Diversity of Cuticular Micro- and Nanostructures on Insects: Properties, Functions, and Potential Applications

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Annu. Rev. Entomol. 2017. 62:185–205

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-031616-035020

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Keywords

exoskeleton, microstructure, nanostructure, adhesion, wetting, optics

Abstract

Insects exhibit a fascinating and diverse range of micro- and nanoarchitectures on their cuticle. Beyond the spectacular beauty of such minute structures lie surfaces evolutionarily modified to act as multifunctional interfaces that must contend with a hostile, challenging environment, driving adaption so that these can then become favorable. Numerous cuticular structures have been discovered this century; and of equal importance are the properties, functions, and potential applications that have been a key focus in many recent studies. The vast range of insect structuring, from the most simplistic topographies to the most elegant and geometrically complex forms, affords us with an exhaustive library of natural templates and free technologies to borrow, replicate, and employ for a range of applications. Of particular importance are structures that imbue cuticle with antiwetting properties, self-cleaning abilities, antireflection, enhanced color, adhesion, and antimicrobial and specific cell-attachment properties.

INTRODUCTION

Nature has produced a vast library of intricate structures for controlling the interface between organism and environment. These are expressed in various forms on and as part of insect cuticle. In many cases, these are readily available for scientists in all disciplines to examine. A fundamental role for the insect integument is that it provides a protective barrier (8, 34, 46, 97, 98). This biocomposite can contain chitin, protein, lipids, waxes, and cement and is secreted across the apical membranes of a sheet of epidermal cells (10). The general morphology of an insect integument, above this sheet of cells, is a series of layers comprising an endocuticle, exocuticle, and epicuticle (inner and outer epicuticle, wax, and cement layer) (10). Hairs/bristles with sockets, sensilla, and scales (modified bristles) are often seen protruding from the integument, and these are a product of clusters of specialized cells (9, 12, 32). They can be architecturally complex and have a similar chitin-based composition to the cuticle (9, 12, 32). Although the structure of the exo- and endocuticle can sometimes play a role, many of the micro- and macro-properties of the insect cuticle, including antiwetting, antireflectance, and iridescence, are consequences of the miniature landscape constructed from patterning of the epicuticle components.

Although the chemistry of insect cuticles has been constrained by biological fabrication routes, available chemical pathways, and synthesis conditions near ambient temperatures, insects have bypassed these limitations via modification of the surface architecture at very small scales. As noted even in early studies, it appears easier for a species to become adapted to an environment by changing the contours and shapes of the cuticular surfaces than by changing the chemistry (107). There are obvious reasons for this evolutionary route; for example, many insects already have a hydrophobic (water repelling) cuticular chemistry and have taken this solution as far as it can go for what can be achieved on the basis of chemistry alone. Thus the only avenue for enhancing this antiwetting attribute, to optimize or maximize function, is to modify spatial organization (micro- and nanoshape, size, and spacing) (8, 26, 33). Some of the most diverse forms of micro- and nanostructuring are present on insect wing membranes that represent large areas of the cuticle and thus present a good focus to illustrate many of the varied forms found at the microscopic level.

This review firstly addresses the morphology of cuticular micro- and nanostructures, suggesting a simplification to seven categories. We then consider the range of functions provided for by these forms. Next, detail is presented for how these forms allow insects to control interactions with fluids, light, and solids. Finally, we address current and potential technological applications, explaining how these examples have and can be used to fabricate new materials, and we provide insight into the direction that research should take in the near term.

OVERVIEW OF CUTICULAR CATEGORIES AND FUNCTIONS

The extent of and complexity in naming micro- and nanostructures has led to a variety of classifications. Lepidopteran wing scales alone comprise a range of categories (e.g., categories 3 to 7 below) (29, 31, 32, 121). For nonambiguous scientific communication, the variety of structuring necessitates specific terminology. But even though there is a significant diversity of cuticular structuring and thus numerous ways of describing, labeling, and grouping cuticular topography, for the purposes of this article, the insect cuticle micro- and nanostructuring can be placed into simple categories reflecting inherent form and complexity:

1. Simple microstructures [dome-like or pillars with all dimensions >100 nm (typically with one or more dimensions >1 μm)]
2. Simple nanostructures (dome-like or pillars with at least one dimension <100 nm)

3. Complex geometric microstructures (varied shape) involving all dimensions >100 nm (typically with one or more dimensions >1 μm)
4. Complex geometric nanostructures (varied shape involving a dimension <100 nm)
5. Scales (flattened hairs or setae usually several microns in one dimension)
6. Hairs/setae (columnar structures, longer than wide, multiple microns in length)
7. Hierarchical structuring (any combination of the previous six categories arranged in a mixed or layered manner to fulfill a function)

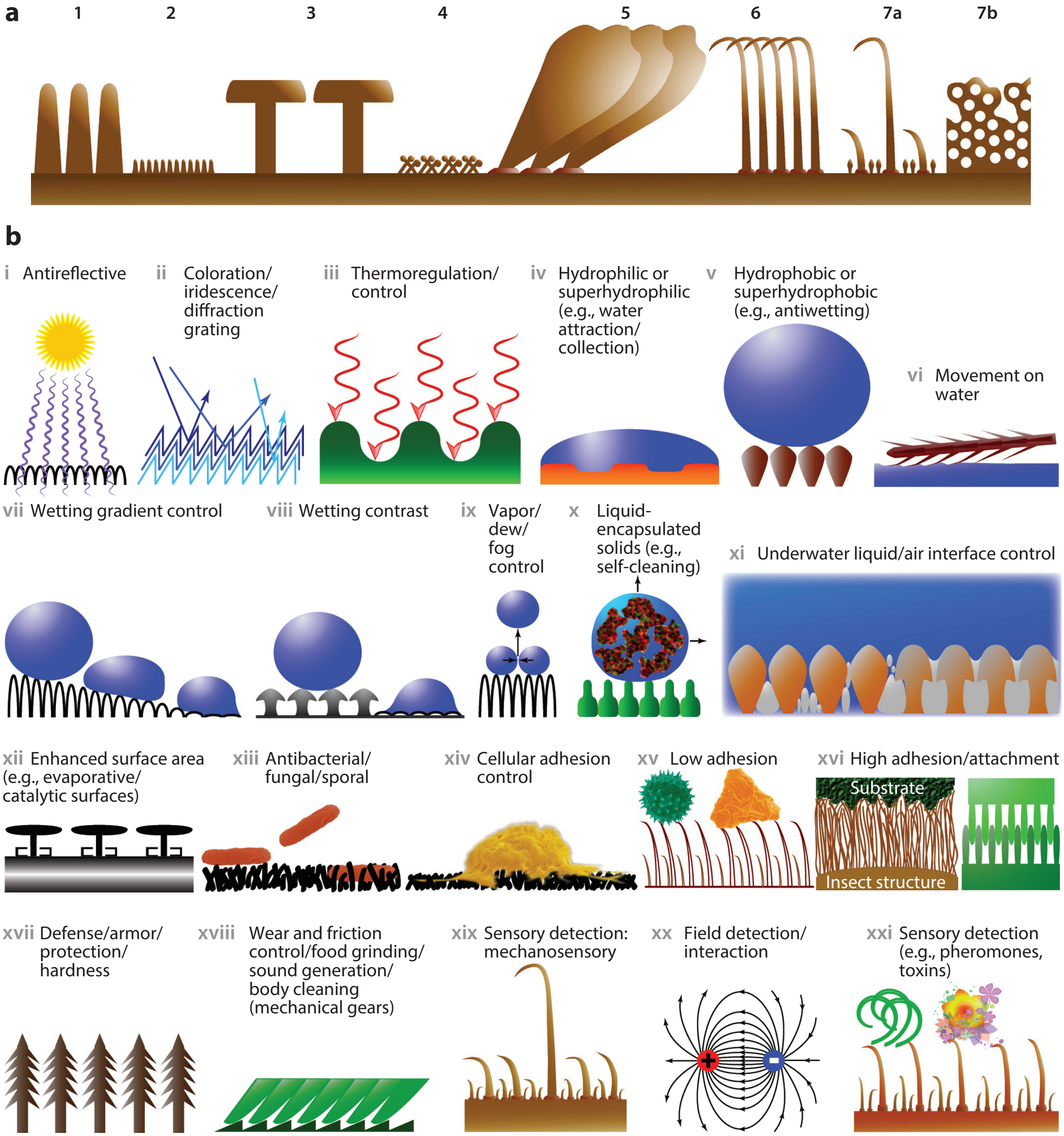
The categories are illustrated in **Figure 1*a***. For simplicity, we define a nanoscale structure as having at least one dimension (e.g., width, diameter, height) less than 0.1 μm (100 nm) with none of the other dimensions exceeding 1 μm (1,000 nm). Microstructures are defined as having all dimensions larger than 100 nm (e.g., height, basal width), and this form of structuring will often have dimensions exceeding 1,000 nm. Complex geometric micro- and nanostructures represent more intricate shapes, typically multiple protuberances, in the appropriate range described.

Diversity of the functions of many of the small-scale structures that can be found on insect surfaces is summarized in **Figure 1*b***. There is an emphasis on nonsensory aspects of the structuring shown. The first three functions illustrated (**Figure 1*b***, subpanels *i–iii*) represent cuticle interaction with light. An arrangement of nanostructures (**Figure 1*b***, subpanel *i*) (i.e., category 2) demonstrates the antireflective property created by dome-like pillars, as found on many compound insect eyes and the surface of some insect wings (such as cicadas) (3, 107). The arrays are structured from the outermost layer of the integument and generally <200 nm in height, while thinner than 100 nm. The second function illustrated is interaction with visible and ultraviolet light (**Figure 1*b***, subpanel *ii*). Cuticular structures comprise ridges, holes, or layers—sometimes in combination, with components in the nanometer range—that constructively or destructively interact with specific wavelengths to produce color and iridescence from white light (categories 1–5 and 7). The use of light is noted for thermoregulation in **Figure 1*b***, subpanel *iii* (categories 1–5 and 7), as suggested in studies of the wings of *Morpho* sp. butterfly (81) and the cuticle of the Oriental hornet (79). A detailed review of mechanisms and examples is presented below in the section titled Insect Cuticle Interactions with Light.

