

Repairable cascaded slide-lock system endows bird feathers with tear-resistance and superdurability

Feilong Zhang^{a,b,c}, Lei Jiang^{a,c,d}, and Shutao Wang^{a,c,e,1}

^aChinese Academy of Sciences Key Laboratory of Bio-Inspired Materials and Interfacial Science, Technical Institute of Physics and Chemistry, Chinese Academy of Sciences, 100190 Beijing, People's Republic of China; ^bBeijing National Laboratory for Molecular Sciences, Key Laboratory of Green Printing, Institute of Chemistry, Chinese Academy of Sciences, 100190 Beijing, People's Republic of China; ^cSchool of Future Technology, University of Chinese Academy of Sciences, 100049 Beijing, People's Republic of China; ^dKey Laboratory of Bio-Inspired Smart Interfacial, Science and Technology of Ministry of Education, School of Chemistry and Environment, Beihang University, 100191 Beijing, People's Republic of China; and ^eChinese Academy of Sciences Center for Excellence in Nanoscience, Chinese Academy of Sciences, 100190 Beijing, People's Republic of China

Edited by J. Aizenberg, Harvard University, Cambridge, MA, and accepted by Editorial Board Member John A. Rogers August 15, 2018 (received for review May 16, 2018)

Bird feathers have aroused tremendous attention for their superdurability against tears during long flights through wind and even bushes. Although feathers may inevitably be unzipped, the separated feather vanes can be repaired easily by bill stroking. However, the mechanism underlying bird feathers' superdurability against tears remains unclear. Here, we reveal that the superdurability of bird feathers arises from their repairable cascaded slidelock system, which is composed of hooklets, a slide rail, and spines at the end of the slide rail as terminating structures. Microscopy with a micronano manipulating system and 3D X-ray microscopy provided high-level visibility into the 3D fine structures and the entire unzipping process of feathers. The hooklets can slide along the slide rail reversibly when suffering external forces, and the sliding hooklet can be locked by the spine at the ends of barbules when larger pulling forces are applied and even slide farther away due to the unzipping of the interlocking structure with large deformation of the barbules. The elongation before separation of adjacent barbs can reach up to 270%, and the separation force can be maintained above 80% of the initial value even after 1,000 cycles of separating and repairing. These results prove that the cascaded slide-lock system ensures the superdurability of bird feathers against tears.

feather | cascaded slide-lock | superdurability | repairable | flexible

fter a long or tumultuous flight through bushes, birds are A often found preening their disordered feathers with their bill, which is considered to repair separated feather vanes (1). To understand the superdurability of feathers against tears, we examined their separation and repair by hand (Fig. 1). With one hand holding the rachis of a feather, the other hand pulled the vanes at the direction from the tip to the calamus (Fig. 1A). The feather vane was stretched and separated along the veins (barbs) in a moment (Fig. 1B, red arrow), while the separated feather vane can be repaired (red dashed line) by stroking lightly with fingers along the direction from the calamus to the tip (Fig. 1C). Remarkably, when pulled at another position (Fig. 1D), the vane was likely to be separated, not along the red dashed line shown in Fig. 1D but along a new one (Fig. 1E, blue arrow), and the separated feather could be repaired again (Fig. 1F, blue dashed line). This separation and repair process can be performed repeatedly, indicating that feathers have a high self-repairing capability.

The fascinating structural features of bird feathers are closely related to the evolution, courtship, and taxonomy of birds and the unique optical and mechanical properties of feathers, which have attracted tremendous attention over the past centuries. Since Hooke (2) drafted the first rough model of feather structures in 1665, many efforts have been made to explore the structure and function of feathers. Microscale hooks and grooves (3–5) and their functions have been observed and illustrated with optical and electron microscopy (1, 6–11). Unfortunately, to

date, the superdurability of feathers against tears has remained linked to the interlocking hook-and-groove model, which cannot yet explain that superdurability adequately. Here, we carried out comprehensive and detailed observations to explore the superdurability of bird feathers and have demonstrated that feathers form a repairable cascaded slide-lock system. The 3D fine structures and the entire unzipping process of feathers were observed via 3D X-ray microscopy and microscopy with a micronano manipulating system, and the feathers' self-repairing capability and superdurability against tears afforded by the cascaded slide-lock system were verified under applied separation forces. These results indicate an important step toward understanding the feather interlocking system, and the cascaded slide-lock system offers insight into the design of smart textiles and flexible devices.

Results and Discussion

Structures of Feathers for the Cascaded Slide-Lock System. Considering the structural and functional similarity of different bird feathers (see the details in *SI Appendix*, Figs. S8–S10), a flight feather from a goshawk was taken as a sample for observation. A feather comprises a shaft (called a rachis) and two rows of side branches (called barbs) on both sides of the rachis (Fig. 24). The barbs are aligned in parallel, with a certain angle relative to the rachis. Similarly, the barbs are composed of overlapped second-order side branches (called barbules) on both sides. The adjacent barbs

Significance

Bird feathers have aroused tremendous attention for their contributions to the unique flight capability of birds against wind and even through bushes. Many studies have attempted to explore the mechanism underlying feathers' superdurability. However, it is not yet clear why feathers are so superdurabile. In this study, we discovered and characterized the sophisticated cascaded slide-lock system of bird feathers, which is composed of flexible hooklets, a slide rail, and spines at the end of the slide rail as terminating structures. This finding demonstrates that the superdurability of bird feathers against tears originates from their cascaded slide-lock system, not from the "hook–groove system" proposed centuries ago.

