

Mimicking Insect Wings: The Roadmap to Bio-inspiration

Jafar Hasan¹, Anindo Roy², Kaushik Chatterjee², Prasad KDV Yarlagadda¹

¹Science and Engineering Faculty, Queensland University of Technology, 2 George Street, Brisbane, QLD 4001, Australia

²Department of Materials Engineering, Indian Institute of Science, C.V. Raman Avenue, Bangalore 560012, India

Authors to whom all correspondence should be addressed:

kchatterjee@iisc.ac.in

y.prasad@qut.edu.au

Abstract

Insect wings possess unique, multifaceted properties that have drawn increasing attention in recent times. They serve as an inspiration for engineering materials with exquisite properties. The structure–function relationships of insect wings are yet to be documented in detail. In this review, we present a detailed understanding of the multifunctional properties of insect wings including micro- and nano-scale architecture, material properties, aerodynamics, sensory perception, wettability, optics and antibacterial activity, as investigated by biologists, physicists and engineers. Several established modeling strategies and fabrication methods have been reviewed to engender novel ideas for biomimetics in diverse areas.

Keywords: Biomimetics, insects, nanoscale architecture nanofabrication, surface science

Introduction

Engineers and scientists have been studying and developing devices by borrowing ideas from nature especially insects, owing to their diversity and abundance. Insects have evolved over millions of years to overcome complex challenges, resulting in some unique properties that have helped them survive. The origin of wings has been regarded as a key evolutionary change among insects, bats, birds and the extinct pterosaurs and contribute towards the diversity of insects¹. Insect wings are corrugated, membranous outgrowths from the exoskeletons and primarily help insects in flight². Largely, insects possess two pairs of wings, namely, the forewings and hindwings. The wings are of different types such as membranous, stiff, hard, scaled and fringed with hairs. The appearance, color and texture vary among different insects and within species. In addition to flight capability, these wings impart several other abilities to insects such as protection, thermal sensing, sound generation, mating, visual recognition, hydrophobicity and antibacterial activity. The aerodynamics and recently-discovered bactericidal behavior of insect wings are some of the key properties that have been investigated extensively.

Insects have fascinated philosophers since ages, as ancient Egyptians are known to have worshipped the dung beetle between 1500 and 2500 B.C. Few of the earliest documented works on insect wings appear to be initiated in the early nineteenth century³⁻⁴. The early investigations on insect wings were only performed by entomologists and curators. But now, many engineers and scientists have been attracted to the wonders of insect wings, especially the unique architecture at the micro- and nano-scales.

We analyzed the more than 2700 scientific publications (excluding book chapters and patents) on insect wings with applications in different areas over the last seven years using the search engine tool Web of Science (Figure 1). The publications were categorized into ten research areas, focusing on different categories of insect wing inspiration. The first area with highest number of publications was flight movements and wing aerodynamics; the second area was bioinspiration and biomimetics; the third area focused on material properties, examining the stiffness and bending of insect wings and the fourth area was

antibacterial or bactericidal properties. Other areas such as wettability, sensing ability and reflectivity have attracted increased interest probably due to the recent progress in characterization techniques.

However, the number of publications does not represent the scientific impact of the specific areas. The Web of Science tool provides the h-index and average citation of all the searched publications. We performed a citation report analysis of the number of publications in the last seven years on insect wings and subject areas (Supporting Information Figure S1), chronicled by their year of discovery. Although subject areas such as roughness, wettability and superhydrophobicity had fewer publications, they had higher average citations. Notably, in the last seven years, 19 papers covering topics of bacteria and insect wings have been cited at least 19 times (Supporting Information Figure S1).

The underlying theme of this paper is bioinspiration from insect wings. Most studies have endeavored to understand wing behavior and characteristics whereas few have focused on actual mimicking vis-à-vis modeling and fabrication. From an engineering perspective, mimicking of the wing or rather its unique properties is as important as understanding the origin of the wing, evolutionary behavior, structure or functions. In this paper, an extensive review on the origin, evolution, structure, composition, classification and multifunctional properties of insect wings is presented. The different multifunctional properties are grouped under bioinspiration sections including micro- and nano-scale topography, material properties, aerodynamics, sensory perception, optics, wettability and antibacterial activity. Followed by bioinspiration, biomimicry is discussed with sections on modeling, simulation and fabrication. In the final section, future perspectives and concluding remarks are postulated. There has been no single commentary, analysis or review of the cumulative work done on the unique and attractive properties of insect wings: this review is an attempt to address that need.

Origin and evolution of wings

The origin of insect wings has been debated since centuries as contrasting theories have been put forth based on the study of fossils. The problem lies in the absence of fossils detailing the transition between

non-winged and winged insects⁵. Majorly, two theories have been proposed by biologists: one is the tergal or paranotal hypothesis and the other is the pleural or gill hypothesis. In the paranotal hypothesis, which was more accepted during the twentieth century⁶, the wings extended from the dorsal body wall or the paranotal lobes to help the insects initially in gliding followed by flying in order to avoid falling from a height⁷⁻⁸. In the gill hypothesis, the wings extended from the leg segments and the branches or exites, which helped the wings to show musculature and articulation⁹⁻¹⁰. The debate on the two hypotheses is essentially based on the possibility of the insect wings to either develop from the pre-existing structures or to develop new structures. Gegenbaur and Muller separately proposed in the 1870s⁶ that insect wings originated from tracheal gills and tergal lobes respectively^{6, 11-12}. Many scientists supported the gill theory or its variation known as the pleural appendage theory in the latter half of the twentieth century⁶. However, in the absence of transition fossils, neither of the theories can be rejected. In 1997, the gill hypothesis again gained wide acceptance due to the innovative work on development genetics by Averof and Cohen¹³. A dual or combined hypothesis proposing the hybrid development of wings from composite structures was put forth in 2010¹⁴, which has been confirmed by several studies and its acceptance is on the rise¹⁵. The contributions of the different tissues or body parts to the origin of insect wings vary with the theory and their specific contribution to the origination remains an active subject of investigation^{5, 16-17}.

Classification, structure and composition

According to the International Commission on Zoological Nomenclature (ICZN), living organisms have a specific taxon classification- kingdom, phylum, subphylum, superclass, epiclass, class, subclass, superorder, order, suborder, superfamily, family, subfamily, tribe, genus, and species ¹⁸. Insects belong to the animal kingdom, arthropoda phylum and insecta class. The identification of insects is a complex and daunting task because of their diversity. The number of described species of insects is close to 1.5 million whereas the mean total estimate is around 5.5 million¹⁹. Generally, insects can be classified into two major subclasses, namely, apterygota (non-winged) and pterygota (winged). Most species come under the subclass

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3 pterygota, which is further divided into palaeoptera (primitive wing) and neoptera (new wing). The
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5 primitive insects that belong to palaeoptera such as dragonflies, damselflies and mayflies have non-folding
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7 wings whereas the neoptera insects can fold back their wings. Insects under neoptera are further subdivided
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9 into exopterygota and endopterygota. The species of exopterygota undergo moderate changes during
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11 development whereas the species of endopterygota undergo complete changes during development or
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13 undergo complete metamorphosis that is found in insects such as beetles, butterflies, ants and moths²⁰.
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17 The identification of insect wings can be done utilizing different wing characteristics in which
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19 reasonable number of factors (or keys) can be taken into account²¹. With the help of DNA barcoding,
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21 available taxonomies and computer software such as Lucid Central, the identification of the insect may be
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23 accurately performed in future. The venation of wings has been used to identify species. The recognition
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25 of features of the venation of insect wings was first generalized by Comstock and Needham in 1898²². This
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27 was further developed such that the common nomenclature of veins and branches exist in numerous wings
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29 among millions of insects ²³⁻²⁴. There are 6 to 8 major longitudinal veins including costal (C), subcostal
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31 (Sc), radial (R), medial (M), cubital (Cu), anal (A) and jugal (J) veins²⁵. Furthermore, the wings have several
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33 fields, joints, cross-veins, flexion and joint lines, branches and sub-branches. The major veins separate into
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35 anterior (convex) and posterior (concave) sectors; the anterior sectors are present on the upper layer whereas
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37 the posterior sectors are present on the lower layer of the wings. The cross-veins, small veins that connect
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39 the longitudinal veins, are more variable than the longitudinal veins and provide information for species
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41 characterization. The topic of venation among insects has been extensively compiled elsewhere ²⁶.
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45 Insect wings have two membranes supported by a rigid network of veins. The wings are made up of
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47 cuticle, which has different functions but majorly acts as an exoskeleton providing shape and support to
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49 structures such as wings²⁷⁻²⁸. The cuticle in various layers of the wings varies in thickness and is composed
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51 of various substances such as chitin and long chain hydrocarbons among orders and species of insects. The
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53 outermost layer of the cuticle is epicuticle; it is very thin and is further divided into outer, meso- and inner
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55 epicuticle²⁹. The composition of the outermost epicuticle layer in several species of dragonflies has recently
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3 been characterized³⁰⁻³¹. In dragonfly wings, the outer layer is made up of long chain aliphatic hydrocarbons
4 and fatty acids such as palmitic acid and stearic acid. The next layer, procuticle, is composed of chitin
5 microfibers and proteins and is further divided into a hard exocuticle and a soft endocuticle. The hardness
6 of the exocuticle layer is attributed to the cross-linking of quinone compounds with individual protein
7 molecules^{27, 32} through a chemical process called sclerotization. In the endocuticle, an elastic protein called
8 resilin is also present that makes the layer softer³³⁻³⁴. The presence of resilin in many insect wings such as
9 beetles, dragonflies and damselflies provides an elastic property, which imparts higher stiffness and lower
10 deformability to the wings against aerodynamic loads³⁵⁻³⁷. Moreover, resilin assists in the folding of wings
11 in order to circumvent any damage during flight³⁵. The folding direction is determined by the distribution
12 of resilin in the radiating and intercalary veins³⁸. In the different wing layers, the cuticle possesses different
13 compositions, orders and thicknesses that vary according to the insect species.
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27 The wings have different phenotypic characteristics such as size, shape, color and veins (Figure 2). The
28 wing growth is dependent on a point in time when the insect body stops growing³⁹. The wing size and shape
29 of the insect may vary due to migration and mate guarding⁴⁰. Some insects may have scales such as those
30 found on the wings of butterflies and moths. The wing coloration arises due to pigmented patterns, melanin
31 production, eyespot concentric rings or structural colors⁴¹⁻⁴².
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40 **Bioinspiration**

