

It's Not a Bug, It's a Feature: Functional Materials in Insects

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Over the course of their wildly successful proliferation across the earth, the insects as a taxon have evolved enviable adaptations to their diverse habitats, which include adhesives, locomotor systems, hydrophobic surfaces, and sensors and actuators that transduce mechanical, acoustic, optical, thermal, and chemical signals. Insect-inspired designs currently appear in a range of contexts, including antireflective coatings, optical displays, and computing algorithms. However, as over one million distinct and highly specialized species of insects have colonized nearly all habitable regions on the planet, they still provide a largely untapped pool of unique problem-solving strategies. With the intent of providing materials scientists and engineers with a muse for the next generation of bioinspired materials, here, a selection of some of the most spectacular adaptations that insects have evolved is assembled and organized by function. The insects presented display dazzling optical properties as a result of natural photonic crystals, precise hierarchical patterns that span length scales from nanometers to millimeters, and formidable defense mechanisms that deploy an arsenal of chemical weaponry. Successful mimicry of these adaptations may facilitate technological solutions to as wide a range of problems as they solve in the insects that originated them.


1. Introduction

The central motivation behind the development of bioinspired materials—indeed, behind all biomimicry—is the idea that evolution by natural selection can be considered as a long-running algorithm for developing solutions to the problem of survival

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in response to a wide variety of environmental pressures.^[1] Since life began in the oceans 4 billion years ago, living organisms have colonized almost every niche on the earth's surface using a diverse array of adaptations.^[2] Engineers seeking to develop solutions to problems with even remote analogues in nature do well to closely investigate the solutions developed by evolution.

Insects are worth particular attention from a bioinspirational perspective given their astounding abundance and diversity; they arguably represent natural selection's wildest success. Around half of all known species of living organism are insects.^[3] Over one million species in the class *Insecta* have been described, with estimates of the total number of insect species ranging from three million to tens of millions. Beetles alone claim 240 000 known species (by comparison, there are around 6000 known species of mammals);^[3] a single tree in Peru was found to house 43 distinct species of ants.^[4] Insects are

ubiquitous, having adapted to nearly all of the environments on earth, though only a handful of species live in the oceans or in polar regions.^[2] Some insects lead solitary lives, while others live in large groups with strict social hierarchies; a single “supercolony” of ants in Hokkaido contains over 300 million workers and 1 million queens.^[4] Insects' Latin-origin namesake translates to “cut into pieces;” this theme extends throughout their body plan, which consists of a three-part form (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and one pair of antennae. These cornerstone appendages, along with countless other structural adaptations such as wings or specialized organs, exist in all shapes and sizes. Adult insects range in length from 0.2 mm (fairyflies of the family Mymaridae)^[5,6] to over 300 mm (stick insects of the family Phasmatidae);^[7] their mass varies 500 000-fold. Accordingly, insects occupy many roles in the global food chain, eating living and dead plants, fungi, other insects, and vertebrates and serving as a common food source for higher animals, including *Homo sapiens*.^[2]

A multitude of selective pressures accompany this diversity of lifestyle, and insects have evolved complex and effective solutions to the particular problems they face. Many of these solutions involve functional materials. Some adaptations, like the photonic structures that give butterfly wings their iridescence, are a part of the anatomy of the insects themselves. Some have their basis in biomaterials secreted from glands, like the wax that honeybees use to form their precisely hexagonal homes. Some insects, like

the ants that cluster to form buoyant rafts and aerial bridges, aggregate to form functional materials with their bodies.

Humans have been entranced by these creatures and their materials since the beginning of recorded history. The practice of beekeeping is at least 5000 years old,^[8] and it is said that the inventor of paper in China around 150 A.D. was inspired by watching vespid wasps make their nests.^[9] The history of scientific discovery owes a lot to insects, as well. The fruit fly, *Drosophila melanogaster*, has been an important model organism in the study of genetics and was the original subject of the studies that discovered sex-linked inheritance and genetic mutation from exposure to radiation.^[10] More recently, studying social insects has led to insights about the nature of adaptive behavior in all social animals, including humans.^[11] Today there are over 100 active peer-reviewed journals dedicated to field, applied, and experimental entomology.

The range of adaptations in insects that have potential for translation to engineering problems is both wide and widely catalogued, but we wager that the majority of today's materials scientists and engineers spend little time reading entomology journals. We therefore intend to bridge an inspiration gap by showcasing some of the most notable ways in which insects have developed specialized anatomy, physiology, and behavior that exploit physical and material principles to ensure their survival (Figure 1). Even basic material adaptations in insects are potentially translatable. For instance, each creature is surrounded by an exoskeleton that imparts long-term functionality and protection despite direct exposure to the stresses of the outside world; such a durable material with tunable mechanical, optical, and surface properties is attractive in a variety of contexts as wide as the insects themselves inhabit. Furthermore, specialized glands allow the emission of a wide variety of secretions, providing insects with the ability to deploy chemical adhesives, coatings, and signals on demand for shorter-term use; this theme perhaps hints that engineered materials could benefit from similar active secretory capabilities. The exoskeleton and secretory glands appear in recurring structural motifs that provide insects with remarkable and diverse functional capabilities (Figure 1). Engineered systems ranging from miniature robots to specially designed functional surfaces to novel drug delivery schemes provide exciting opportunities to apply lessons learned from these creatures.

The sections that follow are organized by function, describing specialized structures for adhesion, movement, interaction with water, and for sensing and production of optical, thermal, vibrational, and chemical signals. Finally, we discuss the special capabilities of insect societies, which perform complex tasks involving specialized materials and often can be considered as materials unto themselves. Each (sub-)section begins with a discussion or case study of the manners in which lessons from insects can be applied to engineering problems, then presents some of nature's most compelling solutions and discusses the physical principles relevant to the task at hand. An overview of insect adaptations arranged by material motif can be found in Table 1.

2. Adhesion

Slippery surfaces and steep slopes are omnipresent in nature. To overcome these obstacles, organisms including (but not



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limited to) marine invertebrates, arthropods, and amphibians have developed organs that promote surface adhesion.^[12–17] Natural adhesives have been the subject of several hundred years of research,^[18,19] and the adhesion techniques of mussels, barnacles, and tree frogs have garnered considerable attention, inspiring an array of synthetic mimics.^[20–22] Adhesives utilized by insects, however, have gone largely understudied when considering their diversity and abundance.^[23] These insect adhesive systems exist as two overlapping categories: physical adhesive structures that mechanically interlock or generate attractive force through van der Waals' interactions, and chemical adhesive secretions that act via molecular bonding, capillary forces, and viscous forces. Some insect adhesives generate impressive forces relative to body weight,^[24,25] however, their strength alone is often outperformed by commercial adhesives which operate in a much different surface-area-to-volume regime. They do, however, excel in rapidly attaching to (and often detaching from) surfaces with a variety of roughnesses and chemistries, and can self-clean after encountering contaminants.^[26,27]

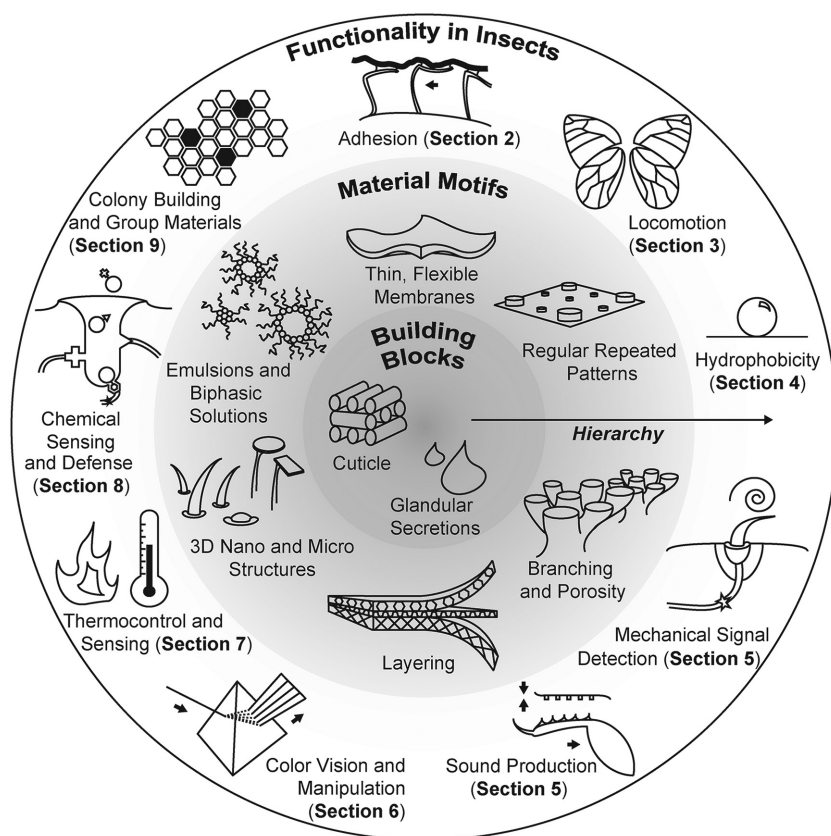


Figure 1. The ability of insects to thrive in diverse environments is linked to two evolutionarily optimized systems: a cuticle-derived exoskeleton with associated functional micro- and nanostructures, and glandular complexes that secrete chemically diverse substances. Most structures rely deeply on hierarchical organization, with structural ordering on length scales ranging from nanometers to millimeters. Insects' structural adaptations function to serve a broad set of insect needs including environmental sensing and control, protection, communication, and locomotion. Numbers in parentheses correspond to the section associated with the particular functionality.

Fibrillar or branching structures are fundamental to many of the adhesive systems found in insects. In fact, variations of these nano- and microstructures exist in other areas of biology as well,^[28,29] suggesting their geometry and mechanism of action are broadly beneficial. Researchers have spent considerable effort trying to replicate the van der Waals-based dry adhesion of gecko foot pads,^[15,29] but insects, none of which have been found to employ purely dry adhesion, indicate that other interactions like hydrogen bonding, viscous forces, and capillary forces can enhance or even dominate overall adhesion capability.^[23,28–31] These additional forces are particularly relevant when adhering to wet substrates, as is necessary in wound dressing and tissue repair. Recent research reported a bioinspired “tough adhesive” designed to stick strongly to biological surfaces for medical applications.^[32] The adhesive is composed of two layers: a lower adhesive layer that binds to material through a combination of covalent bonds, electrostatic interactions, and interpenetration (material mixing), along with an upper matrix designed to dissipate energy when the contact interface is stressed. Here, as discussed in the insect adhesives below, a multifaceted adhesive approach leads to increased versatility and functionality.

2.1. Physical Adhesive Systems

Insects' hardened exterior is made almost exclusively of cuticle: a versatile biomaterial that forms the rigid and multifunctional exoskeleton of all insects (Figure 2). Two types of cuticle microstructures help insect feet adhere to surfaces that have varying degrees of roughness.^[33] The first type, used primarily by flies and beetles, consists of arrays of small fibers (setae) ending in thin spatulas, disks, or points.^[34–36] The fibers are flexible and can bend extensively to accommodate large surface features, while the terminal tips fit within finer features to engage in close-contact van der Waals' interactions.^[37] The second variety, found mainly in stick insects, ants, and cockroaches, are smooth pads with a soft cuticle capable of deforming in response to varied roughnesses. The cuticle has an internal branching structure consisting of rods directed perpendicular to the surface—an orientation thought to help increase contact area and thus strengthen surface-area-dependent attractive forces.^[38] Fuller and Tabor reported that densely arranged surface features smaller than 5 μm present major difficulties for climbing insects,^[39] and certain plant species take advantage of this effect. For instance, pitcher plants, from the carnivorous *Nepenthes* genus, have developed epicuticular wax crystals to serve a variety of purposes from increasing surface microroughness to contaminating adhesive structures with exfoliated crystals in order to capture and consume their insect prey.^[40,41]

A curious example of physical adhesion has developed in the Colorado potato beetle, *Leptinotarsa decemlineata*, to suit its copulation posture.^[42] The tarsal microstructures on the beetles' legs exhibit sexual dimorphism—both male and female beetles have setae that terminate in points and spatulas, but only males have a third style of disk-shaped setae.^[43,44] These terminal disks allow the male to adhere strongly to the smooth back (elytra) of female beetles for extended periods of time during mating.^[45] Unsurprisingly, male beetles can adhere to smooth surfaces slightly better than female beetles, though females can adhere more than twice as strongly to rough, plant-like surfaces.^[42] This observation provided a direct link between structure and function in tarsal adhesive structures. Disk-shaped tips impart a larger surface contact area on smooth surfaces, leading to improved long-term adhesion on those surfaces. Conversely, the flexibility of spear- and spatula-shaped setae makes them well-suited to rough surface adhesion on short time scales (e.g., for locomotion).

As a passive form of defense, many different animals have developed hiding strategies that involve covering themselves with small materials and debris in their surrounding environments.^[46] The most well-researched of insects

Table 1. Insect adaptations sorted by material motif.

Material motif	General functionality	System of interest	Insect and reference
3D nano and microstructures	Adhesion	Adhesive setae	Colorado potato beetles, ^[42] Florida tortoise beetles, ^[606] chrysopoids, ^[47] leaf beetles ^[43]
		Mechanical fasteners	Dragonflies, ^[53] true bugs, ^[55] beetles, ^[56] aquatic true bugs, ^[55] beetles ^[56]
	Chemical sensing and defense	Anatomical allomone structures	Bees, ^[486,491] wasps, ^[486] ants, ^[486] honeybees, ^[497] true bugs ^[473,499,607]
		Defense spines	Lepidopteran caterpillars, ^[485] pine processionary caterpillars, ^[485,490] moths ^[486]
		Built structures	Caterpillars, ^[608–611] moth caterpillars, ^[612] beetles ^[613–615]
		Projectile dispersal	Bombardier beetles ^[467]
	Color vision and color manipulation	1D photonic structures	Beetles, ^[289,291] butterflies ^[289,291]
		Apposition eyes	Ants, ^[361] dragonflies ^[361]
		Bioluminescence	Fireflies ^[616]
		Color vision	Honeybees, ^[617,618] common bluebottle butterflies ^[619]
Disorder-based color		Butterflies, ^[320,323,324] jeweled beetles, ^[329–331] white beetles ^[332,333]	
Photonic crystals		Weevils, ^[290,316,319,321] butterflies ^[290,316,319,321]	
Polarization vision		Flies, ^[369,374] crickets, ^[379] African dung beetles, ^[380,620] bees ^[382,383]	
Locomotion	Rhabdom	Flies, ^[369] bees, ^[370] butterflies ^[370]	
	Locomotive appendage	Beetles ^[621]	
	Locomotive setae	Phantom midges, ^[128] mosquitos, ^[129] gerrormorphan bugs, ^[127] water striders ^[134]	
Mechanosensation	Wing design	Fairyflies, ^[6] thrips ^[124]	
	Campaniform sensilla	Blowflies, ^[215] stick insects, ^[218] flies ^[622]	
	Hair plates	American cockroaches, ^[217] cockroaches, ^[623] hoverflies ^[209]	
Sound production	Near-field detectors	Flies ^[226]	
	Tactile hairs	Desert locusts, ^[207] two-spotted crickets ^[208]	
	Scraper and file	Grasshoppers, ^[264] crickets, ^[264] assassin bugs, ^[624] velvet ants, ^[624,625] mole crickets ^[226,256]	
Thermoregulation	Cooling	Butterflies, ^[626] grasshoppers ^[416,417,512]	
	Thermosensing	Forest-fire-seeking beetles ^[2,394]	
Water active properties	Hydrophobic surface	Termites ^[627]	
	Sub-aquatic exchange	Cattail mosquitos, ^[628] mosquitos, ^[180,181] river bugs ^[191]	
Branching and porosity	Adhesion	Adhesive pads	Stenus beetles ^[70]
	Chemical sensing and defense	Chemoreceptive sensilla	Gypsy moths, ^[433–435] nun moths, ^[433] silk moths, ^[629] tobacco hawk moths ^[440,441]
	Collective materials	Building and fungus cultivation	Termites ^[630]
		Built structures	Honeybees ^[2]
		Group thermoregulation	Termites, ^[528] bees, ^[512,563] wasps ^[512,563]
Wind harvesting	Termites ^[511,631]		
Locomotion	Locomotive appendages	Jumping insects, ^[128] locust, ^[632,633] cicadas ^[634]	
Emulsions and biphasic solutions	Adhesion	Permanent adhesives	Flies, ^[635,636] praying mantis, ^[68] asparagus beetle, ^[637] gum moths ^[57]
	Chemical sensing and defense	Temporary adhesives	Locusts, ^[58] grasshoppers, ^[59] flies, ^[65] beetles ^[65]
		Biphasic secretion	True bugs, ^[469,470] tenebrionid beetles, ^[638] fire ants ^[639]
		Built structures	Green lacewings ^[640]
		Froths and foams	Pyrgomorphid grasshoppers, ^[641] lubber grasshoppers, ^[642] froghopper nymphs ^[474]
		Hemolymph defense	Sawflies, ^[643,644] katydids, ^[450,645] stoneflies, ^[645] stonefly nymphs ^[646]
Projectile dispersal	Stick insects, ^[451,459] termites ^[647]		

Table 1. Continued.

Material motif	General functionality	System of interest	Insect and reference
Layering	Thermoregulation	Cooling	Honeybees, ^[410] mosquitos, ^[411] sawflies ^[412]
	Water active properties	Surface excretion	Leafhoppers ^[166,167,648]
	Collective materials	Built structures	Social wasps ^[649,650]
		Raft building to survive flooding	Fire ants ^[580]
		Bivouac assemblies	Army ants ^[512]
Color vision and color manipulation	Impedance matching	Dragonflies, ^[337] cicadas, ^[339] butterflies, ^[338,341,342] moths, ^[342,343] beetles ^[342]	
Water active properties	Desiccation resistance	Antarctic midges, ^[651] African lake flies ^[652]	
Regular repeated patterns	Collective materials	Defense swarming	Japanese honeybees ^[574]
		Material-like swarm	Honeybees ^[573]
		Magnetic orientation	Termites ^[631]
		Tree nesting	Weaver ants ^[653]
	Water active properties	Designed wettability	Desert beetle ^[161]
	Hydrophobic surface	Planthopper, ^[155] mosquitos, ^[157] green bottle fly ^[160]	
Thin flexible membranes	Locomotion	Locomotive method	Mayflies ^[654]
		Wing design	Bumblebees, ^[102–105] dragonflies ^[94,106,107,112]
	Mechanosensation	Subgenual organs	Ground wetas ^[248,249]
		Tympanum	Cicadas ^[235]
	Sound production	Tymbal sound production	Tiger moths, ^[269] cicadas ^[254,266]
	Thermoregulation	Thermosensing	Dark-pigmented butterflies ^[993,655]
	Water active properties	Hydrophobic surface	Mosquitos ^[178]
		Water-active behavior	Termites ^[177,656]
Chemical/other	Chemical sensing and defense	Hemolymph defense	Monarch butterflies, ^[448] grasshoppers, ^[641] aphids, ^[657]
	Collective materials	Group communication	Honeybees ^[266,550,650]
		Swarm as organism	Midges ^[587]
	Color vision and color manipulation	Pigmentary coloration	Swallowtail butterflies, ^[368] butterflies ^[298,299]
	Thermoregulation	Cooling	Moths, ^[408] bumblebees ^[658]
		Freeze resistance	Spruce budworm, ^[423,659] Alaskan beetles ^[423,659]
Thermosensing		Fruit flies ^[660]	

with this behavior are reduviid nymphs and chrysopoid larvae (**Figure 3**).^[47] Both of these insect subsets rely on adhesive properties of physical microstructures for their camouflaging abilities. Chrysopoid larvae specifically are thoroughly covered in hair-like setae that vary with body position and are specialized for different types of debris. Setae emerging from the back of the larvae are relatively long and flexible (often longer than body-length), are hooked on the ends, and are well-suited to carrying large, light objects.^[48] The setae found on the thorax or abdomen are densely packed and much shorter and stiffer than those on the back, typically have microtextured tips to increase contact area, and assist with carrying smaller objects like dirt or sand grains.^[48] Such selective adhesion properties may also be useful in engineered systems designed to perform a sorting function, e.g., devices that target specific

particles or cells, or machines that separate differently sized parts along an assembly line.

2.1.1. Anatomical Fastening

A variety of different insects have convergently evolved physical methods to fasten two separate anatomical parts together.^[49] Nearly all of these techniques take advantage of complementary lock-and-key structures. Unlike other physical adhesive systems, these were not adapted to stick to generic rough or smooth surfaces, but rather are complete systems of reversible adhesion similar to Velcro.

Dragonflies and damselflies (order Odonata) have a small and delicate connection between the head and the rest of the body

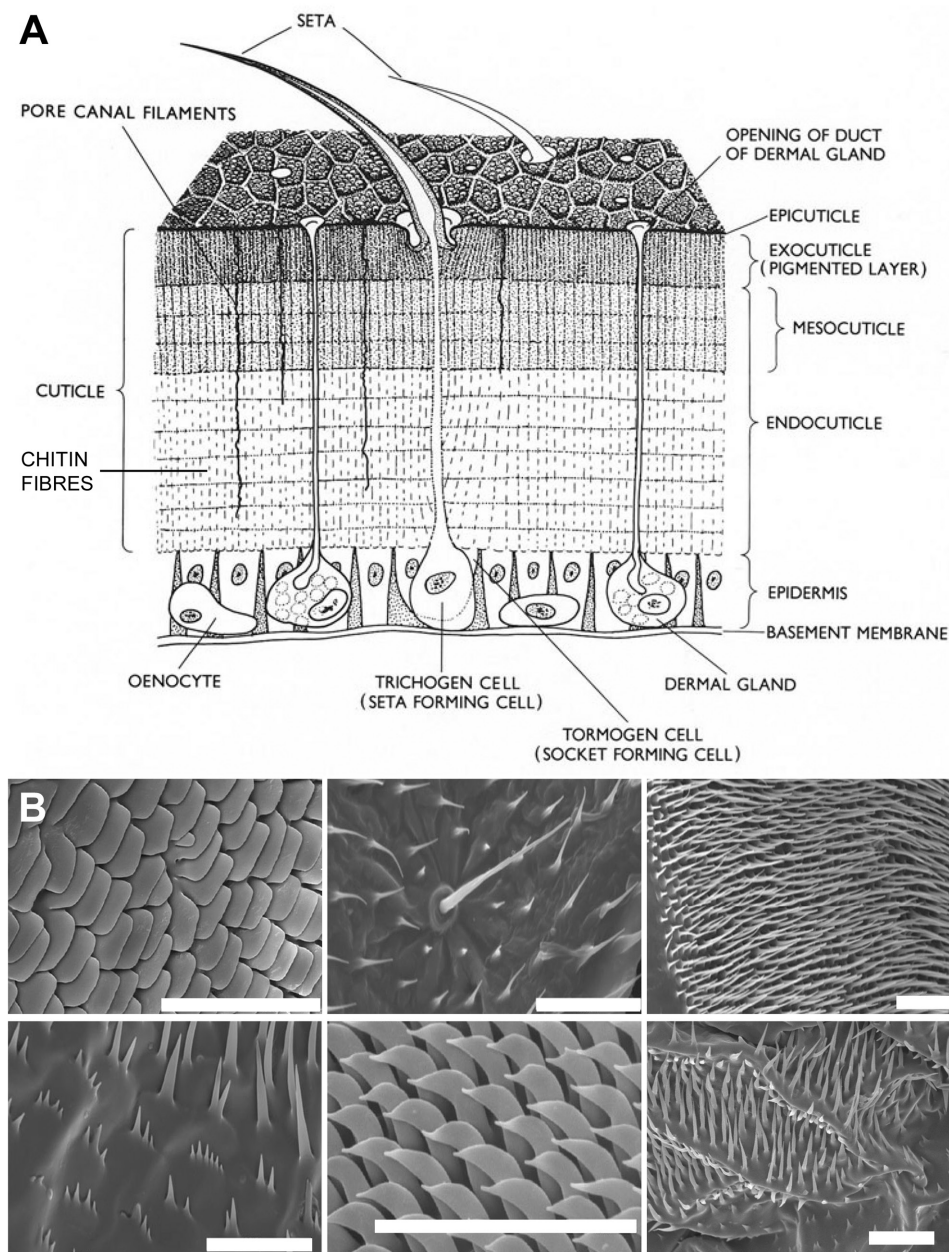


Figure 2. Lamellar structure of the insect cuticle, which forms the majority of an insect's exoskeleton. Three distinct regions of nonliving layers rest on a living epidermal layer that houses various cuticle-producing and microstructure-related cells. The outermost epicuticle layer represents the first line of defense between the insect and its external environment. It often contains lipid secretions, waxes, or other coatings to manipulate wettability, perhaps the most intriguing of which are intricately structured nanoparticles, known as brochosomes, found on the leafhoppers of the family Cicadellidae (see Figure 10). Beneath this layer lies the exocuticle, which undergoes extensive crosslinking and has a relatively high rigidity. In many insects, it hardens rapidly to act as a protective envelope after molting for the prolonged development of softer and more hydrated endocuticle underneath. The exo- and endocuticular layers collectively form what is known as the procuticle, a composite material with protein, polyphenols, water, and lipids, along with crystalline arrangements of the important and abundant linear polysaccharide chitin. A) Cartoon of the structure of cuticle based on TEM images. Adapted with permission.^[661] Copyright 1982, Springer. B) Various morphologies of microtrichia (small stiff hairs) found in the Chinese beetle, *Ulomoides dermestoides*. Scale bars: 20 μm . Adapted with permission.^[662] Copyright 2016, Springer.

(Figure 4A,B).^[50] This fragile joint is beneficial for its extreme flexibility, but poses a problem during relatively high-force actions like feeding, perching, and mating.^[51,52] To avoid potential damage during these activities, dragonflies and damselflies have developed a set of opposing frictional surfaces to provide

support to the neck (Figure 4B,C). The system incorporates four components: arrays of epidermal microtrichia (small stiff hairs on the outer surface), muscles to orient the head and neck surfaces, sensory mechanisms to monitor surface contact, and cells to secrete adhesion-promoting lipid-based substances.^[49]

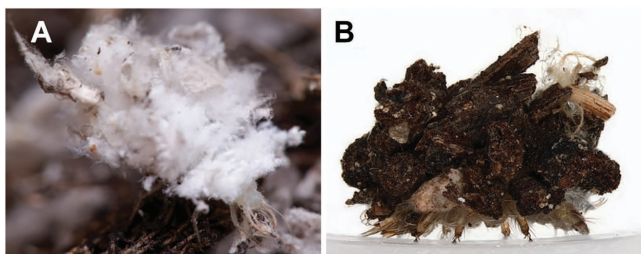


Figure 3. Lacewing larvae employ passive camouflage by carrying around detritus. A) *Apochrysa matsumurae* carrying floculence and cocoon material. B) *Italoachrysa italica* disguised by pieces of woody material. Adapted with permission.^[663] Copyright 2014, Oxford University Press.

