Materials, Structure, and Dynamics of Insect Wings as Bioinspiration for MAVs

Stacey A. Combes

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

1 INTRODUCTION

Insects are the dominant group of animals on Earth – with approximately one million named species, they far outnumber all other terrestrial animals and occur on all continents (Triplehorn and Johnson, 2005). One of the keys to their success has been the evolution of flight, which led to a huge diversification of the primary structure associated with flight, the wings. Insect wings have evolved over hundreds of millions of years to play a wide variety of roles, both related to and independent from flight. This has resulted in numerous design trade-offs, as well as constraints related to available developmental pathways and phylogenetic history (i.e., each species "inherited" a certain wing design from its ancestor, and evolutionary modifications must start from this inherited design).

The earliest insects had four wings (two pairs, with a fore- and hindwing on each side), and some insects such as dragonflies and damselflies have retained four independently functioning wings that produce forces of comparable magnitude (Figure 1a). In many orders of insects, however, one pair of wings has become specialized to produce more aerodynamic force than the other, such as the expanded hindwings of katydids and beetles (Figure 1b, e). Other groups possess forewings that are specialized for force production, and many of these insects have become functionally two-winged by attaching the smaller, flexible hindwings to the forewings (e.g., bees and butterflies; Figure 1f, h). A few groups of insects (e.g., flies) have become truly two-winged, with the hindwings modified into small sensory organs (Figure 1g).

Although the primary function of most wings is to generate aerodynamic forces, complex flight behaviors require more than maximal force production, and the design of insect wings may reflect trade-offs or specialization for other aspects of flight performance, such as efficiency, versatility, maneuverability, or stability. In addition, insect wings must function over an extremely long functional lifespan, often flapping millions of times or more, and must endure collisions and tearing without experiencing structural failure. Wings tend to deform readily and reversibly during collisions, because of either their overall structure (e.g., wing corrugation, see Section 2.2.2; Newman and Wootton, 1986) or special morphological features, such as the transverse "crumple" lines of craneflies (see Section 2.1.3).

It is also important to bear in mind that wings serve other biological functions completely unrelated to flight, and their design may include features that have no effect, or even negative effects, on flight performance. For example, the significance of butterfly wing characteristics such as tails, scalloped edges, and surface ornamentation have been widely

---

Encyclopedia of Aerospace Engineering.
Edited by Richard Blockley and Wei Shyy
ISBN: 978-0-470-68665-2

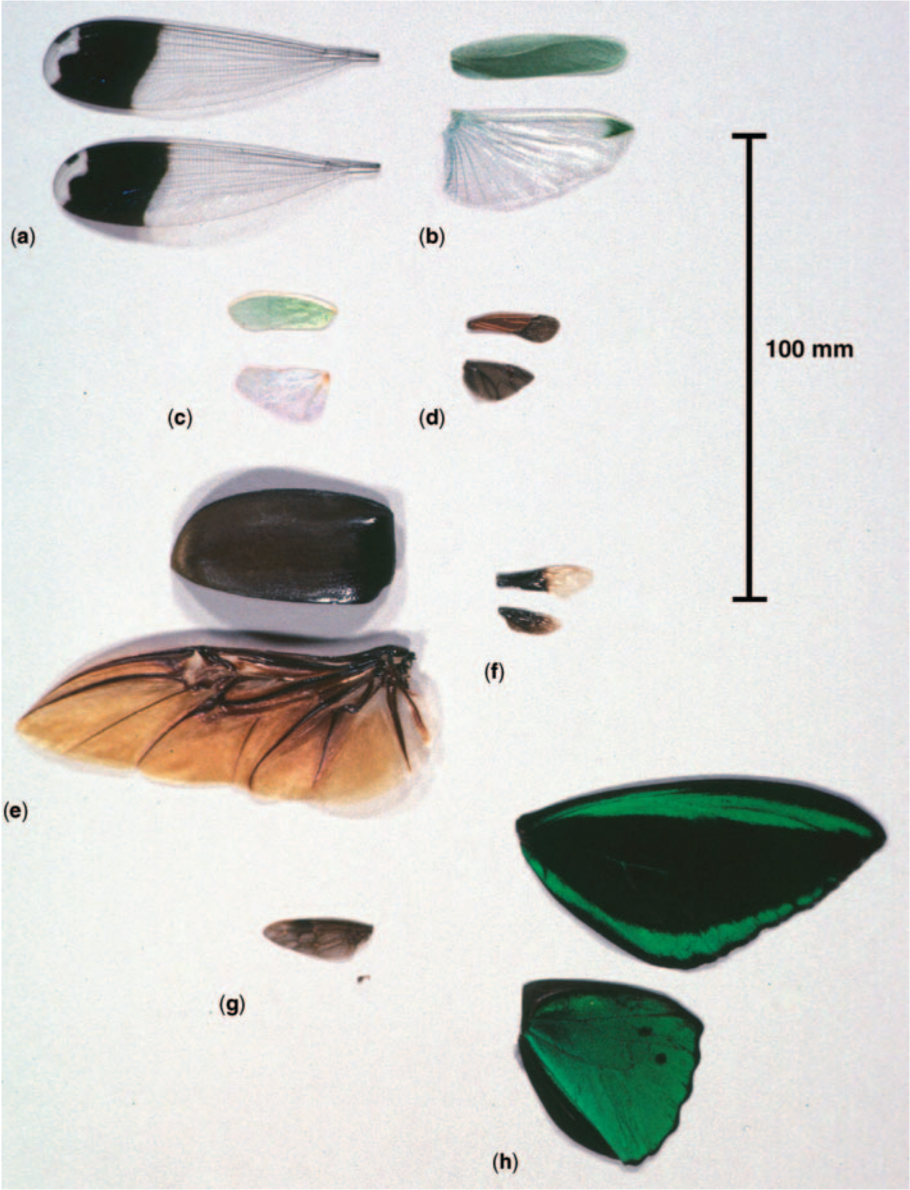

Figure 1. Diversity of insect wings. Forewings and hindwings are shown for each insect (top and bottom, respectively). (a) Helicopter damselfly (order Odonata); (b) Katydid (Orthoptera); (c) Planthopper (Homoptera); (d) Stink bug (Hemiptera); (e) Scarab beetle (Coleoptera); (f) Orchid bee (Hymenoptera); (g) Timber fly (Diptera); (h) Birdwing butterfly (Lepidoptera). Reproduced with permission from Dudley (2000) © Princeton University Press.

discussed, but it is still unclear whether most of these features have any role in flight performance (Wootton, 1992). Some wings are specialized for mechanical protection (Figure 1b, e) or to camouflage insects, while others function in signaling (via sound production or visual signals) or thermoregulation (Figure 1h). Therefore, the assumption that any particular insect wing represents the "optimal" design for flight performance is almost certainly false, although particular features of insect wings may enhance certain aspects of flapping flight performance.