The eight subpanels that follow in **Figure 1*b*** (subpanels *iv–xi*) demonstrate a variety of cuticular micro- and nanostructures that function in interactions with water or fluids. Hydrophilic surfaces allow the spread of fluids. An example is found in the spaced microstructures (categories 3 and 5) present externally toward the end of the proboscis in a number of butterfly species, making up from 5% to 17% of the range of butterfly proboscis lengths (58); above this region, the external surface has a closer-packed surface roughness and is therefore hydrophobic (58). Nanoscale ridges or pillars (categories 2 and 4) may underlie larger hairlike structures (category 6) to provide hydrophobicity at different scales (category 7) (102, 104). A detailed review is presented below in the section titled Insect Cuticle Interactions with Water and Other Liquids. It includes structural arrays that act as wetting gradients (surfaces that vary in wettability and that water is forced to migrate across); vapor, dew, and fog harvesting; and dew or droplet use in cleaning particulates off surfaces, such as insect wings. Control of wetting under water is also illustrated (**Figure 1*b***, subpanel *xi*). This function is represented usually in the form of a field of setae and/or microtrichia (category 6), sometimes hierarchically arranged (category 7), where the array traps air, for example, for respiration (2). In **Figure 1*b***, subpanel *xi*, the cuticular protuberances are represented as stout or capped domes, and the shapes of these affect the size and shape of contained air pockets.

Use of microstructure to enhance evaporation is illustrated in **Figure 1*b***, subpanel *xii* and relates to fluid interactions. This structuring is exemplified by the hierarchically modified cuticle surface (category 7) surrounding the metathoracic scent gland openings of the bug *Graphosoma lineatum*; it is composed of flat plates (<10 μm in diameter) that sit atop a maze of raised walls (in the micron and submicron range). The flat plates and raised walls increase surface area and aid in rapid evaporation (23).

The function and control of adhesion is illustrated in **Figure 1*b***, subpanels *xiii–xvi*. Nanoscale patterning in the form of pillar arrays (category 2), or complex roughness (category 4) composed of a jumble of nanoscale rods, have been shown to limit bacterial, fungal, and spore attachment (47, 51, 106, 108). These types of structures are found on insect eyes (76) and wings (101, 106, 107).



Such nanoscale arrays also affect adhesion of eukaryotic cells, providing inspiration for medical applications (106). The low-adhesion function involved in keeping cuticular surfaces free from environmental particles such as silica, pollen, or spores is also represented under this topic (**Figure 1*b***, subpanel *xv*). Here, micron-sized arrays of hairs and setae (category 6) or nanoscale arrays of pillars (category 2) reduce contact area (106, 108). In contrast, hairs, setae, or smooth, flat pads (categories 6 and 3) can provide an enhanced adhesive function (34, 35) (**Figure 1*b***, subpanel *xvi*). The topic of adhesion is explored in more detail in the section titled Insect Cuticle Interactions with Solid Surfaces: Adhesional Control.

Cuticular micro- and nanostructures also play a role in insect defense, protection, armor, and hardness (**Figure 1*b***, subpanel *xvii*). A classic example for defense is the processionary caterpillar, *Ochrogaster lunifer*, with late instars able to shed over two million barbed setae (10 to 400 μm in length) (category 6) (77). Contact with vertebrates causes urtication, and also, if consumed, the setae can migrate through vertebrate tissue and have been linked to equine amnionitis and fetal loss in horses (77). Armor is demonstrated in the example of overlapping flattened setae (<100 μm in length or width) (category 5) that form a shell protecting *Liphyra brassolis* larvae from arboreal weaver ant attack (22).

Control of friction (108) and control of drag in water (63) are other functions provided by cuticular structures such as nanopillar arrays (category 2) and scales, in the multiple-micron range (category 5) (**Figure 1*b***, subpanel *xviii*). Sound generation, in the form of stridulation, occurs in a broad range of insects and is achieved by the application of a cuticular ridge or protrusion against a row of cuticular pegs, or toothed ridges (e.g., <10 μm high and wide) (category 3). A suitable review of this topic is available by Henrich (11). The concept of mechanical gears is exemplified by opposing rows of toothed protrusions (approximately 20 μm in height) (category 3) that interlock and form the jumping device of nymphs of the flightless planthopper *Issus coleoptratus* (6).

Sensory sensilla are illustrated as the final function in **Figure 1*b***, subpanels *xix–xxi*. Mechanosensory sensilla exist as hairs (category 6) with a socket at the base, enabling bending. They enable insects to feel the world around them, including airflow. A suitable review on the topic is available by Matheson (12). These sensilla are also important in electric field detection (**Figure 1*b***, subpanel *xx*). Bumblebees are able to sense the electrical field of a flower (illustrated in **Figure 1** as field lines) upon approach (96). The charged mechanosensory hairs present on the body bend as a result of attraction as the insect nears an opposite charge held by a flower that has not been visited recently, and this allows detection of the field (96). Chemosensory sensilla (category 6) are illustrated as a final function (**Figure 1*b***, subpanel *xxi*). These perforated sensilla are innervated by dendrites that assist transduction of chemical information. A suitable review is available on this topic by Cribb & Merritt (9). In this current review, we focus specifically on exploring in greater

Figure 1

Illustrations of the categories of micro- and nanostructuring on insect cuticle, and functions and properties that can be attributed to them. (*a*) Categories 1 to 7 demonstrate differences in scaling and shape: category 1 is simple dome-like or pillar microstructures; 2 is simple dome-like or pillar nanostructures; 3 is complex geometric microstructures; 4 is complex geometric nanostructures; 5 is scales; 6 is hairs/setae; and 7a and 7b are hierarchical structuring comprising any of categories 1 to 6. Categories 5 and 6 (scales and hairs, respectively) can be tens of microns in length. (*b*) Functions are noted as text above each panel. Uniformly shaped (e.g., dome-like) structures serve a number of functions, including antireflective, antiwetting, and self-cleaning functions. Hairlike or dome-like structures aid in an insect's interactions with water (e.g., hairs aid water striders to skim across water), and nanoscale domes or rods aid in antibacterial and low adhesive functions. Other functions include defensive barriers (e.g., spikes or scalelike plating), increased attachment to surfaces such as rocks or leaves (e.g., hairlike structures or flattened pads that increase surface area, or interlocking arrays of hairs), thermoregulation (e.g., spacing including ridges, holes, and/or layers of cuticle tuned to specific light wavelengths), and sensing and interaction with electrical fields (via touch-sensitive spines that bend under the influence of such fields).

detail the control of various liquid contacts, interactions with light, and interactions with solids, as these are relevant to many current industrial applications.

INSECT CUTICLE INTERACTIONS WITH WATER AND OTHER LIQUIDS

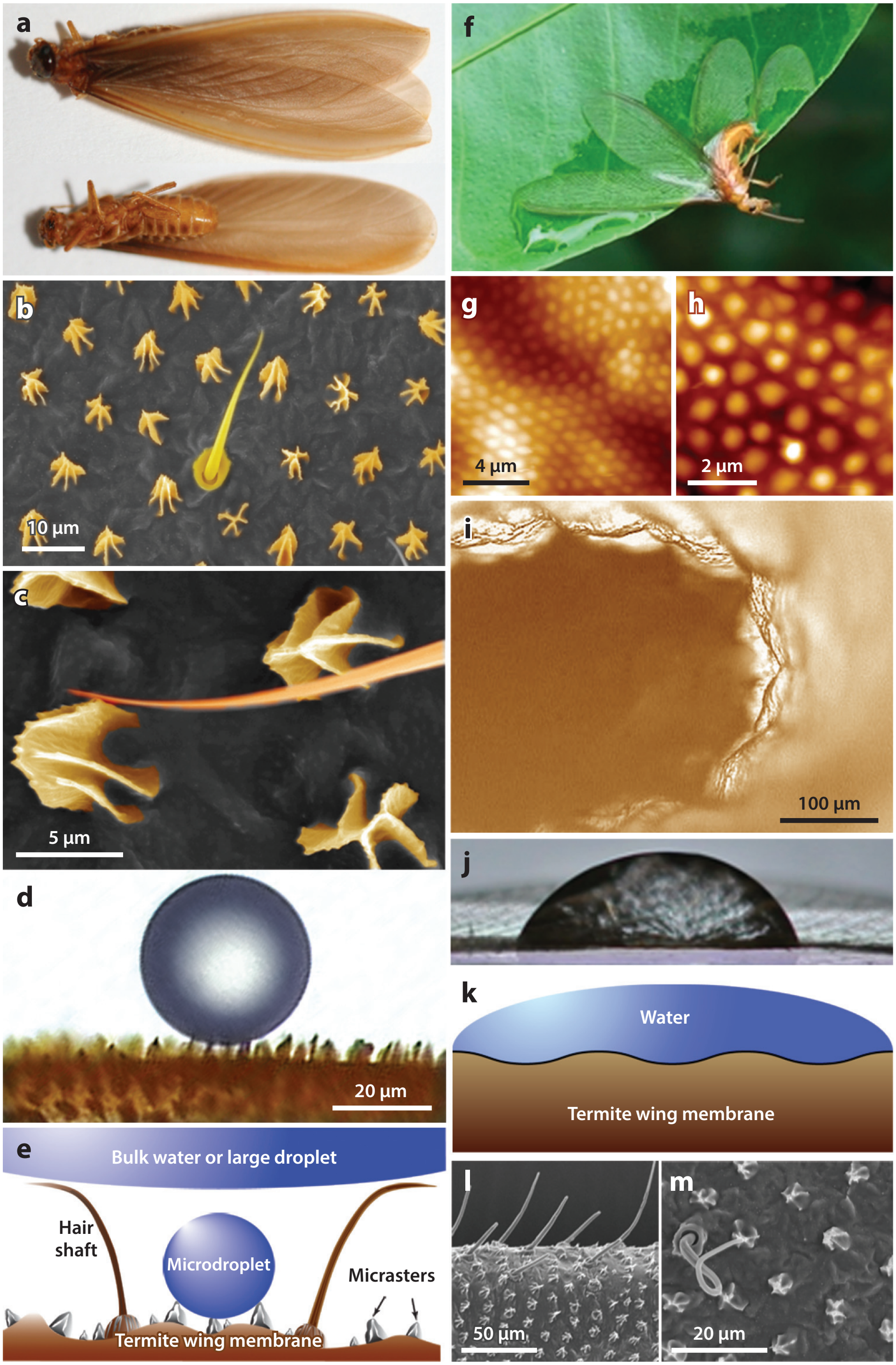
Exploration of the ways that liquids interact with the insect cuticle has been carried out by several research groups (e.g., 20, 21, 60, 94, 101, 103). Interaction with rain, fog, condensation (dew formation), or bodies of water such as lakes, rivers, and puddles affects insect survival. The preferred habitats of insects are a good predictor of the wetting properties of their surfaces and thus of the micro- and nanostructuring that aids functional efficiency.

