigid phase (Saito et al. 2002). During the flexible phase, sponges lack the external ridges found in older sponges that provide stability to the mature structure, and it is possible that increased flexibility during this phase has some functional benefit during this stage of development. Interestingly, structural adaptations at each phase can be used to produce bio-inspired materials for applications that require flexible or stiff structures (Fernandes et al. 2021).

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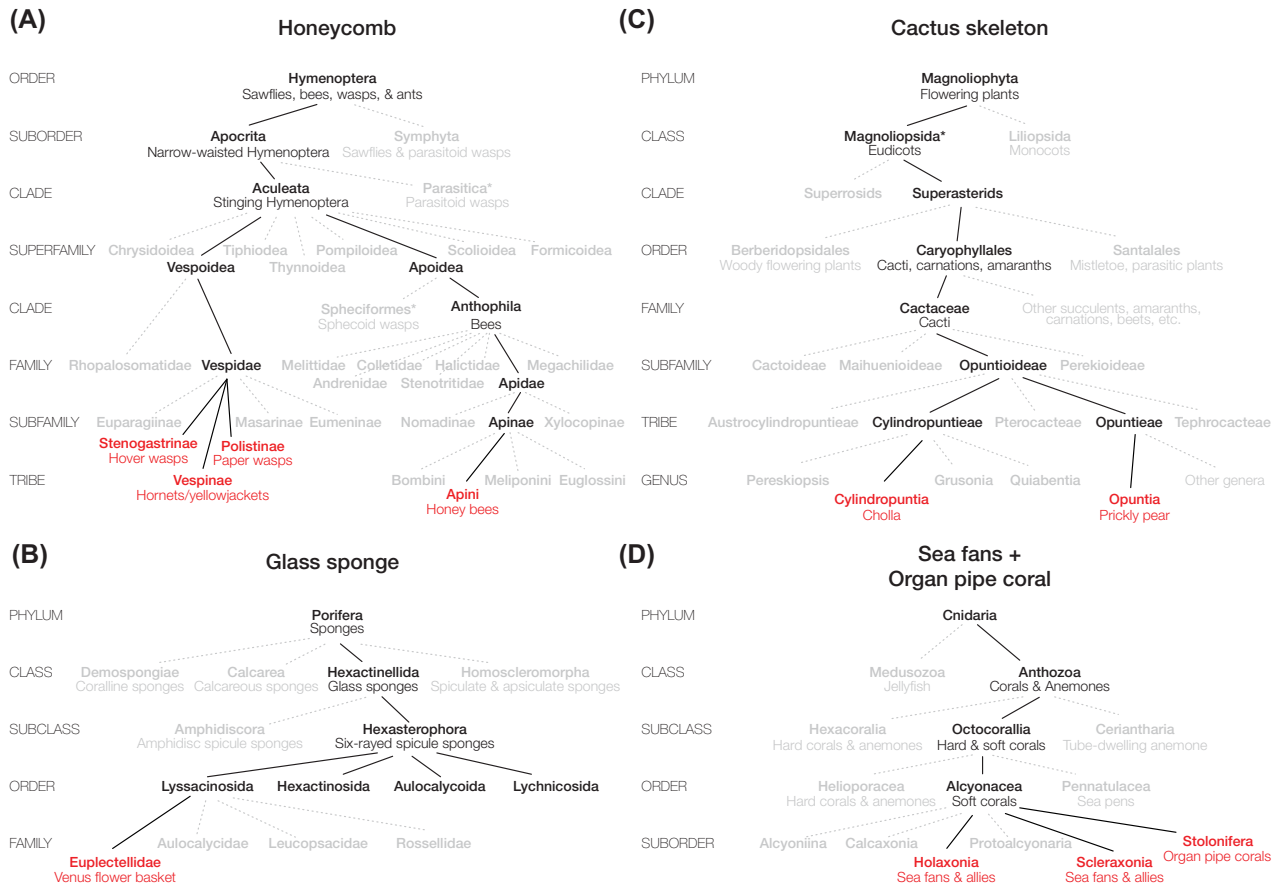

Fig. 2 Evolutionary relationships of natural lattices shown in red. **(A)** Honeycomb structures evolved in insects at least twice independently in the family Vespidae and the tribe Apini; **(B)** All members of the Hexactinellida are considered glass sponges, though unfused, lattice-like skeletons are present only in members of the subclass Hexasterophora, which contains the Venus flower basket; **(C)** complex, lattice-like skeletons evolved in cacti as cylindrical structures in the genus *Cylindropuntia* and flattened structures in the genus *Opuntia*; **(D)** lattice-like structures are present in three suborders of sea fans, with Holaxonia and Scleraxonia featuring laminar structures and Stolonifera featuring three dimensional, organ pipe structures.