41 **Micro- and nano-architecture**

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43 To the best our knowledge, ‘small spots’ – as described by Stainton in 1859 – is one of the earliest reports
44 where microstructures on the wings were observed⁴³. However, there have been earlier endeavors on insect
45 wings where the necessity for a higher microscopic power for examination was mentioned⁴⁴. The small
46 scale features, initially described as micro-sculptures on the wings⁴⁵⁻⁴⁸, are now termed as micro- or nano-
47 patterns, features, structures or spikes/ pillars. The micro and nano-scale architecture, which is typically
48 observed with scanning electron microscopy or atomic force microscopy describes the surface morphology
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of the insect wing membrane (Figure 3, Supporting Information Table S1). Some of the recently-studied nano-scale features of the cicada and dragonfly wings have been characterized as nanopillars (Figures 3A–C). The nanopillars are erect, rod-shaped pillars consistently present on both the dorsal and ventral sides of the wing surface including the veins; their dimensions vary among species and orders of insects. In cicada wings, the nanopillars are hexagonally-packed and the topography arrangement varies among species. The height of each nanopillar varies from 150 nm to 450 nm, the diameter varies from 80 nm to 210 nm and the center-to-center spacing (pitch) varies from 45 nm to 250 nm across the cicada species tested till now⁴⁹⁻⁵⁰. In dragonfly wings, randomly-oriented nanopillars are found, some of which are connected to each other at the top. There have been variations reported within different regions of dragonfly wings (*Sympetrum vulgatum*), where the diameter varies between ~80 nm to 200 nm⁵¹. On statistically testing the variance among different species of dragonflies: 77 % proportion of variation in nanopillar density, 34 % proportion of variation in nanopillar height and 25 % proportion of variation in nanopillar diameter have been reported⁵². Therefore, it is understood that the surface architecture varies largely among species and orders of insects.

It has been postulated that the variation in nanoarchitecture is probably due to differences in taxon, geography, habitat, migratory and foraging characteristics⁵². Recently, the group of Gregory Watson and Jolanta Watson have done work on the characterization of micro- and nano- architecture and the related multifunctional behavior of insect wings^{50, 53-59}. The group has categorized the micro- and nano- architectures of insect cuticles into seven groups, which include simple microstructures, simple nanostructures, complex geometric microstructures, complex geometric nanostructures, scales, hairs/ setae and hierarchical structuring⁵⁷. The presence of architecture at different length scales obviously assists insect wings with various properties and functions, as reviewed in the following sections.

Material Properties

To counter the threats and stresses encountered by flying insects, wings have evolved biomechanical strategies. During the lifetime of the insect, wings undergo high mechanical stresses and millions of cycles

of loading but still maintain excellent resistance to fatigue and fracture^{28, 60-61}. It has been shown that veins reduce crack propagation⁶⁰. Moreover, the fracture toughness of wings is enhanced by 50 % due to the presence of cross-veins⁶¹. Similar to the role of grain boundaries in metals that act as barriers for crack propagation, wings use veins to stop crack propagation; this eventually provides them with enhanced biomechanical properties and scope for inspiration. The wear and tear of wings due to collisions, age and forage have been known to affect performance and functions such as maneuverability, hunting and predator evasion⁶². Recently, the wings of the wasp and bumblebee were experimentally subjected to wear and their response to collision damage was tested⁶³. It was found that both insects exhibit similar behaviors but have different wing venations. The ‘costal break’, which is a flexible resilin joint found on the leading edge of wings of many insects such as wasps, is primarily responsible for mitigating collision damage. However, the costal break is absent in less-rigid bumblebee wings that have a different configuration of veins and may not require buckling during collisions.

Aerodynamics

Insects were the first organisms that developed flight. Many of the maneuvers of flying insects demonstrate their superior flight performances⁶⁴. Due to the small size and high frequency of the wings, insect flight is still not completely understood. The configuration of muscles and wings give rise to direct and indirect flight mechanisms. In direct flights, the muscles of the wings are hinged to the base directly; this is found in primitive four-winged insects such as dragonflies and mayflies. Two groups of muscles, the depressors and the elevators, are known to help these insects during downstrokes and upstrokes in direct flights⁶⁵. In all other insects, the wing movement is determined by deformation of the thorax, which defines the indirect flight mechanism⁶⁵. Here, the vertical and longitudinal muscles govern the movements. When the vertical muscle is contracted, the thorax oscillates giving rise to an upstroke⁶⁶. Similarly, the longitudinal muscle is contracted to shorten the thorax in a downstroke movement⁶⁶. The upward and downward wing movements are facilitated by the indirect vertical and longitudinal muscles.

In addition to normal flying patterns, some insects have the ability to hover, fly backwards and sideways, take-off backwards and land inverted⁶⁷⁻⁶⁸. There are two translational phases, upstroke and downstroke, and two rotational phases, pronation and supination, of wing motion⁶⁹. The highly improbable vertical lift produced by the light-weight insects has been a topic of extensive research⁶⁹⁻⁷¹. There are various mechanisms responsible for the enhanced aerodynamics of insects (Figure 4), of which some are reported⁶⁹ to be distinct yet interactive: (i) Delayed stall: Before the lift, the insect wing flaps at a large angle of attack forming a vortex on the leading edge of the wing. But if the vortex leaves the leading edge, then the lift would be lost and the wing would be stalled (stop ‘lifting’). However, the stall is delayed in an entire downstroke or upstroke and the leading edge vortex (LEV) is maintained on the wings⁷⁰⁻⁷⁴; (ii) Rotational circulation: The mechanism is based on the rotation of wings, which facilitates circulation to generate an upward force and (iii) Wake capture or wing–wake interaction: Immediately following stroke reversal, the wing sheds leading and trailing edge vortices, which helps in generating force (Figure 4). The flow generated by one stroke can enhance the velocity at the start of the next stroke thereby increasing the produced force that cannot be explained by the translational force alone⁶⁹. In the wake capture hypothesis, it is predicted that the wing must continue to generate force even after coming to a complete stop at the end of a half stroke; this was tested by Dickinson et al.⁶⁹. There are numerous other mechanisms, principles and modeling methods that aid in better understanding of the aerodynamic behavior of insect wings such as the clap-and-fling⁷⁵⁻⁷⁶, added mass⁷⁷⁻⁷⁹ and evasion of the Wagner effect⁸⁰⁻⁸¹. Several mechanisms that assist in high frequency flapping have also been postulated including rotational drag and trailing edge vortex⁸²⁻⁸³.

The structure of insect wings has also been studied in relation to aerodynamic functions. For example, the nodus (a specialized wing part) contains resilin, which helps the wing to deform without breaking during flight in dragonflies⁸⁴. However, to save itself from excessive deformation, the nodus can also restrain its displacement in the form of a one-way locking mechanism. The nodus is important in the design of bioinspired flying devices⁸⁵. In the locust, automatic cambering in the hind wings during lift gives it the umbrella effect operating in the vannus⁸⁶. Similar to the spokes and curves during opening an umbrella, the

vannus margin becomes stiff when it is pulled inwards during the stretching of the wing to a certain point⁸⁷. The recent efforts to understand the aerodynamics of the insect wings have been such that the expedition has also moved towards enhancement of flying efficiencies⁸⁸. With the advent of advanced electronics and/or robotics, insect wings are now inspiring the design of flying robots or drones⁸⁹⁻⁹³.

Sensory perception

Insects contain a variety of sensors on the antennae and other body parts. However, there are only two known sensors associated with insect wings till now, namely, gyroscopic and thermoregulatory perceptions. The mechanosensory structures or mechanoreceptors that are present on the halteres as well as the wing cuticle assist the insects in flight maneuvers⁹⁴⁻⁹⁷. The halteres function as vibrating gyroscopic sensors under the Coriolis effect. The receptors or structures, known as campaniform sensilla, are observed to assist as sensors providing feedback regarding body rotations⁹⁸⁻¹⁰⁰. It has been hypothesized that insect wings also assist in thermoregulation, although this serves a secondary function as the temperature control is primarily performed by the main body¹⁰¹⁻¹⁰³. Similarly, the wings assist in other functions such as mating, defense, territorial attack and camouflage¹⁰¹. Inspired by the wings of the glasswing butterfly, a recent study demonstrated that nanostructured surfaces have the potential to be used as intraocular pressure (IOP) sensors in medical devices with multifunctional properties¹⁰⁴. Apart from wings, insects use other multisensory organs such as antennae for sensory perception (smell, sound and humidity)¹⁰⁵⁻¹⁰⁶. During flight, the antennae also provide orientation, maneuverability, stability and speed control¹⁰⁷⁻¹⁰⁸.

Wettability

The wettability of solid surfaces by liquids is a fundamental property of materials that plays a crucial role in a wide range of applications such as optics¹⁰⁹, biomedical implants¹¹⁰, food packaging¹¹¹ and industrial processes including oil recovery¹¹². In nature, many biological materials – including the surfaces of insect wings – are known to exhibit unusual surface wettability. The wettability of numerous insect wings has been estimated by measuring the contact angle of droplets on the wing surfaces (Table 1). It was concluded that the non-wetting or ultra-hydrophobic property is related to the presence of evolutionarily-developed

fine structures on the wing surfaces. If the static water contact angle is greater than 150° and the contact angle hysteresis is less than 10° , the surfaces are called superhydrophobic, self-cleaning surfaces. On the wings of some insects, a water droplet rolls away by collecting surface dust particles thereby making the wing surfaces self-cleaning: a property also found in lotus leaves and termed as the ‘lotus effect’. Barthlott and colleagues examined the wing microstructures on ninety seven insect species and correlated a relationship between surface structures, wettability and effects on contamination¹¹³. They also developed a correlation between wettability and SM index (the quotient of wing surface area to body mass); it was found that insects with high SM index or large wings have more non-wettable surfaces than those with low SM index or small wings.

Various wettability models, such as the Cassie–Baxter and Wenzel models^{114–115}, have been proposed to rationalize the superhydrophobic behavior of a substrate due to topography. In superhydrophobic insect wings, there is a transition from the Wenzel to the Cassie–Baxter state due to the presence of dual-scale roughness or architecture¹¹⁶. Insect wings such as those of cicadas^{50, 59, 117}, damselflies¹¹⁸, butterflies¹¹⁹, termites^{53, 120}, beetles¹²¹, crane-flies¹²² and lacewings¹²³ demonstrate superhydrophobic behavior. The superhydrophobic feature is due to micro- and nano-scale structures that also make the wings capable of maintaining a contaminant-free surface despite the presence of abundant contaminants in their surrounding environments. Due to the arrangement of micro- and nano-structures, the wings of butterflies possess directional wetting or anisotropic wetting, which can serve as an inspiration for the transportation of liquids in microfluidic channels or devices^{124–125}. Insect wings have been used as model substrates to design several functional surfaces with special wettability^{126–129} for practical applications such as self-cleaning windows, windshields, exterior paints for buildings and navigation ships, utensils, roof tiles, textiles and reduction of drag in fluid flow.

