Experimental investigations of the functional morphology of dragonfly wings

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Nowadays, the importance of identifying the flight mechanisms of the dragonfly, as an inspiration for designing flapping wing vehicles, is well known. An experimental approach to understanding the complexities of insect wings as organs of flight could provide significant outcomes for design purposes. In this paper, a comprehensive investigation is carried out on the morphological and microstructural features of dragonfly wings. Scanning electron microscopy (SEM) and tensile testing are used to experimentally verify the functional roles of different parts of the wings. A number of SEM images of the elements of the wings, such as the nodus, leading edge, trailing edge, and vein sections, which play dominant roles in strengthening the whole structure, are presented. The results from the tensile tests indicate that the nodus might be the critical region of the wing that is subjected to high tensile stresses. Considering the patterns of the longitudinal corrugations of the wings obtained in this paper, it can be supposed that they increase the load-bearing capacity, giving the wings an ability to tolerate dynamic loading conditions. In addition, it is suggested that the longitudinal veins, along with the leading and trailing edges, are structural mechanisms that further improve fatigue resistance by providing higher fracture toughness, preventing crack propagation, and allowing the wings to sustain a significant amount of damage without loss of strength.

Keywords: dragonfly wings, SEM, tensile test, nodus, longitudinal corrugation

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1. Introduction

Bionics or biomimetics is a new scientific and technical discipline that attempts to create artificial structures inspired by those found in nature. This multidimensional empirical knowledge involves a wide variety of fields, such as biology, physics, chemistry, mathematics, material science, and biomechanics.

Recent scientific discoveries have shown that all natural materials, tissues, and structures have the most optimized shape and physical appearance. Hence, we dare to say that mimicking nature is the best way to create engineering structures and sustainable products.

One of the most remarkable features of nature is its proficiency in the science of engineering design. Our previous work has showed that insects' wings are one of the best examples of design perfection[1–5] because they are superlightweight composite structures that have complex configurations at both the macro and micro levels. One of the most amazing and interesting wing structures belongs to dragonflies. The wings, as organs of flight, enable the insect to perform a very smooth and stable flight with remarkable agility. A variety of unique flight maneuvers, including flapping, hovering, gliding, and taking off, are demonstrated by dragonflies. In fact, they are one of the fastest and most agile flying insects in the living world.

What is beyond doubt is that both the macro and micro structures of dragonfly wings play an important role in their efficiency, and this is why many researchers have tried to study the effects of these two factors on wing performance and controllability.

Newman's work exhibited the wide range of structural complexities in the vein sections, the shape of the cross-veins and their intersections with the longitudinal veins.[6] The experimental analysis and numerical modeling of veins was performed by Wang *et al.*[7] The experimental data were obtained from scanning electron microscopy (SEM), tensile, and three-point bending tests, and the numerical models were developed using the finite element method. The results showed that the vein has a sandwich microstructure that increases the bending and twisting stiffness of the wings. A micro-CT scanner was used by Jongerius and Lentink[8] to make a three-dimensional (3D) scan of a dragonfly wing. The scans contain a significant amount of accurate and reliable data relating to the wing venation patterns and the thickness distribution of the veins and membranes.

Two-dimensional (2D) cross sections of the wings of a dragonfly were obtained by Okamoto *et al.*[9] The magnified photographs indicated that the wings are corrugated in the chordwise direction. A set of valuable observations was collected by Ren *et al.*[10] to explore these corrugations. Their experimental results revealed that the corrugated angles between the longitudinal veins range from 80° to 150°.

An experimental investigation on the wing membrane was

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done by Song *et al.*[11] It was found that the membrane has a three-layered microstructure with different thickness values. Further, it was observed that the surface of the wing venations is composed of numerous nanometer-scale columns coated by a cuticle waxy layer. This wing covering was thoroughly analyzed by Gorb *et al.*,[12] who used a combination of acoustic microscopy, SEM, and transmission electron microscopy (TEM) techniques to identify the possible functions of this waxy layer. Another valuable study on the wax covering was carried out recently.[13] The authors suggested that the primary function of the mentioned layer is to reduce the surface wettability by water. Other potential functions were also discussed in detail.

Combes *et al.*[14] examined the effects of wing damage on dragonfly flight performance. They suggested that the morphology of the wings has a significant influence on their ability to undergo numerous flapping cycles. A review on the morphologies of dragonfly wings and their mechanical properties was given by Sun and Bhushan.[15] They further used the topology optimization method to design a strong, stiff, and lightweight film.

The above-mentioned studies are a number of remarkable researches on the microstructural features and mechanical properties of dragonfly wings. But, as far as we know, the effects of some wing parameters on its mechanical characteristics are still unknown.[12,16]

The microstructures of dragonfly wings were previously investigated by us.[1–3] We used our knowledge to develop comprehensive numerical models to simulate the wing dynamics. Here, we present our new empirical findings about dragonfly wings and their microstructures.