Author contributions: F.Z., L.J., and S.W. designed research; F.Z. performed research; F.Z., L.J., and S.W. analyzed data; and F.Z. and S.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. J.A. is a guest editor invited by the Editorial Board.

Published under the PNAS license.

¹To whom correspondence should be addressed. Email: stwang@mail.ipc.ac.cn.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10. 1073/pnas.1808293115/-/DCSupplemental.

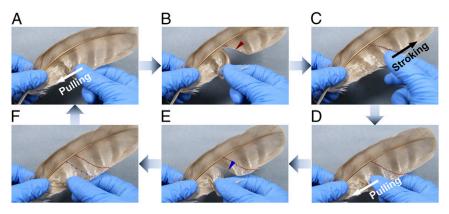


Fig. 1. Diagram of separation and repair of a feather by hand. (*A* and *B*) The feather vane can be stretched and separated along the barbs (red arrow) by pulling on it. (*C* and *D*) Light stroking with fingers can easily repair the separated feather (red dashed line). (D–F) When pulled again, the vane may be separated at another location (blue arrow) and can be repaired again (blue dashed line). This separation-repair process can be continually repeated.

overlap closely, forming dense vanes (Fig. 2B) where hooklets can be found to interlock with the adjacent barbs and strengthen the vanes (Fig. 2 C and D). The 3D X-ray microscopy reconstruction image of adjacent barbs in Fig. 2E shows the in situ 3D structures of a feather. Hooklets protrude from one barbule and hook into the curved margin of the adjacent barbule, which links the adjacent barbs together. Moreover, finer tooth-like spine structures can be observed (details below).

To further explore the fine structures, we separated a single barb from the feather for further observation. The barbules on both sides of the barb shaft (called the ramus) show different structures (Fig. 3 A and B). The barbules close to the tip of the feather have many hooklets (four to five hooklets on one

barbule) protruding from the middle on the ventral side; these structures are called hook barbules and are positioned at an angle of \sim 53° relative to the ramus (Fig. 3*C*; more detail can be observed in *SI Appendix*, Fig. S1 and Table S1). Each hooklet is composed of a drooping ribbon component and a component that gradually transforms from a ribbon to a pillar with a hooked tip (Fig. 3*D* and *SI Appendix*, Fig. S2). The barbules projecting from the other side of the ramus at an angle of ~49° (*SI Appendix*, Fig. S1 and Table S1), called bow barbules, are laminas with dorsally curved margins, and tooth-like spine structures occur at the distal end (called dorsal spines, four to five per barbule) (Fig. 3 *E* and *F* and *SI Appendix*, Fig. S3 *A* and *B*). At the dorsal spines, each lamina splits into several overlapping

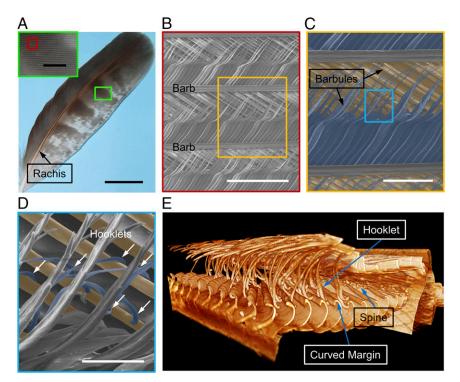


Fig. 2. The hierarchical structures of feathers. (*A*) The vane consists of a number of side branches, which are aligned in parallel, with an angle of \sim 30° relative to the rachis. The primary side branches are called barbs. (*B*) The adjacent barbs overlap closely, forming the dense vane. The second-order side branches, called barbules, occur on both sides of barbs. (*C* and *D*) The hooklets from one barb hook the adjacent barbs and fasten the vane. (*E*) Stereoscopic structure of a feather obtained via 3D reconstruction with a micro X-ray microscope. The hooklets hook the curved margin of the barbules on the adjacent barbs. Finer tooth-like spine structures can be observed. (Scale bars: *A*, 3 cm, and *Inset*, 5 mm; *B*, 500 µm; *C*, 200 µm; *D*, 50 µm.)