Optics

Through evolution, insects have developed unique light manipulation strategies that rely on intriguing combinations of a broad range of optical effects including broad-angle structural color¹³⁰, color-mixing¹³¹,

polarization¹³², antireflection¹³³, iridescence¹³⁴, ultra-blackness¹³⁵ and ultra-whiteness¹³⁶ generated by materials with sophisticated multiscale hierarchical structural arrangements. Such optical effects serve important roles in camouflage, conspecific and heterospecific signaling and so forth. Apart from coloration due to pigmentation, these features on the wing surface are responsible for coherent and incoherent light scattering. The former owes its origin to the periodic regularities of microstructure in the surface layer, which are of the order of the wavelength of light. In a unique phenomenon called iridescence, observed on the wings of many butterflies and moths, there is dependence of the perceived color on the angle of observation. The structures can be thin films¹³⁷, multilayers incorporated into the scale ridging or scale body¹³⁷⁻¹³⁸ or three-dimensional sculptures called photonic crystals^{55, 138-139}. By using the optical principles underlying these natural systems, possible applications in security labelling and anticounterfeiting¹⁴⁰⁻¹⁴², photovoltaic systems such as solar panels^{133, 135, 143-147}, colorimetric sensing¹⁴⁸⁻¹⁵¹, iridescent textile apparel and aesthetic surfaces¹⁵²⁻¹⁵³, water quality monitoring¹⁵⁴⁻¹⁵⁵ and others^{154, 156-158} have been suggested. In many cases, optical properties arise solely due to pigmentation or because of a synergistic effect of the nanostructures and pigments present. Incoherent scattering results when light encounters random irregularities with separations larger than the coherence length of light; this may cause Rayleigh or Tyndall scattering¹⁵⁹.

The colours of butterfly wings are produced from microscopic scales, consisting of an upper and lower lamina linked together by trabeculae¹⁶⁰. Embedded within these scales are melanin pigments that create black and brown undertones. As light scatters within a scale's crystalline structure, it produces iridescent blues, greens and reds. The most vividly studied butterflies are those belonging to the *Morpho* genus^{139, 149, 160-161}. The lustrous blue characteristic of butterflies is due to the constructive interference of light by 'Christmas tree-like' exquisite photonic nanostructures present on their scales, even though the cuticle protein that constitutes these structures is almost transparent¹⁶². These nanostructures possess alternating lamellae layers of materials having high and low refractive indices producing the blue color; vertical and horizontal offsets exist between neighboring 'trees' that eliminate interference among ridges, resulting in

diffuse and broad reflection of a uniform color¹⁶³. Contrarily, the wings of *Papilio Palinurus*, also possessing multilayers, exhibit color mixing because of the juxtaposition of light reflected from the flat and concave regions of the wing, thus flaunting an angle-dependent change in color appearance¹³¹. Yet another species (*Pierella luna*) shows an intriguing rainbow iridescence effect, in which the sequence of colors is reversed (red to blue). This exquisite phenomenon occurs due to decomposition of white light, by redirecting visible colors into specific emergence angles using a diffraction grating¹⁶⁴. Fascinated by these broad range of optical properties incorporated into a single surface, researchers are trying to reproduce similar structures artificially^{157, 163}.

Many insects with flight-dependent lifestyles have optically-transparent wings of 1 to 2 μm ultrathin membranes of chitin. In order to veil glare and reduce thin film interference¹⁶⁵, some insects have developed two-dimensional (2D) photonic nanostructures on their wing surface. Cicada wings have been characterized by highly ordered nano-nipple array structure, which plays a dynamic role in reducing reflection of light over a broad spectral range of wavelengths^{49, 144}. The nanoscale structures introduce a gradient in the refractive index between air and the material by presenting a ‘material–air composite’, thereby reducing the Fresnel reflection and consequently increasing the amount of incident light transmitted across the wings^{143, 147}. The glasswing butterfly (*Greta oto*) has an array of small nanopillars on its wings, imparting omnidirectional anti-reflection behavior¹⁶⁶. Cicada wings have a highly-ordered nano-nipple array structure, which plays a dynamic role in reducing reflection of light over a broad spectral range of wavelengths^{49, 144}. Sun et al. studied the dependence of optical reflectivity and wettability on the surface topography of thirty two species of cicada wing membranes¹⁴⁴. They concluded that a near-linear dependence existed between a decrease in protuberance height and a resulting increase in reflectance intensity. Nanoscale antireflective architecture has also been found in wing scales of *Papilio Ulysses* and *Troides aeacus* butterflies^{142, 167}. The later was found to have a combination of structures of ridges and grooves responsible for light trapping. Some advanced nanofabrication techniques to imitate the anti-reflective surface (ARS) of cicada wings such as soft imprint lithography, reactive ion etching, sol-gel process, micro-injection compression

molding, chemical etching and replica molding have been developed^{146-147, 168-169}. ARSs have the potential to maximize the performance of solar cells, light sensors, high contrast and stealth surfaces. A detailed review of the mathematical principles and manufacturing strategies of ARSs has been published¹⁴³. Cicada wings have also been suggested for direct use as efficient SERS (surface enhanced Raman spectroscopy) substrates¹⁷⁰. The wings of the dragonfly ¹⁷¹ and hawkmoth ¹⁷² have been studied; however, they are yet to be replicated artificially. The wings of dragonfly *Aeshna cyanea* were found coated both ventrally and dorsally with a nanostructured wax coating that is associated with a wavelength- dependent and complex refractive index of 1.38 to 1.40 and has optical absorbance an order of magnitude smaller than butterflies accounting for the transparency ¹⁷³.

Antibacterial activity

The antimicrobial surfaces have the ability to repel microbial cells, mitigate their attachment or kill them upon surface adhesion¹⁷⁴⁻¹⁷⁶. The presence of nanoscale architecture on insect wings renders them antimicrobial by killing the microbe upon contact (Figure 5)¹⁷⁷⁻¹⁷⁸. Ivanova et al. first reported that the wing surface of the *Psaltoda claripennis* cicada, consisting of robust hexagonal arrays of spherically-capped conical nanopillars, was bactericidal rather than antibiofouling, i.e., they kill bacteria rather than merely preventing attachment or halting biofilm formation^{174, 178}. They proposed a contact killing mechanism wherein the nanopillars present on the wing penetrated bacterial cells, causing them to die with no apparent role of surface chemistry¹⁷⁸. Mathematical calculations showed that adsorption of the bacterial cell membrane on the pattern of the cicada wing surface leads to a drastic increase of the total area accompanied by stretching of the membrane; this, in turn, leads to irreversible membrane rupture and death of bacteria¹⁷⁹. A detailed study was published subsequently by Hasan et al.¹⁷⁷ in which the bactericidal activity of cicada wings was tested against seven bacterial species with variable properties covering every combination of cell morphology (rod-shaped and spherical) and cell wall structure (gram-positive and gram-negative bacteria). It was revealed that the surface efficacy is independent of cell shape but depends on the bacterial strain¹⁷⁷. Thus, gram-positive bacterial strains that have a thicker and more rigid cell membrane (due to the

presence of peptidoglycan in higher amounts) were not killed by these nanopillars. Another study investigated the susceptibility of the bacterial cells on the *Calopteryx Haemorrhoidalis* damselfly wing surfaces and the dependence on whether the bacteria are at their early logarithmic or stationary phases of the physiological growth¹⁸⁰. The microbes were more prone to mechanical rupturing during the early phases of growth compared to mature cells. Some comparative studies conducted amongst three different species of cicada wings⁴⁹ proved that the bactericidal effect was strongly affected by variations in nanopillar dimensions (height, tip diameter and spacing between pillars) from one species to another (Table 1). Interestingly, among the three species of dragonflies that inhabit similar environments, the bactericidal efficacy imparted by the nanotopography of protrusions on their wings varied considerably¹⁸¹. Two main lipid components of the insect wings, palmitic (C16) and stearic (C18) acids, have been crystallized to generate 3D structures, which have been reported to exhibit bactericidal activity¹⁸².

The bactericidal insect wings represent an excellent template for the development of synthetic antibacterial surfaces. The aim has been to design a surface that can inhibit the attachment of microbes and effectively halt biofilm formation; this, in turn, prevents any subsequent infection of the surrounding tissue^{175, 183-185}. The first physical bactericidal activity of a hydrophilic, synthetic surface of black silicon (bSi) was reported recently¹⁸⁶. For this work, high aspect ratio-nanopillars were generated inspired from the wings of the dragonfly *Diplacodes Bipunctata*, which proved to be lethal for gram-positive as well as gram-negative bacteria (Figure 5). The biocompatibility of bSi has been further investigated and demonstrated by *in vivo* implant studies. No inflammatory responses were found from the host in animal trials for both ocular and general tissue environments, suggesting possible biomedical applications¹⁸⁴. Several other reports with the aim to engineer the wing-inspired biomaterials have been published (Figure 5)^{185, 187-190}. However, wing-inspired strategies are not limited to implant surfaces but rather have many other potential applications such as reducing nosocomial infections¹⁹⁰⁻¹⁹¹. Recently, Wang et al. incorporated dragonfly-inspired black silicon into a reusable cell, resulting in a bactericidal microfluidic device¹⁹². The device was shown to effectively rupture *Escherichia coli* cells from contaminated water. With adequate scalability, this

could represent a viable method of cleaning bacteria-infected water sources without the need for cleansing chemicals. Generic or selective protection from microbial colonization could be conferred to surfaces for a wide spectrum of applications such as internal medicine, implants, food preparation and agriculture by patterning the material surfaces or depositing coatings inspired from the cicada and dragonfly wings. Recently, titanium dioxide (TiO₂) nanowires have been generated using a simple hydrothermal treatment that mimic the killing behavior of insect wings^{187, 193}. The discovery of bactericidal properties of insect wings has motivated research in diverse fields ^{54, 194-196}.

The antibacterial behavior of insect wings is closely related to nanoscale topography and hydrophobicity. It has been observed that the bactericidal wings are highly hydrophobic or superhydrophobic and have higher roughness or a unique nanoscale topography, all of which may be interrelated. However, the bactericidal activity is species-specific and varies according to the surface topography; this could be an evolutionary or behavioral change. For example, dragonflies have two dominant behaviors: perchers or hawkers. Perchers remain close to plants where they wait for prey while hawkers are in continuous flight hunting for prey. The percher dragonfly would need a wing that can fight microbes due to its surrounding environment that is more prone to microbial attacks. In contrast, the hawker can survive without such a surface property as it spends more time in flight. In fact, it has recently been observed that the wings of perchers exhibit a surface topography that can kill microbes whereas those of hawkers cannot kill microbes efficiently ¹⁸¹.