A good illustration of contrasting micro- and nanostructuring based on environmental challenges is seen by examining wings of termite alates (flying adults) (102, 104). The colonization flight is critical for establishing new colonies (65). This occurs during periods of rainfall to ensure that the soil is wet for ease of nest and soil tunnel construction (75). *Nasutitermes* sp. and *Microcerotermes* sp. typically fly during rain in daylight hours and thus under the camouflage of moving droplets. The small-scale structuring on the wings of these species consists of hierarchical layering (category 7) (**Figure 2*a***) comprising small hairs (category 6) and tiny skeletal-shaped structures (micrasters) (category 3) (**Figure 2*b*,*c***). The hairs repel larger water droplets while the micrasters resist smaller droplets and mist conditions (8, 102) (**Figure 2*d*,*e***). The anisotropic forces exerted by the larger hairs seem to be a contributing factor in the spontaneous and active removal of water from wings (105). The fine structure of the hairs (nanogrooves) (49, 104, 105, 109) and the secondary roughness (nanobumps) on the micrasters enhance the nonwetting properties of the structures. The entire architecture is also constructed to reduce overall weight through minimizing material (102, 104).

In stark contrast, the termite *Schedorhinotermes* sp. typically flies after rainy periods and at night in the cover of darkness (102). They have simplified microstructuring on their wings, comprising micron-sized bumps (curved projections) (category 1) (**Figure 2*g*,*h***) (102). These micropillars give the wing membrane small-scale roughness that, combined with their chemistry, is insufficient to promote hydrophobicity to a level that allows escape from water contact; thus the termite is hydrophilically captured in contact with a water source (**Figure 2*f***) (102). The droplets of water, instead of sitting on the tips of the micropillars, with a thin layer of air beneath [termed the Cassie-Baxter state (52)], extend down between the micropillars and, in this state, spread across the wing. Becoming grounded in moist environments allows the insects to mate in the vicinity of moist soil,

Figure 2

Micro- and nanoarchitecture on the wings of two different termite species, and water behavior on their wing membranes. (*a*) *Nasutitermes* sp. (*b*) Micro- and nanostructuring on the surface of the wing on *Nasutitermes* sp. [scanning electron microscope (SEM) image]. (*c*) Higher-resolution SEM image of panel *b*. (*d*) Droplet (30 μm in diameter) on the *Nasutitermes* sp. wing membrane. (*e*) Diagrammatic representation of the hierarchical structuring on the wing (e.g., panel *b*), showing the interaction with water bodies of various sizes. (*f*) *Schedorhinotermes* sp. (*g*,*h*) Structuring on the *Schedorhinotermes* sp. wing surface [atomic force microscopy images]. (*i*) Optical microscope image of the termite wing folded from exposure to wetting (small droplets), inhibiting flight. (*j*) Large water droplet on the wing of *Schedorhinotermes* sp., demonstrating the hydrophilic contact with water. (*k*) Diagrammatic representation of the termite wing (e.g., of *Schedorhinotermes* sp.), showing the interaction with water where so-called full-surface wetting occurs. (*l*,*m*) Replicated structuring of the topography shown in panel *b*, using a simple molding process. Panels *c* and *f*–*i* reproduced with permission from *PLOS One* (102); panel *e* adapted with permission from *ACS Nano* (104), copyright 2011, American Chemical Society.


a
b
10 μm
c
5 μm
d
20 μm
e
Bulk water or large droplet
Hair shaft
Microdroplet
Micrasters
Termite wing membrane
f
g
4 μm
h
2 μm
i
100 μm
j
k
Water
Termite wing membrane
l
50 μm
m
20 μm

providing a survival advantage and potentially providing a fixing point to aid in removal of wings, which break along a suture line. Contact with water droplets in various forms also inhibits the mobility of the termite, as it is unable to fly from the resultant wing folding (see **Figure 2*i***) (102).

Wings folding in other insects may compromise their survival: Mosquito wings from male and female *Anopheles freeborni* have been shown to spontaneously fold upon exposure to heavy fog (21). Without appropriate micro- or nanostructures for passive water shedding, the insects instead use wing vibrations (flutter strokes) to shed droplets (20). Insect surface topographies that increase the air–water interface and minimize solid–liquid contact area generally lead to higher contact angles (water droplets assume a near-spherical shape). Micro- and/or nanofeatures increase surface roughness to enhance nonwetting behavior and have been observed on various regions, including wings, legs, eyes, and parts of the body of cicadas, dragonflies, damselflies, mayflies, lacewings, alderflies, and springtails (14, 101). Any single category or combination of categories 1–7 may enhance antiwetting for an insect surface (14, 101).

Nonwetting behavior of insect cuticle has been demonstrated for large and fine droplets (rain and mist conditions) and also under condensation conditions involving dew formation (111). In the latter case, energy released as a result of two or more droplets merging propels water droplets off the cuticle surface. This effect is related to the surface area change upon merging. The nonwetting property, resulting from micro- and nanostructuring, transports droplets quickly from the surface, such as from wings in flight. It also allows movement on, and often escape from, the surface of water for locomotion on water, resumption of flight after unintentional collision with water, and egg laying under water. The wings of *Morpho deidamia* butterflies display scales that shed water (category 5) (60). The overlapping scales have porous, asymmetric ridges. Fog condenses as droplets that coalesce and are ratcheted across the wing surface to shed the water. Remarkably, the anisotropic surface works to shed water in static (stationary) as well as dynamic (wing vibrating) states. Reduced wettability also limits conditions favorable for microbial pathogens and removes particles and spores through droplet interactions for self-cleaning (106, 111). Bathlott's group (101) investigated wettability for particulate cleaning for wings of 97 insect species. The group found nano- and microstructures in the form of dense arrays of protrusions, a variety of hairs, and ridges responsible for hydrophobicity. The insects included large-winged families that live around bodies of water (dragonflies, mayflies, stoneflies, alderflies, and caddisflies), as well as insects challenged by water droplets because of the large surface area of their wings (lacewings, scorpionflies, moths, and butterflies).

Cuticular micro- and nanostructures organized into similar spacings with similar heights and widths (forming an array) ensure consistent surface properties of the cuticle over large areas (e.g., **Figure 2*b***). In contrast, nonhomogenous structuring can wet more easily than ordered arrangements (94). Mixing of microstructuring and/or chemistry can provide specific functionality. For example, alternating hydrophobic and hydrophilic regions on Namib Desert beetle cuticle condense and capture water from the atmosphere (74).

Subterranean habitats are in danger of being temporarily flooded. Water present can be contaminated with surface-active substances from decaying plant matter, modifying surface tension. Roughness-induced–nonwetting properties are seen in collembolans that take in oxygen through their thin cuticle and regularly encounter liquids (40, 43–45, 67, 68). Studies examining several species of these hexapods have shown a resistance not only to polar liquids such as water and ethanol but also to nonpolar liquids such as hexadecane and tridecane. The cuticle forms a plastron (air layer), protecting against suffocation upon immersion in water or exposure to low-surface-tension liquids such as alkanes. To contend with such conditions, arthropods such as collembolans also use an architecture consisting of hairs (category 6) and geometric micro- and nanostructuring (categories 3 and 4). The small-scale structuring takes the form of hexagonal or rhombic comblike

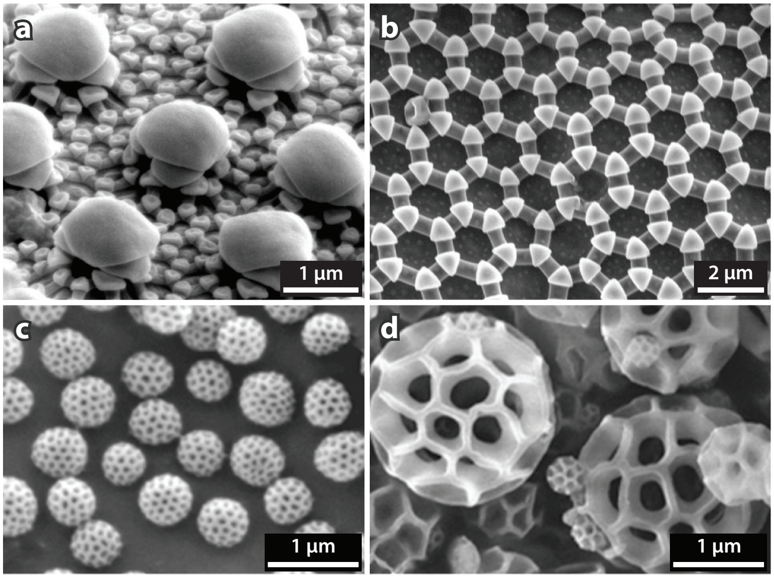


Figure 3

(*a*,*b*) Structuring of antiwetting Collembola cuticle; reproduced with permission from *PLOS ONE* (40). (*c*,*d*) Antiwetting brochosomes from leafhoppers (the leafhopper actively coats its integuments with these intricately structured particles); reproduced with permission from John Wiley & Sons Inc. (83).

patterns (40, 43, 44, 45, 67, 68) (**Figure 3**). A key feature of these geometric structures is the overhangs at the edges, which provide a higher energy barrier for invading liquids and help stabilize liquid above the surface. This hierarchical layering is also resilient to wear, affording mechanical stability, a property suited to a terrestrial organism (43).