Identifying common design principles

A primary characteristic of all models we investigated was a structural hierarchy that ranged from the nanoscale to the macroscale (Fig. 3). Previous studies on the Venus flower basket have identified at least six levels of hierarchy that increase in complexity from the nanometer to centimeter scale (Weaver et al. 2007). The main cylindrical structure is composed by cruciform spicules that come together to form a three-dimensional grid. This grid is then cemented and strengthened by spicule bundles that are arranged vertically, horizontally, and diagonally as well as the addition of external ridges that attach perpendicularly to the structure. The individual spicules that form this structure, which typically range in diameter from 25–50 μm, are themselves complex and consists of a central proteinaceous filament surrounded by concentric layers of silica that aid in crack deflection (Monn et al. 2015; Morankar et al. 2022). Multiple spicule types come together to form the complete structure, including those that form the sieve plate that encloses the top of the sponge, and the long fibrillar spicules that anchor the sponge to the seafloor. The entire structure itself is then covered with a layered silica matrix that strengthens the entire skeletal system.

The Venus flower basket provides the best model of structural hierarchy to date, but we found common patterns across all four biological models. As described above, the mechanical properties of honeycomb relate to the hexagonal shape of their unit cells, but they are also enhanced by the incorporation of silk fibers that reinforce the cell wall (Zhang et al. 2010). The macrostructure of the cholla skeleton arises from a crisscrossing set of helices that follow Fibonacci numbers, with eight bundles spiraling in one direction, and 13 in the other (Altesor and Ezcurra 2003). The microstructure is similar to other woody plants in that it contains lignified vessels, tracheids, and fibers that run in an axial direction with interspersed rays that

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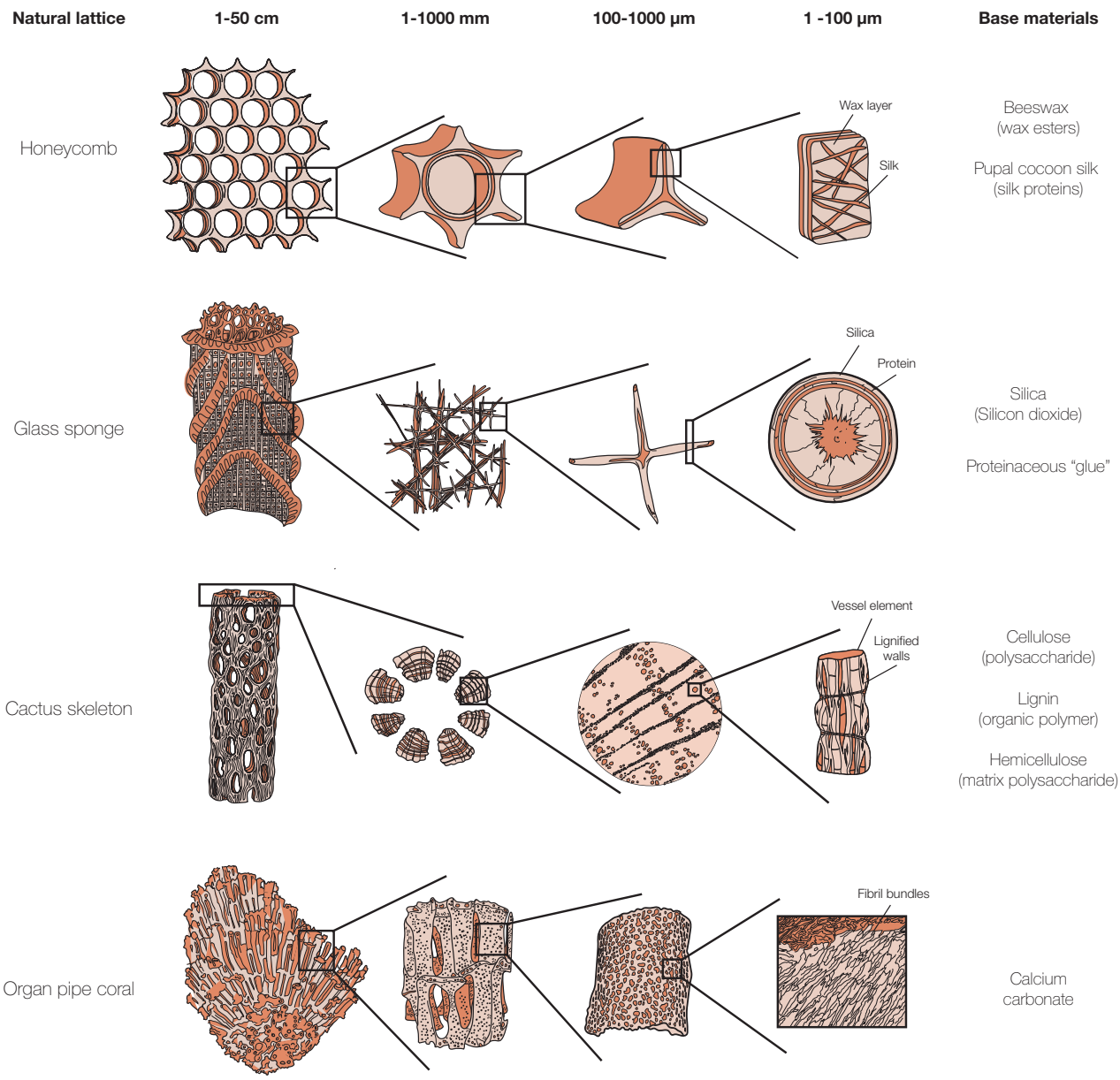