Biomimicry

Modeling and simulation

The efforts to model the unique properties of insect wings has been primarily in two areas: (a) aerodynamic modelling, aiming to realize a special class of unmanned aerial vehicles (UAVs) called the flapping wing micro air vehicles (FWMAVs) and (b) to a lesser extent in antibiofouling surfaces, in which the goal is to elucidate the mechanism of biological interaction. The micro aerial vehicles (MAVs), a miniature class of

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3 UAVs, have been the subject of extensive investigation in recent decades with potential uses in hazardous
4 environments and for remote observations or surveillance. However, the aerodynamic principles governing
5 flight at such small scales are remarkably different from those used in an aircraft¹⁹⁷; this has prompted
6 research towards insect and bird flight, where the flapping wing motion seems to be a concurrent solution⁷¹.
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8 Engineers have attempted to build several prototypes of FWMAVs in the past two decades, of which few
9 have achieved successful flight¹⁹⁸. The calculation of aerodynamic forces and the instantaneous modulation
10 of wing kinematics are crucial in such prototypes since this will ensure control over the orientation of thrust
11 and allow maneuverability and stability. Thus, an aerodynamic model that is capable of accommodating all
12 the high-lift unsteady aerodynamic effects exhibited by true insects is indispensable. A dynamic model also
13 allows parameter variations to be tested in simulation before committing to building a new prototype,
14 thereby saving both time and resources.
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Pertaining to the low Reynolds number (10^2 – 10^3) fluid flow in aerodynamic situations, most models utilize the quasi-steady approximation as a foundation to develop the aerodynamic theory of insect flight^{199–200}. First, an averaged model is constructed assuming that fluid dynamic forces do not depend on their time history but only depend on instantaneous wing kinematics such as velocities and accelerations. This quasi-steady simplification allows change of the angle of attack over time and velocity variation along the wing span to be taken into consideration, unlike steady state models; it also simplifies effects such as added mass, absence of stall and rotational circulation into practicable equations^{69, 71, 201–203}. The mechanisms such as wake capture, Wagner effect and clap and fling are excluded from almost all models due to poor understanding, although there have been attempts to include the latter in quasi-steady models²⁰⁴. Some models that incorporate rotational, translational, added mass and viscous forces encountered during flight have been proposed^{203, 205}. Many models treat the insect body and wings as several connected rigid bodies, in which the bodies representing the wings are associated with certain degrees of freedom (DoF). This allows determination of wing velocities and subsequently, the forces and even torques generated by them²⁰⁶. While greater DoF would permit greater accuracy and robustness in a model, it also introduces new

parameters that lead to greater mathematical complexity. Also, although the rigid wing assumption is useful for understanding the essential flapping-wing aerodynamics, the insect wings undergo three-dimensional elastic deformation in terms of chord-wise, span-wise and twist deformation during flapping flight²⁰⁷. The aerodynamics and structural dynamics of insect wings result in a complex fluid–structure interaction (FSI) phenomena and this enhances the aerodynamic power generated, which must be accommodated into models for greater accuracy²⁰⁸⁻²⁰⁹.

The computational fluid dynamics (CFD) method is capable of computing aerodynamic forces and detailed flow structures by directly solving the Navier–Stokes equations by numerical methods²¹⁰. However, this approach sacrifices simplicity and hence, the applicability of quasi-steady models in FWMAVs. Similar to quasi-state models, CFD primarily involves defining simplified model geometries based upon direct measurements of animals. A kinematic model is then prescribed, replicating the observed parameters at different time points during a stroke and the wing models are encapsulated in overset meshes. The computational background is meshed with refined grids near the wings that become larger and sparser further away from the wing surface. The Navier–Stokes equation can then be applied to calculate aerodynamic parameters. The studies can generate either a two-²¹¹ or three-dimensional (3D) model; the latter is more complicated and has gained prominence amongst researchers only recently after it was demonstrated that 2D models may be inadequate for capturing 3D effects such as span-wise flow in larger insects²¹²⁻²¹³.

The FWMAVs often use rotary electric motors as a means of propulsion for actuators and therefore, the rotary motion needs to be efficiently translated to flapping motion. A recent study demonstrated that the Scotch yoke mechanism for actuators mimics the wing tip motions of *M sexta* better than other mechanisms, making it a viable option for application in a robotic moth²¹⁴. Bio-inspired flight simulators for generating and collecting data rather than constructing MAVs or taking direct measurements from captured insects may help to avoid the tough experimental challenge of large amounts of information capture for proper investigation into 3D near and far flow fields^{197, 215}. Such simulators may be used to optimize the physical

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3 geometry and material properties of components by simulating internal forces and energy losses, thereby
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5 reducing the number of hardware iterations.
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8 Each of the proposed models can address various aspects of insect flight with varying degrees of
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10 accuracy because certain features are encompassed in a model more easily (e.g. wing and body
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12 aerodynamics) than others (e.g. neural circuitry and wing hinge mechanics). Insects rely on the provision
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14 of rich sensory feedback from multiple sensors such as compound eyes, ocelli and antennae, which endow
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16 them with inherent flight stability by allowing them to modulate parameters such as beat frequency and
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18 angle of attack instantaneously. Thus, to achieve similar results in FWMAVs, the models need to be
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20 computationally-robust and capable of modulating power output and structural dynamics according to
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22 sensory inputs⁶⁴. Moreover, notable differences exist in the flight dynamics of large and small insects and
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24 in two- and four-winged ones²¹³, ranging from large differences in stroke amplitude or flapping frequency
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26 to altogether dissimilar flight mechanism⁸³. Therefore, formulating a unified model that applies to a broad
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28 range of insects seems to be a non-trivial task at this point.
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32 In the case of modelling bactericidal insect wings, the bacterial membrane undergoes stretching once it
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34 is in contact with the nanoarchitecture. Therefore, there is a stretching free energy penalty and a decrease
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36 in free energy due to contact adhesion of the membrane with the surface. There also exists an energy penalty
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38 for the bending energy change, which some models choose to ignore since the curvature is negligible
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40 compared to the cell dimensions. In the current models, bacterial cell membranes are assumed to be thin
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42 elastic layers whose structural details and composition can then be neglected. This assumption is reasonable
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44 since the thickness of bacterial cell walls is of an order of magnitude smaller than the dimensions of the
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46 nanostructures. However, complex models are needed that consider randomly-oriented nanopillar geometry
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48 and a dynamic cell rather a simple layer.
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52 The phenomenological model proposed by Pogodin et al. is based on the concept that adsorption of
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54 bacteria onto surface nanopillars is due to the decrease in contact adhesion energy; this leads to a stretching
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of bacterial cell walls suspended between the nanopillars, which causes an increase in the free energy¹⁷⁹. An equilibrium is reached as these competing effects cancel each other. Their model correctly predicts that gram-positive bacteria, possessing comparatively rigid and thick cell walls, are more difficult to deform than the more flexible walls of gram-negative bacteria. This prediction was verified by decreasing the rigidity of surface-resistant strains through microwave irradiation of the cells, which rendered them susceptible to the bactericidal mechanisms of wing surfaces. Li proposed an analytic thermodynamic model, analyzing the total free energy change of bacterial cells adhered to the patterned surface²¹⁶. This model considered all the three processes described above that contribute to a change in free energy. However, the shape of bacterial cells was taken to be spherical because of the difficulty in quantitatively calculating the relation between the geometrical shape parameters during adhesion of rod-shaped bacteria. Ye et al. developed a biophysical model similar to Pogodin et al. that describes the change in total free energy of an adherent *Candida albicans* cell on nanofiber-coated surfaces as a function of the geometry and configuration of the surface topology²¹⁷. Polystyrene (PS) nanofiber-coated substrata were fabricated and experiments were conducted to quantify the cell attachment density for varying fiber diameters at a prescribed spacing in support of their model. Other models that may be useful in further understanding the bacterial killing mechanism include bead model or single chain molecular theory, which is already used in the modelling of membrane phospholipid bilayer²¹⁸.

Fabrication strategies

Bioinspiration involves emulating ideas from nature. A key challenge in this endeavor is the need for fabrication and manufacturing strategies, especially in the mimicking of insect wings. As insect wings possess a variety of unique properties, the fabrication technique must depend on the targeted property. Once the intended property and possible route of fabrication has been designed, currently available techniques may be utilized or it may require the development of new tools. The fabrication of insect wing-inspired structures has been on the rise since micro- and nano-replication strategies have become prevalent in the last decade (Table 2). Earlier, simple ornithopters as micro-air vehicles were made to study aerodynamic

properties and more recently, to study sensing applications²¹⁹⁻²²¹. But to accurately mimic insect wing properties, advanced fabrication methods such as the micro-molding technique, also known as soft lithography, must be used. Here, plastic is pressed on a master mold (or stamp) to replicate patterns. Micro-molding can easily transfer the wing and its corrugated structures²²²⁻²²³. If the right (desired characteristics) plastic is chosen, then this technique can transfer micro-scale defects and features. Other similar techniques such as photolithography, electron beam lithography, hot embossing and nanoimprint lithography have been used in mimicking insect wings^{153, 224-227}. The primary difference lies in using either heat, light or electrons as the source while transferring the features from the mold to the plastic. In some cases, the mold is designed through computer software and then fabricated using laser whereas insect wings are directly used as a mold in others²²⁴. In bio-templating, the wing is used as a mold^{146-147, 154, 227-228}.

In most lithography techniques, the transfer of patterns is completed by a final etching step that is performed by reactive ion etching (RIE) or wet etching techniques. Recently the nanoscale features of dragonfly wings that are more random than patterned were fabricated using a one-step etching technique^{186, 188, 229} in which a few processing parameters can be optimized to generate the random roughness. RIE and lithography have limited scalability in contrast to random wet etching, which is relatively more scalable²²⁹. Similar to wet etching, hydrothermal treatment has also been employed to generate nanopillars on titanium^{187, 193}. Although this treatment involves a greater number of steps and extremely high process temperature, there is more control on geometry compared to random wet etching. The anodization of aluminum is another significant electrochemistry-based process, which is also scalable to generate nanopillars²³⁰. In the first step, electrochemical oxidation occurs and an ordered anodic aluminum oxide (AAO) is formed. In the second step, reduction takes place on the surface such as deposition of metals or galvanic deposition.