1.1 Insect wing motions and flight forces

Although insects occasionally employ steady aerodynamic mechanisms (e.g., during gliding or fast, forward flight), it is becoming increasingly clear that insects primarily use unsteady aerodynamic mechanisms to produce forces during flapping flight (see Aerodynamics, Flapping Wing Aerodynamics). Unsteady aerodynamic forces can be generated during wing translation via formation of a leading edge vortex (LEV; Ellington *et al*., 1996), as well as during stroke reversals, via rotational circulation, wake capture (Dickinson, Lehman and Sane, 1999), and occasionally clap and fling (Weis-Fogh, 1973; Miller and Peskin, 2005).

The major flapping motion of wings is driven by large power muscles inside the thorax, which translate the wing forward and/or down during the downstroke, then backward and/or up during the upstroke, generally at an oblique angle. Smaller muscles at the wing base control wing pitch angle during translation and determine the shape of the wing trajectory, often producing "U" or "figure-8" shaped wing paths. All insects rotate their wings along the spanwise axis to some degree between strokes, revolving backward (supination) before the upstroke and forward (pronation) before the downstroke.

Wings are subjected to three primary types of forces while flapping: intrinsic forces applied by muscles at the wing base to drive wing motions, aerodynamic forces that provide lift and thrust, and inertial forces due to rapid wing acceleration and deceleration during each half-stroke. Although aerodynamic forces tend to receive the most attention, inertial forces caused by rapid flapping can be extremely high, and are often comparable in magnitude to aerodynamic forces (Ennos, 1989a; Bergou, Xu and Wang, 2007). Inertial forces are particularly high during stroke reversals and are thought to supply a significant portion, if not all, of the power required to rotate the wing in preparation for the next half-stroke (Ennos, 1988; Bergou, Xu and Wang, 2007).

Wootton (1992) has described insect wings as being intermediate between structures and mechanisms – functioning at once as levers (transmitting forces from muscles at the wing base to the air), oscillating airfoils (accelerating air to generate and transmit aerodynamic forces to the body), and cantilevered beams (accepting changing patterns of bending and twisting forces without failure). While it could be argued that their flexibility is an inevitable consequence of the properties of biological materials and the need to minimize wing mass and inertial costs, it is becoming increasingly clear that flexibility and controlled deformations are both beneficial and necessary to many aspects of wing functioning.

1.2 Wing deformations and effects on force production

Insect wings are primarily composed of tubular, supporting veins joined by thin, deformable membranes (see Section 2). Two-dimensional images of venation patterns (e.g., Figure 2) are often used to demonstrate wing structure and diversity, but these images can be misleading, as they suggest that wings are flat and rigid. In reality, insect wings are complex, deformable, three-dimensional structures that change shape dynamically as they flap back and forth up to several hundred times per second. Insects have no muscles past the wing base – thus, their wings are largely passive structures that experience dynamic shape changes in response to the forces exerted upon them during flight. Insect wing deformations can vary enormously between species, during different types of flight, and even from stroke to stroke, although general patterns of bending during the stroke cycle can be identified.

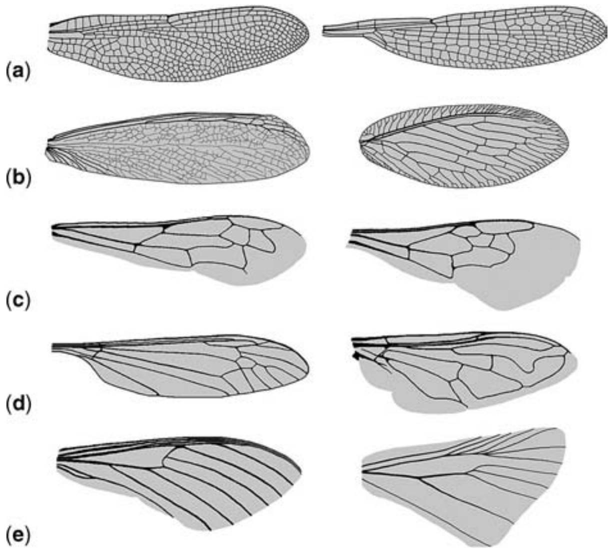

Figure 2. Venation patterns in insect forewings. (a) Dragonfly and damselfly (Odonata); (b) Termite (Isoptera) and lacewing (Neuroptera); (c) Wasp and bumblebee (Hymenoptera); (d) Cranefly and hoverfly (Diptera); (e) Hawkmoth and butterfly (Lepidoptera).

During the downstroke, the wings of most insects are relatively flat, often with a slight camber or twist. At supination, the transition from downstroke to upstroke, the leading edge comes to a halt and rotates to move backward and up. Most insect wings display some degree of ventral flexion during supination, with the tip or even the whole wing bending forward and down (e.g., Figure 3a–c, h). Some wings twist extensively, and a torsional wave passes from the wing tip to the base at supination (e.g. Figure 3c, e). This bending and twisting is essential in order to move the wing into a beneficial orientation for the upstroke (Wootton, 1992).