In this paper, a detailed study of the morphological and microstructural aspects of dragonfly wings is made using an SEM technique to give a better understanding and description of the different parts of the insect wings. The main structural components of the wings are introduced and their specific roles are explained in detail. A number of possible functions are proposed for some parts of the wings. Tensile tests are performed on dragonfly wing samples to validate the assumptions. In addition, for the first time, the different patterns of the longitudinal corrugations of both the forewing and hindwing are explored and their effects are thoroughly discussed. The obtained results are very interesting. The aim of this paper is to provide an overview and to increase the understanding of the unique mechanical-structural characteristics of dragonfly wings.

2. Materials and methods

2.1. Scanning electron microscopy

As is well known, the mechanical performances of biomaterials and biological tissues critically depend on their compositions on the microscopic scale. Based on this argument, it can be concluded that the microstructure of the wing of a dragonfly has a great influence on its functions. Therefore, a Philips XL30 SEM device was used to observe, follow, and characterize the wing morphology and microstructure. To prepare the samples for SEM imaging, an untreated wing was chosen and dried for 24 hours at room temperature. Although the drying process can deform the shape of the wing, it is necessary to obtain high-quality images. After drying, the sample was cut into an appropriate size and fixed onto the stubs using double-sided sticky tape. Then, small pieces of the wing were coated with a thin gold-palladium layer using a sputter coater. Finally, each sample was scanned under the microscope and a number of remarkable observations were made.

It is interesting to note that in order to provide appropriate cross sections of the wing, samples were plunged into liquid nitrogen and held for a few minutes. Thereafter, the brittle samples were taken out and quickly broken into smaller pieces. Finally, the small pieces were investigated under the SEM device along their thickness direction.

2.2. Mechanical testing

Forty fresh samples (20 forewings and 20 hindwings) were carefully taken from dragonflies with the same physical characteristics. All the dragonflies had been gassed with ethylacetate and died only a few seconds before the test began, to preserve their mechanical capabilities. The whole process of sample preparation and testing took about 10 minutes. Mechanical testing was performed using a vertical tensile testing machine with two clamps (Fig. 1(a)). The specimens were placed in the test machine to study the mechanical behaviors of the wing structure under the effect of external tensile forces.

In order to prevent any local damage, slipping or unwanted rupture at the grip interface, four rough rectangles of pasteboard were cut and placed on two sides of each wing specimen (Fig. 1(b)). The rectangle pasteboards were cemented to the wings using a small drop of cyanoacrylate adhesive. Finally, each test specimen was held by the grips of the tensile testing machine at the pasteboards (Fig. 1(c)).

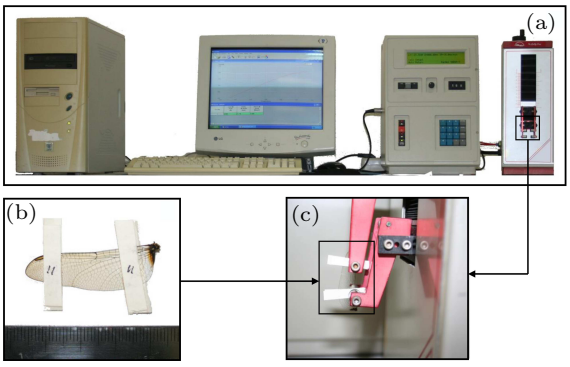


Fig. 1. (color online) (a) A front view of the tensile testing machine. (b) A wing specimen. (c) The specimen in the test rig.

2.3. Section photography

Because of the importance of the size, shape, and pattern of the longitudinal corrugations of dragonfly wings, five forewings and five hindwings were widely investigated. The wings were prepared and placed on a substrate. Four longitudinal sections were made on each wing, and the sections were obtained by slicing the wings with a razor blade, parallel to the spanwise direction. They were then fixed vertically in a soft polystyrene substrate. High-magnification images were taken from the sections, and finally, using a simple image processing technique, the coordinates of all the points on the longitudinal section were determined with respect to a chosen origin.

3. Results and discussion

The typical dragonfly studied in this section is shown in Fig. 2. It is called "Orthetrum sabina", and can be widely found in the north of Iran, flying around the rice fields during spring and summer. The maximum length and width of the forewing and hindwing are 39.12 mm, 9.11 mm, 36.89 mm, and 11.54 mm, respectively, as measured using a digital caliper (Mitutoyo, Tokyo, Japan) with an accuracy of 0.01 mm.



Fig. 2. Photograph of an Orthetrum sabina.

The main component of the external skeleton of the insect is chitin. Chitin, which is a long-chain polymer of N-acetyl glucosamine, is insoluble in water.[17] The essential function of chitin is to prevent the insect from losing too much water, which can be important under dry environmental conditions. Another significant role of chitin is to serve as a mechanically strong layer to protect the insect's wings and body against physical damage, as well as moisture and dirt. In addition, it is very interesting to note that chitin has remarkable antifungal and antibacterial properties.[18,19] These characteristics can defend the body against harmful biological agents.