Another technique is focused ion beam (FIB) milling, in which a focused beam of ions such as gallium can be used to mill or excavate the materials to generate desired geometries¹⁹⁵. Although FIB has never been employed to mimic an insect wing probably because it is slow and expensive, it can be a good

technique to characterize the cross-sections of insect wing nanofeatures²³¹. Sol-gel is a synthetic approach based on bio-templates to make metal oxide nanofeatures¹⁴⁶. Metal oxides such as TiO₂ are rapidly formed in steps of hydrolysis, condensation and drying. This is a low-cost method like most wet chemical techniques. The precision, robustness, cost and ability to replicate complex 3D structures of current fabrication methods are limited²³².

The fabricated materials can be single-layered (consisting of grooves, pillars or other architectures on a single sheet^{154, 228}), multi-layered (prepared by stacking or depositing layers^{132, 233}) or quasi-ordered. Often, the designed process is a combination of techniques such as that performed by Aryal et al. to mimic large-area complex 3D ultrastructures of a Morpho butterfly's wing scale; the process included chemical vapor deposition, photolithography and chemical etching²³⁴. Another combination strategy includes colloidal self-assembly, sputtering and atomic layer deposition to fabricate multiple-layer structures inspired from butterfly wings¹³². Recently, inspired by the wings of *Chorinea faunus* butterflies, Narasimhan et al. engineered a transparent photonic nanostructured silicon nitride (Si₃N₄) membrane exhibiting structurally-induced scattering¹⁰⁴; *in vivo* studies proved this membrane to be suitable for intraocular pressure (IOP)-sensing implants. Some methods to maximize the amount of light energy captured have been devised, inspired from angle-dependent reflection¹⁴⁶⁻¹⁴⁷. These studies highlight the untapped potential of biomimetic surfaces and their likely impact in the near future.

To mimic complete insect wings, fabrication must start at the bottom. Initially, nano-scale or even smaller features need to be fabricated. The corrugations and complex vein systems can be generated using molding techniques. Mimicking insect wings is heavily dependent on physics or rather the growth of nanofabrication tools and processes. Application-dependent techniques can be employed to further characterize and study the fascinating properties of insect wings and a combination of these techniques can possibly offer novel insights.

Conclusions and future perspectives

Despite centuries of investigations on insects, many wing characteristics have not yet been discovered or understood. To start with, there is a lack of search engines or databases on categorization of insect wings. DrawWing is one of the wing-image analysis softwares that has been utilized for identification of insects by giving a numerical description to the wings. A robust digitization is required, which can be accomplished by collaborative efforts between entomologists and computer scientists.

The mechanical, biological, mechano-responsive, optical and aerodynamic properties are not fully understood. Although aerodynamics has been the most researched area with respect to insect wings, there is still scope to investigate the effect of different wing shapes and wing-surface structures on flight kinetics. The optical properties remain another extensive research topic that has inspired scientists to fabricate wing-inspired photonic materials. The surface characteristics such as wettability, anisotropy, reflectance and self-cleaning have been researched by dedicated groups who have characterized the wings of different species but of the same orders. The wings across insect orders can be characterized. There is a need to relate the wing surface with its many functions. A future approach would be to find a mathematical relationship between surface features and different properties or a structure–multifunction relationship, also, the interdependence of properties.

One of the promising fields is the interaction of biological organisms on the surface of insect wings, which came into highlight with the discovery of bacteria-killing cicada wings. Since 2012, efforts to understand and mimic the bactericidal behavior of insect wings have increased rapidly. With the growing concern of multi-drug resistant bacteria and hospital-acquired infections, killing through physical contact offers a novel alternative approach to possibly minimize spread of such infections. Due to the presence of micro- and nano- scale patterns on insect wings, the modelling of geometries is possible and their interaction with cells can be understood in detail. The fabrication of wing-inspired nano-scale patterns is still in its infancy probably because generally, the fabrication tools for nanoscale pillars on surfaces are expensive and technically-challenging. For the generation of patterns, a clean room environment with state-of-the-art

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3 fabrication technologies are required. These techniques are expensive and wing-inspired surfaces cannot be
4 produced at high throughput. In the field of nanotechnology, almost all progress has been made in the area
5 of nanoparticles that are synthesized in solution. Very few techniques offer synthesis of stable and standing
6 nanopillars or nanofeatures on solid substrates similar to the nanoarchitecture found on insect wings.
7 Therefore, there is a need to extensively focus on the fabrication of stable geometries at nano-scale, inspired
8 from insect wing surface topography.
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17 It is also important to consider the application before designing insect wing-inspired surfaces. If the
18 surfaces are designed to resist bacterial infections for biomedical implants, then many other factors play
19 complex roles. There is a race of eukaryotic cells against bacterial cells, which should be given due
20 importance during the design of nanopillars. A rapid initiation of biological cascade occurs at the surface
21 due to monocyte and macrophage adhesion, coagulation, protein adsorption, remodeling, inflammation and
22 deposition of extracellular matrix.²³⁵⁻²³⁶. Therefore, it is plausible that the nanopillars are ineffective against
23 bacterial cells *in vivo*. However, the same nanopillar surface may show efficient bacterial killing *in vitro*.
24 In the case of insect wings, they can easily kill bacterial cells because of the different surrounding habitats
25 and environmental conditions. Although wing nanopillars demonstrate antibacterial activity, mimicking the
26 exact topography may not be a smart design for implants. A better strategy would be to optimize the surface
27 topography in addition to other currently-used modifications or coatings, when considering bioinspiration
28 in the field of medical devices. However, the design of topography of insect wings may benefit other
29 industries such as food processing.
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45 In conclusion, insect wings continue to fascinate and inspire researchers in various fields with their
46 hitherto-unknown properties and several unexplored opportunities that need investigation. There is
47 enormous scope for developing a better understanding of the mechanisms underlying the known properties
48 and finally engineering strategies to replicate them synthetically to address societal needs.
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Supporting Information Statement

Table listing discovery of micro- and nanoscale architecture and wettability of insect wings; Figure illustrating the citation analysis of publications of insect wings in specific areas

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TABLES

Table 1: Bactericidal activity of investigated insect wings

Year	Insect	Species	Geometry	Surface architecture	Bactericidal activity	Refs
2012	Cicada	<i>Psaltoda claripennis</i>	Conical nanopillars	Height: 200 nm, Diameter: 100 nm at the base, 60 nm at the cap, Spacing: 170 nm	First reported mechano-bactericidal surface. Tested against <i>Pseudomonas aeruginosa</i> . Later same species of cicada wing was found to kill only Gram-negative or less rigid bacterial cells.	231, 177
2013	Dragonfly	<i>Diplacodes bipunctata</i>	Nanopillars	Diameter: 50-70 nm, Height: 240nm	Tested against gram-negative <i>P. aeruginosa</i> , gram-positive <i>S. aureus</i> cells and <i>B. subtilis</i> spores.	186
2015	Cicada	<i>Megapomponia intermedia</i> (ME)	Nanopillars	Height: 241 nm, Pitch: 165 ± 8 nm, Diameter: 156 ± 29 nm, Aspect ratio: 1.55	Greater number of dead gram-negative <i>P. fluorescens</i> cells on the ME and CA wings when compared to the AY sample.	49
		<i>Ayuthia spectabile</i> (AY)		Height: 182 nm, Pitch: 251 ± 31 nm, Diameter: 207 ± 62 nm, Aspect ratio: 0.88		
		<i>Cryptotympana Aguila</i> (CA)		Height: 182 nm, Pitch: 187 ± 13 nm, Diameter: 159 ± 47 nm, Aspect ratio: 1.15		
2016	Dragonfly	<i>Diplacodes bipunctata</i>	Nanopillars	Height: 200–300 nm, Diameter: 80 ± 20 nm, Spacing: 180 ± 30 nm.	Tested against gram-negative <i>P. aeruginosa</i> , gram-positive <i>B. subtilis</i> and <i>S. aureus</i> cells and their spores. Killing efficiency: <i>H. papuensis</i> < <i>A. multipunctata</i> < <i>D. bipunctata</i> .	181
		<i>Hemianax papuensis</i>				
		<i>Austroaeschna multipunctata</i>				
2017	Damselfly	<i>Calopteryx Haemorrhoidalis</i>	Nanopillars	Height: 433.4 ± 71.2 nm, Tip diameter: 47.7 ± 11.1 nm, Spacing: 116.1 ± 39.6 nm.	Studied susceptibility of <i>P. aeruginosa</i> and <i>S. aureus</i> at various stages of growth.	180

Table 2: Different kinds of insect wing based bioinspiration to achieve multifunctional materials.

Year	Insect	Bioinspiration	Material; Nanotopology	Geometry	Fabrication Method	Remarks	Ref.
2004	<i>Morpho</i> butterfly	Optics	Quartz patterned substrate, TiO ₂ and SiO ₂ layers on top; Multilayered quasi-ordered structures	Layer thickness: TiO ₂ ≈ 40 nm, SiO ₂ ≈ 75 nm, 14 layers total Substrate unit: 300 x (2000 ± s.d) nm ²	Electron beam lithography and dry etching for patterning the substrate; electron beam deposition for layers	A two-step fabrication capable of emulating almost all aspects of <i>Morpho</i> wings.	237
2005	<i>Morpho</i> butterfly	Optics	Diamond like carbon; Tree like nanostructures	Height: 2.6 μm, length: 20 μm, width: 0.26 μm, Grating pitch: 0.23 mm.	FIB, CVD	Nearly same shape and size as <i>Morpho</i> scales. Process is expensive and slow.	238
2006	<i>Morpho</i> butterfly	Optics	UV curable resin for patterned substrate, TiO ₂ and SiO ₂ layers on top; Multilayered quasi-ordered structures	Layer thickness: TiO ₂ ≈ 40 nm, SiO ₂ ≈ 75 nm, 14 layers total Substrate unit: 300 x (2000 ± s.d) nm ²	Nano casting lithography on substrate, electron beam deposition for layers	Low cost, scalable reproduction method for morpho butterflies. Can be used for other colors too.	163
2006	Butterfly; <i>Morpho Peleides</i>	Optics	Al ₂ O ₃ ; inverted structure of the original	10, 20, 30 and 40 nm thick layers deposited on template	Biotemplating using low temperature ALD	Tunable color depending on layer thickness, successfully replicated morphological and optical properties of the wing.	139
2007	Butterfly; <i>Morpho sulkowskyi</i>	Optics, Sensors	Christmas tree like nanostructures without modification	-	-	Demonstrated vapor selectivity and sensitivity of butterfly scales for the first time	150
2008	Butterfly; <i>Battus Philenor</i>	Optics	Chalcogenide glass	Layer thickness: 0.5 μm.	Biotemplating using conformal-evaporated-film-by-rotation	Replicated optical characteristics of the wing	239
2008	Cicada; <i>Cryptotympana atrata Fabricius</i>	Optics	PMMA polymer films; Conical nanopillars	Height: 440nm, Spacing: 185 nm, Diameter: 140 nm at base and 55 nm at top	Replica molding	Photonic structure with anti-reflective property	168
2009	Cicada	Wettability	PTFE film for membrane, carbon/epoxy fibers for veins	PTFE film: 150 μm Nanostructures on film: Height: 200 nm and width: 1.2 μm; “Veins” carbon/epoxy: 100 μm. Wing mass: 1.9g, wing span: 17.5 cm.	Argon and oxygen ion beam treatment for nanostructures, Thermal treatment	Superhydrophobic, low cost, flexible process, however, inertial characteristics such as bending etc. were not evaluated	127
2009	Cicada; <i>Cyclochila australasiae</i>	Sensors	h-PDMS; Nanopillars	Spacing= 50 nm; Diameter= 110 nm; Height= 200nm.	Nanoimprint Lithography	Integrated a nanoscale biological template with optical fiber to produce	