During the upstroke, both the direction and magnitude of force production depends on the angle of attack that the wing assumes – thus, the farther the wing twists, the closer the force vector approaches the vertical. Insects capable of extensive wing twisting are generally more versatile fliers, as the ability to generate vertical force during the upstroke permits slower flight and hovering; those that cannot twist as much are often restricted to fast flight (Wootton, 1992). During pronation, the transition from upstroke to downstroke, the wing rotates forward for the downstroke, displaying less bending and torsion

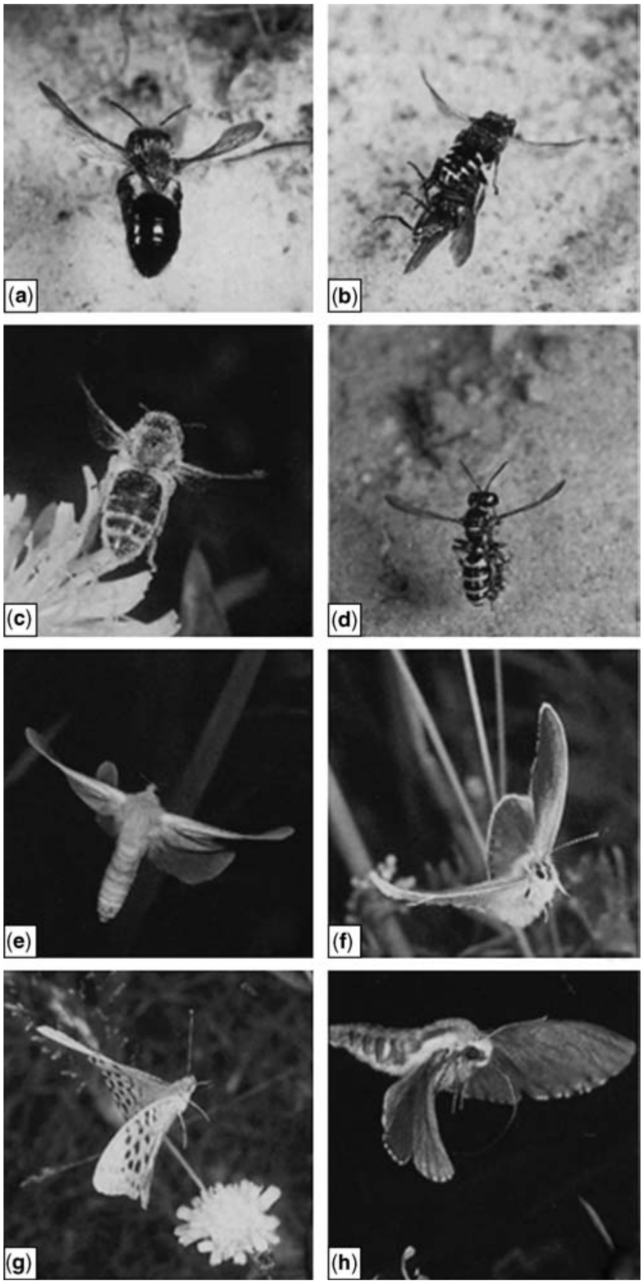

Figure 3. Dynamic wing bending in flying insects. (a–d) Bees and wasps; (e–h) butterflies and moths. Reproduced with permission from Nachtigall (2000) © E. Schweizerbart'sche Verlagsbuchhandlung.

than during supination. Some insects occasionally clap their wings together (or nearly together) at pronation, generating additional aerodynamic force via the unsteady "clap and fling" mechanism first proposed by Weis-Fogh (Weis-Fogh, 1973; see Aerodynamics, Flapping Wing Aerodynamics).

Beyond these general patterns, however, the degree to which insect wings deform during flight has not been well documented. Obtaining precise, fine-scale measurements of dynamic wing-shape changes occurring at high temporal frequencies presents numerous technical challenges. Thus, qualitative descriptions of wing bending based on high quality still photographs (e.g., Figure 3) dominate the literature, although precise, quantitative measurements have been performed recently on hawkmoths, locusts, and hoverflies (Mountcastle and Daniel, 2009; Walker, Thomas and Taylor, 2008a; see Section 2.2.3). Because instantaneous wing shape is determined by the interaction between various flight forces (i.e., intrinsic, aerodynamic, and inertial) and the complex architecture of the wing, deformations are also difficult to predict or model – particularly when aeroelasticity, the mutual interaction between aerodynamic forces and wing shape, is considered. However, experimental studies suggest that in the large wings of hawkmoths, inertial forces (which are easier to predict) are actually far more significant in determining wing deformations than aerodynamic forces (Combes and Daniel, 2003c). Theoretical studies suggest that this result may apply to all wings flapping in air (Daniel and Combes, 2002), and several studies show that the passive, tip-to-base torsional wave seen in many insects at supination is driven partly, if not entirely, by inertia (Ennos, 1988; Bergou, Xu and Wang, 2007).

The influence of flexibility and three-dimensional wing shape on unsteady force production has been addressed in only a handful of studies, with results that are often surprising. For example, while camber and spanwise twist are generally beneficial for steady aerodynamic force production, two physical modeling studies suggest that these attributes have little effect on unsteady translational forces (Dickinson and Götz, 1993; Usherwood and Ellington, 2002a; see Section 2.2.3). However, computational modeling studies suggest that wing flexibility may enhance wake capture during wing rotation (Vanella *et al*., 2009), as well as force production during clap and fling (Miller and Peskin, 2009). In addition, recent experimental work on hawkmoth wings shows that wing deformations, particularly the torsional wave that passes along the wing at supination, result in greater mean advective flows and shift airflow in a direction more beneficial to force production (Mountcastle and Daniel, 2009).

2 STRUCTURAL AND DYNAMIC FEATURES OF INSECT WINGS

2.1 Wing components

2.1.1 Material and structural properties of veins and membranes

Wings are composed primarily of cuticle, a multi-layered material consisting of chitin microfibers embedded in a protein matrix. Cuticle stiffness (*E*, Young's modulus) can vary from 1 kPa to 20 GPa, depending on hydration, sclerotization (the stiffening process that occurs after insects molt), and chitin fiber orientation (Vincent and Wegst, 2004). In wings, the cuticle is arranged into tubular, supporting veins and thin, deformable membranes. Membrane thickness ranges from less than 0.5 μm in small, thin wings to over 1 mm in the protective forewings of beetles (Wootton, 1992), and can vary widely within an individual wing (e.g., 1–6 μm in craneflies and locusts, 10–15 μm in cicadas; Rees, 1975; Smith *et al*., 2000; Song *et al*., 2004). The Young's modulus of locust wing membranes also varies widely throughout the wing (0.3–18.7 GPa; Smith *et al*., 2000). Several studies suggest that wing membranes may function as a stressed skin, contributing to flexural rigidity rather than acting as a purely deformable element (Newman and Wootton, 1986; Kesel, Philippi and Nachtigall, 1998; Wootton *et al*., 2000

Wing veins are typically hollow tubes, with the main longitudinal veins (running from the wing base to the tip or trailing edge) transmitting fluid, oxygen, and sensory information (via nerves). Veins can be thin- or thick-walled, and have round, elliptical, or bell-shaped cross-sections (Figure 4e, f), which affects their bending stiffness along particular axes. Cross-veins connecting the longitudinal veins are rarely fluid-filled, and serve diverse structural roles; for example, cross-veins within the locust hindwing form flattened angle brackets to strengthen some areas of the wing (Figure 4a), and are annulated (ridged like a drinking straw) to promote bending in other areas (Figure 4b; see Section 2.1.2).