Resistance to polar and nonpolar liquids has also been shown in other insect species—for example, on the brochosomes produced by some leafhoppers (83, 84). Although these micron-sized complex structures are not strictly a component of the cuticle, the insects produce them from specialized cells of the Malpighian tubules (83), and this surface coating then acts as the first insect interface with the environment. The structures have a hollow core and are presumably composed of polar proteins (**Figure 3*c*,*d***).

INSECT CUTICLE INTERACTIONS WITH LIGHT

Insects interact with and control light of various frequencies using a number of mechanisms, including structuring at the micron and nanometer levels (13, 95). One of the early examples of light control from nanostructuring was demonstrated in moth eyes (3), where well-ordered nanostructures (pillars) (category 2) approximately 200 nm in height and spacing were described that act as antireflective surfaces on the compound eye. This maximizes the amount of light entering the eye and decreases reflected light, presumably minimizing predation. The tapered projections constitute an optical gradient in which the refractive index changes from that of air at the top of the structuring (refractive index of 1) to solid cuticle at the bottom (refractive index of approximately 1.5) (3, 37, 99). The gradual change in optical index results in less light reflecting from the surface. Similar antireflective structuring of height and spacing has also been shown for compound eyes of other insects, such as a nocturnal grasshopper and an Eocene fly from Baltic amber (around 45 million years ago) (19, 73, 91). More recently, these types of nanoarrays have been identified on the wings of some insects (107, 116, 117) and the functional efficiency for antireflection has been evaluated (95).

Interestingly, recent studies have shown antireflective structuring at the nanoscale level on the wings of some insect species [cicada (*Gudanga* sp.) (47)], and eyes of others [whirligig beetle (Gyrinidae) (4)], is restricted to isolated regions on the cuticle where this functionality is required. For example, in the case of Gyrinidae beetle, the eyes above the waterline have antireflective nanostructuring, whereas this is absent on eyes below the waterline. Inhomogeneous structuring has also been shown to aid in antireflection (e.g., for *Greta oto*, the glasswing butterfly) where reduced reflection by wings occurs even when viewed at high angles. This is a consequence of nonregular arrangement of nanopillar structures (category 2) featuring random height and width distributions (**Figure 4**) (90). A number of insect species with similar topography have been identified (**Figure 4**), and we suggest that this form of structuring (as described in 90), and the associated mechanism for antireflection, may be utilized by numerous other species to aid in reducing reflection and thus reduce predation (47, 94).

Insects may also use micro- and nanostructuring to control physical colors as opposed to chemical coloring (69, 113). These often brilliant colors are typically generated from the interaction of light with fine-scale structuring and layering (both biological and fluid): reflection, interference,

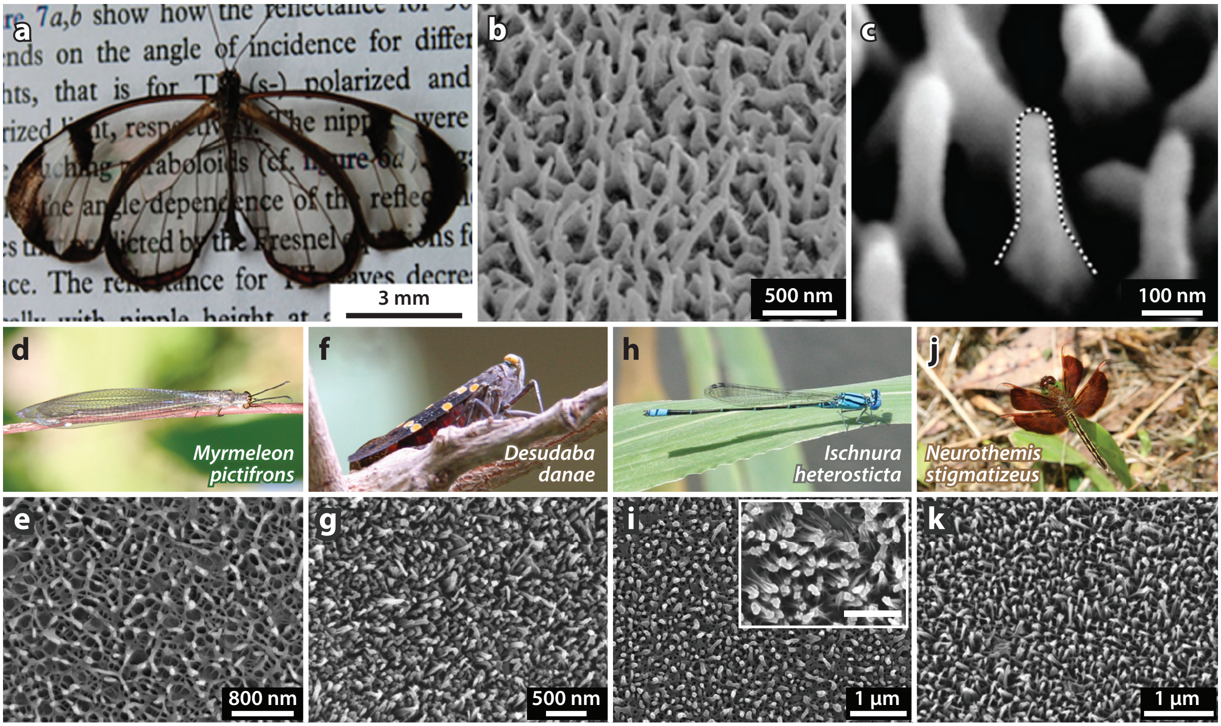


Figure 4

(*a*) *Greta oto*, the glasswing butterfly. (*b*,*c*) Scanning electron microscope (SEM) micrograph of the glasswing wing surface showing nanopillars of random height and spacing that contribute to the antireflective property of the wing. (*d*–*k*) Images showing other insect species that we suggest may utilize random structuring to reduce reflections from their wings and their topographical wing structuring (SEM images). (*d*,*e*) Lacewing. (*f*,*g*) Planthopper. (*h*,*i*) Damselfly [inset in panel *i* shows structuring on abdomen (*blue region*)]. (*j*,*k*) Dragonfly. Panels *a*–*c* reprinted with permission from Macmillan Publishers Ltd, *Nature Communications* (90), copyright 2015.

diffraction, and/or scattering of incident light as a result of structural variations of high and low refractive index materials (56). Butterflies are a good example of such control by way of cuticular scales (category 5) that have a complex architecture of gratings with longitudinal ridges that are joined at intervals by cross-ribs, often forming multiple layers (50). The interaction of light with structures on the cuticle can also be controlled by additional nanoscale beadlike additions observed between the cross-ribs on some butterfly scales (92). But not all nanobeads that produce physical color are above or even within the cuticle, with some being present in arrays in epidermal pigment cells below the cuticle, such as those of the damselfly *Enallagma civile* and dragonfly *Anax junius* (82). For butterflies, the decorated scales on the cuticle effectively increase the amount of reflected light via scattering from the surface and improve visual discrimination between conspecific males and females (92). Control of reflectance or color intensity has also been demonstrated where the nanostructuring of wing scales contributes to blackness (100).

Layering is an important component to color produced by interaction of light waves with cuticle. Iridescent wing coloration in male *Zenithoptera lanei* dragonflies is produced when interference occurs between light waves reflected from layers of melanized and unmelanized cuticle in the wing membrane, with a combined stack-depth of no more than 500 nm (39). A modification in the spacing of the layers can shift the color from blue to green—from these distributed Bragg reflectors—as seen in the damselfly *Matronoides cyaneipenni* (70). For *Z. lanei*, two layers of differently shaped wax crystals (filamentous and leaf shaped) are also present on the dorsal wing and produce diffuse scattering of the light, increasing brightness but reducing chroma (39). Crystalline wax rods, a nanostructural element (category 2) on the exocuticle, have previously been associated with color modification for damselfly bodies (*Calopteryx splendens* and *C. virgo*), along with exocuticle layering to a depth of approximately 1,000 nm (55). Some beetles use over a hundred such layers to achieve color effects (113).

Nanoscale holes and photonic crystals [a honeycomb-like lattice of voids with three-dimensional (3D) periodicity] also provide physical color (99) by providing structures of the correct size to interact with light waves (in the nanoscale range). The tetrahedral crystals appear to be configured for optimal efficiency (99). Thermal effects such as expansion of structures spaced with air pockets, when heated, can affect color (69, 113)—a mechanism that shifts structures from interaction with infrared (e.g., heating mode) to smaller wavelengths (iridescence), as seen in *Morpho* sp. butterfly wings (113). *Vespa orientalis* (Oriental hornet) appears to have developed a light-harvesting cuticle that may generate current (i.e., a solar cell) and be used to heat regions of the body (79). When elements of the system are constructed in the laboratory, light is effectively harvested to create a current (79). The insect cuticle is composed of regular ridges (<200 nm high) and grooves, with a grating-like layering below, separated by pillars (70 nm), and pigment granules packed below that collect the electromagnetic radiation (79).

INSECT CUTICLE INTERACTIONS WITH SOLID SURFACES: ADHESIONAL CONTROL

Insects make use of structuring to produce adhesive mechanisms in a wide range of contexts. Differences in structuring can result in providing strong adhesion for some situations, such as climbing and walking on terrain, or alternatively low adhesion to limit contamination of cuticle by particles and pathogens. Structural and physical aspects comprise two main forms for adhesion: smooth pads and hairy surfaces (category 6) (34, 35). Both mechanisms maximize contact areas on insect legs, aided by flexibility of structures that adapt and conform to the underlying surface profile (35). Density of hairs increases with increased body weight where the number of single contact regions increases (89). Adhesion includes capillary force (wet) and van der Waals (dry) interactions, as demonstrated across the Coleoptera and in the Diptera (31, 57, 72). Other insect orders also demonstrate adhesion with cuticular structures that involves secretions, enhancing surface contact (5, 24, 25). Importantly, adhesional contact to surfaces enables insects to transport themselves across a variety of terrains, and by necessity this locomotion requires that adhesion be fast and reversible [attachment and detachment (78)]. The primary environmental terrain encountered and stage of insect development, or life cycle, partly determine the microstructure that is employed for contact (e.g., 30, 36). Several studies have suggested that the form of structuring for adhesion, composed of hairs, may convey several advantages such as superior adhesion on rough surfaces, easy detachment, self-cleaning, and increased adhesion because of increased surface-to-volume ratio (1, 24, 78). Bullock et al. (5) have highlighted the directional behavior of hair tips and the direction dependence of adhesive pads during locomotion. Adhesional structuring can also be employed for other purposes such as wing fixation, mating, and protection against predation (72).