						highly sensitive SERS probes	
2010	Butterfly; <i>Papilio Blumei</i>	Optics	Pt or Au substrate having an array of concavities; alternating layers of Al ₂ O ₃ , TiO ₂ deposited on top.	Concavities: diameter= 4.5 μm, height= 2.3 μm. Layer thickness: Al ₂ O ₃ = 82 ± 4 nm and TiO ₂ = 57 ± 4 nm.	Colloidal self-assembly, sputtering, ALD	Adjusting fabrication parameters also allows mimicking the wings of either the single colored <i>Papilio Ulysses</i> , or the color mixing of <i>Papilio Palinurus</i> .	132
2011	Butterfly; <i>Morpho Menelaus</i>	Wettability Optics	Al ₂ O ₃ ; Naturally occurring “Christmas tree” structures	Ridge height= 1.8 μm, Spacing= 0.8 μm	Biotemplating using low-temperature ALD method	High aspect ratio nanostructures; Homologous iridescence and diffraction	161
2011	Butterfly; <i>Papilio Palinurus</i>	Optics	Al ₂ O ₃ and TiO ₂ layers on a PS film with concavities	Concavities: 4-5 μm; 5 alternating layers of 20 nm thickness.	Breath figure templated assembly, ALD	Emulated double reflection, polarization and polarization effects exhibited by the insect.	240
2011	Butterfly; <i>Euploea mulciber</i>	Optics Micro and nanoarchitec ture	Co, Ni, Cu, Pa, Ag, Pt, and Au; Metal layers deposited on naturally occurring nanoscale ridges, struts and ribs	Layer thickness: ridges and struts = 20-50 nm, ribs = 20-30 nm.	Selective surface functionalization, electroless deposition	Versatile method, capable of replicating on wide range of metallic substrates	232
2011	Crane fly; <i>Nephrotoma appendiculata</i>	Aerodynami cs	SU-8 for veins, PDMS for membrane	Varying width and thickness of “veins” and membrane; Span of one wing: 7.5-20 μm.	Advanced MEMS technology	Slow and expensive fabrication process; although it faithfully mimicked material conception, weight, venation, size, mass distribution and wing rigidity, wing mass was considerably larger than natural counterparts.	241
2012	<i>Morpho</i> butterflies	Optics Micro and nanoarchitec ture	Alternating layers of SiO ₂ and Si ₃ N ₄ on Si substrate; Tree-like nanostructures	Ridge width: 250 nm, Lamellae width: 50 nm, Period: 500 nm.	CVD, UV lithography, Reactive ion etching, wet etching	Possible to mimic the complexity of most species of butterfly wings using a combination of isotropic and anisotropic RIE.	234
2012	<i>Morpho</i> butterflies	Sensors	Wing scales doped with SWCNTs	Lamallae spacing= 150 nm, ridge spacing= 770 nm	Surface functionalization	Mid-wave IR detection with high sensitivity and response speed	242
2013	Dragonfly; <i>Diplacodes bipunctata</i>	Antibacterial activity	Silicon; Nanopillars	Diameter: 20-80 nm, Height: 500 nm	Reactive ion etching	First reported physical bactericidal activity of any surface.	186
2013	Butterfly; <i>Papilio Blumei</i>	Optics	Si substrate with an array of concavities, with alternating layers of Ta ₂ O ₅ , SiO ₂ on top.	Concavities: 4 μm radii. Layer thickness: Different for each layer.	Self-assembly, electron-beam deposition, and ICP etching.	Multilayerd stacks, no use of bio template	233
2013	Butterfly; <i>Morpho sulkowskyi</i>	Optics	PMMA; several tree-like structures with different dimensions of the ridges	Structures lie flat on the substrate, Height ≈ 150 nm	E-beam lithography	Investigation into how structure geometry affects optical phenomenon	243

						exhibited by the insect.	
2013	Butterfly; <i>Morpho sulkowskyi</i>	Sensors	Honeycomb shaped network of SWCNTs self-assembled on wing scales	-	Biotemplating; self-assembly	Demonstrated laser-triggered remote heating, high electrical conductivity and repetitive DNA amplification	244
2014	Cicada	Antibacterial activity	Titania; Nanowires	Fine: 100 nm diameter; Coarse: 10-15 μm diameter; Height: 3 μm	Alkaline hydrothermal process	Selectively bactericidal while supporting cell proliferation patterns which is dependent on array geometry.	187
2014	<i>Morpho</i> butterfly	Optics	SiO ₂ , TiO ₂ on Si; Nanopillars	Layer thickness: SiO ₂ 73 nm, TiO ₂ 38 nm	Spin coating, dry etching, Cr deposition, SiO ₂ /TiO ₂ deposition	Investigation into effect of nanoscale disorder in <i>Morpho</i> inspired surfaces	245
2014	Butterfly; <i>Pierella luna</i>	Optics	UV curable epoxy resin; Microplate array	Plate: 10 μm long, 8 μm high, 2 μm wide; Spacing: 12 μm perpendicular, 15 μm colinear direction	Replica molding	Fabricated a photonic system with periodic arrangements of diffraction elements, nonexistent in its natural inspiration	141
2015	Butterfly; <i>Papilio blumei</i> , <i>Cicendela chinensis</i> , <i>Papilio peranthus</i> and <i>Suneve coronata</i>	Optics	Cylindrical and triangular grooves with layers of TiO ₂ , Al ₂ O ₃	Nine alternating layers. Depth of grooves not characterized.	Photolithography, Reactive ion etching, PE-ALD	Grooves exhibit polarization and color angle dependence	246
2015	Cicada	Optics	PET; Nanopillars	Different etch times produce pillars with different dimensions	Colloidal self-assembly, Reactive ion etching, wet etching	Study investigates how ARS performance depends on fabrication parameters such as etch time	247
2015	<i>Morpho</i> butterfly	Optics Sensors	PMMA tree-like nanostructures functionalized by FS or 3-aminopropyltrimethoxy silane	Lamellae thickness: 86 ± 6 nm	E-beam lithography, vapor deposition	Capable of quantifying vapors in mixtures, and when blended with a variable moisture background.	148
2015	Cicada	Optics	Si and Ge; Hexagonal nanotip arrays	Different arrays with different dimensions	Plasma etching	Nanotip arrays for efficient light harvesting over a 300–1000 nm spectrum and up to 60° angle of incidence, in both low and high index materials	248
2015	Dragonfly	Antibacterial activity Wettability	Silicon; Nanopillars	Height: 4 μm , Diameter: 220 nm, Random inter-pillar spacing	Deep reactive ion etching	“Super” surface killed gram positive (<i>S. aureus</i>) gram negative (<i>E. coli</i>) and mammalian (Mouse	188

						osteoblasts) with high efficiency	
2016	Butterfly; <i>Trogonoptera brookiana</i>	Optics	SiO ₂ ; Nanoditch array	Cover scales: Ridge width= 383nm, Spacing= 990nm Ground Scales: Ridge width= 508nm, Spacing= 2.08μm	Sol-gel, selective wet etching	Simple biotemplating method for preparing small scale replicas	133
2016	Butterfly; <i>Dione juno</i>	Optics	Fused SiO ₂ substrate and IP-L 780 photoresist; zigzag shapes	Thickness= 0.3 μm, Height= 1.6 μm, various periodicities	Direct laser writing	Demonstrated substrate independent resonance, upscaling using controlled buckling possible	156
2016	Cicada	Optics Wettability	PDMS; Nanopillars	Diameter, top: 150, bottom: 250 nm, Pitch: 720 nm, Height: 200-300 nm	Biotemplating by replica molding	Antireflective and superhydrophobic characteristics were inherited	249
2016	Cicada; <i>Cryptotympana atrata Fabricius</i>	Optics	Biomorphic TiO ₂ ; Nanopillars	Height: 230 ± 42 nm, Spacing: 250 ± 18 nm, Diameter, top: 75 ± 4 and basal: 175 ± 10 nm	Sol-gel process	Demonstrated angle dependent change in antireflectivity	146
2016	Butterfly; <i>Callophrys rubi</i>	Optics	Organic photo resin; 3D gyroid	20 μm X 20 μm X 4 μm samples	Optical two-beam super-resolution lithography	Controllable structural handedness and possible complete band gap	250
2016	Dragonfly	Antibacterial activity	Black silicon; Nanopillars	Height: 652 ± 10.3 nm, Tip diameter: 100 ± 1.8 nm, Density: 12.2 pillars/μm ²	Reactive ion etching	<i>In vivo</i> studies demonstrated biocompatibility, reduced inflammation and bactericidal nature.	184
2016	Dragonfly	Antibacterial activity	Black silicon; Nanopillars	Height: 500 nm; Diameter: 95nm; Spacing: 450 ± 200nm.	Reactive ion etching	Fabricated a reusable, bactericidal microfluidic device with several potential applications.	192
2017	Cicada and dragonfly	Antibacterial activity	Titanium; Nanofibers	Fine: Diameter=34 ± 6.5 nm, Spacing (tip to tip) =171.3 ± 48.3 nm; Coarse: Diameter= 7.78 ± 2.56 nm.	Hydrothermal treatment	Integrated topological and biochemical cues (ligands) to achieve a bactericidal surface that also supports osseointegration.	251