2.1.2 *Wing venation and flexural stiffness patterns*

Insect wing venation is generally denser near the wing base and leading edge (Figure 2), and vein diameter and

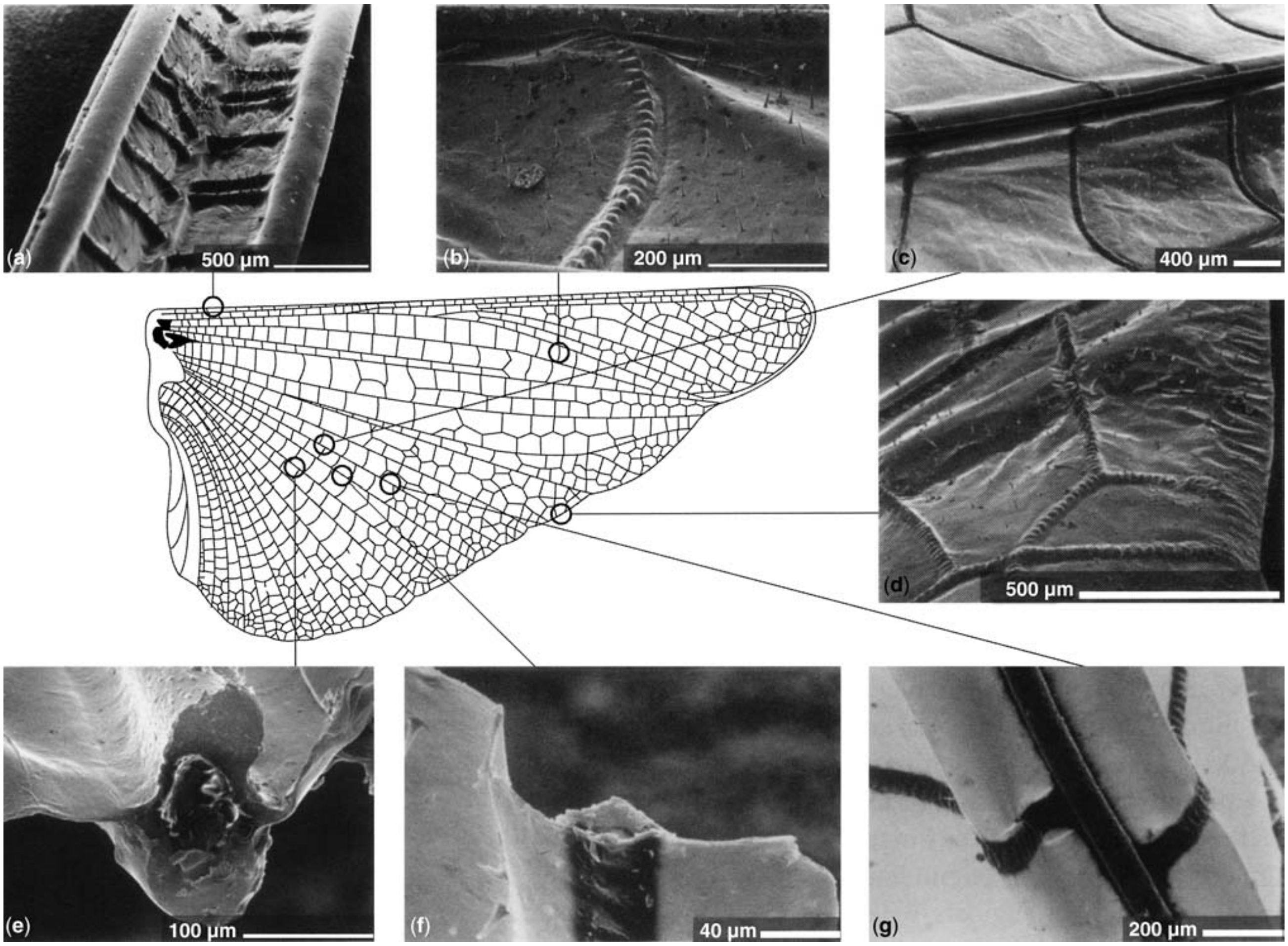

Figure 4. Scanning electron microscope (SEM) images of a locust hindwing. (a) Corrugated leading edge spar reinforced by bracket-like cross-veins; (b) flexible, annulated cross-vein; (c) longitudinal vein with parallel flexion lines and curving, annulated cross-veins; (d) detail of the wing margin; (e, f) cross-sections of longitudinal veins in different regions of the wing; (g) longitudinal vein intersected by two cross-veins bending along flexion lines parallel to the longitudinal vein. Reproduced with permission from Wootton *et al*. (2000) © R.J. Wootton.

cuticular thickness taper from base to tip. This arrangement reflects the distribution of bending stresses in flapping wings (Ennos, 1989a), providing additional strength where bending stresses are highest, and also reducing mass toward the wing tips to minimize inertial power requirements. Beyond these general trends, venation pattern varies widely between groups of insects (Figure 2). Surprisingly, these large differences in venation pattern do not significantly affect average bending stiffness (flexural stiffness, or *EI*) in the spanwise or chordwise direction (base to tip or leading to trailing edge); rather, average stiffness displays a strong scaling relationship, suggesting that overall stiffness is determined primarily by wing size (Figure 5; Combes and Daniel, 2003b).