Fig. 3 Structural hierarchy of natural lattices from the macroscale to the microscale. Each structure is composed of different base materials and evolved independently, but they display a similar structural hierarchy that contributes to mechanical performance of the complete structure.

run radially (De Vivo et al. 2020). A combination of macrostructural (pore collapse and friction) and microstructural (fiber straightening, delamination, pull-out, and rupture) properties provide cholla with high torsional toughness (De Vivo et al. 2020). Organ pipe coral also exhibits structural hierarchy, as they are composed of microscopic spicules as in glass sponges that are arranged into bundles that exhibit different morphology and orientation (Fig. 3). These spicules come together to form the macrostructure, which consists of porous tubes connected by flattened platforms (Spiro 1971). The structural significance of the spicule bundles is not yet known, but it could help compensate for structural toughness compromised by the pore structure required for water flow.

Informing biology and design

One discovery to emerge from our work on honeycomb is that honey bees build hexagonal cells with rounded corners rather than with sharp corners (Goss et al. 2020). Through modelling and mechanical testing, we found that adding corner rounding to honeycomb increases stiffness while reducing corner stress, and further, that there is an optimum value of this rounding that is most efficient (Rajeev et al. 2022). This

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discovery has applications for improving manufactured honeycomb, but it also suggests new opportunities for research on bees and wasps. Different species of honey bees face unique functional challenges. For example, European honey bees build their nests in protected cavities, while a number of Asian honey bee species build their nests in the open, where they are less protected and are likely exposed greater seasonal and diurnal temperature variation. Could bees that construct nests in the open incorporate different design elements that improve damage resistance and performance across a greater range thermal range? Likewise, wasps construct their nests using different materials (paper, mud, or a combination of the two) and may adjust their nest design to compensate for different material properties—a challenge engineers also face when translating design principles to products made using metal, nylon, or other construction materials (Bitzer 1997). We are currently in the process of studying the relationships between cell size, wall thickness, corner rounding, and nest material across a diversity of bee and wasp species to understand how these parameters might also affect bio-inspired applications. Potential insights into how insects fine tune honeycomb cell parameters to conserve material would not have happened if not for collaboration between biologists and engineers. This example highlights how applying comparative methods can enhance collaboration between interdisciplinary team members to address goals in biology and design.

Conclusions

Comparative methods offer a way to increase biodiversity in bio-inspired design and build stronger collaborations with biologists. These methods complement existing approaches to explore a broader diversity of biological models from which to abstract design principles. Current examples of comparative studies in bio-inspired design, while uncommon, offer insight into how these techniques can enhance understanding of biological systems to identify adaptive traits. When successful, these studies can lead to breakthroughs in bio-inspired design as well as biology, which strengthens collaborations and can lead to deeper insights into biological function.

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Conflict of interest

We have no conflicts of interest to declare.

Data availability statement

No new data were generated or analysed in support of this research.

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