Similar to locomotive setae, microtrichia can take on a variety of forms depending on the particular taxa of Odonata (Figure 4D).^[53] When placed into contact, the complementary surfaces do not fully interlock with one another. Instead, deformations of the microtrichia vastly increase surface contact area and prompt the release of wet adhesive secretions, both of which lead to relatively large adhesive forces.^[54]

Examples of quick-release adhesives can be found in many different flying insects that attach their wings to their bodies when not in use. These fastening mechanisms take on a variety of different forms, including snap-like binders in aquatic true bugs (order Hemiptera),^[55] and the pointed, angled structures used by beetles (order Coleoptera).^[56] Aquatic Hemiptera secure their forewings tightly to the thorax while at rest using a knob-and-socket geometry similar to metal snaps used for fastening clothing, but much smaller.^[55] The thorax of these insects contains an array of knobs or button-like protrusions, which are rounded, pear-shaped, or dome-like depending on the species. Each knob is entirely covered with small, densely packed tile-like microtrichia. Some of the microtrichia contain ducts or pores to direct adhesive secretions into the contact zone. The wings contain complementary U-shaped sockets with matching tile-like microtrichia.^[55]

2.2. Chemical Adhesive Systems

The commercial adhesives industry has recently been affected by strict environmental and health regulations. These regulations, in combination with pressures from volatile oil markets, have driven adhesive manufacturers away from fossil-fuel-derived products and toward natural products.^[57] Insects present a multitude of biocompatible, bio-synthesized solutions that could theoretically

be mass-produced using state-of-the-art techniques including recombinant protein expression and microfabrication.

2.2.1. Chemical Adhesives for Stasis and Locomotion

To complement their physical-adhesion-promoting architecture, each of the physical systems described previously also utilizes complementary adhesive secretions. Both fibrous and pad-based tarsal structures secrete an epidermal fluid. This fluid is composed of three key parts: (i) an aqueous portion rich in amino acids and carbohydrates, (ii) oily nanodroplets containing hydrocarbons, and (iii) an emulsifier to stabilize the mixture

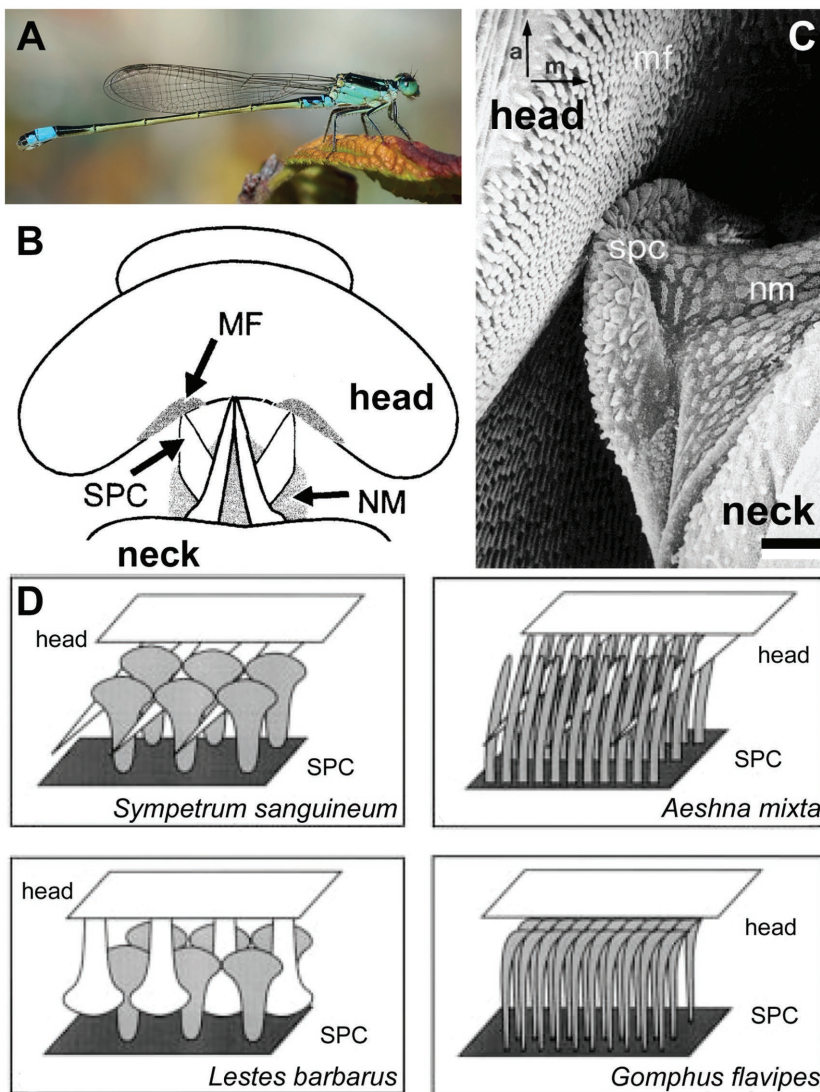


Figure 4. Dragonfly necks are fragile and require a reversible attachment system to secure them during high-intensity maneuvers. A) The damselfly *Ischnura senegalensis*. B) Scheme of the damselfly head, neck, and head arrester system. C) Scanning electron microscopy (SEM) image of head-arresting apparatus on the blue-tailed damselfly, *Ischnura elegans*; MF = microtrichia field on back of head, NM = neck membrane, SPC = postcervical sclerite (movable pad covered in microtrichia complementary to MF). Scale bar: 10 μm . Reproduced with permission.^[664] Wiley. C) Diagrams of various frictional surface motifs found in different families of Odonates as indicated on the lower right of each panel. Reproduced with permission.^[52] Copyright 1999, The Royal Society.

(e.g., cholesterol, monoglycerides, etc.).^[58] A study of the chemical composition of the smooth pad secretions of the migratory locust, *Locusta migratoria*, revealed that there are discernible differences between the composition of the lipid membranes of the pad exterior and the adhesive residue that it leaves behind. The pad surfaces themselves have a much greater proportion of long chained (C_{24} – C_{32}), saturated fatty acids in the form of wax esters, while the secretions contain short chained (C_{16} – C_{20}) unsaturated fatty acids that exist either in their free form or as glycerol esters. Unlike the pads, the secretions also contain significant quantities of carbohydrates (40% of detectable organic components, mostly glucose), which are thought to play a key role in the fluid viscosity and overall adhesive function.^[58]

Several theories attempt to explain the purpose of these locomotive secretions. First, they were thought to be used by insects as a glue-like adhesive. However, Jiao et al. showed that the grasshopper *Tettigonia viridissima* could quickly attach and detach its pads because its adhesive secretions were not sticky in the traditional sense.^[59] An alternative explanation is that a thin film of fluid could facilitate stronger intermolecular forces by playing the role of a coupling agent, adapting to both hydrophobic surfaces and hydrophilic surfaces.^[60] Additionally, the fluid may promote capillary and/or viscous adhesion at the insect–surface interface. Emulsions and colloid-rich solutions can exhibit non-Newtonian behavior, so the oil/aqueous mixture may promote stronger viscous forces under shear stress in the contact region than the viscous forces of a pure aqueous solution.^[61]

Another interesting property of adhesives intended for locomotion is their ability to self-clean.^[26] Insects often travel along surfaces littered with small particles (e.g., dust, pollen, etc.). As with commercial adhesives, one might expect their adhesion ability to decline with time and walking distance, as epidermal surfaces and substances become contaminated. It has been shown, however, that insects retain approximately consistent adhesive strength throughout their lifespan.^[62] Both fibrillar and smooth pad structures are able to remove contaminating particles after only a few steps using several techniques. For example, many insects perform sliding movements while their feet are in contact with a surface in order to induce shear stresses that not only increase viscous adhesive forces, but help to dislodge contaminants.^[63,64] Secreted adhesive fluid also plays a key role in self-cleaning by making it possible to deposit contaminating particles with each step, essentially washing the epidermal layer.^[26]

The ability of certain insects to strongly fasten themselves to a variety of surfaces is also remarkable. For instance, a leaf beetle, *Chrysolina polita*, can withstand drag forces from wind speeds of up to 48 m s^{-1} (170 km h^{-1}), and branch accelerations that can impart forces of around 16 times greater than its body weight.^[34] The beetles are able to achieve this feat using feet with a fibrous exterior in combination with secreted adhesive. In a comparative study of adhesive secretion viscosities, Peisker et al. found that fly secretions (from *Calliphora vicina*) have a much lower viscosity (10.9 mPa s) than secretions from beetles (*Coccinella septempunctata*, 21.8 mPa s).^[65] Both of these insects have fibrous adhesive feet, so the difference can be attributed to the composition of the fluid. This finding provides insight into the role that viscous forces play in general insect adhesion: fly secretions are suited for shorter detachment times to escape from predators, while beetles sacrifice rapid mobility for increased adhesive force.^[65]

2.2.2. Permanent Insect Adhesives

The manner in which female insects position and fasten their eggs on surfaces is critical to reproductive success. Insects accomplish this task by using a thick adhesive coating that can account for $\approx 20\%$ of egg mass.^[66] The sticky substance is typically a permanent glue with the ability to join eggs to both hydrophobic and hydrophilic surfaces, as well as to surfaces covered in dirt or wax crystal contaminants.^[67] Physical properties of this substance vary widely across species, ranging from hydrogels to water-soluble or insoluble liquid glues or light foams,^[66] but the majority share a predominantly (though surprisingly diverse) proteinaceous composition.^[57] For instance, praying mantises (order Mantodea) use a foam-based egg coating that dries rapidly into a cement-like casing and is primarily composed of proteins with α -helical structural motifs in combination with various enzymatic crosslinkers.^[68] One of the strongest measured insect egg-glues, a hydrogel from the gum moth *Opodiphthera* sp., consists of up to 50% protein by dry weight. (Here and throughout this review, “sp.” indicates a single nonspecific species in a genus, while “spp.” indicates multiple species.) Much of this protein has a strong over-representation of glycine residues, which impart flexibility, and serine residues, which encourage hydrogen bonding; these are common characteristics of structural, adhesive, and elastic proteins.^[57] This glue has a dry shear strength of 1–2 MPa with high elastic extensibility and tack, which makes it a biocompatible alternative to currently available “permanent” synthetic adhesives.^[57,69]

2.2.3. Adhesive Prey Capture

Insects also use adhesives to capture prey. A noteworthy example of this behavior is employed by rove beetles, *Stenus* spp. (Figure 5).^[70,71] These beetles have developed a sticky, extensible labium (mouthpart) as a predatory weapon. With no prey present, the labium is stored within a membranous tube inside the beetle’s head. To attack, the beetle rapidly extends its labium (typically on the order of 1–3 ms), drawing the prey into the beetle’s jaw-like mandibles for consumption. The labial structure is terminally tipped with a pair of adhesive pads, so-called paraglossae, each with an intricate, outwardly branching structure.^[72] The surface area and branching extent of these pads differs widely with species and there is a positive correlation between greater surface area/branching and adhesive strength.^[70,73] From an evolutionary perspective, enlargement of these paraglossae likely allowed beetles to target a niche of larger and faster fleeing prey.^[74]

Adhesive attack mechanisms of the *Stenus* beetles are suited to prey with many different physical and chemical surface properties.^[74] As with the locomotive adhesive systems, paraglossae combine a surface mapping microstructure (Figure 5B–E) with a viscous secretion that is produced by specialized glands within the membranous tube. The composition of this fluid, again similar to that found on insect feet, is a combination of two or more immiscible phases containing proteins, carbohydrates, and fatty acids in a viscous milieu.^[75] Two key aspects set the paraglossae apart from

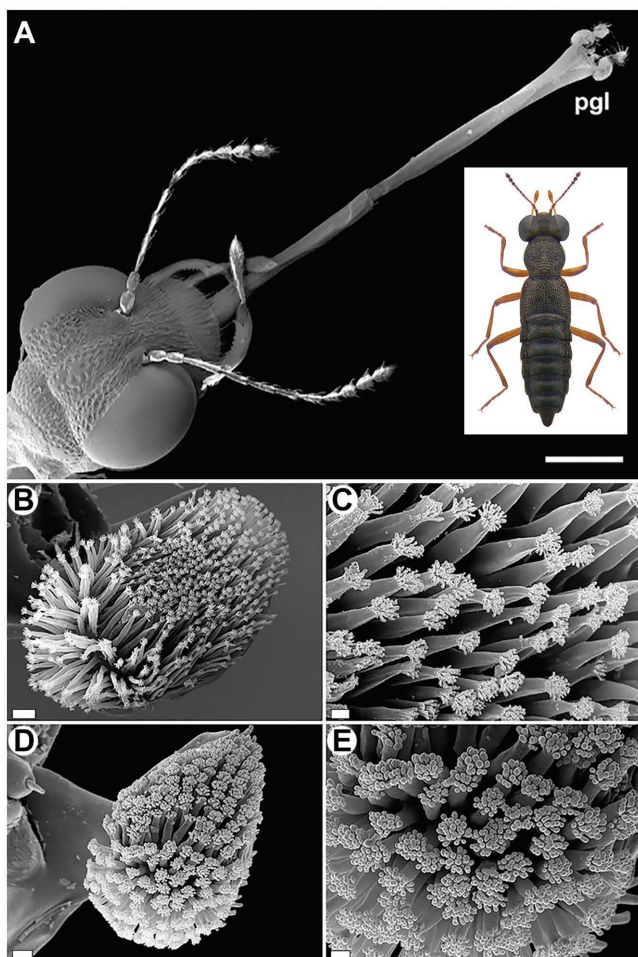


Figure 5. Rove beetles of the genus *Stenus* hunt with an extensible labium tipped with adhesive pads, the paraglossae (“pgl”). A) Extended labium of the *Stenus* beetle used for prey capture.^[73a] Inset: the rove beetle, *Stenus montivagus*. Reproduced with permission.^[73b] Copyright 2009, Udo Schmidt. B,C) Branching structure of paraglossae of *Stenus clavicornis*. D,E) Paraglossae of *Stenus fossulatus*. Note the differences in the extent of branching and spacing. Scale bars: A) 500 μm , B) 10 μm , D) 5 μm , C,E) 2 μm . B–D) Adapted with permission.^[73a] Copyright 2017, Oxford University Press.

their locomotive counterparts. First, their microstructures are almost entirely immersed in secreted fluid. The viscosity of the fluid is therefore assumed to be the dominant adhesive force.^[73] Second, the adhesive strength of these pads is entirely independent of surface roughness. This independence is attributed to the relatively large amount of fluid in combination with the compressive forces generated from rapid protrusion which help to effectively fill voids in the surface.^[72]

3. Specialized Structures for Movement

When insects are not busy performing gravity-defying adhesive walks, many of them also fly or swim to ensure their everyday survival, employing a broad array of physical structures with

unique properties. Each structure is composed of cuticle arranged into macrolayers, thin membranes, porous architectures, or 3D protrusions (Figure 2). Insect appendages combine these material motifs in a way that precisely balances mass, elasticity, force output, and material cost to suit a particular need.^[76–78]

Flying insects in particular have an obvious technological analogue in micro-aerial-vehicles (MAVs), which have generated tremendous buzz for their abundance of potential applications.^[79–81] Flying robots share many design constraints with insects, as their ability to fly relies on striking a delicate balance between the power output of their movement machinery, the amount of available energy, and mass constraints.^[82] Flying robot miniaturization is further complicated by the fact that large aircraft design motifs fail at small sizes due to differences in force scaling.^[80] Researchers recently developed a compelling solution to these problems in the form of a “robotic insect”—a small, battery-powered flying robot with flapping wings.^[83] Its energy-efficient locomotive design is derived directly from insects and it incorporates a switchable, electrostatics-driven adhesive pad that allows it to perch underneath a variety of surfaces. We posit that robotic developments like this are not mere curiosities; they rather represent a shift toward engineered microsystems interacting with weak forces. This is a relatively new size regime for robots, but is one that insects have been inhabiting throughout their existence.

3.1. Insect Wing Morphology and Composition

Nearly twelve thousand vertebrate species and more than one million insect species have developed wings for powered flight.^[84,85] Flying vertebrates have wings containing embedded musculature which they use to actively manipulate wing shape in various flight styles.^[84] The span of an insect wing, however, is almost entirely passive and is controlled only by muscles localized to the wing base.^[86] Therefore, unique morphological and/or compositional features are responsible for any necessary deformations.^[87]

Across all flying insect species, wings provide three key functionalities: (i) they act as levers, relaying force from muscles at the wing base to the surrounding air, (ii) they are oscillating airfoils that direct air through wing strokes to generate lift, and (iii) they act like cantilevered beams, deforming under a variety of forces.^[76,88] To perform each of these tasks successfully, the wings must be lightweight, flexible, and strong, making them intriguing targets for material biomimicry. Quantifying these properties in insects is unfortunately nontrivial, as the delicacy and heterogeneity of wing material is not particularly suited to standard material characterization methods. In response, researchers have developed custom tensile testing apparatuses and have used other techniques like nanoindentation or static bending to measure flexibility descriptors such as Young’s modulus.^[89–91] These systems have determined with reasonable consistency that the Young’s modulus of an insect wing membrane is 2–5 GPa, which is comparable to that of nylon,^[92] though this value can vary with location on the wing, insect species, and general wing structure.^[91]

As is the case for most other structures on insect exteriors, wings are made of cuticle. The cuticle is venated by branching

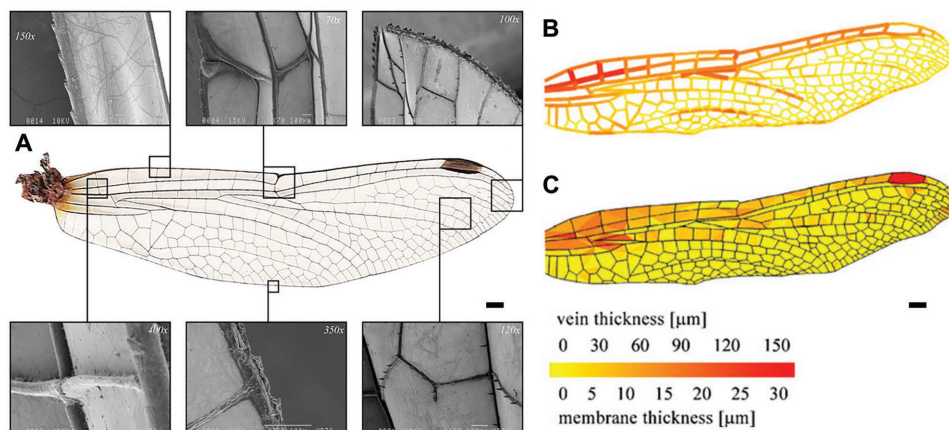


Figure 6. Dragonfly wings are advantageously venated and thickened to provide structural integrity and spatial variation in flexibility. A) Photograph of the forewing of the vagrant darter dragonfly, *Sympetrum vulgatum*, with associated SEM images of the various structural wing features. Distribution of thicknesses of B) veins and C) membrane within the forewing. Scale bars: 1 mm. Reproduced under the terms of the CC-BY license.^[665] Copyright 2010, Jongerius & Lentink.

hollow tubes of varying diameters and wall thicknesses, with elliptical, circular, or bell-shaped cross sections to impart axial-dependent bending stiffness.^[93–95] Generally, veins are larger in diameter and have thicker walls near the wing base where stresses are great, then taper moving out toward the wingtips to reduce inertial forces.^[96] Those veins spanning the leading edge of the wing are largest and carry oxygen, fluids, and neuronal connections. Other, smaller veins are only air-filled and serve to either strengthen or promote bending in particular wing sections.^[76]

Different insects have developed unique and diverse vein branching patterns.^[97] While all patterns tend to promote an exponential decay in bending stiffness from wing base to tip, spatial mapping of veins plays an important role in flexibility variation between the leading and trailing edges of wings (Figure 6).^[98,99] As a method to promote further deformations within this relatively rigid venous structure, the cuticle of certain insect wings contains flexible linear segments, which act as fold lines.^[100] Such bands are distributed independently of support veins—those running radially (base to tip) mediate bending and twisting, while others oriented transversely (leading edge to trailing edge) act as one-way hinges to help the wings bend and reset after the completion of a downstroke.^[100]

Other flex-lines stay rigid during flight movements, but deform reversibly when the wings contact obstacles to prevent structural damage.^[101] A bumblebee is estimated to strike one obstacle per second while foraging for pollen,^[102] which means its wings will sustain $\approx 500\,000$ collisions over its lifespan of a month.^[103–105] After splinting the wings to prevent them from bending, researchers observed an order-of-magnitude increase in the rate of wing loss from collisions.^[101] These damage-minimizing crumple zones are therefore essential to wing longevity, especially in foraging insects.

Wing membranes not only serve as a deformable element, but may also contribute to overall flexural rigidity.^[93–95] Their thickness varies approximately four orders of magnitude across insect species, ranging from less than 500 nm in the delicate wings of fruit flies (*Drosophila* sp.) to thicker than 1 mm in the sturdy fore-wings of beetles (order Coleoptera).^[76] Certain

regions within an individual wing membrane can also vary in thickness and mass. The wings of dragonflies (order Odonata), for example, contain a region called a pterostigma. This dark-pigmented spot sits adjacent to the leading wing edge and is thicker and denser than that of the surrounding cuticle, with a much coarser texture (Figure 6).^[106] It shifts the wing's center of mass toward the leading edge, which provides more gliding stability, helps to regulate wing pitch, and increases asymmetry between upstroke and downstroke in each flap.^[106,107] Membrane composition also varies spatially within wings. The wings of certain beetles and earwigs specifically contain flexible regions rich in a protein called resilin that imparts elasticity.^[108,109] These regions assist with wing folding for storage during rest and with general deformation by reducing the elastic modulus up to three orders of magnitude. Resilin also increases the elastic energy captured during wing movements for better flight efficiency.^[101,110,111]

Unlike typical airfoils, which are smooth and aerodynamically streamlined, the wings of many insects are rough or textured. Some examples of this structuring include the cross-sectional corrugations found in dragonfly wings (Figure 6) and scales on the wings of butterflies and moths.^[112,113] In the dragonfly specifically, it is likely that corrugations improve rigidity between the wing base and tip to compensate for the ultralight and ultrathin membrane composition.^[94,112] Some researchers argue that air vortices fill the voids created by these corrugations and effectively smooth the surface profile, while others assert that dragonfly-wing corrugations trade aerodynamic performance for structural support.^[114,115] Certain insect wings are also cambered near the wing base, meaning that the top (dorsal) side of the wing has a convex structure while the bottom (ventral) side is concave.^[116] This geometry adds an element of asymmetry to wing bending—downward force acting on the dorsal surface of a wing will result in more bending to reduce energy expended during an upstroke, while the wing resists bending under upward force on the ventral surface due to concavity to generate more lift from each downstroke.^[98]

Curiously, fairyflies (family Mymaridae) and small flying insect species from at least six other families do not conform

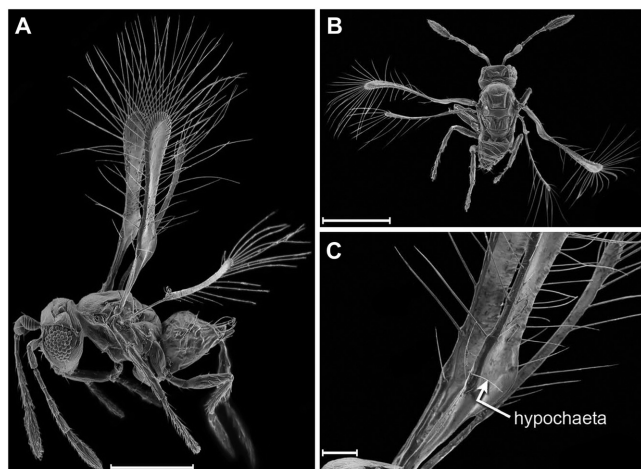


Figure 7. Fairyflies have unique bristle-based wings enabling efficient flight. A) Lateral angle SEM image of the fairyfly *Tinkerbella nana* (Hymenoptera: Mymaridae), the wings are shown at the start of a downstroke. B) Dorsal angle SEM image of fairyfly *Kikiki huna*, the wings are shown at the finish of a downstroke. C) SEM image of a basal wing segment of the fairyfly *Tinkerbella nana*. Scale bars: A,B) 100 μm , C) 20 μm . Reproduced under the terms of the CC-BY license.^[6] Copyright 2013, John T. Huber & John S. Noyes.

to the insect wing morphology described above, and instead have developed wings predominantly made up of long bristles (see **Figure 7**).^[6] The functional basis for this morphology is still up in the air, but likely involves some combination of weight reduction, electrostatic dispersal enhancement (a technique possibly used by ballooning spiders for flight),^[117] mechanosensation, improvement of wing folding, and/or flight efficiency.^[118–121] When moving an appendage through a fluid, the relationship between the velocity of that appendage and the force applied to it depends on the dimensionless Reynolds number, which represents the ratio of inertial forces to viscous forces and is calculated from the fluid's density, viscosity, and relative velocity as well as a characteristic dimension of the appendage. Most biological hairs are sized such that the force generated by their movement is independent of their spacing at relevant speeds.^[122] Fairyfly wings, however, have tiny hairs with diameters between 300 nm and 2.5 μm , expanding the range of velocities where hair spacing has a significant effect on the force generated through movement; the velocity of their wings falls within this range.^[6,123] By actively controlling wing bristle spacing or attack angle, fairyflies are able to optimize their wingbeats to maximize lift and minimize work. In other words, fairyflies reduce their effective bristle spacing on downstrokes to make their wings behave like paddles, and increase this spacing on upstrokes to achieve a more rake-like effect.^[122,124] The force required to separate the wings, which clap together at the top of a wingbeat, also plays a role in this adaptation. Drag forces on one solid insect wing separating from another are more than three times greater than those on a wing translating independently, and this effect increases at lower Reynolds numbers.^[125] The bristled wings of a species of order Thysanoptera, *Thrips physaphus*, experience twelve times lower drag force while separating than solid wings.^[124] By improving flight efficiency, hair-based wings allow smaller insects to fly

for sustained periods of time without large, energy-consuming musculature. A similar design approach may allow even the smallest of MAVs to fly using minimal battery power.