Venation pattern is, however, likely to affect regional variation in stiffness. Measurements of spatial patterns of flexural stiffness in hawkmoth and dragonfly wings show that stiffness declines exponentially from the base to tip and leading to trailing edge in both species, although details of the stiffness pattern (e.g., sharpness of the decline) differ. This exponential decline in stiffness localizes wing bending to particular regions and contributes to the patterns of wing deformation observed during flight (Combes and Daniel, 2003b).

2.1.3 Specialized features of insect wings

In addition to regional differences in wing venation pattern and the material properties of veins and membranes, many insect wings contain flexion lines – bands of flexible cuticle that run along wing membranes and often interrupt supporting veins (veins may be annulated, flattened, or desclerotized where the lines cross them), to promote bending along certain axes of the wing. These lines are sometimes clearly visible and at other times recognizable only by manipulation (Wootton, 1992). Flexion lines can function as two-way joints, or as one-way hinges that contain mechanisms to prevent bending in one direction while promoting it in the other. Many wings contain one to three distinct flexion lines that run longitudinally or radially, facilitating chordwise bending and twisting (Wootton, 1979). Wings may also contain transverse flexion lines running from the leading to the trailing edge, which often function as one-way hinges to promote ventral bending at the end of the downstroke. Some wings possess creases that do not normally bend during flight, but may prevent damage by crumpling reversibly during collisions (e.g., near the tips of cranefly wings).

Fold lines are similar to flexion lines, running longitudinally, transversely, and/or radially (e.g., forming pleats; Figure 4) along the wing. Their primary function is to fold the wings when they are at rest, but wings do bend along many of these fold lines during flight as well. Resilin, a flexible, highly elastic protein, has been found in the fold lines of some beetles and earwigs, potentially assisting in wing folding, preventing material damage, and/or contributing to wing deformations and elastic energy storage during flight (Haas, Gorb and Blickhan, 2000a; Haas, Gorb and Wootton, 2000b). Resilin has also been found in certain chordwise vein junctions of damselfly wings (Figure 6a; Gorb, 1999), suggesting a flight-related function, as damselfly wings do not fold at rest. These flexible joints often contain spikes or other structures that may limit wing flexion in one direction (Figure 6b, c).

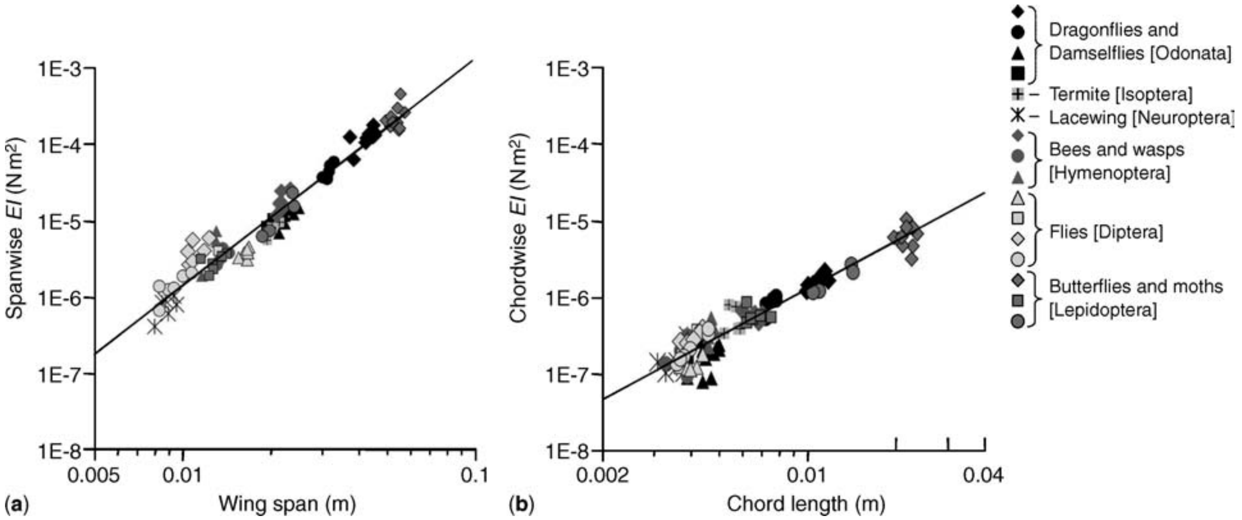

Figure 5. Flexural stiffness vs. span/chord length in 16 insect species. (a) Spanwise flexural stiffness (*EI*) vs. wing span, for log-log transformed data, $y = 2.97x + 0.08$, $r^2 = 0.95$; (b) Chordwise flexural stiffness (*EI*) vs. chord length, for log-log transformed data, $y = 2.08x - 1.73$, $r^2 = 0.91$. Adapted with permission from Combes and Daniel (2003) Ⓒ S.A. Combes.

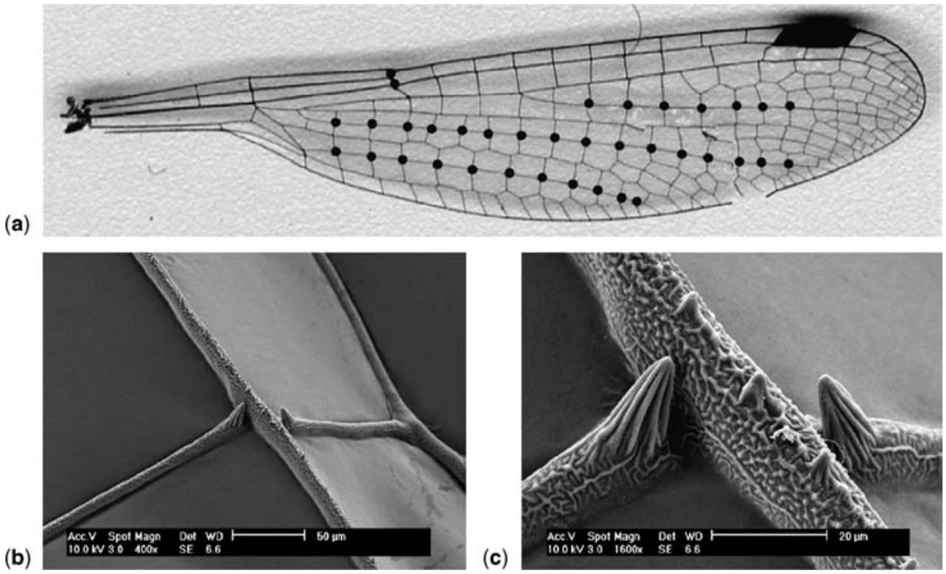

Figure 6. Location and morphology of chordwise, resilin-containing joints in a damselfly wing. (a) Damselfly wing with locations of flexible, resilin-containing joints indicated by black circles; (b, c) SEM images of a resilin-containing joint with spikes that may prevent excessive bending. Images courtesy of James Crall and Seth Donoughe.