As seen in Fig. 2, the insect wing is generally composed of two key components, namely veins and membranes. The veins have been extended as a structural network in the wing to provide a series of rigid frameworks for the membranes. In other words, they are the main supporting elements in the wing construction. They increase its strength and stiffness and improve its functional performance.

There are considerable differences in the shape and size between the veins. This is why they are divided into three types: ambient veins, longitudinal veins, and cross veins. Those veins that encircle the wing, acting as a framework, are commonly called ambient veins. The leading and trailing edges of the wing are supported by an ambient vein. In fact, the ambient vein increases the stiffness of the margin of the wing and also forms its boundary.

Longitudinal veins are those extended from the base to the tip. They provide superior rigidity to the wing structure and protect it from bending and torsional moments. These veins are anchored to the base of the wing and can be easily controlled by the insect. The longitudinal veins are joined together with a series of small light veins called cross-veins, which are irregularly distributed throughout the wing. The cross-veins stiffen the wing and enhance its aerodynamic performance.[20]

The thickness of the veins decreases from the wing base to the wing tip and from the leading edge to the trailing edge. This enables the wing to be more flexible near the tip and the trailing edge. This feature consequently allows the wing to effectively bear both inertial and aerodynamic forces.[8,21]

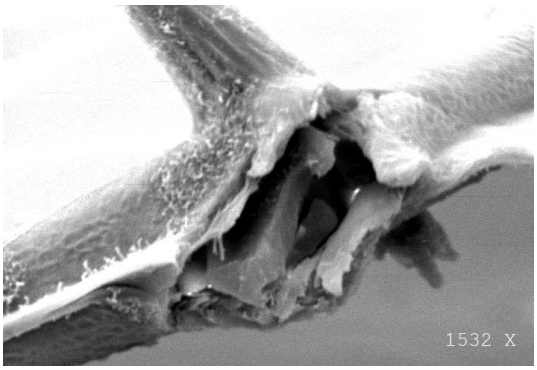


Fig. 3. The hollow microstructure of veins and spins (1532X).

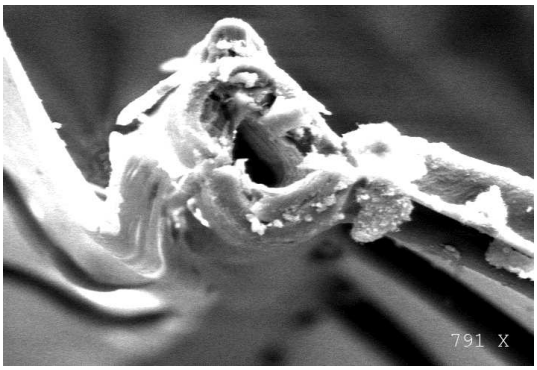


Fig. 4. The microstructure of a tubular vein (791X).

The wing veins have tubular cross sections (Figs. 3–5). These tubular structures are largely made from chitin and protein. Actually, each vein has a sandwich-type configuration

including two chitinous shells separated by a fibrous protein layer, as seen in Fig. 5. This type of biological architecture reduces the weight of the wing and leads to minimum energy consumption. On the other hand, it can increase the stiffness of the structure extremely against bending moments and twisting deformations.[7,22]

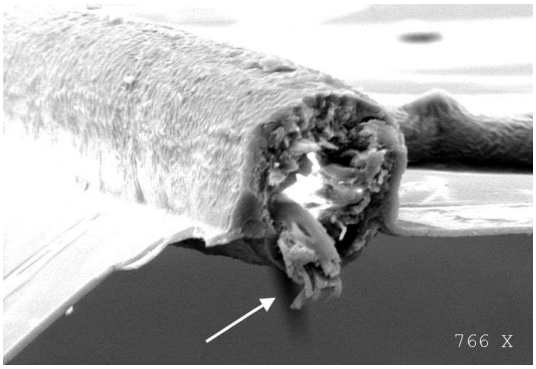


Fig. 5. The fibrous protein layer in the vein wall (766X).

It is expected that the maximum value of the aerodynamic bending load generated during flight is tolerated by the chitinous layers, especially the outer one. This is because the protein layer acts as a ductile material and, as previously reported, it mainly experiences torsional deformations.[7]

The membrane is the ultrathin transparent film, which has been stiffened by the veins. Its primitive function is possibly to prevent the passage of air through the wing. But, we have also demonstrated that the membranes of insect wings, in some regions, act as a stressed skin to stiffen the whole structure.[23–25] It is also subjected to relatively large bending and twisting moments during flight.[26–28]

The membrane has a three-layered microstructure.[11] The central layer is typically thicker than the covering layers. Both covering layers are almost the same in thickness and mechanical property. The same variation is found in the membrane thickness as observed in the veins, and this provides a similar effect on the flight dynamics of the wing.[8]