3.2. Swimming Adaptations

Freshwater aquatic environments contain a disproportionately large amount of animal species. Despite covering only 1% of the surface of the Earth, they are home to more than 10% of taxonomically identified species, 80% of which (up to 200 000) are estimated to be aquatic insects.^[126] At least fourteen orders of insects contain aquatic species, and five of those orders consist mostly or entirely of aquatic insects.^[127] Insects have developed a variety of physiological systems to survive and thrive in water, including systems optimized for feeding, for respiration (discussed in Section 4.2), osmoregulation, and locomotion. Two notable solutions for aquatic movement have been developed by the phantom midge (*Chaoborus crystallinus*), and the mosquito (*Culex pipiens*). Both larvae and pupae of the phantom midge possess a tail fan, which is a structure containing an average of 26 cuticular filaments, ≈ 1 mm in length and 11 μm in diameter (at the base), with 10 μm of base-separation when fully splayed.^[128] Each of these filaments has regions rich in the elastic protein resilin, which helps maintain a splayed state while resting.^[128] To move, the phantom midge curls up its body (fan actively retracted), and then rapidly straightens out while passively splaying the fan. Fan extension increases the surface area of the last abdominal segment by more than 500%, which provides paddle-like thrust and potentially even steering/stability control.^[128] Similarly, mosquito larvae have a brush-like structure emerging from their mouth that resembles a mustache.^[129] The hairs, which number around 1000 per larva and are each ≈ 400 μm long, are arranged in 20–30 rows with even spacing. They are actively swept back and forth at a rate of 11 Hz within a roughly 90° range of motion.^[129–131] This motion produces a one-directional current that propels the larvae without producing any periodic disturbances, which would disrupt both vision (see Section 6) and vibrational sensation (see Section 5).^[129] Techniques that promote uniform (rather than periodic or random) and energy-efficient locomotion are desirable from an engineering viewpoint as they provide maximum autonomy and power to other on-board systems, e.g., cameras or flow sensors.^[132]

Many of the best-known aquatic insects come from the true bugs (order Hemiptera), which includes water striders, water boatmen, backswimmers, and shore bugs.^[126] Legs of insects in this order are well adapted to movement through water or on its surface. Gerromorphans bugs (water striders, shore bugs) have hairs on their legs and bodies that increase surface area and create trough-shaped depressions on the surface of water.^[127] They move across the surface in three distinct fashions: (i) walking by moving three legs at a time as alternating tripods, (ii) rowing by moving the middle legs simultaneously while the hind legs lay flat on the water surface, and (iii) skating with powerful center leg strokes that look like a jump-and-slide.^[133] Water striders in particular are assisted by thin chitinous setae (hairs) 50 μm long that cover the surface of their legs.^[134] These setae are oriented at a 25° angle to the

leg surface, which gives them interesting direction-dependent surface-adhesion properties stemming from the solid–liquid air contact line (see Section 4).^[135,136] When the setae are directed opposite to the motion of the water (against the grain), fluid force pulls them away from the leg surface, increasing both the relative angle between the two and the water–hair contact area. This effect results in greater adhesion to the air–water interface, which the water strider uses both while drifting on the surface and for propelling motions.^[134] When the setae are oriented in the direction of water flow (with the grain), surface adhesion is reduced, which is beneficial for passive gliding after a leg stroke.^[134]

In terms of fluid dynamics, the microhairs help water striders modulate the slip length, i.e., the amount of friction or drag force, between their legs and the fluid. Structured surface features that actively manipulate slip length have, for example, been applied in microfluidic and nanofluidic devices to control flow rates,^[137] and could inspire applications with larger size scales, e.g., to improve watercraft efficiency on the hulls of boats. Passive functional structures such as these have a range of applications limited only by the creativity of the engineer.

4. Water-Associated Structures

Insects have a number of nonlocomotive adaptations that relate to water, as well—they inhabit environments that range widely in terms of their humidity, access to moisture, and prevalence of interfaces, leading to a number of evolutionary pressures with material solutions. Some of these solutions are external: dragonflies, damselflies, and cicadas all have cuticular structures on their wings that protect against interference from raindrops and dirt.^[138–141] Others are internal: to avoid dehydration, various species of midges manipulate their systemic concentrations of osmolytes.^[142–144] Despite their functional and spatial differences, most water-specific adaptations in insects share common mechanisms of action: they either modify wettability through a distinct air–water–surface interface, or they maintain specific osmotic or hydrostatic pressures.

The concept of air-gap-based (super)hydrophobicity, since its introduction in the first half of the 20th century,^[145,146] continues to be applied in new contexts. Advances in micro-fabrication and surface characterization have provided critical physical insight into how micro- and nanostructures modulate wettability.^[147] Aside from choosing substrate materials, engineers ultimately have three control parameters when designing a surface with roughness-induced hydrophobicity: the size, the shape, and the density of fabricated surface features.^[148] As features become smaller and more densely packed, their ability to prevent condensation of fogs and fine mists improves. This effect is optimized when the features are shaped like cones (rather than cylinders), as is the case with the surface of lotus leaves.^[148,149] These general trends represent a useful starting point for surface engineering, but intermediate parameters within each category and the various permutations found among the insect world have yet to be fully explored and may provide more optimized design approaches with advanced functionality.

4.1. Hydrophobic and Hydrophilic Surfaces

Two groups of organisms have developed truly superhydrophobic (water contact angles greater than $\approx 150^\circ$) and self-cleaning surfaces; plants and insects.^[150] Of the plants, lotus leaves have garnered considerable attention for their optimized hierarchical surface patterns that arise from micro- and nano-structured surfaces.^[151–153] Examining the hindwings of the planthopper, *Desudaba danae*, reveals apparent convergent evolution with the lotus (**Figure 8**).^[149] The surfaces of both planthopper wings and lotus leaves are dotted with tapered micropillars with base diameters between 4 and 10 μm and heights between 6 and 10 μm , spaced 15–30 μm apart.^[149] These pillars, and hydrophobic surfaces on insects in general, serve a variety of purposes. They: (i) prevent water (and thus weight) accumulation through antiwetting, (ii) exhibit low adhesion to foreign particles, (iii) promote droplet rolling to encapsulate and remove any contaminants that manage to stick to the surface, (iv) encourage droplet coalescence, which helps protect against the accumulation of water from fine mists, and (v) discourage bacterial growth.^[149,154]

Broadly, these hydrophobic designs can be generalized into at least four groups: simple (e.g., pillar or dome-shaped) micro- or nanostructures, complex (varied shape) micro- or nanostructures, scales (usually 2–3 μm in one dimension), hairs or setae much longer (typically more than 5 μm in length) than their diameters, and hierarchical organizations including any combination of these elements (**Figure 9**).^[155] Regardless of their design motif, hydrophobicity-inducing structures in insects generally seek to maximize the air–water interface area while minimizing the solid–water contact area. This concept of air-gap hydrophobicity, first put forth by Cassie and Baxter in 1944 to explain the hydrophobic nature of duck feathers and how they could serve as bioinspiration for water-repellent clothing, is central to all surfaces in insects whose hydrophobicity is driven by structure rather than chemicals.^[146] The Cassie–Baxter theory describes hierarchical micro- and nanostructures as uniform curved surfaces with a heterogeneous composition (e.g., of air and solid), and posits that the air filling the space between these structures is essentially trapped and behaves like a nonwetting solid.^[146]

Fog forms on a surface when droplets larger than 190 nm in diameter (more than half the shortest wavelength of visible light) condense and accumulate.^[156] This phenomenon poses a challenge to insect vision, as insects lack eyelids and thus have no way to externally remove vision-blocking moisture or other contaminants. Mosquitoes, family Culicidae, have superb vision that can function in poorly lit and damp environments to locate mates, oviposition sites, and blood sources.^[157] To maintain consistent sight and avoid fogging, the surface of each mosquito ommatidium (optical sensory unit, discussed in Section 6.4) is densely coated with nanoscale nipples. These nipples are around 100 nm in diameter and are spaced roughly 50 nm apart in a hexagonal non-close-packed array; they also provide refractive-index matching for improved transparency (see Section 6.2). Their proposed mechanism of hydrophobicity mirrors that of the lotus leaf, planthopper wing, and water strider legs: the nanostructured array contains air gaps that effectively prevent water from contacting a large portion of the surface as in the Cassie–Baxter model of wetting.^[146,149,151,158]

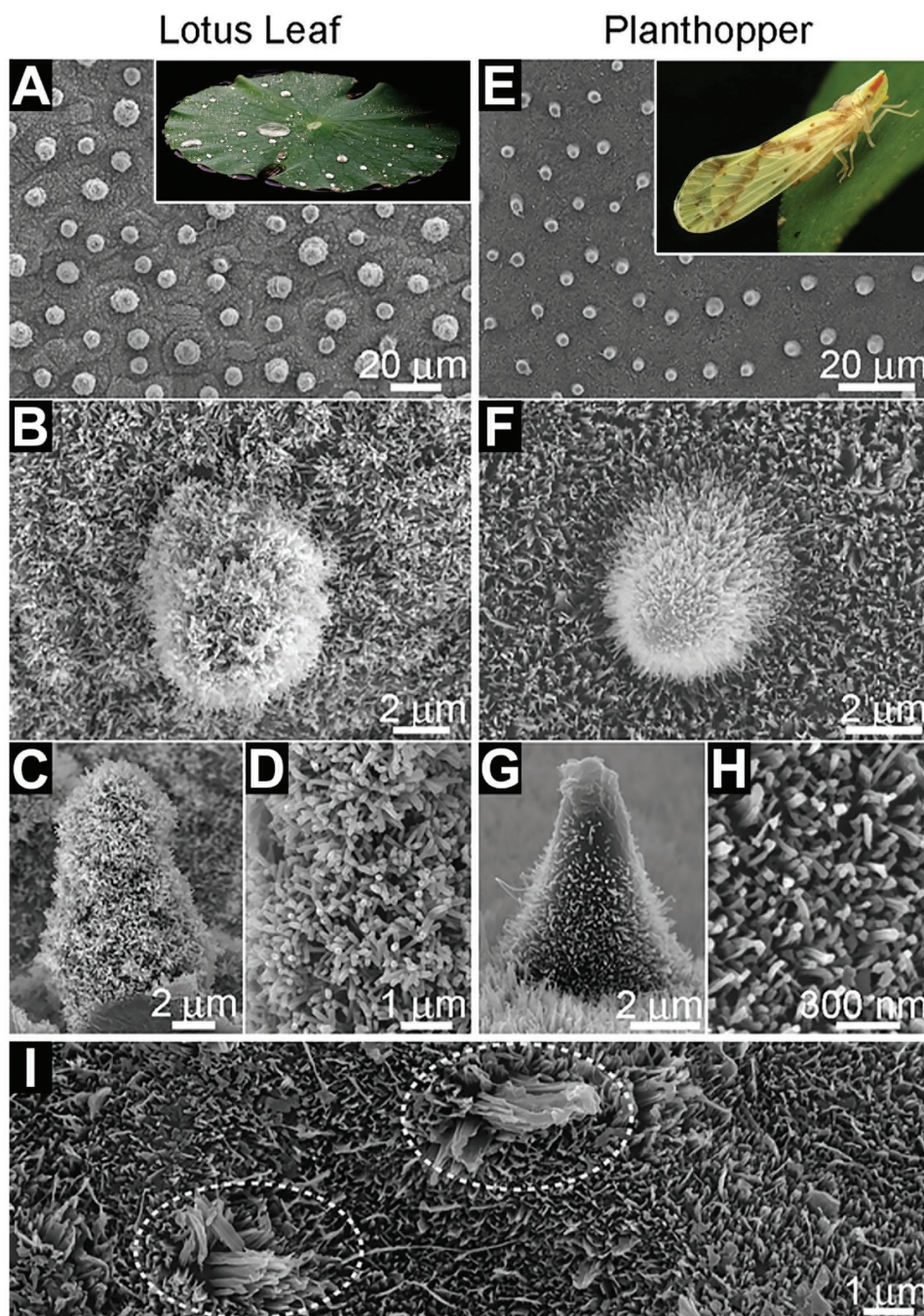


Figure 8. Planthoppers and lotus plants have developed remarkably similar superhydrophobic surface structures through convergent evolution. A–D) SEM images of the surface of the lotus leaf (inset) at varying magnifications. E–H) SEM images of the surface of the planthopper hindwing (inset) at varying magnification. I) SEM image of planthopper hindwing to highlight heterogeneous aspects of the protrusions and their spacing. Reproduced with permission.^[149a] Copyright 2017, American Chemical Society. Inset of (A) Reproduced under the terms of the CC-BY-ND licence. Copyright 2011, Steve Corey,^[149b] inset of (E) Reproduced under the terms of the CC-BY licence. Copyright 2017, Katja Schulz.^[149c]

In other words, the nanometer spacing of surface features creates a complex, nonplanar water–air–insect contact area, which makes it energetically less favorable for water droplets to wet the surface than to remain as spheres in the air.^[136] Additionally, theoretical studies show that it is unfavorable for water molecules to form a network of hydrogen bonds within

nanostructured materials, and specifically between hydrophobic surfaces separated by a critical distance of 100 nm.^[159] Antifog eyes are not unique to mosquitoes; the green bottle fly, *Lucilia sericata*, has also developed a fog-resistant eye surface structure thought to act in a similar manner, with well-ordered bubble-like protrusions ≈ 100 nm in diameter and packed in

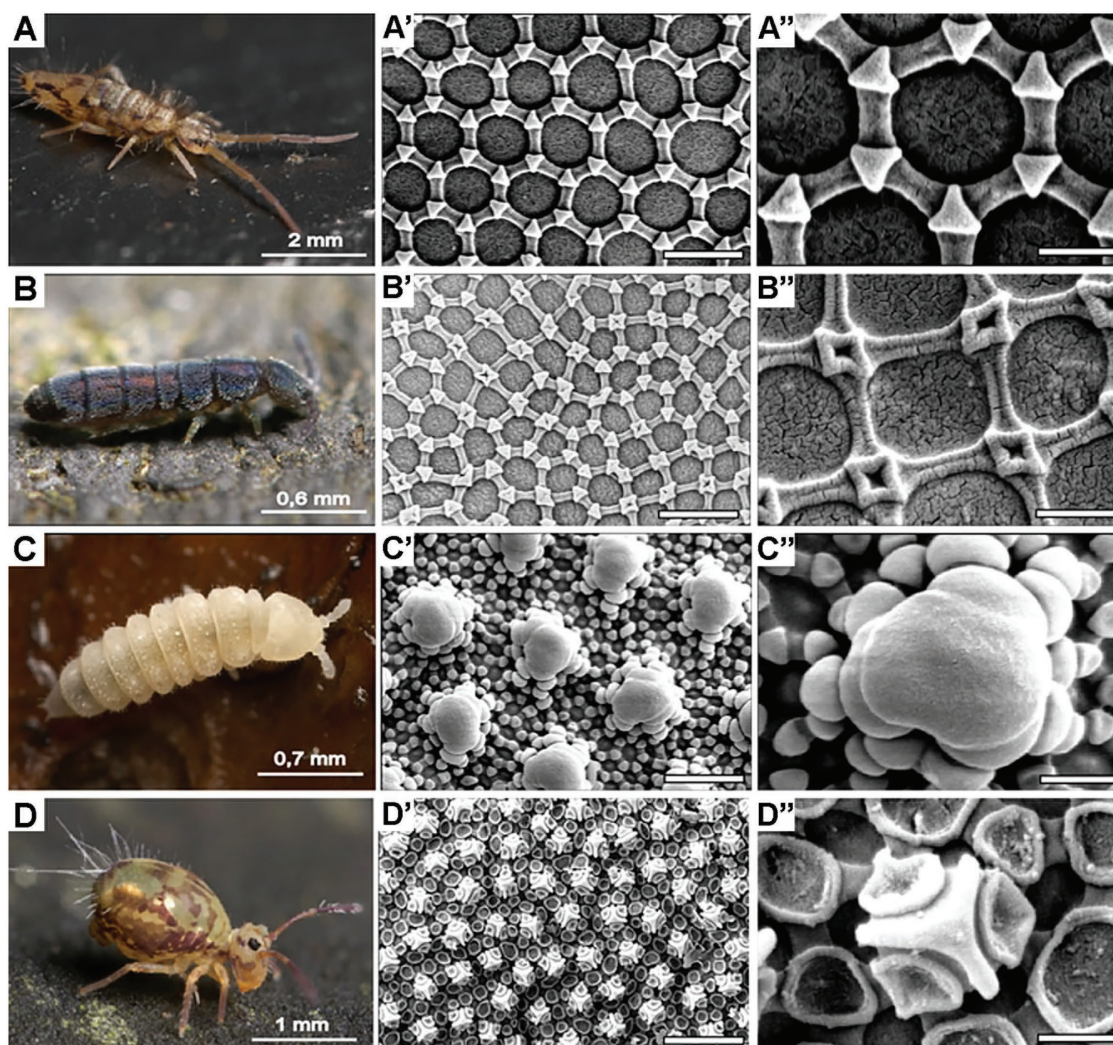


Figure 9. Different orders and life stages of springtails (Collembola) have developed a variety of periodic, hierarchical surface structures with hydrophobic properties. A-A'') Image of *Entomobrya intermedia* and SEM images showing hexagonal and triangular motifs in *P. flavescens*. B-B'') Image of *Vertagopus arboreus*, and SEM images showing irregular square and pentagonal motifs in *I. viridus*. C-C'') Image of *Kalaphorura burmeisteri*, and SEM images showing secondary granular structures and hexagonal motifs in *S. quadrispina*. D-D'') Image of *D. ornata*, and SEM images showing secondary granular structures and variable elliptical patterns in *A. pygmaeus*. Scale bars: A'-D' = 2 μm , A''-D'' = 500 nm. Reproduced with permission.^[666] Copyright 2012, Springer.

close proximity.^[160] Similar optical features have recently been found in many other insect species.^[148]

Other insects including the desert beetle, *Physaterna cribripes*, use fog as an important source of moisture.^[161] When the desert humidity increases to a level where fog or dew can form, usually in the early morning, the beetle angles its elytra (protective wing cover) against the wind, causing droplets to condense on the upper cuticular surface.^[162] These droplets, which are tens of micrometers in diameter, would ordinarily detach from the surface under desert heat and wind conditions, but a specially developed elytral structure of hydrophilic islands on a hydrophobic substrate keeps them in place.^[163-165] The elytra's macroscopic structure is a random array of bumps of around 500 μm in diameter spaced between 0.5 and 1.5 mm from one another. The peaks of these bumps are smooth and hydrophilic, while the troughs between bumps are coated with wax and contain a hexagonal

array of flattened, 10 μm hemispheres that render them hydrophobic. Droplets are attracted to the hydrophilic regions, where they spread to coat their "island" and begin growing upward until they have enough weight to overcome capillary adhesion to the bump.^[164] At this critical mass, they form large droplets that roll into the hydrophobic troughs where they are guided down the surface of the elytra to the beetle's waiting mouthparts.^[161,164]

Not all insects have developed cuticle nanostructures to produce specific interactions with water. Some, like the leafhopper, family Cicadellidae, achieve hydrophobicity by coating themselves in a nanosized proteinaceous powder.^[166,167] The powder is composed of spherical honeycomb-like particles called brochosomes, which have diameters between 200 and 700 nm and walls arranged in pentagonal and hexagonal shapes that open into a hollow center.^[167] Most of these particles have the same truncated icosahedral geometry also found in soccer balls, C_{60}

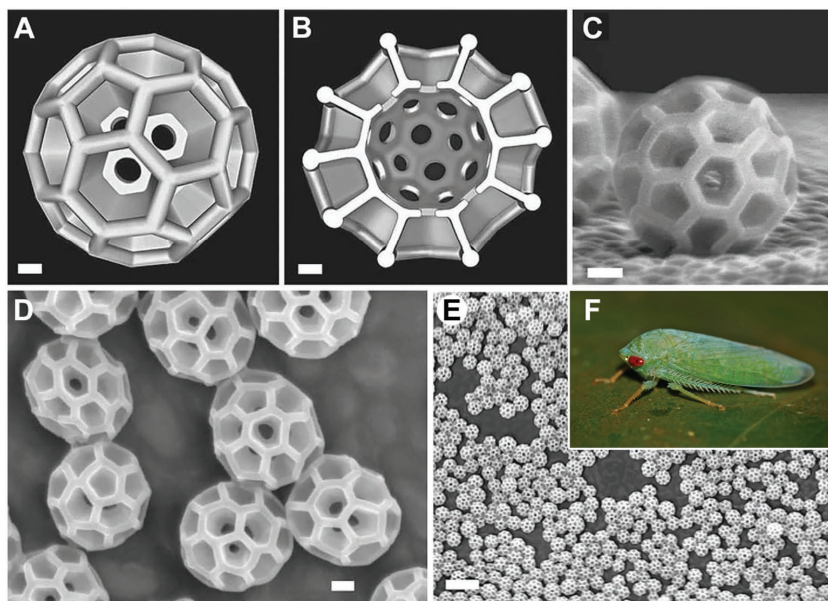


Figure 10. The leafhopper (family Cicadellidae) coats itself with brochosomes—spherical, honeycomb-like particles made of proteins and lipids and less than 1 μm in diameter—to achieve a nearly superhydrophobic exterior. Illustrative model of a typical brochosome with: A) general view and B) cross section. C) Individual brochosome on the surface of *Athysanus agentarius*. D) Touching brochosomes are connected on *A. agentarius*. E) Dense coating of brochosomes on the hind wing of *A. alneti*. F) Photograph of a green leafhopper. Scale bars: A, B) 50 nm, C, D) 100 nm, E) 1 μm . A–E) Adapted with permission.^[667a] Copyright 2013, The Royal Society. F) Reproduced with permission.^[667b] Copyright 2015, Bernard Dupont.

buckyballs, and viral capsids (Figure 10).^[168,169] Their chemical composition is $\approx 60\%$ protein and 40% lipids and/or other compounds; the exact composition varies with species.^[167,170,171] Within the proteins, there are higher than normal representations of glycine residues, which are often found in fibrous structural proteins, and tyrosine residues, which may play a role in polymeric hardening and crosslinking during wall formation.^[172,173] The leafhopper applies these coatings shortly after molting by secreting a colloidal suspension of brochosomes from its hindgut onto its exoskeleton, then grooming itself with rapid leg strokes until the solvent evaporates.^[167,174] Interestingly, the material composition of the brochosomes themselves is only moderately hydrophobic, but they are able to generate near superhydrophobicity when arranged in an ensemble layer by creating a complex water–air–insect interface rife with tiny air gaps (again approximating the Cassie–Baxter regime).^[167] Surprisingly, most leafhopper species actually live far away from water. While their brochosome coatings do defend against atmospheric moisture (e.g., rain), a more likely functionality can be traced to their own liquid excretions. Leafhoppers feed on phloem and excrete a sugar-rich “honeydew,” which is sticky and provides an ideal growth substrate for pathogenic microbes.^[175] In dense populations of leafhoppers, hydrophobic coatings may serve largely to prevent insects from being coated in their own, or their neighbors’, excrement.^[167,176] Protective surface coatings made of actively secreted molecules and particles may also be useful in materials science as such surfaces could reduce biofilm formation or other fouling mechanisms.

Despite the highly optimized nanostructures on their eyes, both male and female mosquitoes of species *Anopheles freeborni*

lack superhydrophobic wing surfaces to passively shed water, so their wings are susceptible to spontaneous capillary-driven folding in high-humidity conditions (e.g., heavy fogs).^[177] When this happens, their wings can become so tightly folded that they take a long time to dry, during which the mosquitoes are grounded. The mosquitoes have developed a modified wingbeat or “flutter stroke” to counter this effect.^[178] Normally, their wingtips oscillate at a frequency around 285 Hz, but when they sense moisture they will occasionally increase this beat rate more than threefold to 875 Hz and decrease its amplitude by nearly 90%.^[178] This flapping regime is poor for locomotion, but generates wing accelerations that are almost double those found in normal flight and sheds water droplets from the wing. Another adaptation, hard landing, is generally employed when the mosquito is hit by a raindrop in mid-flight. When this happens, mosquitoes do not

make any attempt to flap or clear their wings of water and instead begin a freefall dive reaching a terminal velocity of 0.44 m s^{-1} , three times that of a falling dry, anesthetized mosquito.^[179] Upon hitting the ground, mosquitoes shed more than 75% of the associated water droplets, which allows them to resume

4.2. Systems for Sub-Aquatic Exchange

flight and remove the remaining droplets via wing flutter.^[178] The concept of removing water through inertial forces may find uses in future large and small-scale flying structures.