The mass distribution of wings has not been studied extensively, although it is likely to have a significant effect on wing deformations, particularly those caused by inertial forces. The mass of insect wings generally tapers from wing base to tip (Ennos, 1989a), but some groups (e.g., dragonflies and bees) contain a pterostigma, a pigmented spot with greater mass than the surrounding cuticle, located on the distal leading edge (Figure 6a). Adding mass near the leading edge of these wings is thought to help balance the chordwise distribution of mass (which is otherwise located behind the torsional axis), preventing excessive rotational torques and potentially helping to regulate wing pitch during flight (Norberg, 1972).

Finally, many insect wings display diverse surface structures. Small spines project from dragonfly wing veins (D'Andrea and Carfí , 1991), overlapping scales (flattened hair cells) cover the surfaces of butterfly wings, cone-shaped protrusions are distributed along the membranes of true bugs (Heteroptera), and small hairs cover the membranes of fly wings (Wootton, 1992). Some of these features have known non-aerodynamic functions (e.g., sensory, signaling, thermoregulation), but the effects of most surface structures on aerodynamic force production remain unknown. Removal of scales from butterfly wings has been reported to decrease steady lift production (Nachtigall, 1965), but the expected changes in drag were not observed, so these results need to be verified. The addition of perpendicular staples (representing hairs) projecting from the surface of a flat plate accelerated from rest had no effect on unsteady force production (Dickinson and Götz, 1993). However, this model did not reproduce the backward curvature of hairs on fly wings, which may help direct flow over the wing surface (Wootton, 1992), and no other studies have addressed the influence of realistic insect wing surface structures on force production.

2.2 Wing shape

2.2.1 Planform shape

The effect of wing planform (two-dimensional) shape on force production has not been explored as extensively in insects as in birds and bats. Generally, high aspect ratio wings (long, skinny wings, typically with narrow tips) minimize induced drag and provide high lift to drag ratios by reducing the three-dimensional flow effects associated with tip vortices (see Aerodynamics, Flapping Wing Aerodynamics). But these predictions may not apply to gliders at insect-sized scales, where moderately broad wings (with intermediate aspect ratio) appear to minimize drag (Ennos, 1989b); indeed, many of the insects that do glide display unusually broad wings relative to their non-gliding relatives (Wootton, 1992).

Furthermore, predictions of optimal planform shape must be modified when the flapping motions of wings are considered. Because local velocity is highest at the wing tips, distal portions of the wing generate greater aerodynamic force per unit area (Dudley, 2000). Quasi-steady analyses of flapping flight therefore predict that distributing more area toward the wing tips (i.e., increasing r^2, the second moment of area) and/or increasing aspect ratio by extending the span (which increases the relative velocity at the tips) should be beneficial for force production. Theoretical models of flapping, compliant wings confirm that higher aspect ratio wings produce more force, but also suggest that particular combinations of wing shape, flexibility and flapping frequency may produce local optima in fluid dynamic efficiency (Combes and Daniel, 2001).

The formation of leading edge vortices and other unsteady force production mechanisms in rapidly flapping wings may further affect optimal shape predictions. Tripling the aspect ratio of model wings rotating around the sweep axis (i.e., translating continuously with a base to tip velocity gradient) had surprisingly little effect on unsteady force coefficients (Usherwood and Ellington, 2002b). Two different computational models have recently confirmed these results (Ansari, Knowles and Zbikowski, 2008; Luo and Sun, 2005), and have shown that the predicted benefits of increasing aspect ratio are less than expected during unsteady flight because as the span is extended and distal parts of the wing travel further, LEV shedding increases near the tip, reducing overall force generation. Increasing the proportion of area distributed toward the tips (without increasing span) does increase unsteady force production in these models, but this shape change would also increase inertial power requirements. No work has been done on the effects of planform wing shape on unsteady force production during stroke reversals (e.g., rotational circulation, wake capture, or clap and fling).

2.2.2 Corrugation

Dragonflies are well known for the extensive spanwise corrugation of their wings, but corrugation is in fact seen in many insect wings to some extent, especially near the basal leading edge. This corrugation clearly provides structural benefits, increasing spanwise bending stiffness (Rees, 1975) while minimizing material expenditure (Kesel, Philippi and Nachtigall, 1998) and allowing wings to twist extensively (Sunada, Zeng and Kawachi, 1998). For corrugation to be effective, wings must contain structures to prevent chordwise flattening, such as the serial angle brackets in the leading edge of dragonfly and locust wings (Figure 4a; Newman and Wootton, 1986; Wootton *et al*., 2000) or the stiff, cuticular bar near the wing base in flies (Rees, 1975).

Measurements on physical models suggest that corrugated wings in steady flow (i.e., gliding) produce as much lift as technical cambered airfoils, but experience lower drag (Kesel, 2000). However, CFD models accounting for unsteady effects on sweeping wings show that corrugated and flat plates at high angles of attack perform similarly, because the scale of corrugation is small compared to the separated flow region and size of the LEV (Luo and Sun, 2005). Overall, these studies suggest that the aerodynamic performance of corrugated wings is similar to that of either flat or cambered plates, depending on the flow conditions. Corrugated construction therefore provides wings with numerous structural benefits without any apparent detriment to force production.