The entire surface of the membrane is coated with a very thin rough waxy layer, which clearly enhances the strength of the wing and provides strong protection against environmental agents.[29] This layer also has a super-hydrophobic and self-cleaning microstructure (Fig. 6). Self-cleaning reduces energy consumption and hydrophobicity causes a sharp increase in flight agility when the insect flies in a humid place. The waxy layer, however, performs a more important task. It controls the wing surface boundary layer, and in this way fulfills an aerodynamic function.[9,29,30] Actually, the surface roughness of the wing results in a considerable increase in the maximum lift coefficient and the maximum lift to drag ratio.[9]

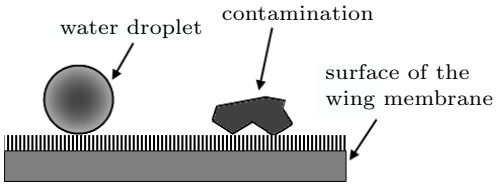


Fig. 6. Schematic view of the hydrophobic and self-cleaning effects of the surface microstructure of the wing.

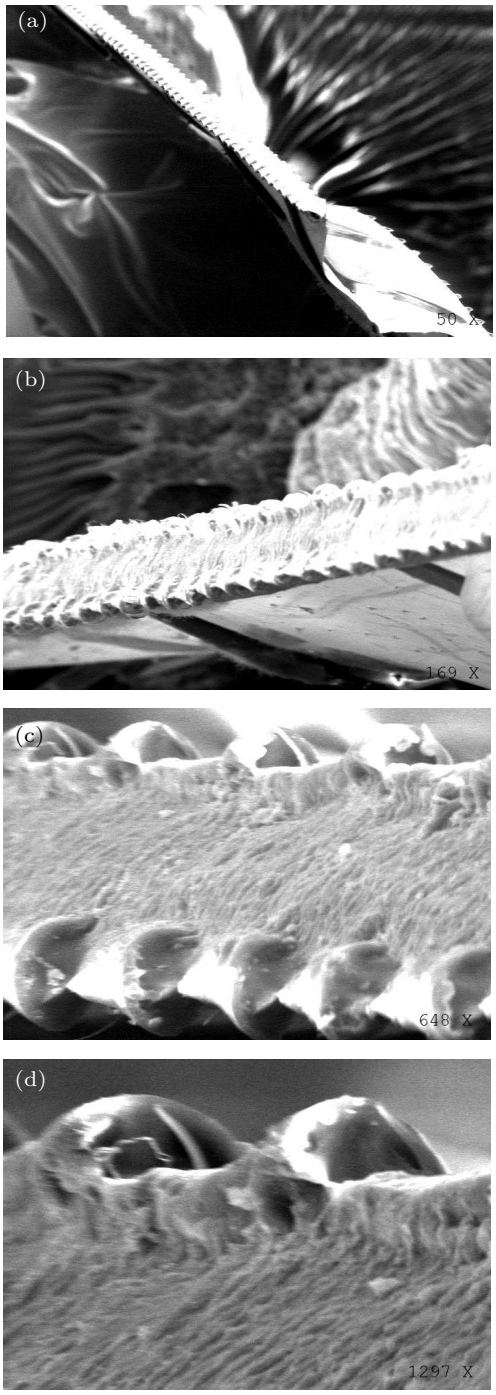


Fig. 7. SEM images of the leading edge of the wing. (a) 50X; (b) 169X; (c) 648X, and (d) 1297X.

The dragonfly wing is divided into different regions with different shapes and areas. These regions are named “cell”. In other words, each cell is an area of membrane separated

by veins. The cells near the leading edge are often square or rectangular, but their shapes and sizes considerably change towards the trailing edge. As depicted in Fig. 2, the trailing edge is mainly composed of non-square cells (e.g. rectangular, pentagonal, and hexagonal ones). Most of the cells in this region are obviously smaller and less uniform in shape. Certainly, the four-sided cells are stiffer than the others. The bending and twisting deformations in a square cell structure are lower than a hexagonal one. This feature allows the wing to be more rigid at the leading edge and more flexible at the trailing edge.

It is supposed that the configuration of the leading edge is very important for the flight capacity of the insect. A three-dimensional configuration is illustrated by Figs. 7(a)–7(d), showing the leading edge of the wing. The leading edge provides exceptional structural strength and stiffness for the wing. It causes a remarkable increase in the flexural stiffness of the wing and significantly improves its aerodynamic and stability characteristics.[6,9,26,27,31]

Electron microscopic images of the trailing edge reveal a series of three-dimensional spade-shaped spines (Figs. 8(b) and 8(c)). It is assumed that these structural elements play an important role in the flight of the insect. They act as Gurney flaps, increasing the lift coefficient as well as stabilizing the flight maneuverability.[32] Figure 8(d) shows the magnified details of the trailing edge.