2017	Butterfly; <i>Morpho didius</i>	Optics	SiO ₂ , SiN _x ; Multilayered conical tree like structures	Approximate ledge height: 30nm	CVD, metal nanoparticle formation, and wet-chemical etching.	High transmission of infrared light, and strong reflection of visible light at high angle	157
2017	Cicada; <i>Cryptotympana atrata Fabricius</i>	Optics Wettability	Biomorphic SiO ₂ ; Conical nanopillars	Height: 190 ± 25 nm, Tip spacing: 290 ± 28 nm, Tip diameter: 63 ± 3 nm, Basal diameter: 260 ± 33 nm	Biotemplating by ultrasonic assisted sol-gel method	Angle dependent antireflection and enhanced hydrophilic properties	147
2017	Cicada; <i>Cryptotympana atrata Fabricius</i>	Optics Wettability Micro and nanoarchitec ture	Polystyrene; Tapered nanopillars	Height: 156, Spacing: 180.	Electroless plating, electroplating, microinjection compression molding	Hydrophobic and anti-reflective replica prepared by biotemplating	169
2018	Dragonfly	Antibacterial activity Micro and nanoarchitec ture	Black silicon; Nanopillars	Multiple samples with varying pillar height and density	Reactive ion etching	Investigation to correlate topographical characteristics to bactericidal efficiency.	189
2018	Generic	Antibacterial activity	Aluminum and its alloys; Hierarchical structure of micro and nanoscale pillars.	Roughness characterized using various roughness parameters such as R _{rms} , R _a etc.	Wet etching	Resisted attachment of drug resistant bacterial strains collected from hospital environments; highly scalable.	229
2018	Butterfly; <i>Morpho sulkowskyi</i>	Optics	ZnO; naturally occurring tree like nanosculptures.	Layers of various thicknesses deposited on the wing nanostructures.	Low temperature ALD (T< 150° C)	Tunable color, providing aesthetic properties, simultaneously enhancing photocatalytic activity. Demonstrated possible uses in water purification.	154
2018	Butterfly; <i>Chorinea faunus</i>	Optics Antibacterial activity Micro and nanoarchitec ture	Si ₃ N ₄ ; Disc-shaped nanostructures	Various radii disc shapes; aspect ratio= 0.45	Phase-separation- based polymer- assembly process	Engineered biophotonic, antibiofouling, nanostructured surface and demonstrated <i>in vivo</i> applicability.	104
2018	Butterfly; <i>Morpho peleides</i>	Optics, sensors	Wing scales embedded into PVA	Natural nanostructures	Infiltrating scales with PVA	Demonstrated pH sensitivity	252

PMMA: poly(methyl methacrylate); PTFE: polytetrafluoroethylene; PET: Polyethylene terephthalate ;
PDMS: Polydimethylsiloxane; PVA: Poly vinyl alcohol

Figures

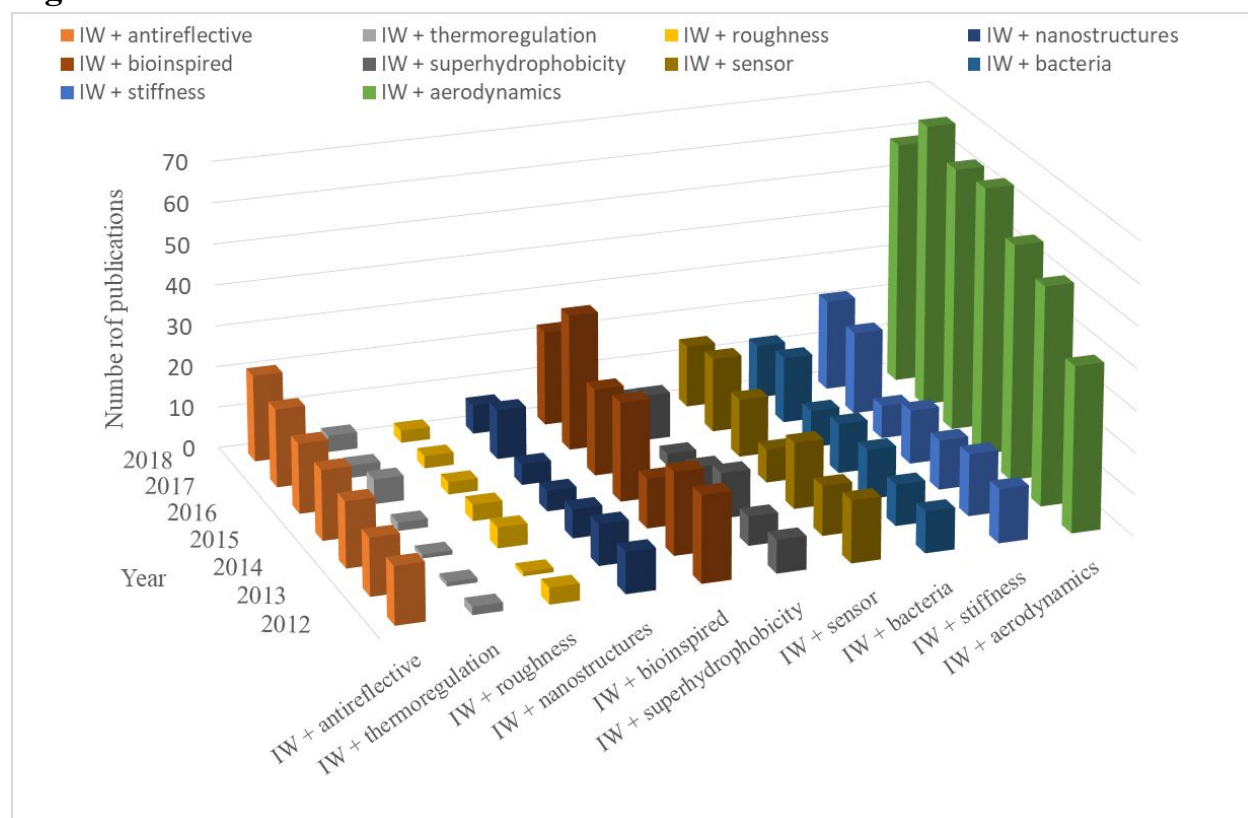


Figure 1: Skyscraper representation of the number of publications including insect wings (IW) in specific areas during the period 2012 to 2018. From the Web of Science search engine, the searches were done using keywords of insect wings and the specific areas. In case of similar words, the OR function was used such as IW + antireflection or IW + reflectivity and IW + bacteria or IW + antibacterial or IW + bactericidal. For simplicity, only one keyword is shown in the axis.



Figure 2: Photographs of (A) Dragonfly, (B) Butterfly, (C) Hoverfly and (D) Damselfly where the insects are displaying their diversity in wing design.

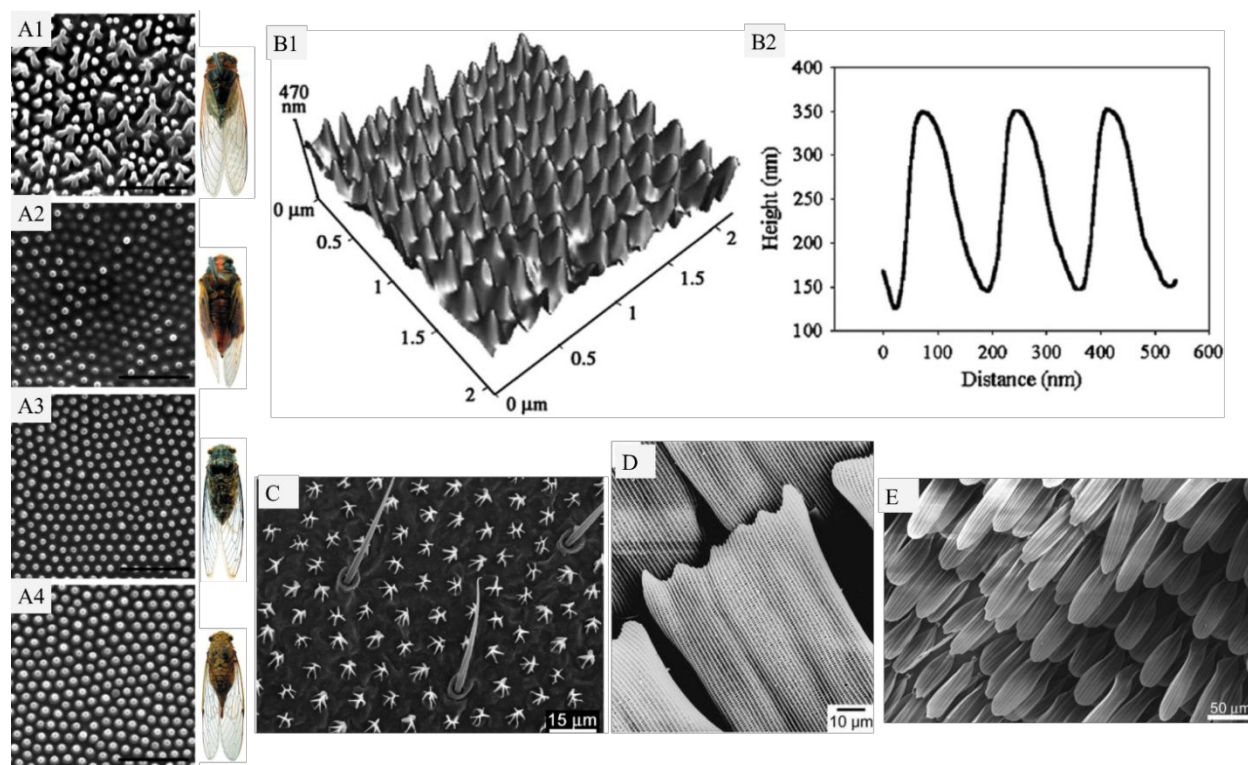


Figure 3: (A1-A4) SEM images and corresponding photographs of the cicada wings of *Chremistica maculate*, *Mogannia conica*, *Meimuna microdon*, *Terpnosia jinpingensis* (scale bars = 1 μm). (B1 and B2) represent the AFM image and height profile of the nanopillars of cicada (*Psaltoda claripennis*) wing. SEM of the micro- and nanostructures on the insect wings of *Nasutiterems walkeri* termite (C), *Speyeria aglaja* butterfly (D), and *Prasinocyma albicosta* moth wing (E). Panels A1-A4 reproduced with permission from ⁵⁰, B1-B2 reproduced with permission from ⁵⁵, C reproduced with permission from ⁵³, D reproduced with permission from ²⁵³ and E reproduced with permission from ²⁵⁴.