Micro- and/or nanostructuring can reduce adhesion and aid in the removal of particles such as silica dust, plant material, and pathogens from the cuticle. The adhesional properties of contaminating particles of various sizes have been investigated for a wide range of micro- and nanostructured insect cuticles (43, 47, 101). Cuticle architectures with an open micro- or nanostructure framework (categories 1–7) demonstrate topographies for minimizing solid–solid contact areas (43, 47, 101). For example Peisker & Gorb (76) have shown that nanostructures (category 2) on the ommatidia of some insects reduce adhesion with particles, helping to optimize functional efficiency of the lens by maintaining a large area free from contaminants. Such structuring allows for a variety of removal mechanisms, such as by wind and self-cleaning droplet interactions. Structuring seen in the springtail (**Figure 3**) has also been shown to exhibit low adhesion with contaminants (43).

Cuticle microstructuring resists adhesion of pathogens, and in some cases the adhesional contacts may kill them (43, 51, 106). For example, the surfaces of springtails (**Figure 3**) have been found to exhibit excellent repellence to bacterial and fungal contamination (43). When they were exposed to *Escherichia coli*, *Staphylococcus aureus*, and *Candida albicans* (representing gram-positive bacteria, gram-negative bacteria, and fungi, respectively) for periods of four days under standard culture conditions, little contamination was observed.

Previous studies of insect structuring have suggested the need for further examinations of the nature of contacts of solid particles and surfaces with insect cuticle in aqueous conditions (47). Insect cuticle resists microbial attack under environmental conditions in the field (**Figure 5*a***). Such observations have helped lead to investigation of a range of insect surface topographies challenged with bacteria (38, 51). For example, some bacteria have been shown to die within minutes of exposure to in situ cuticle structuring (category 1) (51, 106) (**Figure 5*b*,*c***). The specific mechanisms for such antibacterial effects are still not completely understood; however, the process presumably takes place via gravity and nonspecific forces (114). Other species of insects with category 1–4 structuring may also demonstrate antibacterial properties such as those shown in **Figure 5**. The effect is not limited to wings. Aquatic larvae of the drone fly, *Eristalis tenax*, a syrphid that lives in its larvae stage in fetid, microorganism-rich slurry, have unusually banded nanopillars (category 2) over the body, and these appear to limit bacterial attachment when present in an array (42).

The wide range of shape, spacing, height, and size of insect cuticle structures all provide scientists with an extensive number of permutations to explore the range of interactions of eukaryotic cells with structured surfaces. In particular, these types of surfaces can be used to investigate specific cellular responses, such as adhesion, in relation to varied contact conditions (e.g., volume and area) (38). This may entail directional cell guidance (as insect structuring can be anisotropic and of micron dimensions) to varied cell adhesion and adherence (as nanostructure contact control is also possible). Whereas the structuring on the insect surfaces can kill some species of bacteria, the interaction, adhesion, and adherence of eukaryotic cells can take on various forms. Green et al.

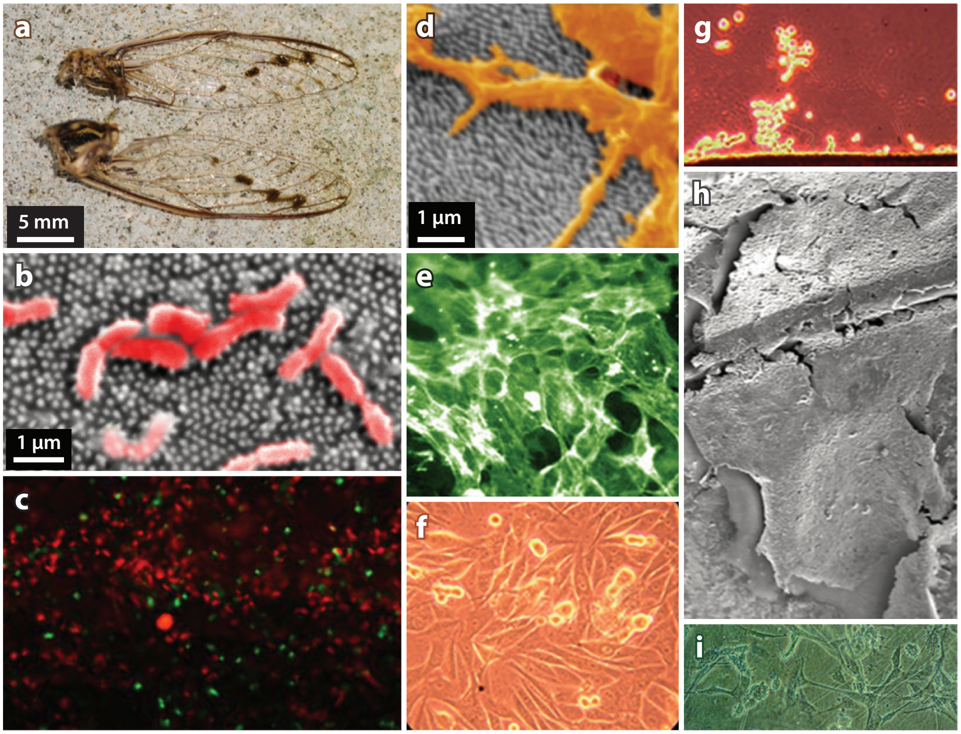


Figure 5

(*a*) Optical image of cicada wings predominantly intact after environmental exposure, whereas the insect body has suffered from environmental degradation during the same time period. (*b*) Scanning electron micrograph shows the interaction of individual bacteria (and bacteria clumps and fragments) on the cicada wing surface. (*c*) Confocal scanning laser micrograph of bacteria on the nanostructure of the cicada wing. Live cells and dead cells are stained; live cells are indicated in green and dead cells are indicated in red. (*d*) Periodontal ligament stem cell; high resolution image in which cicada wing nanostructuring is also visible. (*e*) Human retinal pigment epithelium (ARPE-19) grown on cicada wing. (*f*) C32 melanoma cells on control culture dish showing good adhesion. (*g*) Same cells as in panel *f* grown on the cicada wing demonstrating low adhesion. (*h*) Stem cells grown on a cicada membrane, demonstrating a cell sheet response. (*i*) Human umbilical endothelial cells on cicada wing. Panels *b*, *d*, and *f–i* reproduced with permission from Reference 106; panel *e* reproduced with permission from John Wiley & Sons Inc. (38).

(38) were the first to study such cell interactions with insect cuticles, including cicada and termite wing membranes (categories 1 and 2) (**Figure 5*d–i***). There are at least three distinct adhesional cell responses, comprising (*a*) well-adhered cell interactions, (*b*) cell sheets, and (*c*) loosely adhered cells (106). Examples in **Figure 5** show these responses with a variety of cell lines on cicada wings: human retinal pigment epithelium and human umbilical endothelial, stem, and cancer cells (106). Gaining a better understanding of the way cells adhere (e.g., the three adhesional types) to nano- and microstructures present on insects will provide an avenue for understanding both the interaction of insect surfaces with the microbial environment and the biophysics involved in cell interactions with such substrates. This understanding can assist translation of such patterning into the fields of biological reconstructive techniques such as fabrication of scaffolds for cell regeneration and in vitro growth of cell networks for tissue growth and study, such as in the case of regeneration of ocular epithelium as discussed by Green et al. (38). Recent studies by Makarona et al. (62) and Yang et al. (115) provide review and insight into these fields.

It should be noted that some insect cuticle structuring can also represent an interface that may hold air in aqueous environments, and thus the interaction of living cells with such cuticular arrays may incorporate solid, liquid, and air contacts (particularly at initial stages). The temporal evolution of this three-phase contact may also affect cell responses. Also, the air layer may potentially disrupt certain cellular activities (for example, trap nutrients and waste products). Varied mechanical properties of insect cuticle structuring may also comprise another parameter for cell-response investigations (106). Recent studies on fabricated structuring similar to those exhibited on some insect species (e.g., **Figure 4**) have demonstrated that cocultured cell lines exhibit different responses (15, 86). Such cell selectivity has shown that nanostructuring of particular dimensions can provide favorable conditions for some cells (e.g., endothelial cells) while inhibiting others (e.g., fibroblast cell growth) (15, 86). The tops of the nanostructures can apparently provide insufficient ligand density, spacing, and clustering for the cells to form mature focal adhesions. Density of integrin binding sites may also explain different cell responses. Further studies of insect cuticle with various cell types may provide insights into design for numerous biomedical surfaces where it would be advantageous to enhance the growth of a desired cell type while inhibiting that of another (cell selectivity).

APPLICATIONS AND POTENTIAL APPLICATIONS—NEW TECHNOLOGIES AND STRUCTURES DERIVED FROM INSECT CUTICLE PATTERNING

The range of surfaces, devices, and applications based on potential replication of insect cuticle technologies and structuring in the literature is already significant, considering this has really come to the fore only in recent decades. Applications include, but are not limited to, new superhydrophobic and superoleophilic or superoleophobic coatings, antiwetting surfaces, anti-icing surfaces, fluid separation, microfluidic devices, floatation mechanisms, low-adhesion surfaces, anticorrosion coatings, antibacterial coatings (e.g., catheters, implants), new textiles, protective clothing, printing technologies, counterfeit technologies, sensors, catalytic surfaces (substrates on which chemical reactions occur more quickly), low-wear and friction surfaces, color control (e.g., increasing and tuning color, reflectance, absorption), optical devices (e.g., contact lenses), photonic security labeling, solar cells, reversible couplings, robotic applications, and new and advanced sensors (16–18, 48, 63, 69, 93, 113, 118). A topical area is water collection from fog, to address water shortage issues. Biomimicry of structural hierarchies and replication of islands of hydrophobicity alongside hydrophilic regions have produced various such products (122). Coatings that repel low surface tension oils (superoleophobic) are of particular interest. Arthropods (e.g., springtails) do not use perfluorinated chains, in contrast to human endeavors, and their solution is attractive for copying now that the hierarchical structures involved, and chemistry, are better understood (17). *Hoplia coerulea* beetle scales that change from blue to green upon contact with water, because of their microporous structure, have inspired vapor sensing technology (64). Photonic integrated circuits have been made from the structure of butterfly scales (63). Fabrication has targeted light-harvesting devices modeled on papilionid dark scales (118). A solar cell has been designed from copying the cuticle structuring of the Oriental hornet, *V. orientalis* (79). Structural color has given rise to superparamagnetic colloidal nanocrystal clusters that can be tuned to different colors on the basis of magnetic field exposure and fixed in position as antiforgery protection (63). Cuticular templating has also shown to be useful for optimizing light emission as demonstrated recently by mimicking the nanostructuring of the firefly lantern (53). Pits, pillars, and channels have been replicated on surfaces to provide antifouling functions (63). A highly sensitive strain-gauge sensor has also been developed modeled on nanofibers inspired by the wing-locking device of the beetle *Promethis valgipes* (93). These examples show the breadth of material science solutions that have already come from entomological research. Such applications usually require mimicking structures. A grasp of both the possibilities for application and materials science fabrication techniques are valuable to have in order to be able to assess possible commercialization through biomimicry.