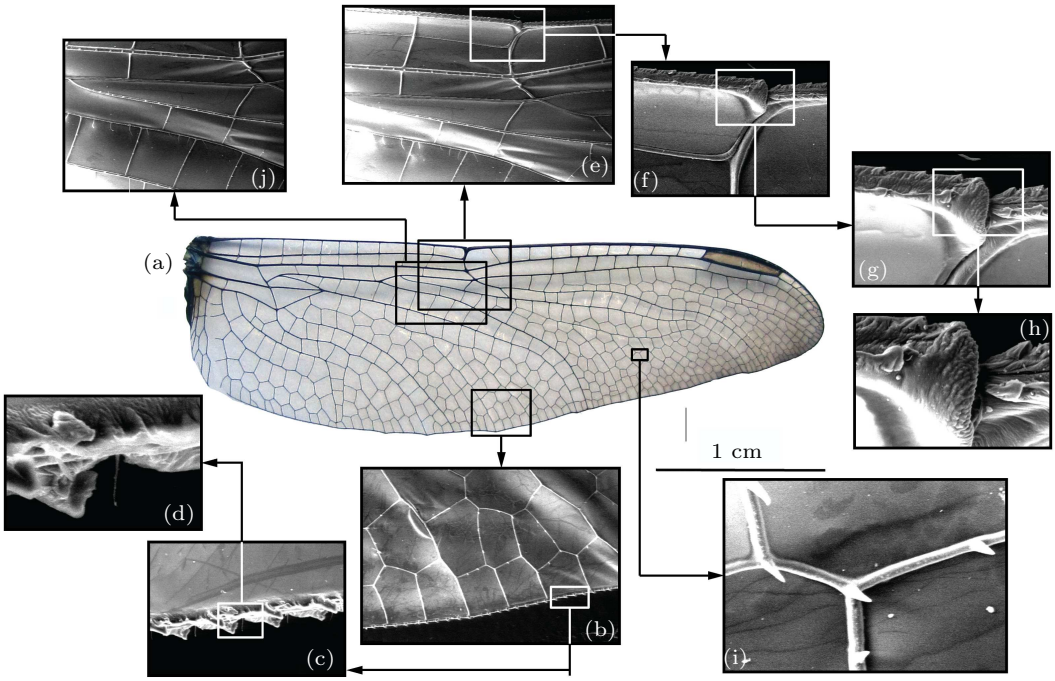


Fig. 8. A selection of SEM images of the dragonfly hindwing. (a) The hindwing of Orthetrum sabina; (b), (c), (d) the trailing edge with three-dimensional spade-shaped spines, 37X, 300X, and 1200X, respectively; (e)–(h) the nodus, 22X, 90X, 181X, and 362X, respectively; and (i), (j) the distributed spines on the wing, 28X and 322X, respectively.

One of the main structural components of the wing is the nodus. As depicted in Fig. 8(e), the nodus is a semicircular spot located at the center of the leading edge. It connects the basal part with the distal part. It is actually a hinge-like structure that increases flexibility and prevents the wing from bending failure. This is because the nodus prevents the bending moment in the center of the leading edge from becoming too high.[33] Likewise, results from previous studies suggest that the nodus has a major influence on the spatial distribution of inertial loads.[8] Closer views of the nodus are provided in Figs. 8(f)–8(h).

Figure 9 shows the initiation of fracture in a dragonfly wing. It is very important to note that all fractures are initiated at the nodus, i.e., the nodus is the critical location with the highest stress concentration when the wings are under tensile forces.

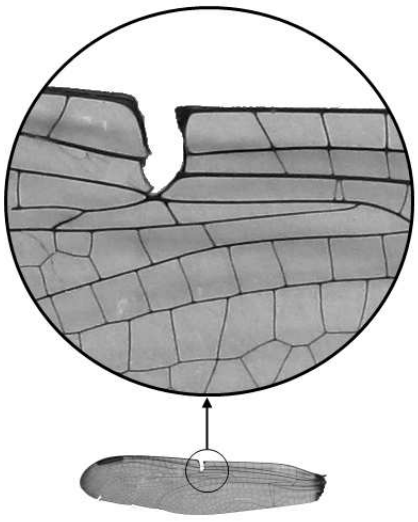


Fig. 9. Limited crack propagation in a test specimen.