The primary survival challenge of aquatic insects (Section 3.2) is maintaining a consistent oxygen supply underwater. To this end, mosquito larvae from *Aedes togoi* float a snorkel-like breathing apparatus on the surface of a body of water to maintain a steady oxygen supply. This appendage contains three main and two auxiliary “hydrofuge lobes” that are coated with oil secretions and arranged into the shape of a hollow cone.^[180,181] The lobes converge to a single point containing an air hole (spiracle) that connects their conical structure to a tracheal trunk and the rest of the larval respiratory system.^[182] The floating mechanism is largely supported by surface tension, which holds the cone base at the water surface and pulls the lobes slightly apart. Lipid-driven hydrophobicity prevents the air-filled inverted cone from flooding and induces a negative water curvature in the gaps between lobes.^[183] When the larva moves downward to submerge itself (e.g., to avoid danger), hydrostatic pressure forces the lobes together, effectively sealing the spiracle until the lobes are again pulled apart by surface tension.^[182] Similar schemes have obvious applications as gas intake or outlet valves in the context of microfluidic actuators.^[184]

Some insects maintain air bubbles within or nearby their exoskeleton for gas exchange (Figure 11). Known as “physical

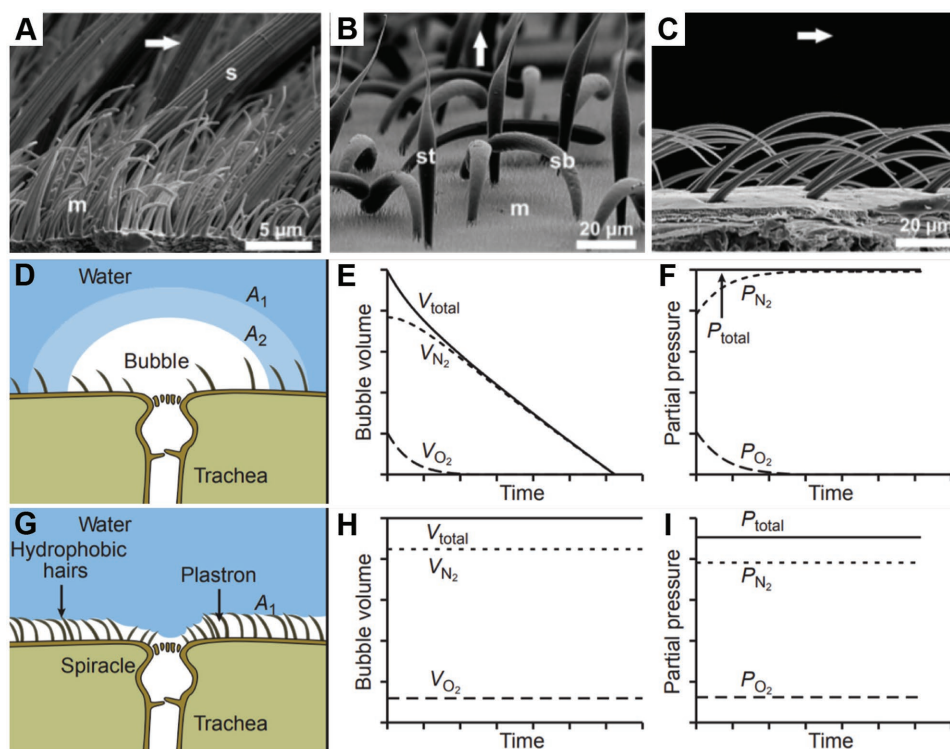


Figure 11. Plastrons facilitate underwater gas exchange by using hydrophobic structures to maintain constant volume and equilibrium pressures. A) SEM image of the water-repelling microtrichia (m) and setae (s) of the abdomen of the common pond skater (*Gerris lacustris*) showing size diversity. B) SEM image of the body of a backswimmer (*Notonecta glauca*), showing the microtrichia (m), as well as sharp-tipped setae (st) and tapered-rod setae (sb). C) SEM image of the waterlily leaf beetle (*Galerucela nymphaea*) showing the uniform orientation of water-active setae on the insect's protective wing covers. All the arrows point toward the tail-end (posterior) of the insect. A–C) Reproduced with permission.^[189] Copyright 2011, Wiley. D–F) Unsupported physical gills decrease in size as the insect uses oxygen, requiring the insect to return to the surface periodically. G–I) Supported physical gills allow insects to remain submerged indefinitely, provided they have low to moderate metabolic rates. D–I) Reproduced with permission.^[194] Copyright 2013, Company of Biologists.

gills,” these bubbles can directly exchange oxygen and carbon dioxide with water and can either be supported by cavities of fixed volume (incompressible) or be nonsupported and free to expand and contract (compressible).^[185] Nonsupported air bubbles shrink as an insect dives: oxygen is used up through respiration, which increases the concentration of nitrogen in the bubble. The resulting gradient causes nitrogen to dissolve into the surrounding water.^[186] Any carbon dioxide produced and released by the insect quickly dissolves into the water as well. This balance of gas concentration and pressure results in a transient system where the insect must periodically return to the surface to replenish the bubble gases.^[187]

Supported physical gills, known as plastrons, are permanent fixtures that allow insects to remain submerged indefinitely in sufficiently oxygenated water.^[188] Unlike nonsupported physical gills, which shrink in response to pressure differences caused by respiration, plastrons have hydrophobic structures that counter the hydrostatic pressure of the water to keep the bubble volume relatively constant.^[189] As an insect absorbs oxygen for metabolic processes, its overall plastron pressure decreases, but the nitrogen partial pressure and plastron volume remain constant. Following this pressure decrease, oxygen diffuses from the water into the bubble, restoring overall plastron pressure and sustaining the resting metabolism of the insect.^[190]

The river bug, *Aphelocheirus aestivalis*, is an aquatic insect that uses a plastron for gas exchange underwater and spends almost its entire adult life submerged. Its particular plastron is made up of cuticular hairs 0.4 μm in diameter and 3 μm long, spaced 0.5 μm apart.^[191] The hairs cover the entirety of the bug's highly flattened exterior, with a total surface area of $\approx 95 \text{ mm}^2$ and an air volume of around 0.14 μL (with roughly a 1:1 hair to air volumetric ratio).^[192] This air pocket represents 8–9% of its body volume, which happens to be very similar to the proportion of lung capacity to body volume in humans.^[192,193] Unlike vertebrates, however, insects employing plastron-based respiration rely entirely on passive diffusion of oxygen through water into their breathing bubbles. These insects are therefore constrained in body size: metabolic rates in insects increase more steeply than surface area with increasing mass. Insects are also often constrained to highly oxygenated aqueous environments.^[194] It then follows that river bugs are likely one of the largest groups of plastron insects.^[192] They are shaped to have a high surface-area-to-volume ratio, they have resting metabolic rates less than half of what is predicted for their size, and they are most commonly found in moving, well-aerated streams.^[195]

Organ-on-a-chip systems have gained popularity for their potential to accurately replicate biological processes entirely in vitro.^[196] These systems, similar to the biological schemes they

attempt to imitate, fully rely on controlled nutrient exchange between moving media and a cellular layer. Devices probing respiratory cells in particular could employ and benefit from a plas-tron-based design to modulate exchange from the gas phase.

5. Sensing and Production of Mechanical Signals

Insects navigate diverse and rapidly changing environments and do so while performing complex tasks like flying, mating, grooming, and foraging, among others. Making matters more difficult, all arthropods (including insects) are encased in a rigid exoskeleton similar to a medieval suit of armor. This exoskeleton provides essential benefits, but poses a major challenge in sensing and interacting effectively with the outside world. To solve these problems, insects have developed mechanosensory organs that provide spatial and force-responsive feedback. These organs are similar to (and often complement) the appendages that insects use for locomotion; they are largely comprised of cuticle arranged in material motifs that impart various material properties like strength, elasticity, durability, and vibrational resonance.

5.1. Detection of Mechanical Signals in Insects

The large majority of insect mechanosensory tools rely on approximately the same signaling mechanism based on ionic gradients, which is also employed by cochlear (hearing) hair cells in vertebrate organisms.^[197] The dendrite of a mechanosensory neuron sits within a highly resistant epithelial cell layer separating potassium-rich endolymph from potassium-deficient central hemolymph. Adenosine triphosphate (ATP) driven potassium pumps in the membranes of the epithelial cells maintain this transepithelial gradient and potential of 30 mV or more.^[198] When the dendrite is mechanically stimulated, mechanotransduction potassium channels open, rapidly depolarizing the associated neuron and alerting the insect to the presence of a stimulus. The large negative transmembrane resting potential of the neuron in combination with the large positive epithelial potential leads to signal transduction on the scale of microseconds, in accordance with the Hodgkin–Huxley model.^[199] Analogous to how signals from the human retinae are mapped into a complete visual image, insects are thought to process signals from mechanosensory arrays in aggregate, likely allowing them to interpret air currents, body movements, communication signals, and surface features as a “map” of their surroundings.^[200]

Understanding mechanotransduction in biology requires thorough characterization of its fundamental components: the relationship between the physical properties of mechanosensory organs and their associated stimuli, and the ways in which signals from those organs are processed and subsequently influence an organism’s behavior. The examples we present below aim to connect structural aspects of insect mechanosensors (e.g., morphology, elasticity, and anatomical position) with the forces they transduce. Such structure–force relationships are a central theme in the development of stretchable sensory electronics, which have applications in prosthetics, robotics, and biological monitoring.^[201,202] Mechanical durability is critical in

both manufactured and biological structures, as many of these devices and structures must last the lifetime of a product or insect despite exposure to wear and tear. Chortos et al. recently developed novel stretchable transistors by incorporating layers of carbon nanotubes within a polymeric material to measure stresses and strains applied to the material.^[203] The spatial orientation of the nanotube layers can be programmed to detect stretching or forces applied in desired directions, just as the orientation of cuticle microstructures of insects influences their specificity. The transistors themselves can be embedded into a variety of elastomer scaffolds; the composition of those scaffolds could potentially be optimized for durability or elasticity using various cuticle design principles found in insects.

5.1.1. Tactile Hairs

The most prevalent organ morphologies used by insects for mechanical transduction are bristle-like structures generally known as tactile hairs. These hairs consist of hollow shafts, each attached to a single sensory neuron, and act as lever arms that relay a mechanical force to corresponding mechanotransduction channels.^[204] Physically, they are thick, terminate in sharp points, and receive extra structural support from specialized cells.^[205] Each hair has directional selectivity that varies with aspects like hair morphology, shaft angle relative to the cuticle, and ion channel location and/or type.^[206,207] Additionally, insects often possess two distinct types of associated sensory neurons: rapidly adapting (i.e., respond quickly to changes in stimuli) and slowly adapting (i.e., respond throughout the duration of the stimuli). Hair length varies between the two. Two-spotted crickets, *Gryllus bimaculatus*, for instance, have tactile hairs ranging in length from 30 to 1500 μm .^[208] Long cricket hairs stimulate neuron dendrites, which are slowly adapting; these first-order differentiators are sensitive to changes in displacement and generate action potentials over the duration of a stimulus. The neuron dendrites associated with shorter hairs are rapidly adapting second-order differentiators that respond to changes in velocity.^[208] This difference stems mainly from the ion channels for mechanotransduction within the dendrites themselves rather than from the mechanical properties of the hairs—e.g., the short hairs of crickets remain pivoted past threshold under sustained stimulus, but their associated neurons do not transmit signals outside of the stimulus onset or offset. Together, these hairs allow the creatures to sense miniscule changes in air currents, including the wingbeats of predators in the presence of a steady wind. Studies on the desert locust, *Schistocerca gregaria*, revealed that in particular mechanical activation thresholds can vary considerably between the two types of mechanosensors, with roughly a 40° deflection threshold for rapidly adapting hairs and a 10° threshold for slowly adapting hairs.^[207]

Head stabilization is essential to insect agility and visual navigation. Dragonflies accomplish this task by temporarily fastening their heads to their necks using an intricate, interlocking physical adhesive structure as discussed in Section 2. On the other hand, the hoverfly, *Episyrphus balteatus*, has a more developed structural and muscular head support than

dragonflies, which it is able to manipulate with the help of tactile hair feedback.^[209] This feedback acts in combination with visual cues to orient both the head and body of the hoverfly in a horizon-locked position. Head positioning is also important for walking insects, which face disruptions from step movements as well as inconsistent surface topographies. For example, in complete darkness, the bull ant, *Myrmecia pyriformis*, is able to maintain a consistent head position using feedback from joint-positioned hairs, which monitor positions and forces on each ant limb to determine the direction of gravity.^[210,211]

There is little variability in the structure and ubiquity of tactile hairs between different insects,^[212–214] and the hairs play an integral role in the survival of insects. This convergent mechanosensory system is therefore thought to be extensively refined by evolutionary selection pressures.^[200]

5.1.2. Campaniform Sensilla

Another class of mechanosensory organ, known as campaniform sensilla, are dome-shaped cuticle components that respond primarily to stress and strain.^[215] Similar to the tactile hairs, each sensillum is innervated by a single neuron, which rests within a socket underneath a dome composed of cuticle. Mechanotransduction channels in the dendrite of this neuron are activated when the dome flattens, caused either by compression or tension of the sensillum.^[216] The domes themselves are generally elliptical rather than circular, which imparts directional selectivity through axial orientation: a compression along the short axis or tension along the long axis will, for example, lead to dome flattening and thus neuronal activation.^[217] In the blowfly, *Calliphora vicina*, specifically, the average length of the long axis of a sensillum is about 9 μm , and the spacing between two sensilla is roughly 20 μm .^[215] Groups of sensilla also exist arranged side by side in close proximity, often forming structured rows.^[215] These groups are most commonly found in regions of the insect anatomy subject to larger strains (e.g., joints). Dendrites of each sensilla can be either rapidly or slowly adapting as well, allowing detailed sensory feedback.^[218] Like the tactile hairs, campaniform sensilla represent a mechanical force sensor with a unique morphology that may be replicated in next generation stretchable electronics.

5.2. Detection and Production of Vibrational Signals

Hearing loss affects one in six adult humans,^[219] and is one of the most widespread chronic conditions in adulthood. With an aging population and increasing headphone use, the prevalence of hearing loss is expected to escalate in the coming years.^[220,221] Current commercial hearing-aids have low satisfaction rates:^[222] they are expensive, they are often energy inefficient, and they suffer from a poor signal-to-noise ratio, amplifying background noise and constraining their users to a voice-volume comprehension threshold more than 30 dB greater than that of listeners who do not require a hearing-aid.^[223] There is hence a need for miniaturized, biologically compatible systems that can efficiently detect, and also produce (see below), sounds in distinct frequency ranges.

Insects are able to “hear” sounds through a variety of structures, very few of which resemble vertebrate ears. Sound is a vibration that propagates as a mechanical pressure wave through a transmission medium, such as air, water, or a solid substrate. As the majority of insects are land-based animals, air is the most prominent carrier medium. It is, however, a compressible medium of low density. This means that although sound waves propagate a considerable distance through air, their intensity diminishes much faster than in solid or liquid media, and at an exponential rate described by Stokes’ law of attenuation.^[224] Organs that can detect airborne sounds at a great distance (far-field) are therefore much more sensitive than those that are only receptive to sounds or vibrations produced in their immediate vicinity (near-field).

Near-field detectors are very common in the insect world, ranging from Johnston’s organs at the base of mosquito antennae to rear-projecting antennae-like organs in cockroaches, even including the tactile hairs discussed previously.^[225] These detectors are used by flies (*D. melanogaster*) to sense the wingbeat frequencies of mates and by caterpillars to respond to the wingbeat frequencies of predators.^[226,227] Near-field detectors are most often found on rigid projections that resonate with ambient vibrations; their main limitation, apart from requiring close proximity to the source, is that they are generally only receptive to low frequencies (less than 500 Hz) with high intensities.^[228] Tympanal organs in insects—far-field detectors—can sense the pressure wave of a sound field from more than 10 m away, and frequencies ranging from 2 to over 100 000 Hz.^[229] These organs are composed of three components: a tympanal membrane, an air-filled sac pressed against the membrane, and a chordotonal sensory organ.^[230–232] The chordotonal organ is a cellular complex that ultimately houses a dendrite for the associated neuron(s), while the tympanum is a thin cuticle membrane similar to the head of a drum.^[229]

Unlike vertebrate organisms, which have ears in close proximity to their cranial regions, insect ears exist at various positions on the body, including the head, wings, mouthparts, and legs.^[230–232] Such diversity in spatial distribution and frequency detection range is the result of imprecisely convergent evolution; insects have evolved tympanal hearing almost thirty independent times.^[233] By comparison, vertebrate hearing is thought to have evolved only once.^[234] The mechanics of insect hearing also vary considerably, from the intricate lever system joining thousands of auditory neurons in cicadas,^[235] to the simple, two-auditory-cell tympanum complex of Noctuid moths.^[236] Body size is a constraining factor in the evolution of tympanal organs, as the membrane requires either a minimum diameter or extreme tension to respond effectively to sound delivered at all but the very highest carrier frequencies. For example, a 0.5 mm diameter tympanum may respond maximally to 100 kHz sound delivered above a threshold amplitude of 60 dB sound pressure level (SPL) (= 20 mPa).^[237] Thus, the smallest insects generally do not possess tympanal organs and lack the ability to hear far-field sound.^[238]

5.2.1. Subgenual Organs

The development of “smart material” systems with the ability to detect and locate self-damage has garnered increasing interest

in recent years. These kinds of systems offer the prospect of efficient and low-cost monitoring of integrity in both micro-scale technological devices and macroscale civil structures.^[239] Vibration sensors can detect large changes in global vibration through a material that arise from a general loss of material stiffness. These sensors often struggle to detect small cracks that can quickly propagate beneath the surface and can lead to structural failure.^[240] Several potential solutions to this problem exist: (i) incorporating a massively parallelized array of micro-sensors, e.g., “sensory skin,” that provides a detailed force-map of the entire structure;^[241,242] (ii) improving upon the design of current vibrational sensors and their associated processing algorithms to locate cracks more effectively, or (iii) employing some combination of these first two strategies.

Certain insects transmit and receive vibrational messages through the substrates they stand on for defense and other intraspecific purposes.^[243–245] Land bugs from more than ten families produce low-frequency (50–200 Hz) vibrations using muscle contractions to rapidly percuss their hard abdominal (tergal) plate against a plant substrate.^[246,247] The resulting vibrations travel well through the low damping substrate—measured intensity values of a 124 Hz signal through a cyperus stem were found to be consistent tens of centimeters from the source.^[243] Unsurprisingly, the organs that can detect these signals most sensitively, called subgenual organs, are located in the leg and are in direct contact with the substrate (subgenual means “below the knee”).^[198] Ground weta species from the genus of *Hemiandrus* do not have tympanal organs in the classic sense, and while they have tactile hairs that are receptive to near-field vibrations, they are thought to be insensitive to far-field airborne sound.^[248] They compensate for this deficiency with a sensitive intratibial structure known as a subgenual organ, which has different shapes and attachments depending on the desired physiological activation (e.g., frequency range).^[249] For instance, the subgenual organ in *H. hemideina* is pillow-shaped and acts as a precisely sized inertial mass which resonates with vibrational stimuli.^[250] Alternatively, the organ of *H. pillatarsis* is wafer-like, spanning the internal body fluid (hemolymph) channel in the tibia, with a thick attachment to one interior cuticle wall and a thinner attachment on the opposite side. This morphology allows it to function like a hinged plate: longitudinal waves traveling through the substrate, for example, act on the pliant region of the wafer, which swings back and forth stimulating the dendrites of sensory neurons.^[249] Other *Hemiandrus* species, as well as many other insects outside of that genus, have developed variants of these organs to perform the same function on different substrates at different frequencies and present intriguing targets for future morphological and biophysical investigation in the context of smart materials.^[249]

5.2.2. Sound Production in Insects

In acoustic communication, sound waves are generated specifically to be heard by the intended receivers.^[251] Hence, the sound needs to have sufficient acoustic power and has to be controlled to contain specific information. Sound production usually occurs by the active modification of specialized external

organs. In a first approximation, the minimum source size for good source-to-medium matching has a radius of about 1/6 or 1/4 of the intended sound wavelength for a monopole or a dipole source, respectively.^[252–254] Due to their small size, invertebrates are therefore limited to producing sound either at high frequencies or at low acoustic power. As a consequence, noisy insects either are relatively big, use high frequencies or resort to other acoustic tricks.^[255] For instance, several species of mole crickets dig tunnels in the ground with megaphone-shaped entrances.^[256,257] When the males sing from just inside their burrow openings, the shape of the tunnel amplifies the sound. This strategy results in roughly a twenty-fold increase in sound production, generating sounds that can be heard 600 m away.^[258]

Evolution has brought forward two major mechanisms to produce sounds in large insects: stridulatory organs, in which two components are actively rubbed against each other, and sound-radiating surface organs called tymbals. Small insects also produce sound by wing beating.^[259] Sound production in insects is often sexually dimorphic and restricted to the males. These sounds are often used in mating ritual or territorial behavior; however, some are used as a warning or defensive signal (so-called acoustic aposematism). Excellent reviews have covered large areas of sound production^[251,259,260] and perception.^[261]

Stridulation is the act of producing sound by rubbing together body parts that contain structured vibrational elements. Insects perform this task ad nauseam by rubbing one structure with a well-defined lip (the so-called “scraper” or plectrum) across a finely ridged surface (the “file”) or vice versa, generating vibrations in the process (Figure 12A–D). The sounds produced by stridulation are normally called “chirp” and “chirrup”. Insects are capable of generating a diverse range of songs that can be loud, musical, or highly patterned. This behavior is quite common in large insects and spiders, but is also found in some vertebrates such as fish and snakes. The position on the body and the anatomical features of the plectrum and the file can differ enormously in different invertebrates. What is largely conserved, however, is the mechanical durability of these organs, derived from the strength of their associated cuticular projections (Figure 2).

The most common system, used by grasshoppers and many other insects, involves rubbing a scraper located on the leg (e.g., in beetles)^[257,262,263] or the trailing edge of the wings (e.g., mole crickets, *Gryllus* sp, and grasshoppers, *Chortippus* sp.)^[264,265] against a hardened file on the underside of the adjacent wing. Both the scraper and the file are optimized for chirping and are coupled to thin, rigid parts of the wing (see Section 3.2) to promote acoustic coupling (Figure 12A–D). Each time the scraper passes over a tooth in the file, the thin, papery portions of the wings vibrate and amplify the sound. The nature of the sound that is produced depends on the resonance frequency of the wing determined by its cuticle rigidity, as well as the rate at which the teeth of the file are struck, which can vary from 7–65 Hz (bush crickets vs mole crickets).^[254]

Tymbals, like wings, are corrugated exoskeletal membrane structures made of cuticle, but they are used to produce sounds rather than for locomotion. Insects generate clicking sounds by contracting and displacing these membranes, analogous to

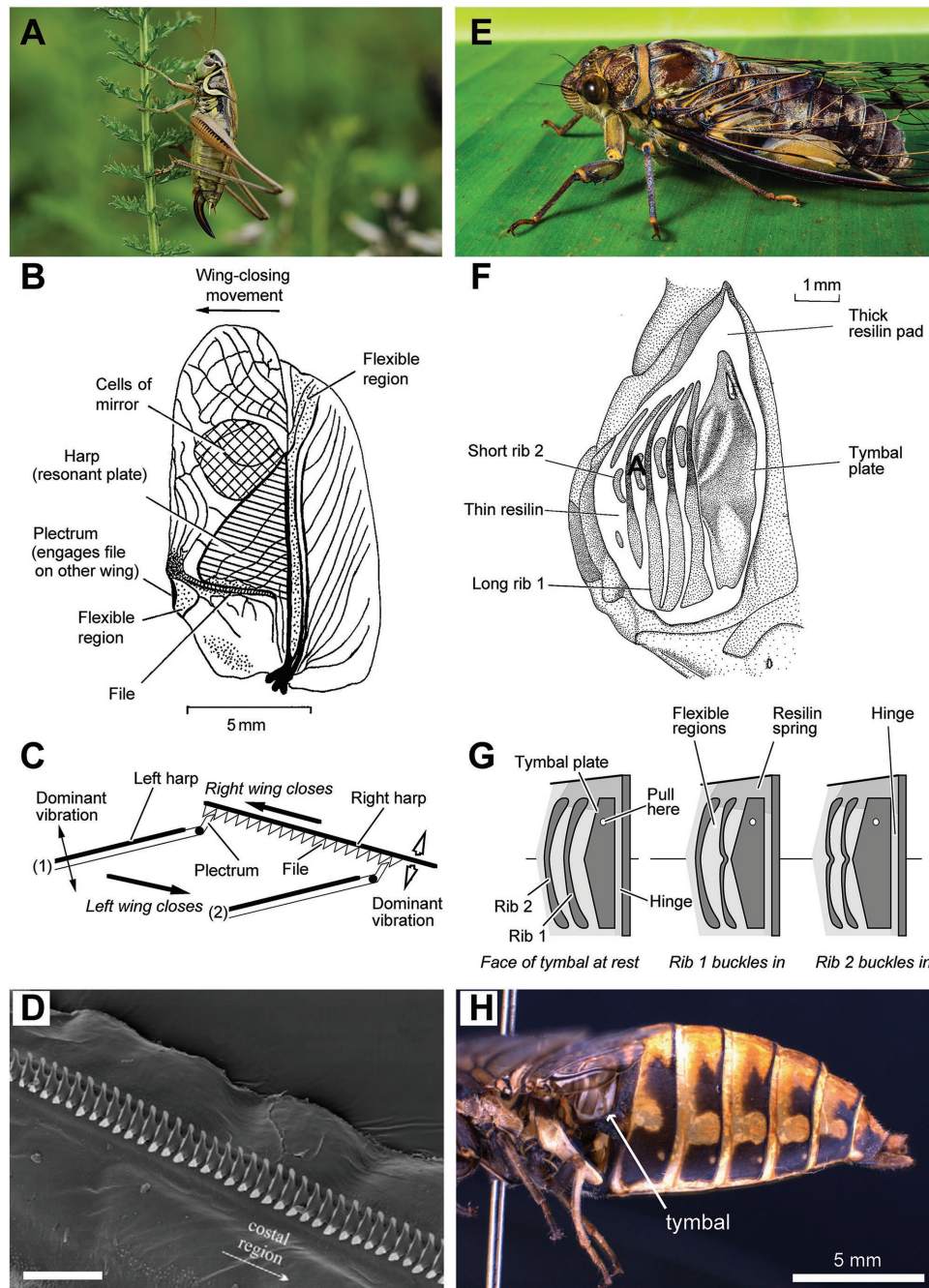


Figure 12. Sound production in insects is due to two different mechanisms. A–D) Stridulation or E–H) tymbals. A–D) Crickets produce sound by stridulation, a scheme involving scraping a file along a ridged surface (plectrum). A) Habitat image of a cricket.^[254a] B) Drawing of the underside of the wing showing the harp (the main resonator), the file, and the plectrum on the wing. C) Diagram explaining the main mechanism of excitation that results in sound production. B,C) Reproduced with permission.^[254b] Copyright 1999, Company of Biologists. D) SEM image of the file of a *Gryllus bimaculatus* cricket. Reproduced with permission.^[668] Copyright 2009, Company of Biologists. E–H) Cicadas generate their characteristic sounds using tymbal organs, which produce sound via the dynamic buckling of a membrane. E) Habitat image of a cicada.^[669a] F) Schematic drawing of a single tymbal organ showing the different components. G) Diagrams of the mode of excitation of sound resonances in the tymbal organs. As the membrane's ribs buckle inward, clicks are created. F,G) Reproduced with permission.^[669b] Copyright 1995, Company of Biologists. H) Lateral view image of the pygmy bladder cicada, *Xosopsaltria thunbergi*, showing the position of the tymbal. Reproduced with permission.^[670] Copyright 2016, Oxford University Press.

production of sound by an electronic loudspeaker. This mechanism is most prominently found in tiger moths (*Arctiinae*) and cicadas (*Cicadoidea*), producing deafening songs with peak intensities of over 100 dB.^[266]

Cicadas have paired tymbals that are located on the sides of their abdominal base (Figure 12E–H). The tymbals are regions of the exoskeleton that are modified to form a complex membrane with thin, membranous portions and thickened ribs

(Figure 1F,G). A contraction of the tymbal muscle causes the membrane to buckle inward, producing a loud click. As the membrane snaps back, it clicks again. Serial muscle contractions cause these membranes to vibrate rapidly; this vibration is transferred to enlarged air-filled chambers derived from the tracheae, where it resonates and is amplified.^[254,266–268]

Tiger-moth tymbals are modified regions of the thorax that produce high-frequency, tuneable clicks in the 40–80 kHz range.^[269] Sounds from these clicks, unlike cicada songs, serve a dual purpose and are used both as mating signals and in acoustic aposematism against bats. The moths are advertising to bats that they are toxic and the sounds “jam” the sonar of moth-eating bats to deter them.^[270,271] Although placing a sound-producing insect directly in your ear may not be a pleasant thought, insect-sized and structured tymbals could be paired with insect-inspired sound reception mechanisms to generate energy-efficient and frequency-targeted hearing assistance for humans.

6. Sensing and Manipulation of Light

Most animals have used light as a primary information carrier for communication^[272] since the emergence of vision after the Cambrian explosion about 500 million years ago.^[273,274] In particular, intricate optical structures deliver specialized signals that are processed into information by complex visual systems, the eyes.^[275,276] The cuticle exoskeleton of certain insects contains ordered, quasi-ordered or disordered nanostructures that reflect light in particular wavelength ranges and can produce vibrant colors, while cuticle on the exterior of other insects forms nanostructured layers that prevent light reflection entirely, rendering them transparent. Mechanisms to manipulate light have developed alongside those to detect it; the surface of some insect eyes is patterned with nanoscale features that promote efficient light transmission and also act as a hydrophobic deterrent for vision-blocking condensation (Section 4). This light-control toolkit is essential for insect survival, and has provided inspiration for engineered systems that harness fundamental physical phenomena to produce and detect visual signals.