There are numerous pathways to potentially replicate insect structuring; for example, simple templating can reproduce relatively complex features of insect cuticle (**Figure 2*l*,*m***) (54, 108). More elaborate techniques are also employed, each with its inherent strengths and weaknesses: electron beam lithography, electrospinning, sol-gel, layer by layer techniques, etching, chemical vapor deposition, electrochemical techniques, imprint lithography, self-assembly colloidal techniques, plasma chemical techniques, polymerization reactions, and hydrothermal reactions (7, 30, 41, 53, 59, 110).

An awareness of fabrication processes helps in the assessment of the feasibility of translation from insect science to device. For example, ordered 3D macroporous structures such as those found on the weevil *Pachyrrhynchus congestus pavonius* that result in its spectacular orange coloration or that are responsible for the iridescent blue on *Morpho* sp. butterfly wings are challenging to fabricate but have been prepared using poly(methyl methacrylate) (PMMA) as a template (113) or prepared from self-assembling latex particles (spheres and anisotropic spheroids) (120). The *M. peleides* wing structure with its violet–blue-range optical properties has been replicated using Al_2O_3 deposited in a layer via a low-temperature atomic layer deposition process (63). The quasi-honeycomb structures found in the scales of some *Papilio* species that reduce reflectance, always appearing dark brown or black, can be fabricated using an aqueous sol-gel process ending with a metal replica (118). Microfibers and silks produced with knot-like bumps can gather water from air and direct it along the shaft, as has been found for the silk of the spider *Uloborus walckenaerius*. These structured microfibers have been fabricated with PMMA electrospinning in the presence of titanium tetrachloride (TiCl4) hydrolyzed nanoparticles, as a fog (122). The elytra of the desert beetle *Stenocara* sp., which harvests water, have acted as inspiration for many hydrophilic-hydrophobic patterned substrates. An example of such a fabrication process is calcined copper microgauze treated with 1*H*,1*H*,2*H*,2*H*-perfluorodecanethiol ethanol solution then deposited on a polystyrene sheet (122). The advances in 3D printing technologies may also yield viable avenues for replication of such complex insect structures.

Areas in which micro- and nanoarchitecture of insect cuticle may be applied in future research and technological and commercial applications are numerous, with many still to be discovered and explored. They include the following:

1. Tunable colors involving interphase physical interactions from fluid composition directly controlling optical properties, and humidity-controlling light-switchable colors from physical changing of spatial distances of macromolecular structures (e.g., 18, 63, 69, 81, 85, 88, 99, 112, 113, 119)
2. Micro-robot design—for example, drone technology based on principles of insect micro- and nanostructuring encompassing adhesion, reflections, water repellence, and weight reduction properties (e.g., 27, 61, 106)
3. Platforms used as biosensors/devices, implants, contact lenses, and catheters that are modeled after insect surfaces that selectively control adhesion and growth as well as (alive or dead) state of target cells (e.g., 106)
4. Novel platforms and devices incorporating switching between binary states or along gradients for magnetism, color, or adhesion (e.g., 28)
5. Micro- and nanostructuring for adhesive advancement (e.g., 71)
6. Material durability, wear resistance, and self-repairing structuring (e.g., 66)

7. Micro- or nanotags or identifiers developed from micro- and nanostructures (e.g., regions with stacked 3D ridges or possibly so-called micro-javelins and micro–ball bearings) incorporating surface polarity gradients (e.g., 80)
8. Insect farming to harvest natural and genetically engineered species for producing commercially specific micro- and nanostructures as well as micro- and nanoarchitectures [an extension of harvesting insects for the textile industry (87)].

Entomologists and other researchers continue to identify, label, and characterize surfaces that enable an understanding of how nature utilizes minute structures of the insect cuticle. This library of free technology will increase for some time as we further examine the biodiversity available. The examples provided have been chosen to ignite further interest from a range of researchers to enhance speculation and investigation of relationships between structure, form, properties, and functions, leading to potential applications for new industries of the future.

CONCLUDING COMMENTS

Insect cuticular structures can be represented as seven categories: simple microstructures, simple nanostructures, complex geometric microstructures, complex geometric nanostructures, scales, hairs/setae, and hierarchical structuring. The same type of structure can provide for more than one function—for example, as seen with simple nanostructures that can reduce wetting and also reduce reflection and channel light. **Figure 1** provides a graphical summary for both structural category and function, and the text has been used to elaborate the detail. Although a range of functions has been presented, this review has focused in particular on the role of cuticular structuring for interactions with light, water, and solids (specifically related to adhesion). Numerous examples have been presented to show how these structure-function solutions translate into novel technical applications that are being or have been commercialized. Many more opportunities remain for insect science. There is a need though for researchers to be aware of current fabrication technologies in order to assess the feasibility of translation from observation to device. To aid this, the review has provided an introduction to such techniques and elaborated on their use for biomimicry of insect science examples. Promising applications for the near future appear to lie specifically in the areas of color manipulation (e.g., sensors that change color), improvements in energy harvesting, and autonomous vehicles, or drones, structured to better handle environmental challenges. Dynamic solutions that incorporate reversible binary shifts, or gradations, offer novel solutions to the technological problem of tuning responses and sensors and are particularly appealing. On the medical front, immediate opportunities exist in relation to patterning of the surfaces of medical implants and devices to reduce microbial growth, and for the use of insect micro- and nanostructures to enhance tissue scaffolds and as substrates for tissue regeneration in vitro for study or implantation.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Arzt E, Gorb S, Spolenak R. 2003. From micro to nano contacts in biological attachment devices. *PNAS* 100:10603–6

2. Balmert A, Bohn HF, Ditsche-Kuru P, Barthlott W. 2011. Dry under water: comparative morphology and functional aspects of air-retaining insect surfaces. *J. Morphol.* 272:442–51
3. Bernhard CG, Miller WH, Móller AR. 1963. Function of corneal nipples in compound eyes of insects. *Acta Physiol. Scand.* 58:381–82
4. Blagodatski A, Kryuchkov M, Sergeev A, Klimov AA, Shcherbakov MR, et al. 2014. Under- and over-water halves of *Gyrinidae* beetle eyes harbor different corneal nanocoatings providing adaptation to the water and air environments. *Sci. Rep.* 4:6004
5. Bullock JMR, Drechsler P, Federle W. 2008. Comparison of smooth and hairy attachment pads in insects: friction, adhesion and mechanisms for direction-dependence. *J. Exp. Biol.* 211:3333–43
6. Burrows M, Sutton G. 2013. Interacting gears synchronize propulsive leg movements in a jumping insect. *Science* 341:1254–56
7. Celia E, Darmanin T, de Givenchy ET, Amigoni S, Guittard F. 2013. Recent advance in designing superhydrophobic surfaces. *J. Colloid Interface Sci.* 402:1–18
8. Chapman RF. 1998. *The Insects: Structure and Function*. Cambridge, UK: Cambridge Univ. Press
9. Chapman RF. 2013. Chemoreception. Revis. updat. BC Cribb, DM Merritt. In *The Insects: Structure and Function*, ed. SJ Simpson, AE Douglas, pp. 771–92. Cambridge, UK: Cambridge Univ. Press. 5th ed.
10. Chapman RF. 2013. Integument. Revis. updat. H Merzendorfer. In *The Insects: Structure and Function*, ed. SJ Simpson, AE Douglas, pp. 463–500. Cambridge, UK: Cambridge Univ. Press. 5th ed.
11. Chapman RF. 2013. Mechanical communication: producing sound and substrate vibrations. Revis. updat. R Henrich. In *The Insects: Structure and Function*, ed. SJ Simpson, AE Douglas, pp. 824–56. Cambridge, UK: Cambridge Univ. Press. 5th ed.
12. Chapman RF. 2013. Mechanoreception. Revis. updat. T Matheson. In *The Insects: Structure and Function*, ed. SJ Simpson, AE Douglas, pp. 738–70. Cambridge, UK: Cambridge Univ. Press. 5th ed.
13. Chapman RF. 2013. Visual signals: color and light production. Revis. updat. P Vukusic, L Chittka. In *The Insects: Structure and Function*, ed. SJ Simpson, AE Douglas, pp. 793–823. Cambridge, UK: Cambridge Univ. Press. 5th ed.
14. Cong Q, Chen G-H, Fang Y, Ren L-Q. 2004. Study on the super-hydrophobic characteristic of butterfly wing surface. *J. Bion. Eng.* 1:249–55
15. Csaderova L, Martines E, Seunarine K, Gadegaard N, Wilkinson CDW, Riehle MO. 2010. A biodegradable and biocompatible regular nanopattern for large-scale selective cell growth. *Small* 6(23):2755–61
16. Darmanin T, Guittard F. 2014. Recent advances in the potential applications of bioinspired superhydrophobic materials. *J. Mater. Chem. A* 2:16319–59
17. Darmanin T, Guittard F. 2015. Superhydrophobic and superoleophobic properties in nature. *Mater. Today* 18:273–85
18. Deparis O, Mouchet S, Dellieu L, Colomer J-F, Sarrazin M. 2014. Nanostructured surfaces: bioinspiration for transparency, coloration and wettability. *Mater. Today* 1(Suppl.):122–29
19. Dey S. 1988. Scanning electron microscopic detection of corneal anti-reflection coating in the grasshopper, *Epacromia dorsalis* and its physiological significance. *Vis. Res.* 28:975–77
20. Dickerson AK, Hu DL. 2014. Mosquitoes actively remove drops deposited by fog and dew. *Integr. Comp. Biol.* 42:1–6
21. Dickerson AK, Liu X, Zhu T, Hu DL. 2015. Fog spontaneously folds mosquito wings. *Phys. Fluids* 27:021901
22. Dupont ST, Zemeitat DS, Lohman DJ, Pierce NE. 2016. The setae of parasitic *Liphyra brassolis* butterfly larvae form a flexible armour for resisting attack by their ant hosts (Lycaenidae: Lepidoptera). *Biol. J. Linn. Soc.* 117:607–19
23. Durak D, Kalender Y. 2009. Fine structure and chemical analysis of the metathoracic scent gland secretion in *Graphosoma lineatum* (Linnaeus, 1758) (Heteroptera, Pentatomidae). *C. R. Biol.* 332:34–42
24. Federle W. 2006. Why are so many adhesive pads hairy? *J. Exp. Biol.* 209:2611–21
25. Federle W, Riehle M, Curtis ASG, Full RJ. 2002. An integrative study of insect adhesion: mechanics and wet adhesion of pretarsal pads in ants. *Integr. Comp. Biol.* 42:1100–6
26. Feng X-Q, Gao X, Wu Z, Jiang L, Zheng Q-S. 2007. Superior water repellency of water strider legs with hierarchical structures: experiments and analysis. *Langmuir* 23:4892–96