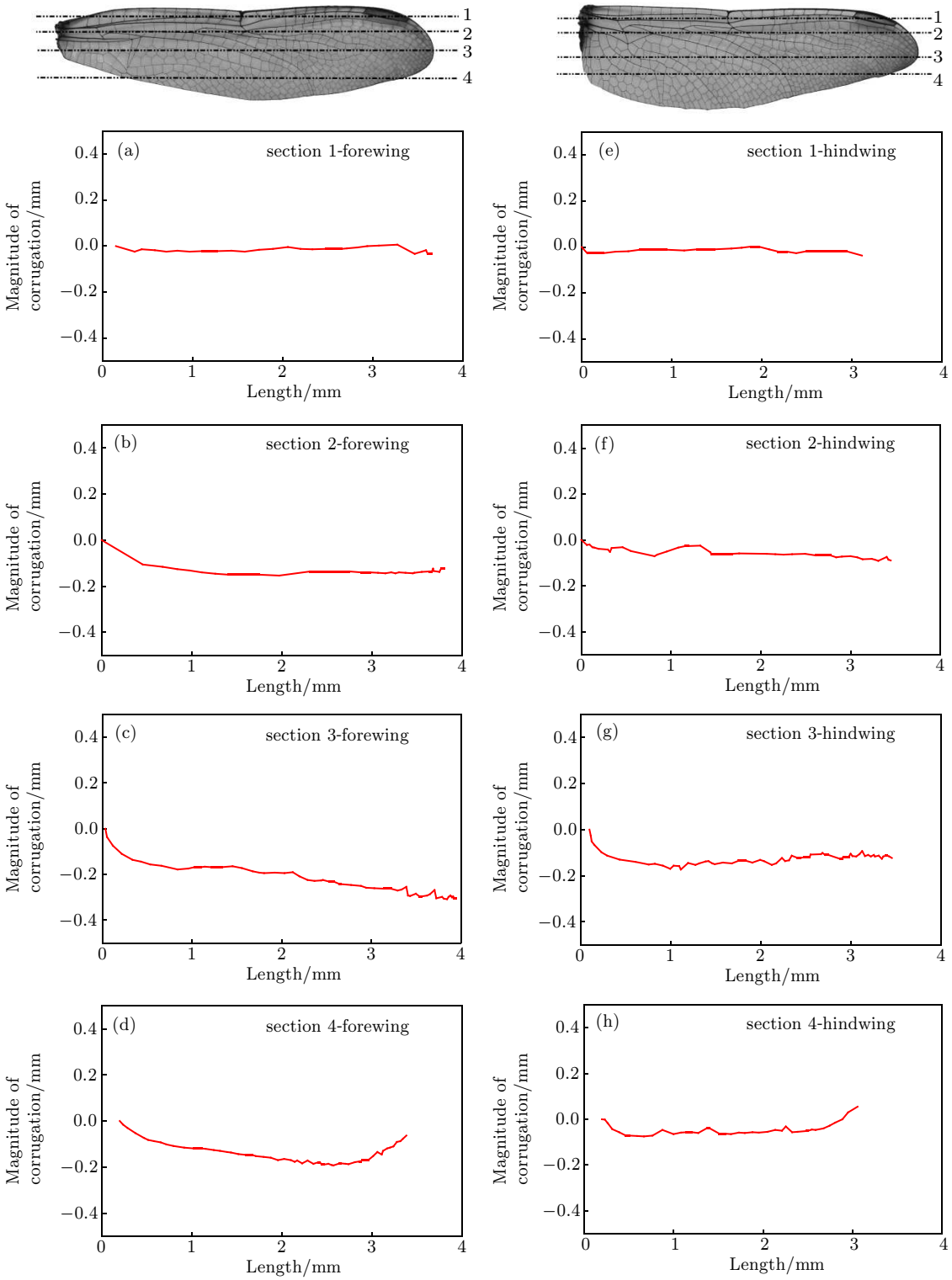


Fig. 10. (color online) The different patterns of the longitudinal sections of both the forewing and hindwing. (a) Section 1, (b) section 2, (c) section 3, and (d) section 4 of the forewing. (e) Section 1, (f) section 2, (g) section 3, and (h) section 4 of the hindwing.

Another important consideration in the design of dragonfly wings is the pterostigma. The pterostigma is a dark, thickened, and blood-filled membrane structure near the tip of the wing. The pterostigma has a favorable aerodynamic function. It increases the stability of the wings by moving the centre-of-mass towards the leading edge and passively controls the angle of attack of the wing during flapping flight.[34–38] It is also believed that the pterostigma reduces wing flutter during gliding and therefore raises the maximum speed at which gliding can occur.[34] Additionally, it can be utilized as a visual marker to detect and court females.

The SEM images reveal that a number of tiny and narrow spines are densely distributed on the veins all over the wings (Figs. 8(i) and 8(j)). The spines each have a hollow

microstructure (Fig. 3). They are usually cone-shaped with a dome-like tip. It is assumed that the spines are efficient and effective mechanisms to provide an optimized flow of air above the wing surface.[1] Additionally, we propose that another function of the spines is to facilitate convection cooling of the insect wings, because they increase the contact surface area between the air and the wing.

Cross-sectional corrugations at the middle and trailing edge increase the lift coefficients at all Reynolds numbers. These corrugations also decrease the drag force acting on the wing.[39] Another important role of the cross-sectional corrugations is to improve the flexural rigidity of the wing structure.[40]

Different patterns of the longitudinal corrugations of both the forewing and hindwing are plotted in Fig. 10. The patterns are related to four longitudinal sections on each wing. Figure 10(a) illustrates the pattern of the forewing corrugation in section 1. As seen in this figure, the magnitude of the longitudinal corrugation remains without significant changes all the way through this section. As can be seen from Fig. 10(b), in section 2, there is an increase in the magnitude of the corrugation near the base, while it remains almost constant in the longitudinal direction. In section 3, a continuous increase in the magnitude of the longitudinal corrugation, from the base to the tip, can be observed with respect to the base point (Fig. 10(c)). The pattern of the longitudinal corrugation in section 4 is shown in Fig. 10(d). The drawn pattern indicates that the magnitude of the corrugation is increasing, but near the tip an abrupt change occurs in the corrugation slope.