2.2.3 Camber and twist

The wings of many insects exhibit some degree of camber at rest, particularly near the base, with a convex upper surface and a concave lower surface (Wootton, 1993). In addition, many wings undergo dynamic camber changes during flight, displaying instantaneous camber of up to 10% of chord length in locusts and up to 12% in hoverflies (Walker, Thomas and Taylor, 2008a). Dynamic camber is thought to be driven in some cases by “smart” structures, which automatically depress the flexible trailing edge during translation in response to aerodynamic and inertial forces. In some groups (e.g., dragonflies and flies), short, transverse veins or triangular groups of veins near the wing base act as levers, transmitting forces between the longitudinal veins they connect via flexible hinges (Ennos, 1989c; Wootton, 1991). In addition, Ennos (1988) has proposed that wings with a corrugated leading edge spar will automatically generate camber by transmitting torsional forces generated at the leading edge to veins that branch obliquely and curve backward toward the trailing edge. In addition to camber, some insect wings display innate spanwise twist at rest (with the wing tip pitched down), and many species exhibit significant dynamic twisting during flight (e.g., up to 25° in hawkmoths, 30° in locusts, and $>50^\circ$ in hoverflies; Walker, Thomas and Taylor, 2008a; Willmott and Ellington, 1997).

The aerodynamic effects of wing camber and twist in flying insects remain unclear. Cambered insect wings perform better than flat wings in steady flow (Ellington, 1984), and dynamic twist may improve force production in sweeping wings by providing a nearly constant angle of attack along the span (Walker, Thomas and Taylor, 2008b). However, physical models of unsteady, translational force production have not provided any evidence for the aerodynamic benefits of camber or wing twist in rapidly flapping insect wings. Cambered plates accelerated from rest (in pure translation) produce the same amount of force as flat plates (Dickinson and Götz, 1993), and neither camber nor twist has any effect on unsteady force production by sweeping model hawkmoth wings (Usherwood and Ellington, 2002a). However, rigid three-dimensional models may overlook some aspects of unsteady force production in translating, flexible wings that change shape continuously, and the effects of wing camber and twist on force production during stroke reversals have not yet been explored.

Regardless of whether or not wing profile affects unsteady force production, it is likely to have a substantial effect on the mechanical behavior of wings. For example, cambered plates twist and bend more easily when pushed on their convex surface than on their concave surface (Ennos, 1995); thus, camber may contribute to the observed dorsal–ventral asymmetry in wing flexural stiffness (Combes and Daniel, 2003b), as well as to the pronounced ventral flexion that occurs in many insect wings during supination (Figure 3; Wootton, 1992). Wing camber also leads to asymmetric twisting behavior in butterfly wings, permitting wings to twist extensively during supination but restricting their motion during pronation (Wootton, 1993).

3 CONCLUSIONS

This chapter highlights the need for further studies linking insect wing structure, and particularly wing flexibility, to dynamic shape changes and force production during flapping flight. Experimental work on the functional morphology of insect wings has been limited primarily to static testing, due to various technical challenges. These tests cannot accurately reproduce the complex and often unpredictable deformations of flapping insect wings in response to unknown and spatiotemporally variable forces. Significant advances in physical and computational modeling have been vital to uncovering previously unknown mechanisms of unsteady aerodynamic force production. However, incorporating wing flexibility and complex morphological features into these modeling approaches remains challenging because of the fundamental difficulties involved in scaling both material and fluid dynamics, and the computational expense associated with solving the Navier–Stokes equations for oscillating, compliant structures. The development of new experimental platforms capable of quantifying force production by real insect wings moving through controlled, complex trajectories at insect-like frequencies would allow us to begin exploring the many unanswered questions surrounding the link between insect wing structure, dynamic shape changes, and flight performance.

ACKNOWLEDGMENTS

The author would like to thank James Crall for helpful discussions and assistance with literature review.

REFERENCES

Ansari, S.A., Knowles, K. and Zbikowski, R. (2008) Insectlike flapping wings in the hover part 2: effect of wing geometry. *J. Aircraft*, **45**(6), 1976–1990.

Bergou, A.J., Sheng, X. and Wang, Z.J. (2007) Passive wing pitch reversal in insect flight. *J. Fluid Mech.*, **591**, 321–337.

Combes, S.A. and Daniel, T.L. (2001) Shape, flapping and flexion: wing and fin design for forward flight. *J. Exp. Biol.*, **204**, 2073–2085.

Combes, S.A. and Daniel, T.L. (2003a) Flexural stiffness in insect wings. I. Scaling and the influence of wing venation. *J. Exp. Biol.*, **206**, 2979–2987.

Combes, S.A. and Daniel, T.L. (2003b) Flexural stiffness in insect wings. II. Spatial distribution and dynamic wing bending. *J. Exp. Biol.*, **206**, 2989–2997.

Combes, S.A. and Daniel, T.L. (2003c) Into thin air: contributions of aerodynamic and inertial-elastic forces to wing bending in the hawkmoth Manduca sexta. *J. Exp. Biol.*, **206**, 2999–3006.

D'Andrea, M. and Carfí, S. (1991) Spines on the wing veins in Odonata: are they aerodynamic? in *Form and Function in Zoology* (eds G. Lanzavecchia and R. Valvassori), Selected Symposia and Monographs U.Z.1., 5, Mucchi, Modena, Italy, pp. 281–290.

Daniel, T.L. and Combes, S.A. (2002) Flexible wings and fins: bending by inertial or fluid-dynamic forces? *Integr. Comp. Biol.*, **42**, 1044–1049.

Dickinson, M.H. and Götz, K.G. (1993) Unsteady aerodynamic performance of model wings at low Reynolds numbers. *J. Exp. Biol.*, **174**, 45–64.

Dickinson, M.H., Lehman, F.O. and Sane, S.P. (1999) Wing rotation and the aerodynamic basis of insect flight. *Science*, **284**, 1954–1960.

Dudley, R. (2000) *The Biomechanics of Insect Flight*, Princeton University Press, Princeton, NJ.

Ellington, C.P. (1984) The aerodynamics of hovering insect flight. Part IV: aerodynamic mechanisms. *Phil. Trans. Roy. Soc. Lond. B*, **305**, 79–113.

Ellington, C.P., van den Berg, C., Willmott, A.P. and Thomas, A.L.R. (1996) Leading-edge vortices in insect flight. *Nature*, **384**, 626–630.

Ennos, A.R. (1988) The importance of torsion in the design of insect wings. *J. Exp. Biol.*, **140**, 137–160.

Ennos, A.R. (1989a) Inertial and aerodynamic torques on the wings of Diptera in flight. *J. Exp. Biol.*, **142**, 87–95.