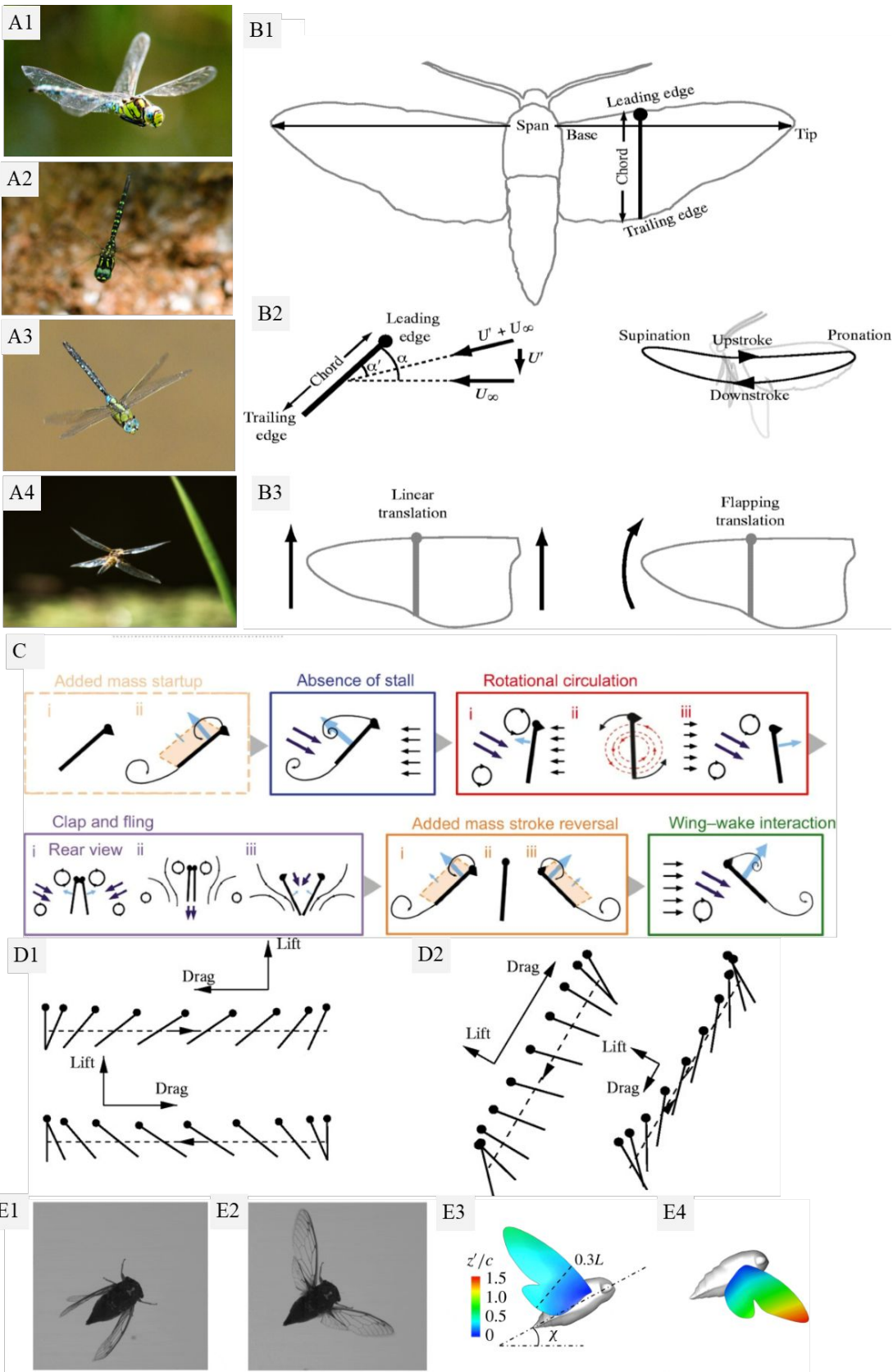


Figure 4: (A1-A4) Photographs of dragonflies depicting flight maneuvers, (B1-B3) Schematic of an insect wing leading edge, chord, trailing edge and various strokes used in various phases of insect kinematics, in B2, U_{∞} is the free stream velocity, U' is the downwash velocity, α is the geometric angle of attack that the wing section makes with free stream velocity, α' is the aerodynamic angle of attack which is the angle between the wing section and the free stream velocity deflected due to downwash, (C) Schematics of various complex aerodynamic mechanisms as discussed in the aerodynamics section, (D1-D2) Horizontal and inclined hovering of various insects (E1-E4) Photos and model images representing a downstroke and upstroke motions of a cicada. Panel B reproduced with permission from ⁷⁸, panel C reproduced with permission from ⁷¹, panel D reproduced with permission form ²¹¹ and panel E reproduced with permission from ²⁵⁵

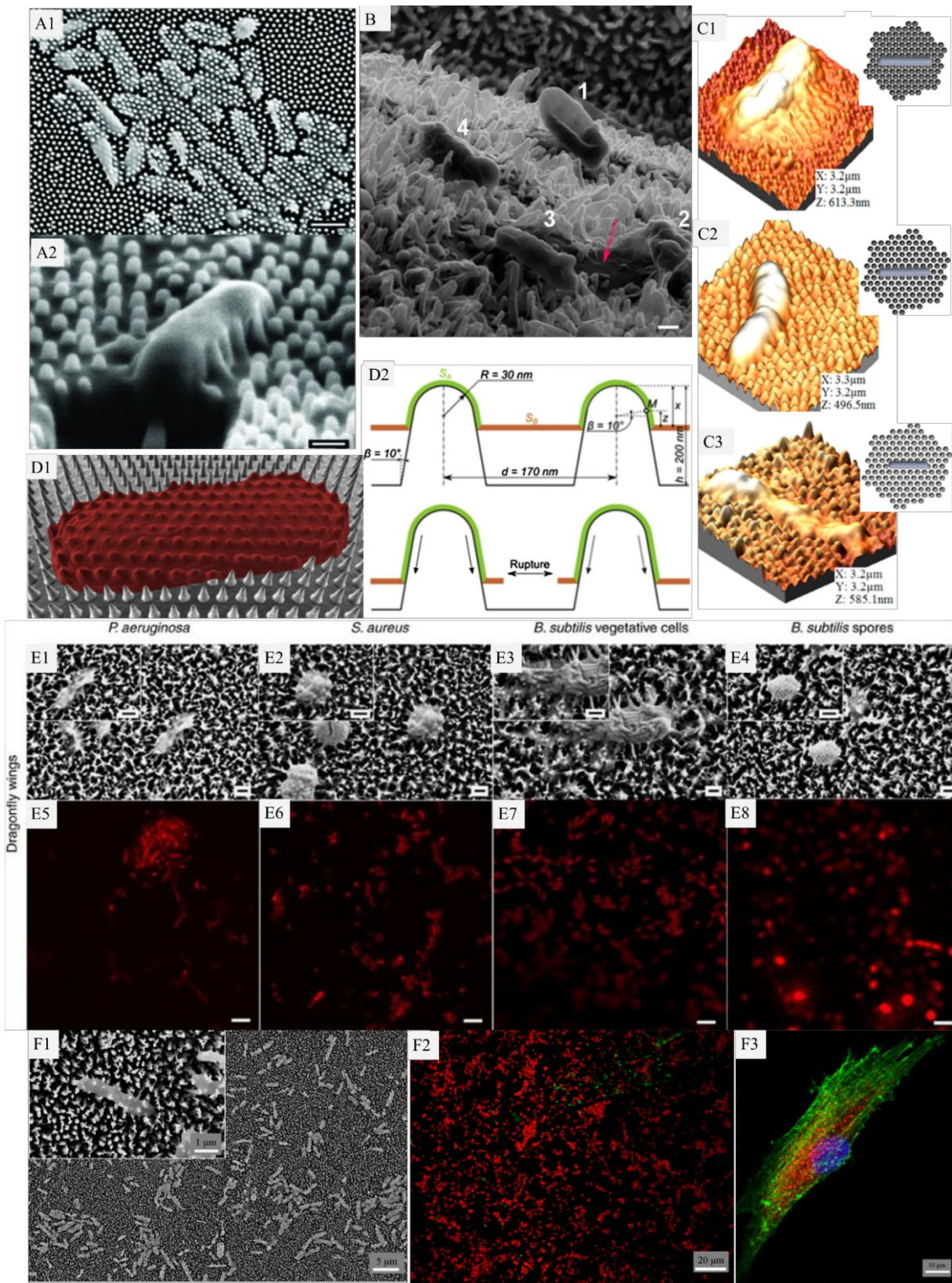


Figure 5: (A1-A2) SEM images showing bactericidal effect of cicada wing nanopillars against *P. aeruginosa* cells. The bacteria cells settle down at the wing surface, where the cells appear lysed by the nanopillar architecture (A1 scale bar = 1 μm , A2 scale bar = 200 nm), (B) Different *E. coli* cells are affected upon contact with the dragonfly wing nanopillars (scale bar = 200 nm). The nanopillars of dragonfly are not patterned like that on cicada wings but the effect is similar, (C1-C3) AFM images and corresponding schematic of the single bacterial cell interacting with three different species of cicada wing nanopillars. The nanopillars are seen to have different nanotopography and their effect on bactericidal activity was studied. (D1-D2) Schematic and geometric model representation of the bacterial cell interaction with the nanopillars of the cicada wings. The top figure shows the bacterial cell being stretched by the nanopillar which is represented by green color, whereas the stretched part of the cell membrane are suspended between the nanopillars which is represented by the orange color. The bottom figure shows the ruptured cell where the cell has reached its limit to stretch. (E1-E8) SEM and fluorescent microscopic images of different bacterial strains on the dragonfly wing surface (E1- E4 scale bars = 200 nm, E5 – E8 scale bars = 5 μm). (F1-F2) SEM and fluorescent microscopy image of *E. coli* cells on wing inspired nanostructured titanium surface. The fluorescently labeled cells are red indicating that that the cells are non-viable or damaged, (F3) shows a human mesenchymal stem cell attached on the nanostructured titanium surface depicting cytocompatibility for orthopedic applications. The cell is stained for parts of the cell indicating adhesion such as paxilin (red), actin filaments (green) and nucleus (blue) (scale bar = 10 μm). Panel A reproduced with permission from ²³¹, B reproduced with permission from ¹⁷⁶, panel C adapted and reproduced with permission from ⁴⁹, panel D reproduced with permission from ¹⁷⁹, panel E reproduced with permission from ¹⁸⁶, panel F reproduced with permission from ¹⁸⁵.

Mimicking Insect Wings: The Roadmap to Bio-inspiration

Jafar Hasan¹, Anindo Roy², Kaushik Chatterjee², Prasad KDV Yarlagadda¹

¹Science and Engineering Faculty, Queensland University of Technology, 2 George Street, Brisbane, QLD 4001, Australia

²Department of Materials Engineering, Indian Institute of Science, C.V. Raman Avenue, Bangalore 560012, India

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