The corrugation patterns of the hindwing, along the spanwise direction, are shown in Figs. 10(e) and 10(f). The profiles of the corrugation of the hindwing, in sections 1 and 2, are approximately the same as those of the forewing. But, from a morphological point of view, there are differences in the corrugation pattern between the wings in sections 3 and 4. In fact, in section 3, unlike in the forewing, the slope of the longitudinal corrugation of the hindwing after a rapid increase slightly decreases (Fig. 10(g)). Finally, in section 4, near the base, an increase occurs in the magnitude of the corrugation, but after that a continuous decrease takes place (Fig. 10(h)).

It is clear that the longitudinal bending of the wings increases with the increase in the longitudinal corrugations towards the tip. On the other hand, the experimental results from the tensile loading of the wing samples indicate that these corrugations have a great influence on the load-bearing capacity of the wings. The longitudinal corrugations also increase the elongation ability and longitudinal flexibility of dragonfly wings. In fact, these corrugations are anti-failure mechanisms that prevent structural damage due to external applied loads. A force-elongation diagram of a dragonfly hindwing is given in Fig. 11. It appears that each peak on this diagram corresponds to the tensile rupture of one of the reinforcing longitudinal veins. The first peak is related to the tensile resistance of the first longitudinal vein (costa). Once the initial crack starts to grow, it rapidly reaches the next longitudinal vein. Indeed, the membrane between two longitudinal veins experiences a catastrophic failure. Then, it can be concluded that the longitudinal veins are the main components that increase the fracture toughness values of the wings.

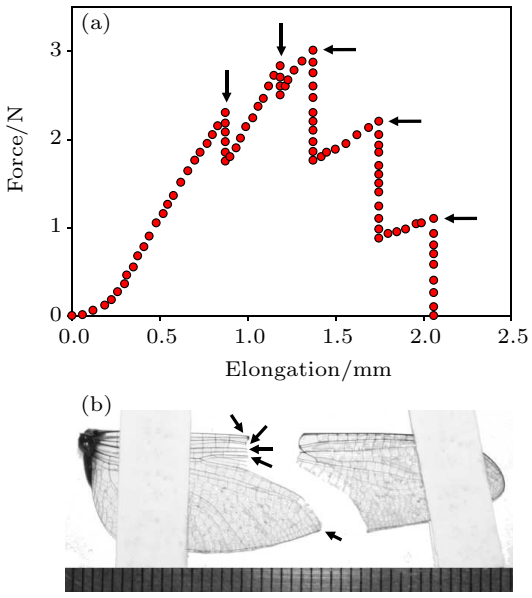


Fig. 11. (color online) (a) Force-elongation diagram of a hindwing. (b) The top view of a fractured hindwing under tensile loading. The fracture is initiated from the nodus, rapidly passes through the membrane, and when it reaches the next longitudinal vein it is stopped.

The fracture strains obtained from the tensile testing experiments for the forewing and hindwing are 5.65% and 5.58%, respectively. These values are obviously higher than the fracture strain of the chitin (1%–2%), which is the main component of the insect wing and body. The mechanical behavior of the wings subjected to tensile loads needs further investigation, and the results will be presented in our future work.

4. Conclusion

In this work, detailed observations on dragonfly wings are performed using SEM. The obtained images are employed to study the surface morphologies and microstructures of the wings. A vertical tensile testing machine is used to explore the mechanical behaviors of the wings under tensile forces.

The SEM images taken from the leading and trailing edges display a crimped structure. This structure effectively increases the stiffness of the wing and potentially prevents crack initiation and tearing. In total, the reinforced wing structure seems to be an effective design that prevents crack propagation by providing tough barriers in front of the crack tips.

The typical images of the fractured surfaces due to tensile loads indicate that the nodus is the critical region of the

wing. The relatively extensive elongations of the samples under tensile loading conditions verify that the longitudinal corrugations are beneficial as anti-failure patterns because they significantly improve the load-bearing capacity of the wing. They also increase the flexibility of the wing structure, thereby affecting its fatigue resistance.

Moreover, concerning the hollow shape and microstructure of the spines, it can be proposed that the combination of multiple spines and longitudinal corrugations can provide an optimized fatigue resistance when the wings are subjected to dynamic loading conditions. The spines may also have an effective role in normalizing the wing temperature due to the increased surface area of the wings. The results from the present study may be useful in the further development of new designs inspired from dragonflies.