27. Floreano D, Wood RJ. 2015. Science, technology and the future of small autonomous drones. *Nature* 521:460–66
28. Fox JD, Capadona JR, Marasco PD, Rowan SJ. 2013. Bioinspired water-enhanced mechanical gradient nanocomposite films that mimic the architecture and properties of the squid beak. *J. Am. Chem. Soc.* 135:5167–74
29. Gao X, Jiang L. 2004. Water-repellent legs of water striders. *Nature* 432:36
30. Garrod RP, Harris LG, Schofield WCE, McGettrick J, Ward LJ, et al. 2007. Mimicking a Stenocara beetle's back for microcondensation using plasmachemical patterned superhydrophobic-superhydrophilic surface. *Langmuir* 23:689–93
31. Ghiradella H. 1998. Hairs, bristles, and scales. *Microsc. Anat. Invertebr.* 11:257–87
32. Ghiradella H. 2010. Insect cuticular surface modifications: scales and other structural formations. In *Advances in Insect Physiology: Insect Integument and Colour*, Vol. 38, ed. J Casas, SJ Simpson, pp. 135–80
33. Gibson CT, Watson GS, Myhra S. 1996. Determination of the spring constants of probes for force microscopy/spectroscopy. *Nanotechnology* 7:259–62
34. Gorb S. 2001. *Attachment Devices of Insect Cuticle*. Dordrecht, Neth.: Kluwer Acad. Publ.
35. Gorb SN. 2005. Uncovering insect stickiness: structure and properties of hairy attachment devices. *Am. Entomol.* 51:31–35
36. Gottardo M, Vallotto D, Beutel RG. 2015. Giant stick insects reveal unique ontogenetic changes in biological attachment devices. *Arthropod Struct. Dev.* 44:195–99
37. Grann EB, Moharam MG, Pommet D. 1995. Optimal design for antireflective tapered two-dimensional subwavelength grating structures. *J. Opt. Soc. Am. A* 12:333–39
38. Green DW, Watson GS, Watson JA, Abraham SJK. 2012. New biomimetic directions in regenerative ophthalmology. *Adv. Healthc. Mater.* 1:140–48
39. Guillermo-Ferreira R, Bispo PC, Appel E, Kovalev A, Gorb SN. 2015. Mechanism of the wing colouration in the dragonfly *Zenithoptera lanei* (Odonata: Libellulidae) and its role in intraspecific communication. *J. Insect Phys.* 81:129–36
40. Gundersen H, Leinaas HP, Thaulow C. 2014. Surface structure and wetting characteristics of Collembola cuticles. *PLOS ONE* 9:e86783
41. Guo Z, Liu W, Su B-L. 2011. Superhydrophobic surfaces: from natural to biomimetic to functional. *J. Colloid Interface Sci.* 353:335–55
42. Hayes MJ, Levine TP, Wilson RH. 2016. Identification of nanopillars on the cuticle of the aquatic larvae of the drone fly (Diptera: Syrphidae). *J. Insect Sci.* 16:36
43. Helbig R, Nickerl J, Neinhuis C, Werner C. 2011. Smart skin patterns protect springtails. *PLOS ONE* 6:e25105
44. Hensel R, Finn A, Helbig R, Braun H-G, Neinhuis C, et al. 2014. Biologically inspired omniphobic surfaces by reverse imprint lithography. *Adv. Mater.* 26:2029–33
45. Hensel R, Helbig R, Aland S, Braun HG, Voigt A, et al. 2013. Wetting resistance at its topographical limit: the benefit of mushroom and serif T structures. *Langmuir* 29:1100–12
46. Hepburn HR. 1985. Structure of the integument. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology: Integument, Respiration and Circulation*, Vol. 3, ed. GA Kerkut, LI Gilbert, pp. 1–58. Oxford, UK: Pergamon Press
47. Hu HM, Watson JA, Cribb, BW, Watson GS. 2011. Fouling of nanostructured insect cuticle: adhesion of natural and artificial contaminants. *Biofouling* 27:1125–37
48. Hu HMS, Watson JA, Cribb BW, Watson GS. 2011. Multi-functional insect cuticles: informative designs for man-made surfaces. *World Acad. Sci. Eng. Technol.* 59:1370–74
49. Hu HM, Watson GS, Cribb BW, Watson JA. 2011. Non-wetting wings and legs of the cranefly aided by fine structures of the cuticle. *J. Exp. Biol.* 214:915–20
50. Ingram AL, Parker AR. 2008. A review of the diversity and evolution of photonic structures in butterflies, incorporating the work of John Huxley (The Natural History Museum, London from 1961 to 1990). *Phil. Trans. R. Soc. B* 363:2465–80
51. Ivanova EP, Hasan J, Webb HK, Truong VK, Watson GS, et al. 2012. Natural bactericidal surfaces: mechanical rupture of *Pseudomonas aeruginosa* cells by cicada wings. *Small* 8:2489–94

52. Jopp J, Grüll H, Yerushalmi-Rozen R. 2004. Wetting behavior of water droplets on hydrophobic microtextures of comparable size. *Langmuir* 20:10015–19
53. Kim J-J, Lee Y, Kim HG, Choi K-J, Kweon H-S, et al. 2012. Biologically inspired LED lens from cuticular nanostructures of firefly lantern. *PNAS* 109:18674–78
54. Koch K, Schulte AJ, Fischer A, Gorb SN, Barthlott W. 2008. A fast, precise and low-cost replication technique for nano- and high-aspect-ratio structures of biological and artificial surfaces. *Bioinspiration Biomim.* 3:046002
55. Kuitunena K, Gorb SN. 2011. Effects of cuticle structure and crystalline wax coverage on the coloration in young and old males of *Calopteryx splendens* and *Calopteryx virgo*. *Zoology* 114:129–39
56. Land MF. 1972. The physics and biology of animal reflectors. *Prog. Biophys. Mol. Bio.* 24:75–106
57. Langer MG, Ruppersberg JP, Gorb S. 2004. Adhesion forces measured at the level of a terminal plate of the fly's seta. *Proc. R. Soc. B* 271:2209–15
58. Lehnert MS, Monaenkova D, Andrukh T, Beard CE, Adler PH, Kornev KG. 2013. Hydrophobic–hydrophilic dichotomy of the butterfly proboscis. *J. R. Soc. Interface* 10:20130336
59. Li Y, Zhang J, Yang B. 2010. Antireflective surfaces based on biomimetic nanopillared arrays. *Nano Today* 5:117–27
60. Liu C, Ju J, Zheng Y, Jiang L. 2014. Asymmetric ratchet effect for directional transport of fog drops on static and dynamic butterfly wings. *ASC Nano* 8:1321–29
61. Ma KY, Chirarattananon P, Fuller SB, Wood RJ. 2013. Controlled flight of a biologically inspired, insect-scale robot. *Science* 340:603–7
62. Makarona E, Peter B, Szekacs I, Tsamis C, Horvath R. 2016. ZnO nanostructure templates as a cost-efficient mass-producible route for the development of cellular networks. *Materials* 9:256
63. Malshe A, Rajurkar K, Samant A, Hansen HN, Bapat S, Jiang W. 2013. Bio-inspired functional surfaces for advanced applications. *CIRP Ann. Manuf. Technol.* 62:607–28
64. Mouchet SR, Tabarrant T, Lucas S, Su BL, Vukusic P, Deparis O. 2016. Vapor sensing with a natural photonic cell. *Opt. Express* 24:2267–80
65. Nalepa CA, Miller LR, Lenz M. 2001. Flight characteristics of *Mastotermes darwiniensis* (Isoptera, Mastotermitidae). *Insectes Soc.* 48:144–48
66. Naleway SE, Porter MM, McKittrick J, Meyers MA. 2015. Structural design elements in biological materials: application to bioinspiration. *Adv. Mater.* 27:5455–76
67. Nickerl J, Helbig R, Schulz HJ, Werner C, Neinhuis C. 2013. Diversity and potential correlations to the function of Collembola cuticle structures. *Zoomorphology* 132:183–95
68. Nickerl J, Tsurkan T, Hensel R, Neinhuis C, Werner C. 2014. The multi-layered protective cuticle of Collembola: a chemical analysis. *J. R. Soc. Interface* 11:20140619
69. Niu S, Li B, Mu Z, Yang M, Zhang J, Han Z, Ren L. 2015. Excellent structure-based multifunction of *Morpho* butterfly wings: a review. *J. Bion. Eng.* 12:170–89
70. Nixon MR, Orr AG, Vukusic P. 2013. Subtle design changes control the difference in colour reflection from the dorsal and ventral wing-membrane surfaces of the damselfly *Matronoides cyaneipennis*. *Opt. Express* 21:1479–88
71. O'Rorke RD, Steele TWJ, Taylor HK. 2016. Bioinspired fibrillar adhesives: a review of analytical models and experimental evidence for adhesion enhancement by surface patterns. *J. Adhes. Sci. Technol.* 30:362–91
72. Pang C, Kwak MK, Lee C, Jeong HE, Bae W-G, Suh KY. 2012. Nano meets beetles from wing to tiptoe: versatile tools for smart and reversible adhesions. *Nano Today* 7:496–513
73. Parker AR, Hegedus Z, Watts RA. 1998. Solar–absorber antireflector on the eye of an Eocene fly (45 Ma). *Proc. R. Soc. B* 256:811–15
74. Parker AR, Lawrence CR. 2001. Water capture by a desert beetle. *Nature* 414:33–34
75. Pearce MJ. 1997. *Termites Biology and Pest Management*. Oxfordshire, UK: CAB Int.
76. Peisker H, Gorb SN. 2010. Always on the bright side of life: anti-adhesive properties of insect ommatidia grating. *J. Exp. Biol.* 213:3457–62
77. Perkins LE, Zalucki MP, Perkins NR, Cawdell-Smith AJ, Todhunter KH, et al. 2016. The urticating setae *of Ochrogaster lunifer*, an Australian processionary caterpillar of veterinary importance. *Med. Vet. Entomol.* 30:241–45