6.1. Mechanisms of Color Production

Insects have evolved a diversity of mechanisms that interact with incident light and allow them to create a dynamic form of information. The remarkable displays of insects have long fascinated biologists, physicists, and natural philosophers alike, including Newton, Darwin, and Rayleigh.^[277] Numerous recent reviews discuss the physical aspects of insect displays,^[273,277–286] as well as their function in animal communication.^[275,276,287]

In general, there are two main classes of animal coloration: pigmentary coloration due to the wavelength-selective light absorption by chemical dyes and structural coloration due to the interaction of incident light with ordered, quasi-ordered or disordered nanostructures causing interference.^[277,288,289] Both coloration mechanisms feature unique optical properties that can combine in nontrivial ways and modulate optical properties with potential applications ranging from displays, to brilliant durable paints, to adaptive camouflage and transparent materials.^[287,290–293]

Interferometric modulator displays are a low-power micro-electromechanical display technology based on structural coloration, enabling full visibility in direct sunlight, unlike conventional liquid-crystal display screens.^[294,295] The concept is relatively simple: each pixel in the display contains a fixed, semitransparent membrane separated a distance (air-gap) of $\approx 1 \mu\text{m}$ above a reflective, moveable thin-film stack. Both the membrane and stack reflect light, and their separation determines the relative phase of the aggregate light output. When the films are oriented at a distance such that all reflected light in the visible spectrum destructively interferes, the pixel is black, but when the stack is actuated to a distance that produces constructive interference of visible light, it takes on a color determined by its particular distance-dependent phase shift.^[296] This “color” state is a direct analog to structural color in many insects, and represents just one of the many examples of potential light-active microstructured devices that can incorporate insect-inspired design.

6.1.1. Pigmentary Coloration

Pigmentary coloration is the most abundant coloration principle found in animals. It is based on the deposition of different chemical pigments in the outer body layer that selectively absorb incident light. Pigments are responsible for most of the yellow, orange, red, and brown-black colors observed in insects. It is curious to note that most insects are not capable of synthesizing green- or blue-colored pigments (except for a few species, e.g., *Graphium* spp.^[297]) and instead rely on nanostructural features to reflect these colors. The pigments are usually dispersed throughout randomly ordered structures so that any incident light that is not absorbed is scattered diffusely. Pigmentary colors hence appear identical in color from all viewing angles and are often described as dull and lusterless. Pierid butterflies are an exception to the dull appearance as they have evolved a way to create an intense pigment-based color. In the wing scales of these butterflies, the pigments are condensed in randomly ordered rice-grain-shaped granules.^[298,299] This arrangement greatly increases the effective refractive index of the granules, resulting in a much increased scattering strength and a higher reflectivity than if the pigment was randomly distributed throughout the wing scale.^[300]

6.1.2. Structural Coloration

Insects’ most stunning visual displays arise from the interaction of light with nanostructures, resulting in structural coloration. To cause constructive interference of visible light, photonic structures must consist of at least two materials with different refractive indices (RI) and with periodicities on the mesoscale (i.e., $\approx 200 \text{ nm}$).^[277,301] Such photonic structures are often assemblies of dielectric materials with negligible light absorption such as insect cuticle (RI ≈ 1.55)^[302] and air (RI = 1), but also feature assemblies of pigmented material, e.g., melanin-containing layers, to achieve the desired refractive index contrast.^[286,303,304]

Among insects, the striking palette of colorations is due to the plethora of nanomorphologies.^[305–307] Simply speaking,

the photonic structures in insects can be treated as periodic optical materials (so-called photonic crystals), and described using photo-physical terminology.^[289,301,308] Morphologies can be categorized by their translational periodicity as 1D, 2D, and 3D photonic crystals, where the structure is locally periodic in one, two, and three dimensions, respectively. Each different morphology changes the way light interacts with the structure, as do local defects and disorder. Insect nanomorphologies range from ordered structures starting from thin films^[309–311] and multilayer structures^[277,282,304,312,313] to 3D photonic crystals to quasi-ordered and fully disordered structures,^[314–320] each with different optical properties.

1D photonic structures, such as thin films or multilayer structures, are probably the most encountered nanostructure in nature.^[289,291] These are responsible for the iridescent, metallic colors of many beetles and butterflies (Figure 13A–C). As opposed to pigmentary colors, structural colors reflect light directionally and show a brilliant iridescence; in other words, light is strongly blueshifted for large angles of light incidence. Furthermore, light reflected by 1D photonic structures is strongly polarized under high incident angles of light (in particular above Brewster's angle, in the range of $\approx 60^\circ$ – 90°).

Photonic crystals are photonic structures that are periodic in all three spatial dimensions. In insects, these are found in wing scales of nearly all families of butterflies, weevils, and beetles and are composed of cuticle sculpted into 3D minimal surfaces (Figure 13D–F).^[314–320] Light–matter interaction in these photonic crystals becomes highly dependent on the orientation of the photonic crystal, as well as the direction of incident light. Due to the low refractive-index contrast of cuticle and air (≈ 1.55), these photonic crystals cannot build a full photonic bandgap, but show a pronounced iridescence due to partial optical bandgaps that can be well explained by photonic bandgap modeling.^[315] The minimal surfaces most often found in insects approximate the geometry of either a diamond (e.g., in weevils)^[321] or a gyroid (e.g., in butterflies).^[290,316,319] How these differences are related to differences during cell development is still an open debate.^[322] It is noteworthy that the photonic crystals in insects often appear in rather disordered orientations and commonly provide a green color by additive color mixing of the different reflections from differently oriented crystals, presumably to provide camouflage in a foliaceous habitat.^[321]

Insects also employ disorder to alter their optical appearance. Local disorder in *Morpho* butterflies provides a large range of viewing angles with stable color by introducing disorder in the

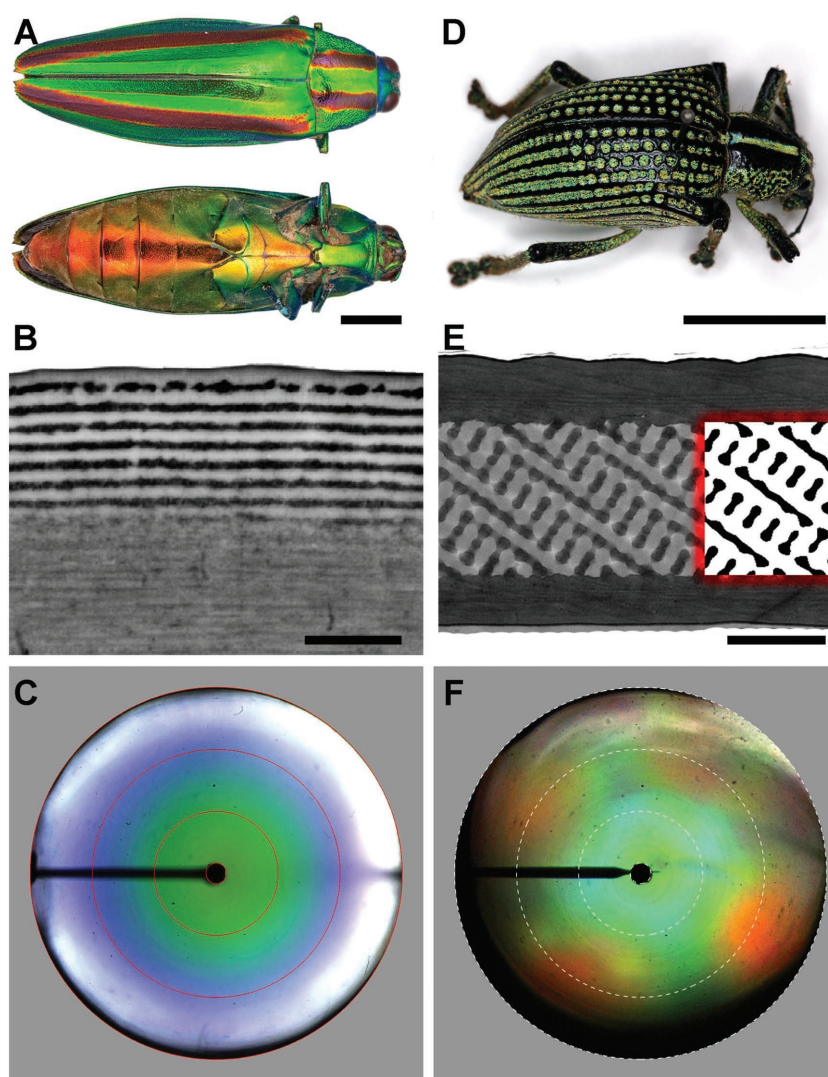


Figure 13. Insects employ ordered photonic structures for brilliant coloration. A–C) Multilayer structures (here in the elytra of a Japanese jewel beetle) impart a metallic, deeply colored appearance with an alternating arrangement of chitin and melanin layers (B) that result in an isotropic reflectance (C). D–F) 3D photonic crystals (here in the wing scales of the diamond light weevil) are structured in all three spatial directions (E) resulting in a strong angle-dependent light reflectance (F). Scale bars: (A,D) 1 cm, (B,E) 1 μm . A) Reproduced with permission.^[671] Copyright 2013. IOP Publishing. B,C) Reproduced with permission.^[313] Copyright 2011. The Royal Society. D–F) Reproduced with permission.^[315] Copyright 2012. The Royal Society.

scale ridge reflectors (Figure 14A).^[277,323,324] A certain degree of disorder can also smooth the reflectance of multilayer structures by suppressing higher-order reflections caused by perfectly ordered structures.^[325] Multilayer structures can be chirped, i.e., have a varying distance between layers of refractive index,^[292] or twisted, resulting in strongly circularly polarized reflected light.^[326–328] A combination of chirping with a twisted Bouligand-type helicoidal structure causes the brilliant silver and golden reflections of jeweled beetles (Figure 14B).^[329–331] Disorder in all directions results in a white color. This principle is optimized in white beetles, where a disordered network of chitin shows the highest scattering strength of any measured material (Figure 14C).^[332,333] Perfect white materials from extremely thin

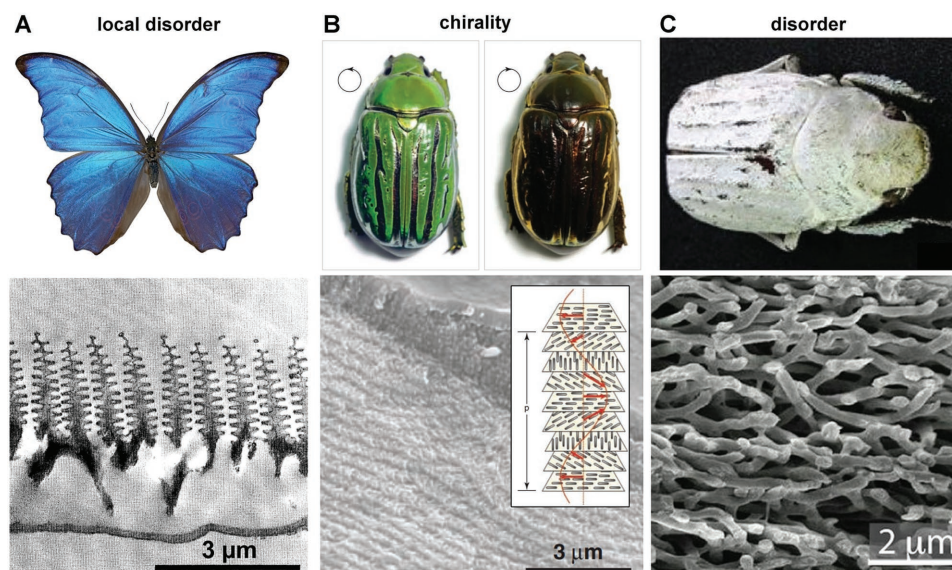


Figure 14. Order and disorder in photonic structures can lead to unique optical effects. A) Local disorder in the ridge reflector of the butterfly, *Morpho rhetenor*, results in stable blue color. Adapted with permission.^[672] Copyright 1999, the Royal Society. B) Bouligand-structure in jeweled beetles, *Chrysina gloriosa*, results in a circularly polarized optical signal. Adapted with permission.^[326] Copyright 2009, The American Association for the Advancement of Science. C) Fully disordered chitin network in white beetles, *Lepidiota stigma*, results in brilliant whiteness. Adapted under the terms of the CC-BY license.^[332] Copyright 2014, Matteo Burrese.

disordered nanostructures may find applications ranging from paper to food.

Evolution of insect displays has brought forward an amazing variety of photonic nanostructures suited for different signaling purposes. The effect of the incident angle of the light on the color reflected by these structures allows insects to create a dynamic form of information, particularly as colorful body parts are moved in time and space resulting in color signal with various temporal resolutions. Colors serve multiple roles in insects, often several at the same time: to increase visibility to potential mates, to warn predators of toxicity, and/or to camouflage against predators on the hunt.^[273,275,276]

6.2. Transparency

Another way insects avoid detection is by employing transparency. Transparency can provide almost perfect camouflage for the animals able to achieve it. Many marine animals such as jellyfish are highly transparent.^[334] However, achieving transparency is easier in dim lighting or turbid seawater than in well-illuminated environments in air, where small transparency mismatches are easily seen. Nonetheless, this effect of optimized light guidance through a structure is observed on the wings and eyes of certain insects, providing potential inspiration for engineered transparent materials.

Transparency is the physical property of allowing light to pass through a material without being scattered or absorbed. In more physical terms, the reflectivity is minimal, while the transmittivity approaches unity. Glass is transparent in the visible wavelength range, but each glass surface still reflects about 4% of incident light due to the refractive-index mismatch of

glass ($RI \approx 1.5$) to air ($RI \approx 1$), which results in a visible reflection described by Fresnel's equations.^[335,336] To minimize this effect, materials in natural systems are often structured so that the refractive index changes gradually between them; this is known as impedance matching.^[335] Evolution has selected for several tricks using nanostructures that exploit this effect.

Transparent insect wings are a prominent example of impedance matching. While most wings are relatively unstructured thin films of chitin,^[311] some dragonflies, cicadas, and butterflies have optimized the transparency of their wings by employing a local nanostructure (Figure 15A).^[337–341] In the wings of these insects, the thin film of chitin that forms the wing membrane is covered on both sides by small conical or nipple-shaped nanopillars that provide impedance matching (Figure 15B). It is crucial for the pillars to be smaller than the wavelength of light to prevent interference effects, resulting in a maximum size of about ≈ 250 nm. Furthermore, height and positional disorder of the nanopillars facilitate broadband omnidirectionality of the transparency effect, resulting in a reflectance below 0.05% for viewing angles below 50° and reaching a maximal value of 5% at an angle of incidence of $\approx 80^\circ$.^[338]

Optical-impedance-matching mechanisms are useful not only for transparency but also to optimize light transport into a structure. This phenomenon is critical for ensuring optimal light transmission to optical sensors in insect eyes. This is particularly true for insects living in low-light conditions, such as moths and other nocturnal insects, which feature similar nanopillars covering their facet lenses (Figure 15C,D).^[342–345] These so-called corneal nipple arrays optimize light flux into the eye and photon detection by the photoreceptors. As a positive side effect, the surface reflection of the eyes is minimized during daytime, suppressing a detectable reflection of the inactive insects by predators. Insects can form a diverse array of

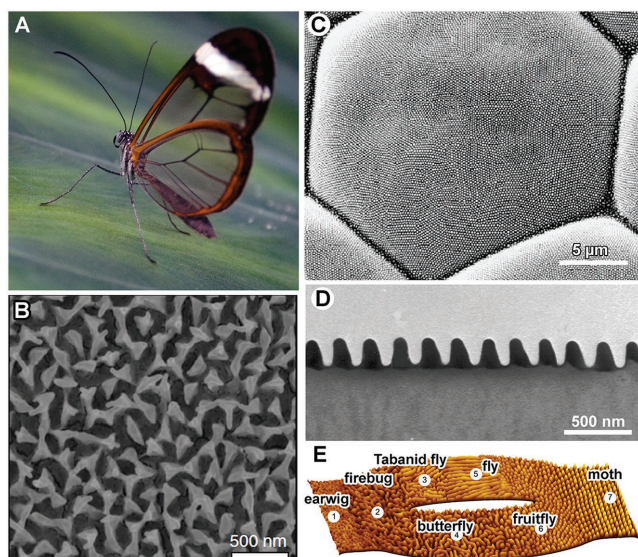


Figure 15. Insect wings and eyes carry nanostructured antireflection coatings to achieve near-perfect transparency. A) Glasswing butterflies, e.g. *Greta morgane*, feature largely transparent wings. Reproduced under the terms of the CC-BY license.^[338a] Copyright 2008, Wikimedia-User: Weir-doldhattie. B) Close-up SEM image of glasswing butterfly wings showing a disordered arrangement of protrusions. Reproduced with permission.^[338b] Copyright 2015, Nature Publishing Group. C) SEM image of the cornea of a moth shows subpatterning on each facet lens. D) TEM cross-section of the corneal surfaces of a moth. Reproduced with permission.^[343] Copyright 2006, the Royal Society. E) The structural diversity of corneal nipple arrays can be vast across different insect lineages. Reproduced with permission.^[344] Copyright 2015, National Academy of Sciences.

nanostructures (Figure 15E) whose developmental pathway is unknown but is hypothesized to be based on a Turing-like patterning of the outermost corneal layer during development.^[344]

6.3. Bioluminescence

Fireflies (members of the beetle family Lampyridae) are winged beetles famous for their conspicuous use of bioluminescence during twilight to attract mates or prey. Fireflies produce a “cold light,” ranging from yellow (520 nm) to pale red (670 nm), produced in their lower abdomen in the so-called lantern. The chemical process enabling firefly light production has been investigated for more than a century.^[346–348] The most common model for light production involves luciferin, the enzyme luciferase, and oxygen. To emit light, a two-step reaction takes place in the light-emitting organ: luciferin complexes with luciferase and ATP in the presence of Mg^{2+} to form an “active intermediate,” luciferyl adenylate. The active intermediate form only needs oxygen to complete the photochemical reaction. With the addition of the oxygen, the active intermediate forms a cyclic peroxide, luciferyl adenylate, that decomposes and while doing so emits light.

When these chemicals are mixed together *ex vivo*, they typically produce a steady constant glow unless oxygen is added last, in which case the reaction generates a flash resembling that observed *in vivo*.^[348,349] The effect is strongly dependent on the specific luciferin–luciferase pair; the most common pair emits green light.

The lantern features a special morphology that allows optimized light emission.^[347,348,350] Each lantern is a flat slab of tissue with a dorsal and a ventral layer. The dorsal layer contains uric acid crystals to reflect light away from the light produced in the cells in the ventral, or photogenic, layer. Most fireflies can modulate their light emission to some extent and some fireflies can actually flash by turning the lantern reflectance sharply off and on similar to a lighthouse. This is achieved by different lantern morphologies and controlling the influx of oxygen.^[348] Each firefly species has its own specific light-pulse pattern, which acts as a communication signature: the female is usually at rest at the edge of the forest and males fly around sending and receiving signals. Over time, the females respond to species-identical males to reveal their location.^[351]

The light source (the reaction center) is contained inside a high-refractive-index medium, imposing boundary constraints on the morphology of the lantern in order to optimize light extraction to the outside air due to total internal reflection at large incidence angles.^[352,353] Bay et al. have recently shown that the structure of the cuticle outside of the light-emitting organ increases the efficiency of the light emission by $\approx 10\%$.^[352] The light-extraction efficiency of synthetic electroluminescent devices, e.g., organic light-emitting diodes (OLEDs), suffers from the same refractive-index-mismatch,^[354] and the insight from the firefly lantern structure has been used to improve light-extraction from OLEDs by up to 55%.^[353]

6.4. Insect Eyes

Unlike humans, insects have faceted, compound eyes that consist of numerous anatomically identical units (Figure 16). Insect eyes are classified according to the optical system that they employ to focus incident light efficiently onto the light-sensitive parts of their photoreceptors as either apposition or optical superposition eyes.^[355–359]

Apposition eyes are the main type of eyes found in insects (Figure 16C). Here, each facet is a separate light detector. It consists of a facet lens that caps an ommatidium, which is an assembly of photoreceptor cells, pigment cells, and (crystalline) cone. Incident light is focused through the lens into a long, cylindrical waveguide-like structure called a (fused) rhabdom. Rhabdoms consist of an assembly of smaller structures, rhabdomeres (see below), which contain the photoreceptors’ visual pigment molecules.^[360–362] Optical superposition eyes are mainly employed by nocturnal moths, and use multiple facet lenses to focus light onto separate photoreceptive rhabdoms (Figure 16D).^[360,361,363]

Apposition eyes have a higher spatial resolution than superposition eyes, while superposition eyes have a higher light sensitivity.^[361,364] Moths are therefore able to live a nocturnal lifestyle that is unavailable to butterflies, which are active during the day.^[355,365] Insect eye facets are relatively small, with diameters ranging between 10 and 50 μm .^[366] The number of facets per eye can vary significantly, ranging from ≈ 100 in ants up to 30 000 in some dragonflies.^[361] A low number of facets renders ants nearly incapable of forming an image, while dragonflies have superior resolution.

Rhabdomeres—structures containing many microvilli with high concentrations of light-sensitive pigments called

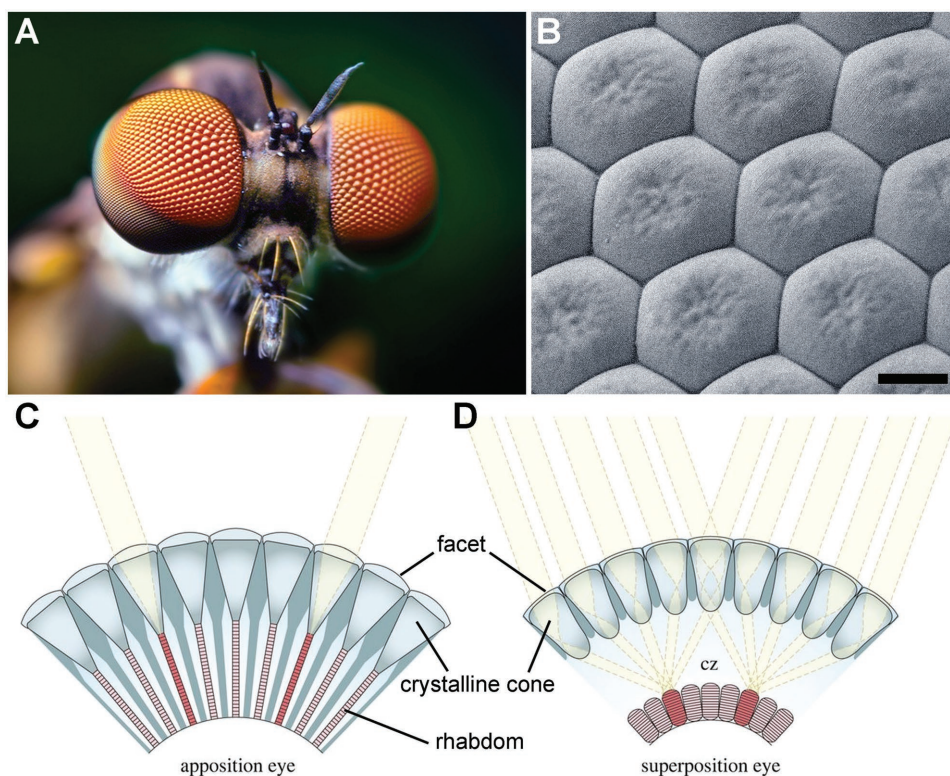


Figure 16. Insect eyes can contain thousands of lenses that direct light toward a photoreceptive rhabdom. A) Close-up photograph of a robber fly showing the regular arrangement of facet lenses. Reproduced under the terms of the CC-BY license.^[355a] Copyright 2005, Opo Terser. B) Close-up SEM of a few facet lenses highlighting the hexagonal shape, scale bar: 10 μm . C, D) Schematic drawing of apposition (C) and superposition (D) eyes. Reproduced with permission.^[355b] Copyright 2017, the Royal Society.

rhodopsins—facilitate detection of light by transducing light absorbed by these pigments into a neural signal.^[367,368] In flies, the eight rhabdomeres in each ommatidium remain independent, each acting as a unique optical waveguide.^[369] In bees and butterflies, nine rhabdomeres fuse together to act as one efficient optical waveguide, and are collectively referred to as the rhabdom.^[370] Rhabdoms are often surrounded by heavily pigmented iris cells that may alter the spectral composition of incident light to support color vision or to suppress stray light entering the ommatidium through the sides or from neighbouring rhabdoms.^[371]

6.4.1. Navigation with Polarization

As sunlight, moonlight, or starlight passes through the atmosphere, it is scattered by gas particles in accordance with common scattering laws^[335,372] and generates a (linear) polarization pattern that contains information about the position of the light source and the observer.^[373–375] A recently developed bioinspired camera system captures the light polarization pattern across the entire sky in a single image by using a wide-angle lens in combination with a triplet linear polarizer.^[376] This device, ultimately a visual compass and optical global positioning system, allows its user to navigate or geolocate outdoors using purely optical information, and could be applied to pre-existing cameras in robotic systems as a simple

and energy-efficient complement (or alternative) to standard guidance methods.