Ennos, A.R. (1989b) The effect of size on the optimal shapes of gliding insects and seeds. *J. Zool., Lond.*, **219**, 61–69.

Ennos, A.R. (1989c) The comparative functional morphology of the wings of Diptera. *Zool. J. Linn. Soc.*, **96**, 27–47.

Ennos, A.R. (1995) Mechanical behaviour in torsion of insect wings, blades of grass and other cambered structures. *Proc. R. Soc. Lond. B*, **259**, 15–18.

Haas, F., Gorb, S. and Blickhan, R. (2000a) The function of resilin in beetle wings. *Proc. R. Soc. Lond. B*, **267**, 1375–1381.

Haas, F., Gorb, S. and Wootton, R.J. (2000b) Elastic joints in dermapteran hind wings: materials and wing folding. *Arthropod. Struct. Dev.*, **29**, 137–146.

Gorb, S. (1999) Serial elastic elements in the damselfly wing: mobile vein joints contain resilin. *Naturwissenschaften*, **86**(11), 552–555.

Kesel, A.B. (2000) Aerodynamic characteristics of dragonfly wing sections compared with technical aerofoils. *J. Exp. Biol.*, **203**, 3125–3135.

Kesel, A.B., Philippi, U. and Nachtigall, W. (1998) Biomechanical aspects of the insect wing: an analysis using the finite element method. *Comput. Biol. Med.*, **28**, 423–437.

Luo, G. and Sun, M. (2005) The effects of corrugation and wing planform on the aerodynamic force production of sweeping model insect wings. *Acta Mech. Sinica*, **21**, 531–541.

Miller, L.A. and Peskin, C.S. (2005) A computational fluid dynamics of 'clap and fling' in the smallest insects. *J. Exp. Biol.*, **208**(2), 195–212.

Miller, L.A. and Peskin, C.S. (2009) Flexible clap and fling in tiny insect flight. *J. Exp. Biol.*, **212**, 3076–3090.

Mountcastle, A.M. and Daniel, T.L. (2009) Aerodynamic and functional consequences of wing compliance. *Exp. Fluids*, **45**(5), 873–882.

Nachtigall, W. (1965) Die aerodynamische Funktion der Schmetterlingsschuppen. *Naturwissenschapter*, **52**(9), 216–217.

Nachtigall, W. (2000) Insect wing bending and folding during flight without and with an additional prey load. *Entomol. Gener.*, **25**(1), 1–16.

Newman, D.J.S. and Wootton, R.J. (1986) An approach to the mechanics of pleating in dragonfly wings. *J. Exp. Biol.*, **125**, 361–372.

Norberg, R.Å. (1972) The pterostigma of insect wings an inertial regulator of wing pitch. *J. Comp. Physiol.*, **81**, 9–22.

Rees, C.J.C. (1975) Form and function in corrugated insect wings. *Nature*, **256**, 200–203.

Smith, C.W., Herbert, R., Wootton, R.J. and Evans, K.E. (2000) The hind wing of the desert locust (*Schistocerca gregaria* Forskål). II. Mechanical properties and functioning of the membrane. *J. Exp. Biol.*, **203**, 2933–2943.

Song, F., Lee, K.L., Soh, A.K., Zhu, F. and Bai, Y.L. (2004) Experimental studies of the material properties of the forewing of cicada (Homòptera, Cicàdidae). *J. Exp. Biol.*, **207**, 3035–3042.

Sunada, S., Zeng, L. and Kawachi, K. (1998) The relationship between dragonfly wing structure and torsional deformation. *J. Theor. Biol.*, **193**, 39–45.

Triplehorn, C.A. and Johnson, N.F. (2005) *Borror and DeLong's Introduction to the Study of Insects*, 7th edn, Thomson Brooks/Cole, Belmont, CA.

Usherwood, J.R. and Ellington, C.P. (2002a) The aerodynamics of revolving wings. I. Model hawkmoth wings. *J. Exp. Biol.*, **205**, 1547–1564.

Usherwood, J.R. and Ellington, C.P. (2002b) The aerodynamics of revolving wings. II. Propeller force coefficients from mayfly to quail. *J. Exp. Biol.*, **205**, 1565–1576.

Vanella, M., Fitzgerald, T., Preidikman, S., Balaras, E. and Balachandran, B. (2009) Influence of flexibility on the aerodynamic performance of a hovering wing. *J. Exp. Biol.*, **212**, 95–105.

Vincent, J.F.V. and Wegst, U.G.K. (2004) Design and mechanical properties of insect cuticle. *Arthropod. Struct. Dev.*, **33**, 187–199.

Walker, S.M., Thomas, A.L.R. and Taylor, G.K. (2008a) Photogrammetric reconstruction of high-resolution surface topographies and deformable wing kinematics of tethered locusts and free-flying hoverflies. *J. Roy. Soc. Interface*, **6**(33), 351–366.

Walker, S.M., Thomas, A.L.R. and Taylor, G.K. (2008b) Deformable wing kinematics in the desert locust: how and why do camber, twist and topography vary through the stroke? *J. Roy. Soc. Interface*, **6**(38), 735–747.

Weis-Fogh, T. (1973) Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. Exp. Biol.*, **59**, 169–230.

Willmott, A.P. and Ellington, C.P. (1997) The mechanics of flight in the hawkmoth *Manduca sexta*. I. Kinematics of hovering and forward flight. *J. Exp. Biol.*, **200**, 2705–2722.

Wootton, R.J. (1979) Function, homology and terminology in insect wings. *Syst. Entomol.*, **4**, 81–93.

Wootton, R.J. (1991) The functional morphology of the wings of Odonata. *Adv. Odonatol.*, **5**, 153–169.

Wootton, R.J. (1992) Functional morphology of insect wings. *Ann. Rev.*, **37**, 113–140.

Wootton, R.J. (1993) Leading edge section and asymmetric twisting in the wings of flying butterflies (Insecta, Papilionoidea). *J. Exp. Biol.*, **180**, 105–117.

Wootton, R.J., Evans, K.E., Herbert, R. and Smith, C.W. (2000) The hind wing of the desert locust (*Schistocerca gregaria* Forskål). I. Functional morphology and mode of operation. *J. Exp. Biol.*, **203**, 2921–2931.