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References

[1] Rajabi H, Moghadami M and Darvizeh A 2011 *J. Bionic Eng.* **8** 165
[2] Darvizeh M, Darvizeh A, Rajabi H and Rezaei A 2009 *Int. J. Multiphysics* **3** 101
[3] Darvizeh A, Rajabi H and Khaheshi A 2011 *International Bionic Engineering Conference*, September 18–20, 2011, Boston, USA, p. 3
[4] Darvizeh A, Rajabi H, Khaheshi A, Etedadi J and Sobhani M K 2011 *International Bionic Engineering Conference*, September 18–20, 2011, Boston, USA, p. 7
[5] Darvizeh A, Rajabi H, Khaheshi A, Sobhani M K and Etedadi J 2011 *International Bionic Engineering Conference*, September 18–20, 2011, Boston, USA, p. 13
[6] Newman D L S and Wootton R J 1986 *J. Exp. Biol.* **125** 361
[7] Wang X S, Li Y and Shi Y F 2008 *Compos. Sci. Tech.* **68** 186
[8] Jongerius S R and Lentink D 2010 *Exp. Mech.* **50** 1323
[9] Okamoto M, Yasuda K and Azuma A 1996 *J. Exp. Biol.* **199** 281
[10] Ren H H, Wang X S, Chen Y L and Li X D 2012 *Chin. Phys. B* **21** 034501
[11] Song F, Xiao K W, Bai K and Bai Y L 2007 *Mat. Sci. Eng. A* **457** 254
[12] Gorb S N, Kesel A and Berger J 2000 *Arth. Struct. Dev.* **29** 129
[13] Wan Y L, Cong Q, Wang X J and Yan Z 2008 *J. Bionic Eng.* **5** 40
[14] Combes S A, Crall J D and Mukherjee S 2010 *Biol. Lett.* **6** 426
[15] Sun J and Bhushan B 2012 *Compt. Rend. Mec.* **340** 3
[16] Gorb S N, Tynkkynen K and Kotiaho J S 2009 *Int. J. Odonat.* **12** 205
[17] Nakatani H and Hiromi K 1974 *J. Biochem.* **76** 1343
[18] Jing Y J, Hao Y J, Qu H, Shan Y, Li D S and Du R Q 2007 *Acta Biol. Hung.* **58** 75
[19] Kulikov S N, Tiurin Iu A, Fassakhov R S and Varlamov V P 2009 *Zh. Mikrob. Epidem. Immun.* **5** 91
[20] Thomas M A, Walsh K A, Wolf M R, McPheron B A and Marden J H 2000 *Proc. Natl. Acad. Sci.* **97** 13178
[21] Machida K, Oikawa T and Shimanuki J 2006 *Key Eng. Mat.* **326** 819
[22] Li Yand and Wang X S 2008 *Adv. Mater. Res.* **33** 785
[23] Ennos A R 2011 *Solid Biomechanics* (New Jersey: Princeton University Press) p. 95
[24] Wootton R J, Evans K E, Herbert R C and Smith C W 2000 *J. Exp. Biol.* **203** 2921
[25] Newman D J S 1982 "The Functional Wing Morphology of Some Odonata", Ph. D. dissertation (Exeter: University of Exeter)
[26] Combes S A and Daniel T L 2003 *J. Exp. Biol.* **206** 2979
[27] Combes S A and Daniel T L 2003 *J. Exp. Biol.* **206** 2989
[28] Wootton R J 1990 *Sci. Am.* **263** 114
[29] Kreuz P, Arnold W and Kesel A B 2001 *Ann. Bio. Eng.* **29** 1054
[30] Wang Z J 2005 *Ann. Rev. Fluid Mech.* **37** 183
[31] Marrocco J, Venkataraman S and Demasi L 2009 *Proceeding of the Applied Computational Science and Engineering Student Support (ACSESS)*, March 27, 2009, San Diego, USA, p. 13
[32] Bechert D W, Meyer R and Hage W 2000 *Fluids Conference and Exhibit*, June 19–22, 2000, Denver, USA, p. 1
[33] Machida K and Shimanuki J 2005 *Proceedings of SPIE — The International Society for Optical Engineering, Third International Conference on Experimental Mechanics and Third Conference of the Asian Committee on Experimental Mechanics*, November 29, 2004 Singapore, p. 671
[34] Chapman R F 1998 *The Insects: Structure and Function*, 4th edn. (Cambridge: Cambridge University Press) p. 788
[35] Norberg R A 1972 *J. Comp. Phys.* **81** 9
[36] Li Z X, Wei S, Tong G S, Tian J M and Loc V Q 2009 *J. Zhejiang Univ. Sci. A* **10** 72
[37] Sudo S, Tsuyuki K, Ikohagi T, Ohta F, Shida S and Tani J 1999 *JSME Int. J. Series C* **42** 721
[38] DiLeo C and Deng X 2009 *Adv. Robotics* **23** 1003
[39] Kim W K, Ko J H, Park H C and Byun D 2009 *J. Theor. Biol.* **260** 523
[40] Ree C J C 1975 *Nature* **256** 200