Like this artificial imaging system, many insects (notably bees) can detect the polarization of light.^[377] Polarization detection is facilitated by the spatial arrangement of the microvilli that make up the rhabdom, as well as by the distribution of the photoreceptor molecules on the microvilli. Due to the cylindrical shape of the microvilli, twice as many light-sensitive chromophore groups of the rhodopsin molecules are aligned parallel to the long axis of each microvillus than orthogonal to it. This arrangement facilitates detection of light polarized parallel to the microvilli.^[378]

Polarization vision in flies occurs in a narrow dorsal rim via UV photoreceptors.^[369,374] Crickets have developed a prominent dorsal area, recognizable by smooth facet lenses and ommatidia that are devoid of screening pigment that feature exclusively blue-sensitive photoreceptors.^[379] African dung beetles^[380,381] and bees^[382,383] navigate using the polarization pattern created by of the sun, the moon or the milky way on cloudless nights.^[2]

6.4.2. Simple Eyes—Ocelli as Light Detectors

Vision systems that are designed and optimized for a particular task are valuable in applications with extreme mass and energy constraints, like miniature flying robots.^[296,384,385] With this in mind, Pericet-Camara et al. developed a simple, bioinspired “artificial eye” containing three photodetectors and weighing

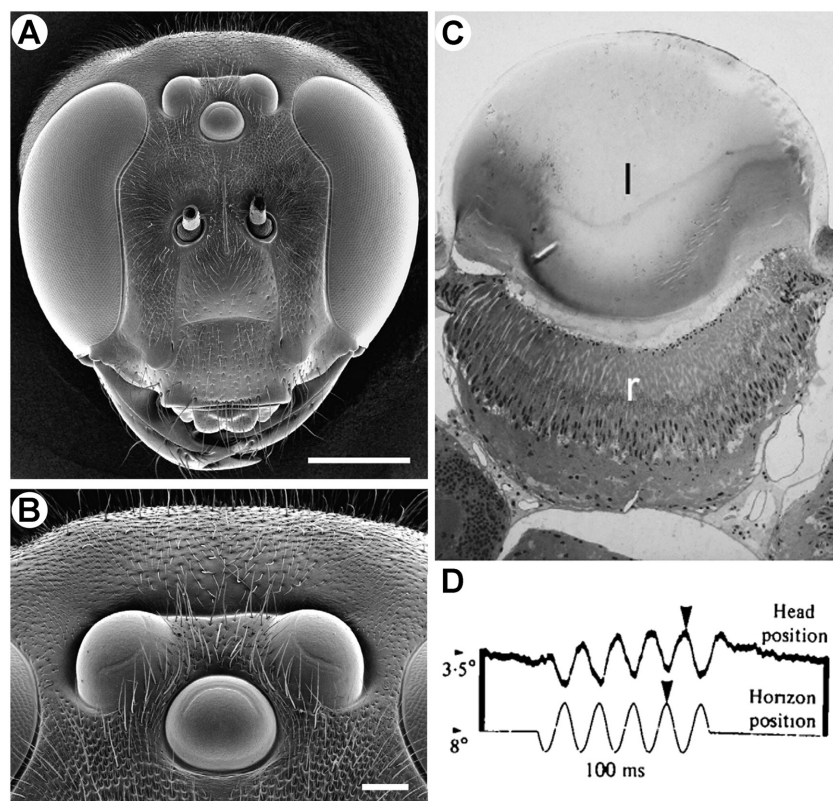


Figure 17. Ocelli are simple light detectors. A, B) SEM images of the head of a nocturnal halictid bee showing three ocelli between the two compound eyes. C) Light microscopy cross-sectional image of the median ocellus showing the lens (l) and the retina layer (r). A–C) Reproduced with permission.^[389] Copyright 2006, Elsevier. D) Adjustment of the head position with regard to the horizon. This rapid tracking is assumed to be supported by ocelli. Reproduced with permission.^[390] Copyright 1981, Company of Biologists Ltd.

only 2 mg that could detect movement at rates up to 300 Hz with minimal power consumption.^[386] Its flexible footprint makes it well-suited to problems requiring rapid visual sensing in a compact format.

The inspiration for this microsized camera—small simple eyes, so-called ocelli, containing a single facet lens—complements compound eyes in many insects.^[361,387] An ocellus typically consists of a lens element (cornea) and a layer of photoreceptors (rod cells). Due to the low refractive power of the cornea, ocelli typically cannot form images on the photoreceptor layers, although some exceptions have been reported.^[388] As a consequence of the large aperture and the resulting low f -number of the lens, ocelli can detect lower light levels and have a faster response time than compound eyes. Ocelli are typically found on the dorsal (top) surface of the head of many insects and coexist with compound eyes (Figure 17).

The number, forms, and functions of the dorsal ocelli vary significantly throughout insect orders, and ocelli tend to be larger and more strongly expressed in flying insects (particularly bees, wasps, dragonflies, and locusts)—and they tend to be larger in nocturnal insects, where they are typically found as a triplet.^[389] Two lateral ocelli are directed to the left and right of the head, while a central (median) ocellus is directed frontally. Due to their fast response time, ocelli are commonly thought

to function in flying insects to assist in maintaining flight stability as they are fit to quickly measure changes in perceived brightness (Figure 17D).^[390,391]

7. Thermal Sensing and Regulation

Temperatures vary widely across insect habitats, and fluctuations occur over a broad range of time scales. While responding to months-long temperature changes (e.g., seasons) is important for overwintering and survival of species on the long run, short-term changes in temperature, which include night versus day, and even sun versus shade, are important for the day-to-day survival of each individual. The variability and consistency of temperature fluctuations are important components that shape the thermal niches and habitats of insects.^[392] Insects employ solutions to heat-regulation problems that span the scientific disciplines, ranging from biological controls (e.g., varying metabolic rate) to physical techniques (e.g., structural coloration (Section 6)) and chemical approaches (e.g., antifreeze protein synthesis).

7.1. Thermal Sensing

Several insects have developed mechanically actuated heat detectors. In particular, members of the forest-fire-seeking beetles, *Melanophila*, fly to forest fires (and other sources of immense heat) to lay their eggs in freshly killed conifer trees, as they are not able to overcome the resinous natural defense reaction of living trees.^[2,393,394] Forest-fire-seeking beetles detect forest fires using specialized infrared-detecting pit organs located on either side of the thorax near their middle legs (Figure 18). Each sensory organ consists of a spherical cuticular structure ≈ 12 – $16 \mu\text{m}$ in diameter with a central cavity that is connected to the distal process of a nerve cell. Adjacent to each sensory organ, a gland continuously cleans the sensor by secreting strands of wax.^[394] Infrared (IR) light is detected via absorption of light in the pit organ leading to a pressure difference detected by a force sensor.^[393,395] In a way, these beetles hear IR light. Forest fires burn at temperatures between 400 and 1200 °C, thus emitting IR wavelengths in the range of 2–4 μm .^[396] *Melanophila* IR cells are able to detect and respond to wavelengths exclusively in this region.^[397] These findings strongly indicate that *Melanophila* beetles can detect a 10-hectare fire from a distance of 12 km due to atmospheric transparency at these wavelengths.^[393]

Engineered IR detectors fall within one of two general categories: light-based or temperature-based.^[398,399] The large majority of IR-sensor development has focused on photons, because methods to directly transduce changes in heat via IR absorption have traditionally been slower and

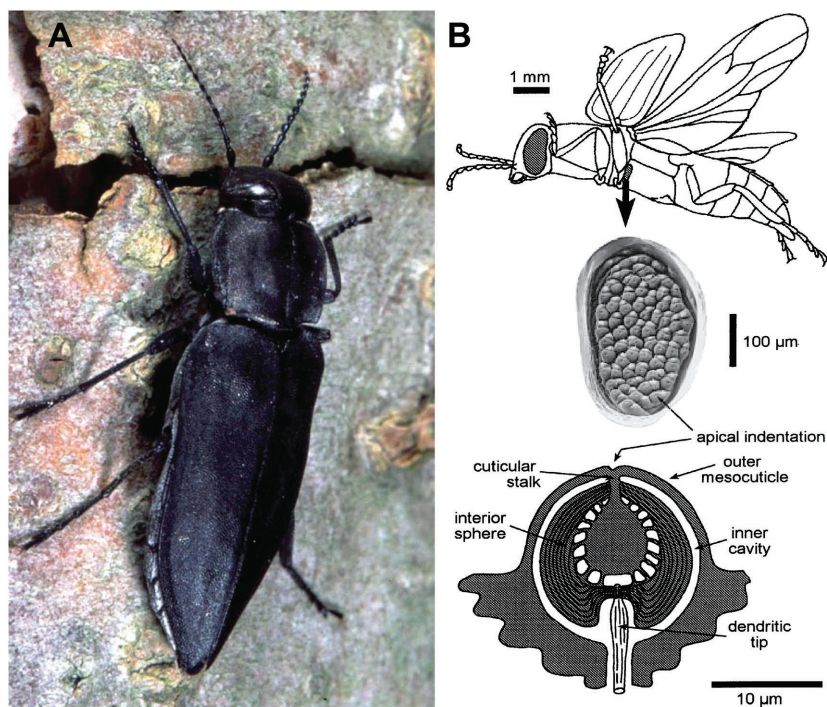


Figure 18. Forest-fire seeking beetles use their IR-sensing pit organs to detect forest fires. A) Habitat picture of *Melanophila acuminata*. Reproduced with permission.^[393a] Copyright 2009, Helmut Schmitz. B) Schematic drawing of the location and function of the pit organ. The beetles lift their middle legs to fully expose the pit organs, in which dendrites detect the expansion of an endocuticular sphere in response to the absorption of infrared radiation. Reproduced with permission.^[393b] Copyright 1998, Springer.

less sensitive than their photon-detecting counterparts.^[400] Biology has prompted a new look at these transducers, however, and several different bioinspired designs have emerged. Recently, Jiang et al. developed a thermal–pneumatic IR sensor that works by monitoring displacement of a thin (20–60 nm) membrane that spans and seals a small, gas-filled compartment.^[401] While testing this device, buckling in the polymeric compartment-containing substrate was observed, leading to the development of a thermal buckling sensor.^[402] This new sensor is based on thermal-expansion mechanisms and has a temperature resolution that is an order of magnitude (10 mK vs ≈ 100 mK) lower than most thermal IR sensors. With a footprint of only 15 μm , the sensor is just one example of many potential bioinspired designs that exploit material properties to achieve energy-efficient, compact sensors.

7.2. Temperature Control

Effectively distributing food resources is of immense interest to the growing global population; more than US \$750 billion of perishable food goes to waste each year, much of which is tied to elevated food temperature during transport and storage.^[403] Long-distance, cold-chain food shipments are energetically and financially expensive, so efficient mechanisms to maintain stable food temperatures over long time periods are desirable. Despite their small size, insects have found unique

design principles to regulate temperature, all of which are biocompatible. Curiously, one insect-related thermoregulation solution has been adopted in the food industry. Unilever recently filed a patent on incorporating genetically modified freeze-resistant proteins (discussed below) into ice-cream production.^[404] With the addition of small amounts of these proteins, the company claims that the ice cream can be deep-frozen to temperatures lower than -40 °C without any risk of ice-crystal formation (normally inducing freezer burn) when thawed back to the temperature of common household freezers (-4 to -16 °C). Deep-frozen ice-cream would take much longer to melt if exposed to elevated shipping temperatures, lowering the risk of spoiling. This concept may be extendable to other, more nutritious, perishables.

Biologically, thermoregulation describes an organism's ability to maintain a stable body temperature T_b (either above or below ambient temperature), by physiological or behavioral means.^[405–407] Many insects have a largely variable T_b and yet maintain a substantial independence from strongly varying ambient temperatures.

Two types of thermoregulatory mechanisms exist in insects; those that manipulate internal heat production and those that manipulate external heat exchange. Flight is

fundamentally linked to thermoregulation, as flight is an energetically expensive form of locomotion that usually requires a high metabolic rate to supply sufficient energy. In order to fly, an insect's flight muscles must be capable of high mechanical power output, which in turn produces large amounts of heat.^[406,408] Under mild conditions, the heat generated by a flying insect dissipates without causing any damage. However, if the flying insect is also exposed to external sources of heat like sunlight or a higher than normal ambient temperature, it needs to thermoregulate to maintain a nonlethal body temperature.

7.2.1. Keeping Cool

During high-speed flight, insects may lose heat by convection because increased air flow facilitates convective cooling. Nonetheless, the T_b of moths increases with flight velocity.^[408] This temperature increase happens because the moth flight muscles work at higher frequency during rapid flight, which increases thoracic heat generation. To prevent dangerous internal temperatures, moths dissipate heat by moving hemolymph from their thorax (where flight muscles are located) to the abdomen. The heart of these moths makes a loop through the center of the thorax to promote heat exchange and to use the abdomen as both a heat sink and a radiator.

Alternatively, insects can dissipate heat through evaporation. Normally, water reserves in insects are too small to permit

evaporation as a routine method of cooling, but this approach has been observed in insects living close to an abundant water supply (vegetation, plants, or blood). Honeybees flying at high T_b extrude a water droplet from their mouth, as do bees at ambient temperatures above 46 °C, to lower T_b by as much as 5 °C.^[409,410]

Malaria-transmitting mosquitoes, *Anopheles* sp., whose preferred T_b is ≈30 °C, thermoregulate each time they take a blood meal on a warm-blooded animal by emitting a droplet composed of urine and fresh blood that they keep attached to their anus. The liquid of the drop evaporates and dissipates the excess heat gained from ingesting a relatively large volume of warm blood.^[411] Similarly, sawfly larvae produce a fluid anal secretion that they spread over their bodies to cool down by as much as 7 °C when the temperature is above the lethal 42 °C.^[412]

Structural and pigment-based cuticle coloration (Section 6) can also influence insect body temperature. Dark-colored (or melanic) insects, which generally contain significant amounts of melanin pigment, absorb more IR radiation (and thus heat) than their light-colored counterparts.^[280,413,414] For example, light-colored individuals of *Colias* butterflies in alpine populations are more active in warmer conditions than darker individuals, while these melanic individuals can fly longer in cold conditions.^[415] Some insects can even actively change coloration with temperature; grasshoppers are black below a threshold temperature (≈10 °C) but rapidly turn a light blue at elevated temperatures, probably to prevent overheating.^[405,416,417] Similar modifications are also reported for damselflies and dragonflies.^[418] The transition temperature may be correlated with habitat as the color change could provide camouflage while the animal is inactive. The precise nanostructural mechanism behind this color change is not known. Its mode of action may be amenable to synthetic materials.

7.2.2. Freeze-Avoidance

The exact definition of low or high temperature is relative. While 10–15 °C induces chill coma or death in tropical insects, insects in temperate or polar regions often remain active well below 0 °C.^[419] Insects living in habitats at extreme latitudes cannot easily avoid cold and have developed the ability to survive sub-zero temperatures by either preventing their body fluid from freezing (freeze avoidant) or adapting in such a way to be able to withstand the freezing of their body fluid (freeze tolerant). In both cases, the insects survive by expressing anti-freeze proteins (AFPs) within their cells. AFPs, first identified in the blood of Antarctic fish, allow animals to avoid freezing in environments colder than the colligative melting point of their bodily fluids.^[420–422] AFPs adsorb to the surface of ice and prevent water from joining the crystal lattice, thereby preventing freezing of a solution in the presence of ice until a new, lower freezing point is reached.^[423,424] AFPs create a difference between the melting point and freezing point; this phenomenon is known as thermal hysteresis, and it allows insects to survive while their body temperature is below the melting point.

Insect AFPs share a similar amino acid motif^[425–427] that is fundamentally different from those found in fish or plants, granting them a greater degree of thermal hysteresis that allows

them to survive at lower temperatures. In insects, AFPs consist of varying numbers of 12- or 13-mer amino acid residue repeats that are folded into a repeating barrel structure of ≈8–13 kDa total weight. Throughout the protein length, at least every sixth residue is a cysteine. Disulfide mapping of the insect AFPs indicates that all cysteines form disulfide bridges,^[428] which impose significant folding constraints and help to align the important hydroxide-rich sides that bind to water molecules. Indeed, the cysteines act to stabilize the proteins and properly align the residues that hydrogen bond to ice or ice-nucleating sites. AFPs have been identified in more than fifty insect species.^[424] Not surprisingly, insect AFPs are 10–30 times more effective than fish AFPs, given the far lower temperatures that some land-based insects must survive. During the extreme winter months, the spruce budworm, *Choristoneura hebenstreitella*, resists freezing at temperatures approaching –30 °C, while the Alaskan beetle *Upis ceramoides* can survive in a temperature of –60 °C.^[423]

8. Chemical Sensing and Defense

To a far greater extent than vertebrates, insects navigate their world largely by detecting and deploying chemical stimuli. Insects use smell to find their food and mates,^[429] and they produce volatile signaling molecules called pheromones to convey a wide range of messages to the organisms around them. Insects must, however, surmount a fundamental difficulty in order to send and receive chemical communication effectively: the world is big, and they are small. The volumes of an insect's pheromone or allomone emissions are usually single microliters at most, so the volatile signaling compounds become extremely diluted upon evaporation. As a result of this dilution, insects have evolved sophisticated chemical sensors that give neurons maximal exposure to the environment while providing protection and selectivity as needed, as well as various methods of dispersing their chemical signals in a manner that ensures proximity to their targets.

The fields of chemical sensing and drug delivery both also face the dilution problem; in both contexts, insect-inspired innovations have recently been applied to overcome it. Insects' wide variety of mechanisms for chemical detection and dispersal typically involve high surface areas and/or sophisticated means of moving molecules across skin or cuticle, strategies that also have utility in engineered contexts.

8.1. Chemical Sensing

The signal-to-noise problem faced by insects in chemical communication is analogous to challenges faced in engineered methods for selective single-molecule detection and analysis. One such technique, nanopore-based resistive pulse sensing, detects the translocation of particles through a single nanoscale pore in a membrane by measuring transient reductions in ionic current across the membrane. It is often advantageous to use solid-state membranes made of silicon, as pores of any desired size may be fabricated according to the analyte of interest, but such substrates are plagued by nonspecific interactions between solutes and the pore walls, causing clogging and other problems. Recent research from our group has taken

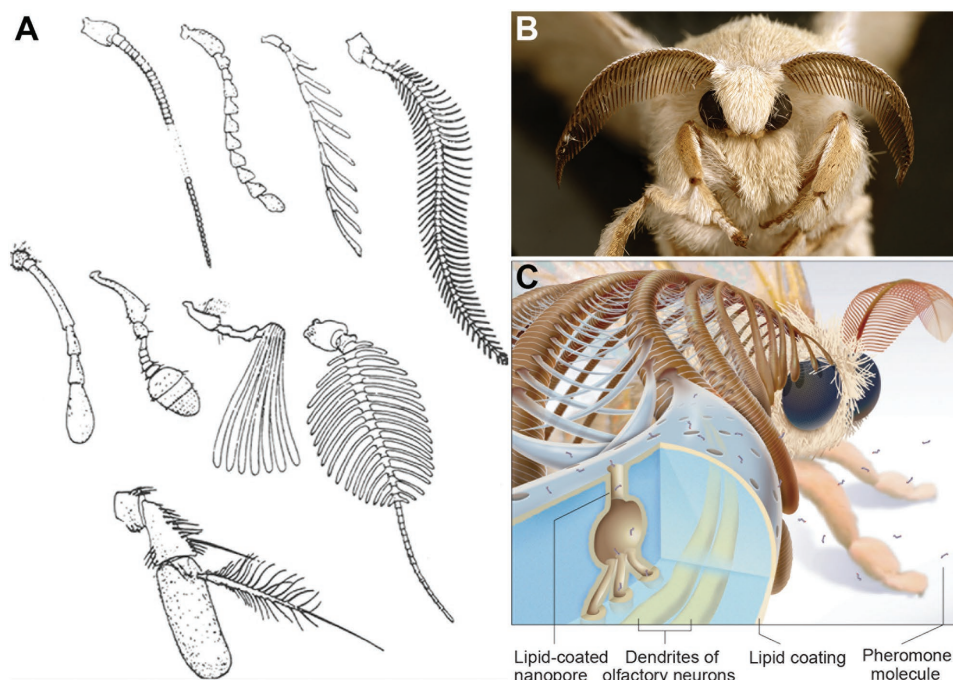


Figure 19. Insect sensilla and antennae have evolved in different morphologies. A) Various antenna morphologies. Reproduced with permission.^[438a] Copyright 1999, Springer. B) Habitat image of the silk moth, *Bombyx mori*. Reproduced under the terms of the CC-BY license.^[438b] Copyright 2010, CSIRO. C) Close-up view of a sensillum from *B. mori* showing pheromone access to dendrites via nanoscale pores. Reproduced with permission.^[431] Copyright 2011, Nature Publishing Group.

inspiration from the lipid-bilayer-lined pores in the walls of sensilla in moth antennae, which also have the function of detecting and identifying chemicals in small amounts. Moth sensilla provide a nonstick fluid coating (Figure 19C,^[430–432]) and selective odorant-binding proteins and neural receptors enable moths to distinguish between odorants as described below.^[430,433–435] Similarly, selective conjugation of an analyte to a lipid membrane imparts selectivity to synthetic nanopore systems while minimizing nonspecific adsorption.^[431,432] By convention, an insect recognizes airborne chemicals by smelling them (olfaction), while it recognizes aqueous chemicals by tasting them (gustation). The mechanism for both modes of sensing is, however, nearly identical.

Like some mechanosensors (see Section 5), the basic chemoreceptive structures in insects are called sensilla. Sensilla take various shapes involving cuticular projections containing pores or pits (Figure 19A,B), but the role of each chemoreceptive sensillum is the same as in the mechanical sensors: to bring the dendrites of the detecting sensory neurons into direct contact with the outside world while providing them with a protective barrier that facilitates chemical transport. The pores on a sensillum mediate access to the sensory neurons. External gustatory sensilla are typically hairs containing only a single apical pore that will be touched directly to food or fluid; they are typically also mechanosensitive. Gustatory sensilla appear on insects' mouthparts, but also on other parts of their bodies such as their legs, wings, and genitals, allowing them to sample food before ingesting it.^[436]

Sensillar dendrites contain highly specific receptors in the form of membrane proteins on their exterior membranes, which initiate action potentials in response to chemical signals

that exceed a threshold concentration. This selectivity allows complex signaling and specific messaging between insects.^[430] The gypsy moth, *Lymantria dispar*, uses the (+) enantiomer of a compound called disparlure as a sex pheromone but is antagonized by the (–) enantiomer. Its close relative, the nun moth *L. monacha*, also uses disparlure, but is able to avoid attracting gypsy moths by producing mostly the (–) enantiomer.^[433–435]

Most of an insect's olfactory sensilla are located on its antennae, which have evolved as specialized sensory structures to detect mechanical and thermal stimuli in addition to chemicals. Due to the low concentration of odorant molecules in air and their importance in signaling, many insects have been evolutionarily pressured toward developing incredibly sensitive olfactory systems. For this reason, olfactory sensilla tend to have thousands of pores lining their walls (Figure 19C) to give the sensory dendrites of each sensillum maximum exposure to the environment. Different types of sensilla have evolved to optimally detect different types of analytes; double-walled sensilla are thought to be more sensitive to polar molecules, while single-walled sensilla have evolved close-packed arrays of pore tubules specialized for the transport of nonpolar odorants.^[430,437] Many insects have multiple types of sensilla decorating their antennae,^[438] giving them a wider scope of substrates (Figure 19A).

Other adaptations improving olfactory sensitivity involve increasing the surface area of the antennae by various types of branching in order to provide space for more sensilla (Figure 18A). The moths in particular have developed spectacular antennae in the shape of combs or feathers. Extensive branching increases the surface area of the antennae of the silkworm, *Bombyx mori*, sixfold from 4.8 to 29 mm² (Figure 19).^[438,439]

The tobacco hawk moth, *Manduca sexta*, packs around 150 000 sensilla of various types onto each of its antennae; it has over 260 000 antennal neurons connected to the environment by hundreds of millions of pores.^[2,438,440,441] *Bombyx*, with fewer sensory neurons than *Manduca*, is able to alter its behavior in response to ambient pheromone concentrations of around 10^{-16} mol L⁻¹.^[442] Some calculations imply that it may take fewer than 100 molecules in total to exceed the threshold for a response.^[2] Detection systems with this sensitivity threshold are clearly attractive for engineered sensors, especially those designed to characterize challenging analytes such as, for instance, amyloid-beta, a peptide that has implications in Alzheimer's disease and forms transient, heterogeneous aggregates that tend to stick to surfaces.^[431,432]

8.2. Chemical Defense

Insects produce an impressive arsenal of defensive chemicals (or "allomones"), which can either inflict actual harm upon attackers or simply ward off predators by their repulsive smell or taste.^[2] Insect allomones vary widely in chemical structure, with molecular weights ranging four orders of magnitude from 17 (ammonia)^[443] to 1.7×10^5 atomic mass units (antlion ALMB-toxin).^[444] Allomones can be biosynthesized by the insects themselves or sequestered from the plants they eat.^[445–448] The chemical structures of insect allomones have been thoroughly reviewed elsewhere;^[449,450] the astounding diversity of pharmacologically active compounds biosynthesized by insects makes them interesting as a natural product library for pharmaceutical research.^[451–453] Allomones are only useful insofar as they can reach their targets, however, so insects have evolved a repertoire of both specific and nonspecific defensive chemical dispersal mechanisms.

The Coandă effect describes the phenomenon whereby fluid passing over a convex surface stays attached to that surface.^[454] Ambient pressure forces the fluid stream into the low-pressure zone generated between the fluid and the adjacent surface, causing the stream to effectively conform to surface geometry. This effect, used on the microscale by insects to target predators with jets of fluid, can be exploited in nearly any engineering design problem where moving fluids interact with surfaces. For instance, Lee et al. recently employed the Coandă effect to generate increased lift in an unmanned aerial vehicle.^[455] By directing a single propeller downward over a symmetrically curved structure, the researchers considerably improved flight efficiency and stability relative to commercial multicopter drones.^[455] Cardiologists are also examining this effect, as it strongly influences artificial valve design and the forces acting on materials implanted in the heart and vasculature.^[456] Other fundamental mechanisms that underlie insect chemical defense strategies are also interesting in the context of directing fluids, a task shared by a variety of applications.

8.2.1. Projectile Dispersal

A variety of exocrine glands are largely responsible for the production and expulsion of chemical defense in insects. These glands can appear anywhere on an insect, from salivary ducts

in the animal's mouthparts to anal glands near the posterior tip and anywhere in between. While some glands simply allow the chemical cocktail they produce to ooze forth from an orifice, others eject their cargo as sprays, jets, or mists, typically by contracting the surrounding musculature in a controlled manner.^[457,458] In some cases, they can shoot their secretions quite precisely, even around corners. Stick insects (*Phasmidae*), which can exceed 30 cm in length, are capable of discharging streams of an irritating, tear-inducing secretion containing a diverse array of allomones upon provocation.^[451,459] The streams are issued from one or both of its prothoracic glands, which can be aimed accurately;^[459,460] phasmids can fire up to five consecutive discharges^[459] over distances of up to 50 cm.^[450] These discharges can take the form of sprays or fine jets tens of micrometers in diameter.^[459,461,462] The form of the discharge depends on the pressure, viscosity, and surface tension of the secretion, the dimensions of the aperture, and the steadiness of the duct over time.^[463] The control mechanisms of these aspects may be inspiring for engineered jets and sprays.