78. Persson BNJ, Gorb S. 2003. The effect of surface roughness on the adhesion of elastic plates with application to biological systems. *J. Chem. Phys.* 119:11437–44
79. Plotkin M, Hod I, Zaban A, Boden SA, Bagnall DM, et al. 2010. Solar energy harvesting in the epicuticle of the oriental hornet (*Vespa orientalis*). *Naturwissenschaften* 97:1067–76
80. Potyrailo RA, Starkey TA, Vukusic P, Ghiradella H, Vasudev M, et al. 2013. Discovery of the surface polarity gradient on iridescent *Morpho* butterfly scales reveals a mechanism of their selective vapour response. *PNAS* 110:15567–72
81. Pris AD, Utturkar Y, Surman C, Morris WG, Vert A, et al. 2012. Towards high-speed imaging of infrared photons with bio-inspired nanoarchitectures. *Nat. Photonics* 6:195–200
82. Prum RO, Cole JA, Torres RH. 2004. Blue integumentary structural colours in dragonflies (Odonata) are not produced by incoherent Tyndall scattering. *J. Exp. Biol.* 207:3999–4009
83. Rakitov RA. 2004. Powdering of egg nests with brochosomes and related sexual dimorphism in leafhoppers (Hemiptera: Cicadellidae). *Zool. J. Linn. Soc.* 40:353–81
84. Rakitov RA, Gorb SN. 2013. Brochosomal coats turn leafhopper (Insecta, Hemiptera, Cicadellidae) integument to superhydrophobic state. *Proc. R. Soc. B* 280:20122391
85. Rassart M, Colomer J-F, Tabarrant T. Vigneron JP. 2008. Diffractive hygrochromic effect in the cuticle of the hercules beetle *Dynastes hercules*. *New J. Phys.* 10:033014
86. Reynolds PM, Pedersen RH, Stormonth-Darling J, Dalby MJ, Riehle MO, Gadegaard N. 2013. Label-free segmentation of co-cultured cells on a nanotopographical gradient. *Nano Lett.* 13:570–76
87. Rivers VZ. 1999. *The Shining Cloth: Dress and Adornment That Glitters*. London and New York: Thames and Hudson
88. Saranathan V, Seago AE, Sandy A, Narayanan S, Mochrie SGJ, et al. 2015. Structural diversity of arthropod biophotonic nanostructures spans amphiphilic phase-space. *Nano Lett.* 15:3735–42
89. Scherge M, Gorb SN. 2001. *Biological Micro- and Nanotribology: Nature's Solution*. Heidelberg, Ger.: Springer-Verlag
90. Siddique RH, Gomard G, Holscher H. 2015. The role of random nanostructures for the omnidirectional anti-reflection properties of the glasswing butterfly. *Nat. Commun.* 6:6909
91. Stavenga DG, Foletti S, Palasantzas G, Arikawa K. 2006. Light on the moth-eye corneal nipple array of butterflies. *Proc. R. Soc. Lond. B* 273:661–67
92. Stavenga DG, Stowe S, Siebke K, Zeil J, Arikawa K. 2004. Butterfly wing colours: Scale beads make white pierid wings brighter. *Proc. R. Soc. Lond. B* 271:1577–84
93. Sun J, Bhushan B. 2012. Structure and mechanical properties of beetle wings: a review. *RCE Adv.* 2:12606–23
94. Sun M, Liang A, Watson GS, Watson JA, Zheng Y, et al. 2012. Influence of cuticle nanostructuring on the wetting behaviour/states on cicada wings. *PLOS ONE* 7:e35056
95. Sun M, Liang A, Zheng Y, Watson GS, Watson JA. 2011. A study of the anti-reflection efficiency of natural nano-arrays of varying sizes. *Bioinspir. Biomim.* 6:026003
96. Sutton GP, Clarke D, Morley EL, Robert D. 2016. Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *PNAS* 113:7261–65
97. Vincent JFV. 2002. Arthropod cuticle: a natural composite shell system. *Composites Part A* 33:1311–15
98. Vincent JFV, Wegst UGK. 2004. Design and mechanical properties of insect cuticle. *Arthropod Struct. Dev.* 33:187–99
99. Vukusic P, Sambles JR. 2003. Photonic structures in biology. *Nature* 424:852–55
100. Vukusic P, Sambles JR, Lawrence CR. 2004. Structurally assisted blackness in butterfly scales. *Proc. R. Soc. B* 271:S237–39
101. Wagner P, Neinhuis C, Barthlott W. 1996. Wettability and contaminability of insect wings as a function of their surface sculptures. *Acta Zool.* 77:213–25
102. Watson GS, Cribb BW, Hu HM, Watson JA, 2011. Contrasting micro/nano architecture on termite wings: two divergent strategies for optimising success of colonisation flights. *PLOS ONE* 6:e24368
103. Watson GS, Cribb BW, Watson JA. 2010. Experimental determination of the efficiency of nano-structuring on non-wetting legs of the water strider, *Acta Biomater.* 6:4060–64
104. Watson GS, Cribb BW, Watson JA. 2010. How micro/nanoarchitecture facilitates anti-wetting: an elegant hierarchical design on the termite wing. *ACS Nano* 4:129–36

105. Watson GS, Cribb BW, Watson JA. 2010. The role of micro/nano channel structuring in repelling water on cuticle arrays of the lacewing. *J. Struct. Biol.* 171:44–51
106. Watson GS, Green DW, Sun M, Liang A, Xin L, et al. 2015. The insect (cicada) wing membrane micro/nano structure—nature's templates for control of optics, wetting, adhesion, contamination, bacteria and eukaryotic cells. *J. Nanosci. Adv. Tech.* 1:6–16
107. Watson GS, Myhra S, Cribb BW, Watson JA. 2008. Putative functions and functional efficiency of ordered cuticular nanoarrays on insect wings. *Biophys. J.* 94:3352–60
108. Watson GS, Watson JA, Hu S, Brown CL, Cribb BW, Myhra S. 2010. Micro and nanostructures found on insect wings—designs for minimising adhesion and friction. *Int. J. Nanomanuf.* 5:112–28
109. Watson JA, Cribb BW, Hu H-M, Watson GS. 2011. A dual layer hair array of the brown lacewing: repelling water at different length scales. *Biophys. J.* 100:1149–55
110. Watt AJA, Watson JA, Watson GS. 2014. Microwell depth control on a polydimethylsiloxane polymer using a simple colloidal self assembly process. *Sci. Adv. Mat.* 6:1–5
111. Wisdom KM, Watson JA, Qu X, Liu F, Watson GS, Chen C-H. 2013. Self-cleaning of superhydrophobic surfaces by self-propelled jumping condensate. *PNAS* 110:7992–97
112. Wu L, Zhang W, Zhang D. 2015. Engineering gyroid-structured functional materials via templates discovered in nature and in the lab. *Small* 11:5004–22
113. Xu J, Guo Z. 2013. Biomimetic photonic materials with tunable structural colors. *J. Colloid Interface Sci.* 406:1–17
114. Xue F, Liu J, Guo L, Zhang L, Li Q. 2015. Theoretical study on the bactericidal nature of nanopatterned surfaces. *J. Theor. Biol.* 385:1–7
115. Yang S-P, Wen H-S, Lee T-M, Lui T-S. 2016. Cell response on the biomimetic scaffold of silicon nano- and micro-topography. *J. Mater. Chem. B* 4:1891–97
116. Yoshida A, Motoyama M, Kosaku A, Miyamoto K. 1996. Nanoprotuberance array in the transparent wing of a hawkmoth, *Cephonodes hylas*. *Zool. Sci.* 13:525–26
117. Yoshida A, Motoyama M, Kosaku A, Miyamoto K. 1997. Antireflective nanoprotuberance array in the transparent wing of a hawkmoth, *Cephonodes hylas*. *Zool. Sci.* 14:737–41
118. Zhang D, Zhang W, Gu J, Fan T, Liu Q, et al. 2015. Inspiration from butterfly and moth wing scales: characterization, modelling, and fabrication. *Prog. Mater. Sci.* 68:67–96
119. Zhang J, Zou Q, Tian H. 2013. Photochromic materials: more than meets the eye. *Adv. Mater.* 25:378–99
120. Zhang Y, Wang J, Huang Y, Song Y, Jiang L. 2011. Fabrication of functional colloidal photonic crystals based on well-designed latex particles. *J. Mater. Chem.* 21:14113
121. Zheng L, Wu X, Lou Z, Wu D. 2004. Superhydrophobicity from microstructured surface. *Chin. Sci. Bull.* 49:1779–87
122. Zhu H, Guo Z, Liu W. 2016. Biomimetic water-collecting materials inspired by nature. *Chem. Commun.* 52:3863–79