Bombardier beetles (**Figure 20A**) present perhaps the most spectacular example of projectile defense found in insects. While all ground beetles (*Carabidae*) have paired pygidial glands for synthesis and dispersal of allomones, the *Brachininae* and *Paussinae* subfamilies of ground beetles have evolved an extremely specialized variant of these structures that sequentially combine the ingredients to a highly exothermic reaction, resulting in the synthesis, heating, and explosive release of an irritating *p*-benzoquinone spray at 100 °C with accompanying steam and a popping hiss. The spray is pulsed at around 700 Hz, reaches velocities of 10 m s⁻¹,^[464] can be aimed precisely with a full 360° range and can hit targets up to 7 cm away.^[465,466]

Bombardier beetles are the only known animals capable of containing a hot explosion inside their bodies as a part of normal anatomical function,^[467] a feat they achieve in a reaction chamber (**Figure 20B–D**) with several material adaptations that help maintain structural integrity and passively regulate the rate of the process. Most of the chamber is constructed from stress-resistant cuticle, but flexible seams that often contain resilin allow expansion in response to overpressure (**Figure 20C**). Inside the chamber, an enzymatic secretion produced from adjacent accessory glands catalyzes an oxidative reaction that exothermically generates benzoquinones from a fuel solution of hydrogen peroxide, hydroquinones, and hydrocarbons. The fuel is stable without the enzymes, and is stored in a bellows-like reservoir until a valve leading to the reaction chamber is opened.^[467] Less than a millisecond after the valve opens, the explosion resulting from the contact of the fuel with the enzymes displaces a flexible expansion membrane (**Figure 20B**) that closes the valve again, giving the jet its pulsed character and automatically regulating the consumption of fuel for longer, less self-destructive pulses than if the fuel were to all enter the chamber at once.^[464] The secretion that catalyzes the reaction is dense and sticky and is held to the inner surface of the reaction chamber by an impressively diverse array of microsculptures, including branched spines, haired walls, spiny hairs, spiny lobes, small spinules, and a honeycomb-like floor, which minimize catalyst loss due to washout between blasts (**Figure 19D**). The "turret" at the abdominal apex contains resilin to minimize recoil.^[467] In *Brachininae*, aiming is accomplished by the rotation of the abdomen,^[465] but *Paussinae* have evolved a different strategy

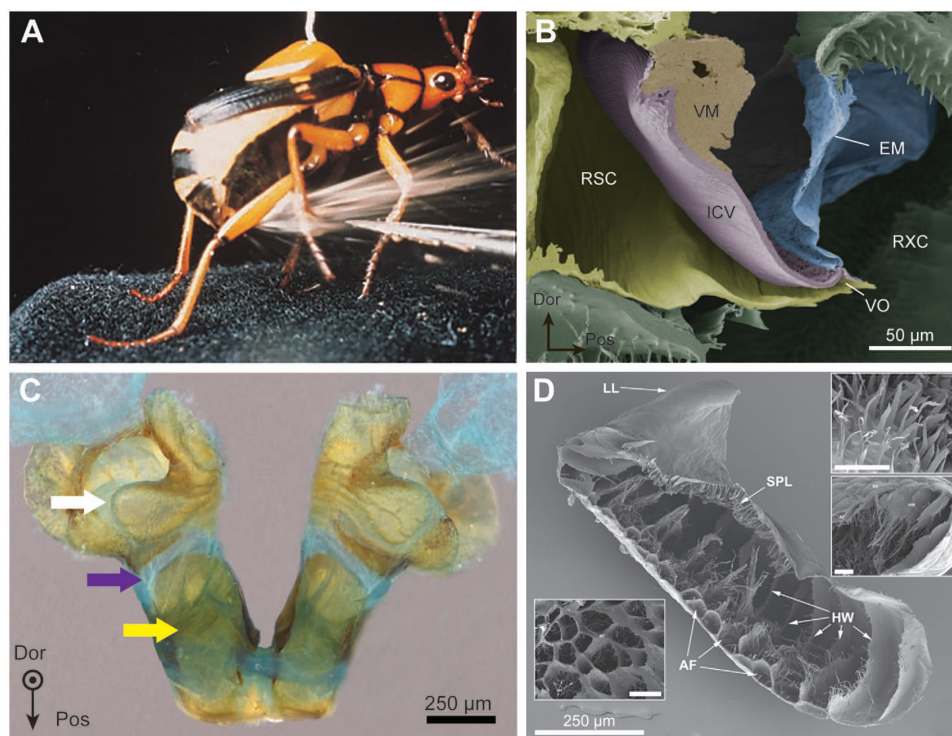


Figure 20. Bombardier beetles use specialized reaction chambers to contain pulsed explosions. A) The African bombardier beetle, *Stenaptinus insignis*, aiming its spray forward. Reproduced with permission.^[465] Copyright 1999, National Academy of Sciences. B) False-color SEM image of the inter-chamber valve (ICV) leading from the reservoir chamber (RSC) to the reaction chamber (RXC). After an initial contraction of the valve muscles (VM), the valve opening (VO) opens and shuts passively by the elastic action of the resilin-containing expansion membrane (EM) in response to changes in pressure caused by the explosive reaction. C) Optical microscopy image of the double-barreled pygidial gland of the beetle *Brachinus elongatulus* containing the reaction chamber. Resilin has been stained blue. The white arrow points to the reaction chamber's flexible midline crease; the purple arrow points to the junction between the reaction chamber and the exit channel (yellow arrow). Reproduced with permission.^[464] Copyright 2015, The American Association for the Advancement of Science. D) SEM of the different microstructured compartments of the reaction chamber of *Pheropsophus occipitalis*. Insets feature different varieties of microsculpturing: spiny lobes (SPL), hairy walls (HW), and alveolate floor (AF); inset scale bars: 50 μm . Reproduced with permission.^[467] Copyright 2015, Elsevier.

for directing jets forward involving a pair of grooved flanges in the rear of their wing covers. When the beetle's spray is aimed at the flanges, it is deflected up to 50° due to the Coandă effect.^[454,466]

8.2.2. Biphasic Liquid Secretions

Like the bombardier beetle, many insects that generate highly toxic or irritating compounds avoid poisoning themselves by synthesizing a less harmful precursor inside endocrine glandular cells, then secreting it into the lumen of a reservoir lined with an impermeable cuticle to be enzymatically converted into its final form before expulsion.^[468,469] In some members of the true bugs of suborder Heteroptera, the enzymes in the lumen reside in an aqueous phase while the reactive irritants occupy the organic phase. This observation is likely generalizable to a greater swath of the insect population.^[469,470]

Some tenebrionid beetles have developed an intriguing adaptation to maximize the efficacy of their biphasic sprays that takes advantage of gravity and different density of the two sprays.^[471] The beetles stand on their heads when threatened, raising their abdomens skyward before squirting their secretions; as a result, only the supernatant irritant-bearing

low-density organic phase of the mixture is expelled, leaving the aqueous enzyme-containing phase behind.^[472]

Insects frequently deposit their allomones as foams, the process of which encourages the evaporation of volatile odorants, often makes a sound, and leads to a highly visible product to warn potential attackers. Foams are also spatially efficient, so insects will often cover most or all of themselves or their offspring in a protective blanket of toxic foam using relatively little liquid exudate.^[473]

Frog hopper nymphs are well-known for covering themselves with a frothy foam known as "cuckoo-spit"^[474,475] after settling on a feeding site. As in the grasshoppers, this froth is an effective deterrent to predators,^[476] but it also serves to create a "microhabitat" that may protect the nymph against desiccation.^[475] The foam is stabilized by surface-active mucopolysaccharides^[477] and parallel silk-like proteinaceous fibers^[478] that reduce local evaporation rates by 65%.^[479]

8.2.3. Anatomical Structures for Allomone Injection

Several insects have evolved structures specifically to pierce the skin of threatening vertebrates and inject allomones. Though

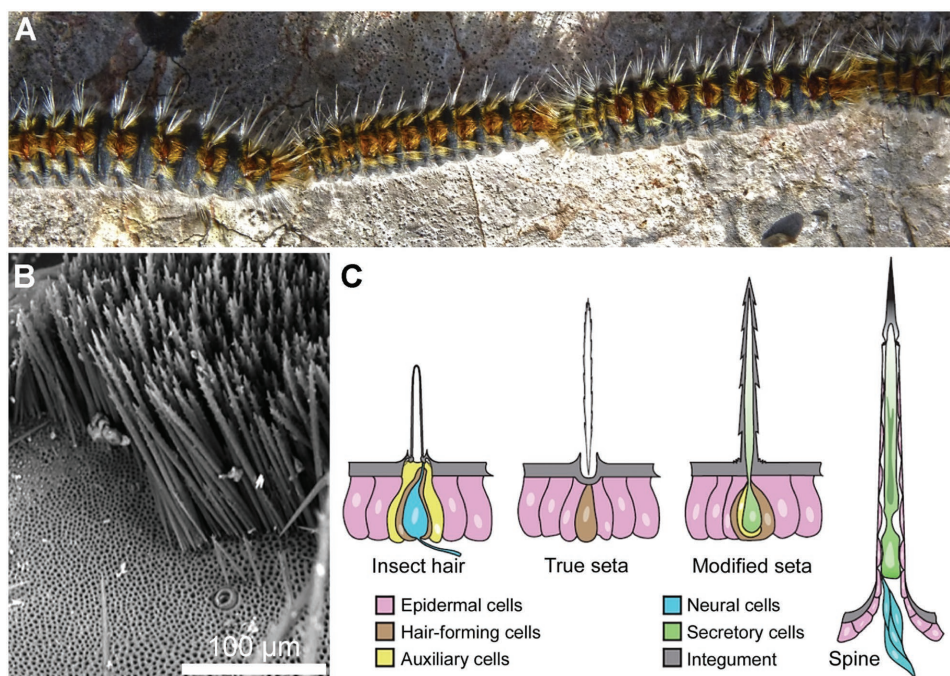


Figure 21. Various anatomical means of injecting allomones have evolved in insects for predation and defense. A) A single-file line of pine processionary caterpillars, *Thaumetopoea pityocampa*, covered in urticating hair-like setae.^[673a] B) SEM image of true setae in *Thaumetopoea pinivora*. The pores on the bottom left are sockets where some detached setae were previously affixed. A,B) Reproduced with permission.^[673b] Copyright 2015, Springer. C) Comparative diagrams of normal insect hair, true seta, modified seta, and spine. Reproduced with permission.^[485] Copyright 2011, Annual Reviews.

the context is very different, traversing the epidermal layer for sample delivery and withdrawal is a task shared by the medical community. Certain patients must receive pharmaceutical compounds intravenously quite often, motivating the development of optimized technologies for subcutaneous access. Diabetics, for example, must collect blood samples to measure glucose levels multiple times per day,^[480] and do so by puncturing their own skin with a metal lancet needle, which can be painful. Insect-inspired structures are particularly relevant in alleviating some of this burden, as many insects have developed appendages to effortlessly and painlessly puncture the skin of mammals; in fact, over 500 species of insects feed on human blood, and countless more pierce skin as a mechanism of defense.^[481] This sharp-tipped efficiency has attracted the attention of subcutaneous-injection-device manufacturers and researchers alike, leading to bioinspired microneedles. Oka et al. developed one of the first mimics inspired by mosquito mouthparts (proboscis),^[482] and they have been followed by designs based on caterpillar spines^[483] and others.^[484] Research in the microneedle field continues to grow, and the multitude of skin-piercing organs in insects have a wealth of insight to offer in this effort.

Lepidopteran caterpillars are known for having a wide variety of arrangements of “urticating,” or poisonous, hairs and spines that are often numerous and ostentatious, serving both as a direct threat to potential attackers and as an effective aposematic mechanism. Urticating structures have been reviewed extensively;^[485–487] the three most prevalent defensive apparatuses in caterpillars are true setae, modified setae,

and spines (Figure 21). True and modified setae are barbed hairs that grow from a modified cell at the base of the hair, while spines are more complex projections of the epidermis containing a number of specialized cells; all these structures are chitinous and hollow, but they vary widely in size. Functionally speaking, spines and modified setae are similar in that both have sturdy bases and sharp tips, both can contain venom provided by specialized secretory cells, and both primarily function by sticking into attackers tip-first.^[485] Caterpillars can pressurize the lumen of the secretory apparatus to inject considerable volumes of poison;^[486] the tips of spines and hairs also often detach easily into the skin of the attacker.^[488,489]

True setae have a fundamentally different mechanism of action. These are typically much smaller than other urticating structures at 100–500 µm long and only 2–10 µm in diameter. The bases are pointed and form a bottleneck at the base of the hair. True setae function by detaching from the integument of the caterpillar upon contact with a surface; they then pierce the skin of an enemy with the pointed base end.^[485,486] The pine processionary moth caterpillars (Figure 20A), named for the long, continuous single-file lines they crawl in,^[490] can have 60 000 hairs per square millimeter^[485] in the folds between abdominal tergites, which “gush out” of the folds “like an eruption” upon mechanical provocation.^[486] In white-marked Tussock moth larvae, the setae are so light and attached so delicately that the caterpillars can dislodge them into the surrounding atmosphere by simply wagging their back end upon the appearance of a threat.^[486] Contact

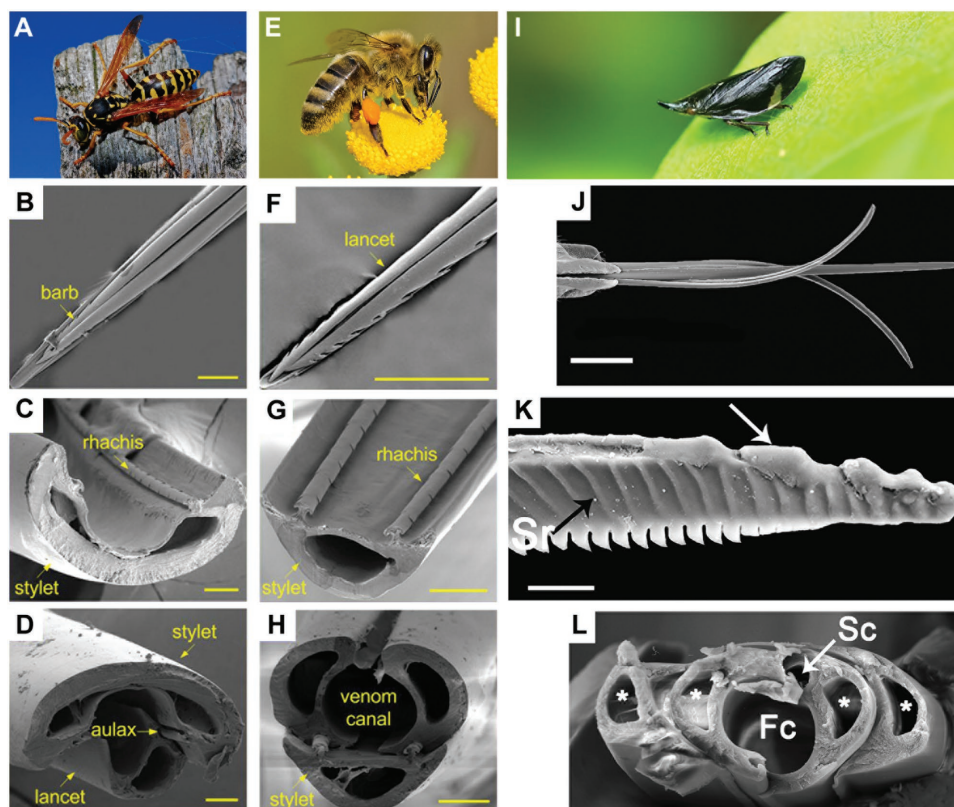


Figure 22. Paper wasp and honeybee stings share morphological characteristics with the piercing mouthparts of Hemipterans. A–D) Paper wasp sting tip. A) Paper wasp, *Polites sp.* B) The stylet sheath is wider than the lancets, allowing wasps to pull out the sting after insertion into a host and thus avoid sting autotomy. C) Cross-section of wasp stilet showing the main shafts (rhachis) that the lancets move along. D) Cross-section of stilet and single lancet showing grooves inside the lancet that run complementary to the rhachis on the outside. E–H) Honeybee sting tip. E) Honey bee, *Apis cerana*. F) The lancets are wider than their stylet sheath, leading to sting autotomy, i.e., irreversible embedding of the sting into the host. G) Cross-section of honeybee stilet showing rhachises. H) Cross-section of stilet and lancets, showing venom delivery canal formed by interlocking lancets. F–H) Reproduced under the terms of the CC-BY license.^[674] Copyright 2015, Company of Biologists. I–L) Spittlebug stylets. I) Spittlebug, *Philagra albinotata*. Reproduced with permission.^[675a] Copyright 2008. J) Stilet bundle emerging from tip of spittlebug rostrum. K) Detail of mandibular stilet showing serrate ridge (Sr). L) Cross-section of stilet bundle showing interlocking stylets, food canal (Fc), salivary canal (Sc), and dendritic canals (asterisk). Scale bars: B,F) 500 μm , C,D,H,K) 20 μm , J) 300 μm , L) 15 μm . J,K) Reproduced with permission.^[675b] Copyright 2015, Elsevier.

with true setae causes allergic reactions and skin irritation in mammals; however, the mechanism of action is not well-understood. The composition of the setae is complex, with a chitin skeleton surrounded by proteins, lipids, wax, and mucopolysaccharides, all of which are foreign to mammals. Additionally, chitin is hypothesized to promote inflammation and immune responses.^[485]

Many female members of Hymenoptera, a large insect order that includes all bees, wasps, and ants, have a venomous sting derived from an egg-placing device (ovipositor) on the tip of their abdomen for defense (and often predation). The process of stinging involves many parts of a complex apparatus moving in harmony, with muscles pulling on rigid levers connected by flexible, resilin-bearing linkages.^[486,491,492] The chitinous, needle-like tip that pierces the skin is composed of three distinct parts: two independently moving lancets with barbed tips and a fixed track called a stylet with rails called rhachises (Figure 22); the venom flows between the three components. A sensory sheath covered in hair projects above the tip; this sheath directs the sting into more vulnerable positions^[486] and produces pheromones that encourage stinging among other

colony members in social hymenoptera.^[493] After the tip is initially extended, the lancets dig into the victim and retract in an alternating fashion, boring deeper and deeper into the skin with the help of the barbs. In many insects, the lancets are attached to valves that pump venom out of a reservoir upstream of the sting as they bore into the enemy.^[486] The venom of bees in particular contains a compound called melittin, an amphiphilic peptide that self-assembles into oligomeric pores in enemy lipid membranes to induce cell death.^[494–496]

A number of mechanisms exist that allow sting removal. Vespid stylets are wider than their lancets, allowing the lancets to retreat and shield their serrated barbs before extraction (Figure 22A–D).^[497] Furthermore, some of their serrations are simply sharp enough to sever most fibers blocking the way back to the skin surface.^[486,497] However, honeybees, who frequently face vertebrate predators seeking the valuable honey in their hives, have evolved mechanisms such as large lancet barbs, preformed breaking points,^[486] and narrow stylets^[497] to ensure that their stings and all the attendant machinery stay lodged in the victim rather than remaining attached to the body of the attacker (Figure 22E–H). The process of

wrenching the sting from the abdomen results in the certain death of the attacking bee. Counterintuitively, this is understood as adaptive; the life of an individual worker bee is of little consequence to a colony, while its sacrifice results in a more effective deterrent than if it were able to remove itself from its enemy. When a bee's sting is left behind, its poison apparatus still functions, emptying its contents into the enemy and making it significantly more difficult for the predator to avoid further exposure to venom; these suicidal attacks result in more painful wounds than stings that are successfully extracted.^[498]

Many insects of the diverse order Hemiptera have evolved a remarkably similar anatomy on their front end in the form of a fearsome beak called a rostrum that they use to feed on vertebrates and invertebrates alike. Like bee and wasp stings, rostra contain a bundle of barbed shafts that burrow into the body of their prey after the exoskeleton is pierced (Figure 22I–L). Unlike stings, these projections are long and flexible, penetrating deep into the prey and whipping around radially as they spray saliva, causing severe mechanical and chemical damage within seconds.^[499,500] Furthermore, the task of this instrument is more complex than hymenopteran stings, as it serves simultaneously as a syringe that injects a potent cocktail of lytic proteins to liquefy the innards of the prey^[501,502] and as a straw to extract the resulting slurry.^[503] The barbed shafts contain grooves that they use to lock together, forming two channels that are sealed off from one another while still allowing the shafts to move independently (Figure 22L).^[499] At the point inside the rostrum where they diverge, the tip of a rigid structure that comes between them has a complex X shape that directs the grooves into each other like the fastener of a zip-locking bag.^[503] Some hemipterans can extract over 94% of the nutrients in the carcass of prey up to five times their body weight (including fish, snakes, and turtles) in the span of 2 h.^[500]

9. Material Properties of Insect Nests and Aggregates

Up to this point, we have focused on adaptations that benefit the fitness of individual insects. Social insects, e.g., ants, termites, bees, and some wasps, have evolved cooperative behavior, leading to solutions that benefit entire colonies. Social adaptations can be significantly more complex than individual ones, often manifesting as structures on the

scale of meters rather than micrometers. Termites, for example, build “cathedrals” up to nine meters high, which rank among the largest structures made by animals (Figure 23).^[504] Ants and termites practice agriculture in the form of mutualisms with

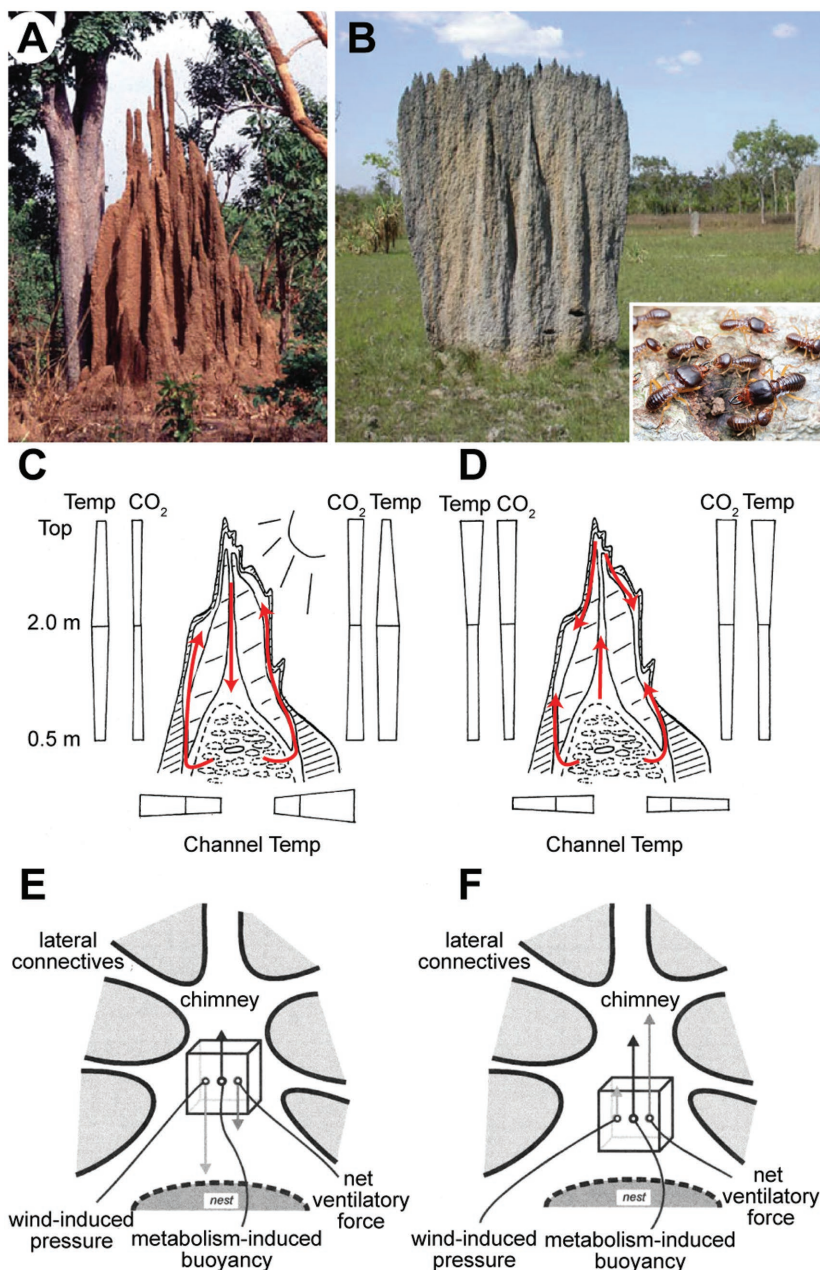


Figure 23. Termites build enormous nests that serve as collective organs for thermal homeostasis and gas exchange. A) “Cathedral” built by the termite *Macrotermes bellicosus* in the savannah. The high surface complexity contributes to efficient gas exchange. B) The magnetic termite, *Amitermes meridionalis*, builds ridge mounds aligned in a north–south direction for passive heat regulation over the course of a day. A,B) Reproduced with permission.^[523a] Copyright 2010, Springer. Inset: Habitat image of termites. Reproduced with permission.^[523b] Copyright 2015, Marcus Ng. C,D) The route of gas flow in *M. bellicosus* savannah nests is different in the day (C) and at night (D). Adapted with permission.^[570] Copyright 2000, Oxford University Press. E,F) Another termite, *M. michaelseni*, builds wind-catching nests. The direction and strength of the wind changes the direction of gas flow through a central chimney. Adapted with permission.^[511] Copyright 2001, The University of Chicago Press.

fungi, which they cultivate in their nests.^[4,505] Bees and wasps make large-scale nests with remarkably precise lattice patterns out of digested material (**Figure 24**).^[506] Alone, no insect could accomplish tasks on this scale and level of sophistication.

Termites have no preordained blueprint for the towers they build, nor do wasps receive instructions to fan their nest from a single commander. Insects collectively accomplish complex actions such as nest-building and homeostasis despite a limited individual repertoire and a lack of a central control

locus via the principle of self-organization. Specifically, each individual has a set of behavioral prescriptions that determine its response to stimuli as diverse as temperatures that exceed a threshold, pheromones released by nestmates, or an encounter with a half-built structure. Collectively, these behaviors lead to feedback loops, in which an insect is stimulated by the product of its own and/or another insect's actions to produce an effect that in turn stimulates more insects, a phenomenon known as stigmergy.^[507–511] In insects, positive

feedback causes building behaviors, signal amplification, and decision-making; negative feedback causes behavior that brings the environment closer to an ideal state, leading to homeostasis of gas concentrations and temperature in insects capable of directly impacting these conditions, usually with their wings.^[512] The behavioral patterns in individual insects have been selected over time because the emergent feedback loops they create have proved to be adaptive to the colony as a whole, which is often called a “superorganism.”^[513,514]

Examinations of the stigmergic behavior of insects have led to innovations in computing based on a consideration of feedback loops generated by individual actors with prescribed behavioral scripts. In the context of foraging, stigmergy allows honeybees and ant colonies to deduce the shortest path to a food source. Multiple insects search randomly for food and return to recruit others with pheromone trails when they have found it, and the shortest paths begin recruitment earlier and eventually develop the strongest pheromone trails, as more round trips can be taken down shorter paths in a given time.^[515] The researchers who discovered this capability in ants developed a stochastic mathematical model to describe the foraging behavior,^[515] and in the early 1990s, Dorigo realized that a similar stochastic approach using a population of “artificial ants” could be generalized for solving multiparametric optimization problems with varying degrees of constraint through positive feedback.^[516] Since then, “ant-colony optimization” has proven to be a scalable and flexible problem-solving approach with particular utility to problems such as routing, resource allocation, and scheduling, in which the computation time scales exponentially as the complexity of the system increases. Ant-colony optimization does not compute the exact best solution to such problems, but provides a high-quality solution in a relatively short time. Additionally, as in actual ant colonies, this approach is capable of adapting to a system that changes over time, making it useful for solving the

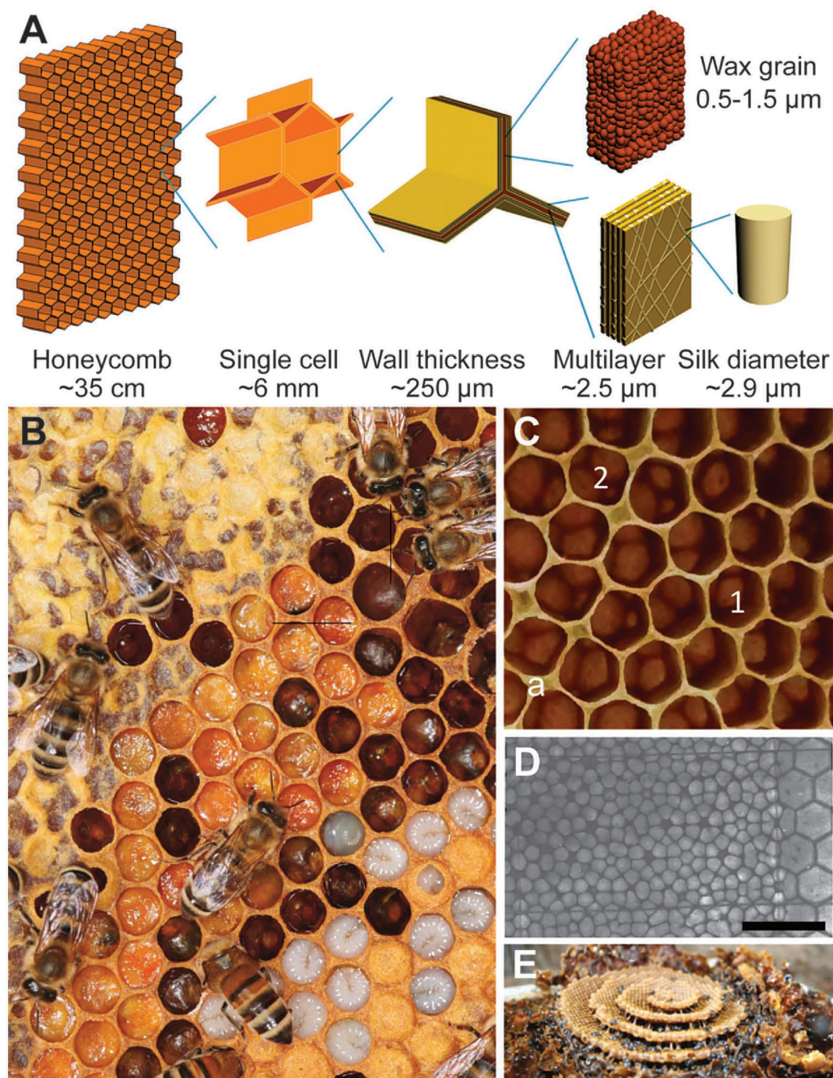


Figure 24. Bees assemble complex honeycombs as a multifunctional storage unit. A) The honeycomb is a hierarchical structure containing periodic architectural motifs with length scales across five orders of magnitude. Reproduced with permission.^[543] Copyright 2010, National Academy of Sciences. B) Honeycombs serve as storage for pollen, honey, and brood. Reproduced with permission.^[506] Copyright 2008, Springer. C) Honeycombs deviate from their usual hexagonal lattice when two constructions are attached together, creating occasional 5- and 7-sided cells. Reproduced under the terms of the CC-BY license.^[534] Copyright 2016, Francesco Nazzi. D) Bees build unusual and complex honeycomb geometries on patterned substrates. This substrate has a pattern of large hexagonal ridges (shown on the right). Scale bar: 25 mm. Reproduced with permission.^[536] Copyright 1983, Entomological Society of South Africa. E) Some bees have different geometric “rules” for honeycomb building, resulting in architectures like this spiral made by the dwarf honeybee, *Tetragonula carbonaria*. Reproduced with permission.^[539] Copyright 2012, Springer.

dynamic routing problems commonly encountered in mobile telecommunications.^[517,518]

9.1. Insect-Built Materials and Structures

Most taxa of social insects build chambered nests for protection and homeostasis and much like the magnetic termites, they shape these structures based on individually detected environmental stimuli (see Sections 5–7). These nests are often hierarchical (Figure 24A), and are both complex and central to survival. As presented below, termite mounds function as respiratory organs,^[511,523,528] and colonies of bees would be unable to survive winters without storing large amounts of honey in their combs.^[506]

Magnetic organizational control has been incorporated in a variety of techniques involving magnetic particles;^[519,520] it is also used by insects. The “magnetic” termite, *Amitermes meridionalis*, builds wedge-shaped mounds that reliably run along a north–south axis (Figure 23B). This adaptation is linked with thermoregulation, as orienting the nest in the north–south direction gives it a sun-facing surface area that is large during the cool mornings and evenings and minimal during midday.^[521–523] Experiments involving exposure to controlled magnetic fields in the lab^[524,525] indicate that the termites build both their nests and the structures within them directionally in response to an internal “compass” that likely consists of magnetite nanoparticles in the thorax and abdomen.^[526] In a similar fashion, Ding et al. recently demonstrated a method using external magnetic fields to create photonic crystals (see Section 6.1) by organizing a population of sub-micrometer-length magnetic ellipsoids.^[527] The researchers were able to control the color of the resulting ellipsoidal superlattice simply by changing the size of the ellipsoids.

9.1.1. Complex Structural Designs Built by Insects

Bees and wasps are master builders; they each construct large arrays of regular hexagons for their nests (Figure 24B). Bees’ honeycombs are capable of supporting large masses; each kilogram of beeswax is capable of supporting about 22 kg of honey.^[2] In addition to being mechanically robust, regular hexagons have the smallest perimeter of any polygon that fills a plane without gaps, making them the most materially efficient geometry for the packing of honey, pollen, and brood.^[529] Each honeycomb is a staggered bilayer of hexagonal cells that open outward on each side; the rhombic junctions between the two layers meet at the angle that gives the minimum surface area of base comb.^[530] The cells begin as close-packed cylindrical holes; their triple junctions thin over time, turning into corners.^[531] The question of whether the hexagons arise due to active shaping by bees^[510,532] or passive thermoplastic flow into an equilibrium state at elevated temperatures^[531,533] has not been definitively answered^[534] and is still a matter of active debate. A focal point of the discussion is the glass transition of beeswax, which is around 40 °C, a temperature that the wax approaches but does not seem to reach during comb formation.^[506,532] Regardless, the geometry of the lattice is regulated, with

remarkably uniform wall thicknesses and an angle consistently 9°–14° above the horizontal, ostensibly to prevent honey from leaking out of uncapped cells.^[2,506]

Intriguingly, bees are able to adapt their comb structures stigmergically in response to their environment and to previous construction and/or obstacles. Bees typically begin building a comb at multiple locations in parallel that then merge into a single structure. Bees are able to “retouch” the combs to come together harmoniously. Hexagonal cells are the dominant shape, but pentagons and heptagons are not uncommon as interstitial binders; a cell simply takes on the same number of sides as the number of its nearest neighbors (Figure 24C),^[534] though there are limits to the surface patterns they can successfully accommodate.^[535] Furthermore, if bees are provided with a patterned substrate, they will construct honeycombs in periodic arrangements defined by the substrate pattern that can be more complex than a normal hexagonal lattice (Figure 24D).^[536] Bees are strongly driven to align their combs with one another; in an early experiment, a researcher placed a beeswax foundation in a perpendicular alignment to two adjacent combs and found that the resulting comb twisted a full 90° on its way down in order to align the lower cells with the neighboring combs.^[537,538] Finally, some bees follow different stigmergic assembly “rules” altogether, leading to different architectures—one species of dwarf honeybee produces “spiral combs” that climb upward in space (Figure 24E), while another produces disordered “semi-combs.”^[510,539,540]

The wax that bees use for their comb originates in glands under the “wax mirrors,” or smooth areas of cuticle on the abdomen. These glands secrete anisotropic wax crystals that the bees masticate, turning them into stiff, isotropic comb wax that is easier to manipulate at elevated temperatures using a combination of lipolytic saliva and mechanical forces.^[538,541,542] Although this conversion process allows the bees to sculpt the wax into combs, it is at first glance curious that bees actually make their wax less strong, more easily fracturable, and more susceptible to deformation at high temperatures before using it to construct their homes. Nests made entirely of new comb wax should completely collapse at 45 °C, but are able to avoid this fate due to the actions of the developing brood they were built to house. Before pupation, larvae cover the walls of their cells with a silk cocoon, which vastly improves the tensile strength, breaking strain, stiffness, and fracture energy of the comb; although it is still sensitive to temperature increases, its structural integrity at 45 °C surpasses that of new comb wax at room temperature. As multiple brood generations are raised, the wax is imbued with thickening layers of silk, becoming a fiber-reinforced composite material similar to fiberglass or reinforced concrete with impressive load-bearing characteristics.^[541,543]

9.1.2. Communication in Large-Scale Nests

Bees communicate in a number of different chemical, physical, and optical ways; communication among honeybees has been extensively reviewed.^[544–548] Several signaling mechanisms involve using vibrations to call attention to a message. A number of “waggle dances” are used to convey information about foraging, food supplies, and nesting. The dances contain

vibrating “steps” at various frequencies, mostly clustered from 15 to 20 Hz^[549] or from 200 to 300 Hz.^[550–553] The open cells of a honeycomb resonate around 20 or 250 Hz, thereby amplifying vibrations at these frequencies and turning the honeycomb into a mechanism for wide signal broadcasting.^[554] Bees that dance on empty, uncapped cells are able to recruit around twice as many bees than those that dance on capped brood cells;^[555] these followers are also recruited from a greater distance.^[550,556] Another vibration-mediated behavior known as “shimmering” arises in the giant honeybee, *Apis dorsata*, upon the emergence of a threat such as a predator. Shimmering behavior is a social motion, similar to “the wave” in football stadiums,^[557] in which the bees on the surface of a nest all periodically (<1 Hz) raise their abdomens in a manner that propagates across the surface, often emanating from a central locus. This behavior has an aposematic function, but it also causes the entire comb to vibrate as an underdamped oscillator, alerting all the bees in the colony to the presence of a threat nearly instantaneously.^[557]

9.1.3. Thermoregulation in Complex Nests

Thermoregulation principles (Section 7) allow bees and wasps to actuate their flight muscles to significantly raise the temperature of their thoraxes at the cost of metabolic energy. This ability is used to raise larvae and pupae within a specific temperature range; the brood nests of honeybees maintain a temperatures between 30 and 36 °C while ambient temperatures range from –40 to 40 °C.^[512] This remarkable capacity for homeostasis has inspired comparisons of bee colonies to “a mammal in many bodies.”^[558] Worker bees practice a number of tending behaviors to keep the brood warm. A bee can climb into a brood-adjacent empty cell and warm its neighbors for up to 45 min. The thin cell walls provide negligible resistance to heat conduction.^[559–561] To heat individual cells containing pupae, bees press their thoraxes up against cell caps, which are put on cells at the pupation stage of the brood they carry.^[562]

Bees and wasps can also cool their nests when temperatures grow too hot. In one famous experiment, researchers placed a beehive on a lava field in full sunlight where the ambient temperature reached 60 °C, but the bees managed to hold their nest’s core temperature at 36 °C, an incredible act of heat dissipation.^[512,563] The winged social insects are able to accomplish such forceful thermal control using two primary techniques. First, bees fan their nests with their wings to circulate air. This is straightforward when a nesting area has at least two entrances, as the bees can simply drive an air current in one direction through the area. When a nest is built in an area with only a single exit, however, bees create a pulsed current: they fan air out of the nest, lowering the internal pressure, then wait as air passively fluxes inside. Cycles of this “breathing” occur about three times per minute.^[512,564,565] The second technique, evaporative cooling, is often used in concert with the first in both bees and wasps. When stores of water (often kept as a component of nectar or honey) are depleted, workers will leave the nest and actively forage.^[512,566]

The worker castes of termites and ants lack both the specialized flight muscles that enable bees and wasps to produce

heat and the possibility of fanning to dissipate heat or circulate gases.^[564] Thermal and chemical homeostasis is no less important for these insects than for the flying social insects as both ants and termites are prone to desiccation and sensitive to fluctuations in temperature.^[4,523] Successfully tending brood and fungus, which they grow to help digest food and heat their nests, requires still more stringent homeostatic controls. Given their limited capacity as direct homeostatic actors, many ant and termite species build nests that are structured to maintain a stable temperature and favorable gaseous environment despite external fluctuations.

The spectacular constructions that termites build from soil and fecal matter enable homeostatic mechanisms that passively regulate the heat and gas exchange of the colony and fungal combs (Figure 23). They have been likened to organs, an apt comparison given their respiratory function and circulatory nature^[511,567,568]—some termite colonies can exchange hundreds of thousands of liters of air per day.^[569] Colonies of *Macrotermes bellicosus* build differently shaped mounds depending on their habitat. In the savannah where sunlight is direct, they build cathedral-like mounds with high surface complexity (Figure 23A), whereas they build less contoured dome-shaped mounds in shaded forest settings. High surface complexity facilitates not only convective gas exchange, but also significant heat loss to the environment; forest mounds, which have fewer surface features and thicker insulating walls to conserve heat, thus have higher nest CO₂ concentrations and lower overall fitness.^[528] The savannah mounds have a network of air channels near the surface that connect with a large central chimney at the top and bottom of the nest; this architecture directs the airflow in response to thermal gradients that change over the course of a day. During the daytime, the sun heats the air in the channels, causing rising flow near the surface of the nest and downward flow in the chimney (Figure 23C). During the night, the fungus combs are the dominant heating element, causing gas to rise throughout the nest and exchange through the walls (Figure 23D). The circular flow of the daytime is the more efficient gas exchange process, so nest CO₂ concentrations are lower during the day than at night,^[570] but the thermoregulation is quite effective: temperatures fluctuate less than 2 °C even as ambient temperatures vary by up to 35 °C.^[528,571]

9.2. Insect Swarms as Functional Materials

The bodies of social insects can also form functional aggregations.^[572] Honeybee swarms seeking to find a new nest begin as broodless populations with one queen and 20 000–60 000 bees in total. The swarming bees settle on a branch and aggregate in a beard-like mass for days, sitting nearly motionless as scouts seek a suitable site for nest construction. During this time, the swarm maintains a remarkably stable core temperature of 35 ± 1 °C despite ambient temperatures that can dip below 5 °C.^[573] The bees accomplish this feat by altering their spacing and metabolic rate. When the temperature outside is high, the swarm forms a loose cluster with air channels flowing through it; at low environmental temperatures, the swarm packs together into a tight cluster. While clustering in response to cold weather, the bees on the “mantle,” or surface, of the swarm have significantly

lower body temperatures than the ones in the core. At extremely low temperatures, the core temperatures actually increase a few degrees above 35 °C; this is likely a means of keeping the body temperature of the mantle bees above 15 °C, a threshold below which they grow unresponsive.^[573]

An extreme manifestation of similar behavior emerges when a nest of Japanese honeybees (*Apis cerana japonica*) is approached by a giant hornet (*Vespa mandarinia japonica*). The approach of a solitary hornet is life-threatening for the colony, as hornets mark their prey sites with a pheromone that recruits a swarm. A group of 20–30 hornets can easily massacre a colony of tens of thousands of bees, as each hornet can kill up to 40 bees in a minute. As a result, the bees have evolved a unique defense mechanism in response to this marking behavior: as the hornet approaches, over 500 workers swarm it and form a tightly packed ball. The internal temperature of the ball rises to 47 °C, a “sweet spot” that is lethal for the hornet (which cannot live above 44–46 °C) but not for the bees (which cannot live above 48–50 °C); after 20 min in this configuration, the hornet is killed. No stinging occurs during this process.^[574,575]

Army ants (notably *Eciton burchelli*) are particularly known for their collective behavior outside the nest: they lack permanent nests altogether, instead spending their entire lives in temporary bivouacs composed of 200 000 to 600 000 workers that move their sites daily. The workers use their claws to link their legs and bodies together, forming layered clusters that can

measure up to 80 cm across (Figure 25A).^[512,572,576–578] These bivouacs have an internal structure, with the largest workers and brood larvae positioned toward the outside of the cluster as they are more resistant to desiccation.^[572,579] Bivouacs are actively thermoregulated via the opening and closing of ventilation channels;^[576] this sheltered and climate-controlled environment is suitable for brood-rearing.^[572,579]

Fire ants native to the rainforests of Brazil, *Solenopsis invicta*, are known for forming floating rafts in response to habitat flooding (Figure 25B); they are able to survive floating on these rafts for up to 12 consecutive days.^[580] While an individual ant has a somewhat hydrophobic integument (contact angle $\theta_e = 102^\circ$) and is denser than water, ant aggregations become over five times less dense and significantly more water-repellent ($\theta_e = 133^\circ$) in accordance with the Cassie–Baxter law as their newfound collective buoyancy decreases their area fraction of water contact.^[581]

Recent years have seen a number of studies that obtain quantitative measures of the remarkable properties of ant aggregations, which can be compared with other types of “entangled active matter” such as cells, which also have actively regulated physical bonds.^[582,583] Using classic measurement strategies such as tensile testing,^[584] parallel-plate rheometry,^[585] spreading drop measurements,^[581] and Hele–Shaw cells for flow measurement,^[583,586] the material properties of insect populations can be quantified. Accordingly, ant aggregates are classified as viscoelastic pastes with shear-thinning and self-healing properties.^[583–585] Though they lack physical bonds and so cannot be considered to be entangled matter, insects in flight also form aggregates with quantifiable physical properties. Swarms of midges, *Chironomus riparius*, have been studied as a model organism; an intriguing series of recent studies borrows the language and characterization models of materials science to classify midge swarms according to their response to perturbations^[587] and has made mathematical analogies between the driving forces defining aggregation behavior (likely mediated by long-range acoustic interactions) and tensile strength among solids^[588] and gravitational forces.^[589–591] Social behavior in insects should not be considered without an acknowledgment of the complex and multiparametric nature of the evolution of interactions.^[592] Still, characterization methods from materials science hold promise for quantifying and modeling the behavior of active and self-healing materials, biological and otherwise.^[583,585,592]

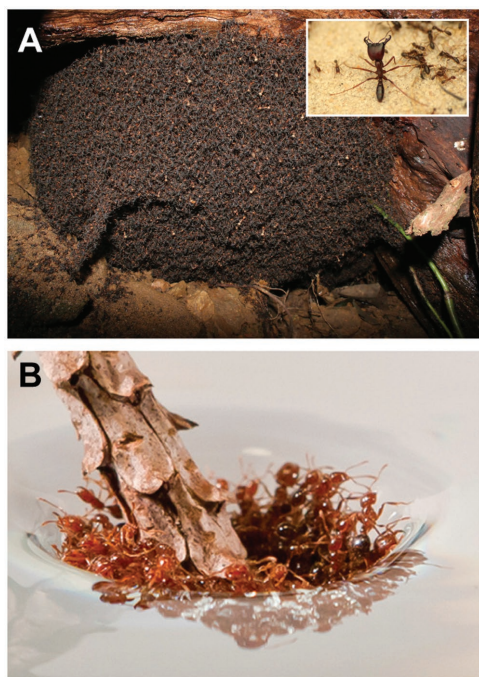


Figure 25. Aggregates of ants can work together to perform sophisticated tasks collectively. A) Army ants, *Eciton burchelli*, have no fixed nest, instead forming “living nests” known as bivouacs. Reproduced with permission.^[581a] Copyright 2017, Daniel Kronauer. Inset: habitat image of army ants showing soldier and worker castes. Reproduced under the terms of the CC-BY license.^[581b] Copyright 2006, Axel Rouvin. B) Fire ants, *Solenopsis invicta*, form floating rafts with strong buoyant forces that float even when prodded with a stick. Reproduced with permission.^[581c] Copyright 2011, National Academy of Sciences.

10. Outlook

We have provided a glimpse of insects’ bounty of extraordinary adaptations. We are hopeful that readers might now or in the future identify a problem they share with an insect that has evolved an efficient solution. While the descriptions presented here are intended to highlight some of the most compelling functional materials in insects, they represent a minuscule fraction of all the adaptations that over one million known insect species have to offer. This number is vast and approximates the total amount of all other identified living organisms,^[3] but it is not a full account of all the insects on earth—we are likely not even halfway to a full taxonomy. Though the margin of error is

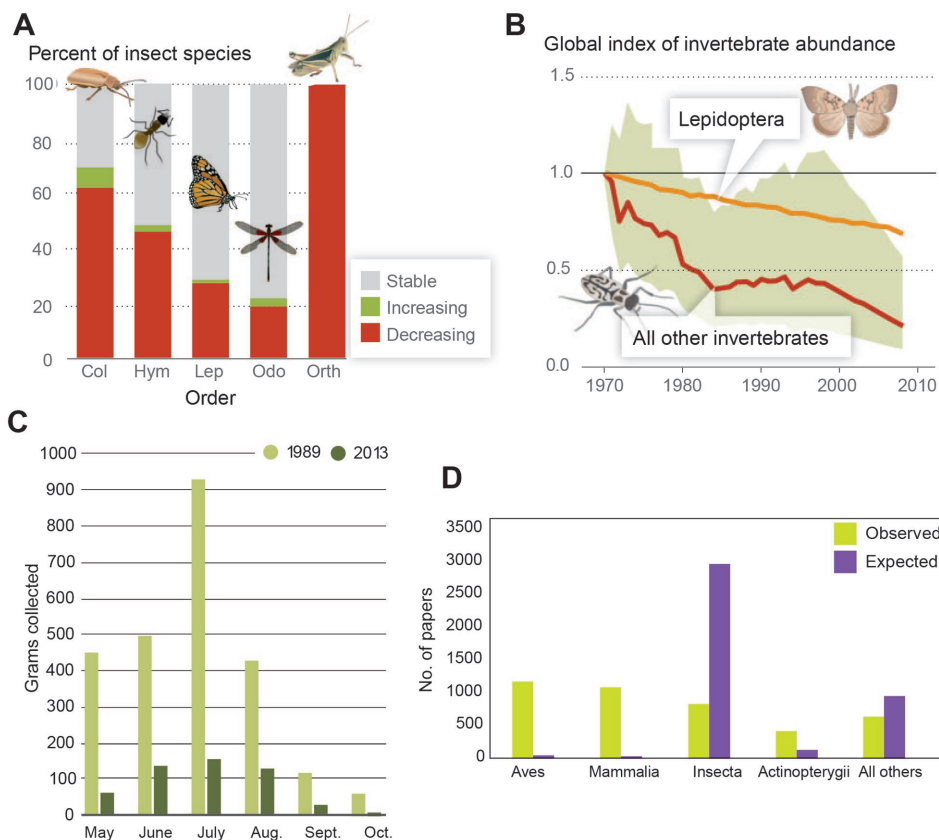


Figure 26. Decreases in the abundance and biodiversity of insects since the 1970s have coincided with a decrease in the stature and funding of entomology research. A) Population trends in insects documented by the International Union for Conservation of Nature. Insects with documented population trends account for less than 1% of known species; this figure is significantly higher for vertebrate species. B) Trends in insect abundance from long-term monitoring of 452 species of insect. Lepidopteran populations decreased by 35% since 1970; the decrease is much larger for non-Lepidopteran invertebrates. A,B) Reproduced with permission.^[595] Copyright 2014, The American Association for the Advancement of Science. C) The mass of insects collected in traps in the Orbroicher Bruch nature reserve in northwest Germany experienced 78% overall declines over a span of 24 years. The data were collected by the Krefeld society, a group of mostly amateur entomologists. Reproduced with permission.^[604] Copyright 2017, The American Association for the Advancement of Science. D) Number of papers published in the journal “Animal Behavior” on the most commonly covered animal taxa. “Expected” proportion is based on the relative proportion of described species in each taxon. “Animal Behavior” was chosen to reflect the broad state of the field of animal behavior; this meta-analysis was published in that journal. Reproduced with permission.^[601] Copyright 2017, Elsevier.

high, the actual figure likely approaches a total of five million insect species.^[593,594]

It is also shrinking. Both the abundance (Figure 26A–C) and the diversity of insects are in bad decline; overall insect populations have decreased 45% in the past 40 years.^[595] This downturn is taking place in the context of an anthropogenic “sixth extinction wave” on the same scale as Earth’s five previous mass extinctions.^[596] Across terrestrial animals, the main contemporary causes of declining populations and extinctions (“defaunation”) are all results of human impact on the biosphere: overexploitation, habitat destruction, interactions with invasive species, and climate change.^[595] Given the importance of insects in the global food chain and as pollinators, the consequences of these declines will be deeply felt, both ecologically and economically. For example, downturns in bee diversity in the UK and The Netherlands have been strongly correlated with the decline in plants pollinated by those bees;^[597] over 75% of the world’s crops require pollination, accounting for ≈10% of

the economic value of the global food supply.^[595] The total value of services performed by insects in the USA alone has been estimated at \$57 billion annually, which, in addition to the obvious line items (such as pollination and feeding higher animals), also includes less visible benefits, like the \$380 million that dung beetles save American ranchers every year by burying livestock feces.^[598] However, as insects are assigned conservation statuses at far lower rates than vertebrates,^[594,595] it is difficult to assess the magnitude and nuances of the defaunation threat.

Against this backdrop, entomologists (without whose heroic field work this review would not exist) have been pushed to the margins of the scientific community after facing stiff competition over a shared funding pool from the “new biology” of genetic engineering since its advent in the 1970s.^[599] Even within the field of zoology, entomology research is underrepresented in major ecology^[600] and animal-behavior journals (Figure 26D);^[601] this ongoing “ghettoization” to specialized journals has likely contributed to a bleak funding landscape

exacerbated by the wide reliance by funding institution on impact factors as a metric of worthiness.^[600] Taxonomists in particular, on whom we depend to quantify the extent of global defaunation, have been pushed to near-extinction, their work being regarded as “dated” and funded meagerly.^[602,603] As a consequence, data gathering on insect abundance trends is, as in a recent report in *Science*, being left to amateurs rather than career scientists.^[604] While community engagement and citizen science are admirable and should be encouraged, they cannot be relied on to meet a challenge of this magnitude, which will require sustained investment.^[605]

A second goal here is therefore to assert the value of basic scientific research. The impact of the entomologists whose observations are catalogued here will likely reverberate for generations in cross-disciplinary ways. Like all enterprises motivated by exploration, the value that is eventually derived from this type of work is impossible to foresee at the outset, instead becoming apparent over time in response to new insights, societal needs, and scientific discourse. Traditionally, institutions with some degree of freedom from market and political forces have enabled scientists and their benefactors to take a long view. As this insulation becomes more difficult over time, new funding paradigms and public policy innovation may be required in order to ensure that ambitious, long-term efforts can continue to be sustained.

If we are to meet the challenges of anthropogenic defaunation and climate change, we will rely on a host of inventive engineered solutions. As we have seen, life has a way of adapting to survive in the face of environmental pressures; bioinspiration enables us to appropriate some of nature’s prior evolutionary playbook to surmount pressures of our own. It will ultimately be poetic if mimicking the adaptations that insects rely on for their individual survival contributes to the conservation of their taxon as a whole.

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Conflict of Interest

The authors declare no conflict of interest.

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