BIOPHYSICS AND COMPUTATIONAL BIOLOG

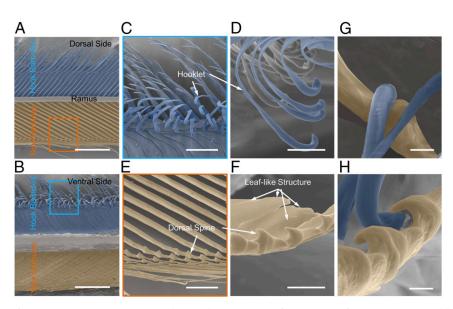


Fig. 3. The fine structures of hook barbules and bow barbules. (*A* and *B*) The structure of a single barb from the dorsal view (*A*) and ventral view (*B*). Side branches on both sides of the barbs exhibit different structures called hook barbules and bow barbules. (*C* and *D*) A hook barbule bears approximately four pendulous, backward-facing hooklets in the middle. (*E* and *F*) The bow barbule, with a sharply curved margin, carries approximately four tooth-like spine structures, called dorsal spines, with a scalene triangle shape at the distal end. (*G* and *H*) The hooklets and the curved triangle dorsal spines match in size and shape. (Scale bars: *A* and *B*, 500 µm; *C* and *E*, 50 µm; *D* and *F*, 20 µm; *G* and *H*, 5 µm.)

leaf-like structures (Fig. 3F and SI Appendix, Fig. S3 C and D). The hooklets of the hook barbules can hook the curved margins of the bow barbules on the adjacent barbs, which maintains the feather vane flexible and stable against wind. Moreover, the hooklets on the hook barbules and the dorsal spine, which feature a curved triangle shape, on the bow barbules completely match in size and shape (Fig. 3 G and H); thus, the structures can form a terminal interlocking system to prevent the hooklets from sliding out of the curved margin under external forces. Moreover, the overlapped leaf-like structures can be separated from each other when pulled (SI Appendix, Fig. S3D), helping unzip the interlocked hooklets and dorsal spines instead of breaking them. Such elegant structures ensure a rather large force for separating adjacent barbs without causing damage. These findings suggest a more complex feather interlocking system than the hook-and-groove model.

The Cascaded Slide-Lock System in Feathers. To further explore the function of the unique structures, we used optical microscopy and scanning electron microscopy coupled with a micronano manipulating system to observe the separation of two adjacent barbs when pulled (Fig. 4 and Movie \$1). In the original state, the hooklets on hook barbules drooped freely and hooked the curved margin on the adjacent bow barbules (Fig. 4A). When external force was added, the hooklets were stretched and hooked the curved margin of the bow barbules (Fig. 4B and Fig. 4D, i). With the increase in the pulling force, the hooklets slid along the curved margin as a slide rail accompanied by slight bending of the barbules (Fig. 4D, i-ii). At a certain force, the hooklets slid to the distal end of the bow barbules, met the dorsal spines, and formed interlocking structures (Fig. 4C and Fig. 4D, ii-iii). The interlocking structures could stop the hooklet from sliding away from the bow barbule. With a large increase in the pulling force, both the hook barbules and bow barbules were bent (Fig. 4D, iii-iv, and Movie S1). Finally, when the bending degree exceeded a certain threshold (SI Appendix, Fig. S4, the mechanical analysis of the separation process), the interlocking structures could be unzipped, and the hooklet moved to another dorsal spine or directly away from the bow barbules (Fig. 4D, ivvi). According to the force analysis of the hooklet during the

separation process, the factor determining whether the hooklet will slide is the angle θ between the pulling force on the hooklet and the advancing direction (SI Appendix, Fig. S4). When θ is smaller than the threshold (arccot μ , where μ is the friction coefficient between the hooklet and the curved margin of bow barbules), the hooklet will slide away. The dorsal spines change the advancing direction and increase θ ; thus, the hooklets cannot move away unless a much larger increase in the pulling force bends the barbules and decreases θ to the threshold (SI Appen*dix*, Fig. S4). Further details related to the separation process are presented in Movie S1. If the external force were removed before the hooklets moved away from the bow barbules, the hooklets would move back close to the initial position (Fig. 4D, i-v, and Movie S2). Considering these elegant structures and their function, we propose that the superdurability of feathers originates from their cascaded slide-lock system (Fig. 4D).

To help describe the feather structures and the separation process, we created an animated 3D movie showing how all of the feather features interact during the separation process: the hooklets slide along the curved margin of a bow barbule; when the hooklets meet the dorsal spine, interlocking structures form and stop the hooklet from sliding away; increasing the external force bends the barbules, and the interlocking structures are unzipped, resulting in the separation of the barbs (Movie S3). We also printed a simplified mechanical model based on our proposed cascaded slide-lock model of the feather; the model featured a flexible hooklet, slide rail, and sliding-terminated structures (SI Appendix, Fig. S5A). As a control, a 3D printed model based on the traditional "hookgroove" model was also generated (SI Appendix, Fig. S5A, Right). As shown in SI Appendix, Fig. S5B, the separation of the samples based on our proposed cascaded slide-lock model requires a much larger external force (SI Appendix, Fig. S5B, Top) than that of the sample based on the hook-groove model (SI Appendix, Fig. S5B, Bottom). These results indicate the advantage and validity of our proposed cascaded slide-lock feather model.

The Self-Repairing Capability and Superdurability Against Tears of the Cascaded Slide-Lock System in Feathers. Furthermore, we measured the separation force of a feather's cascaded slide-lock system by sticking one side (\sim 6 mm wide) of two closed adjacent

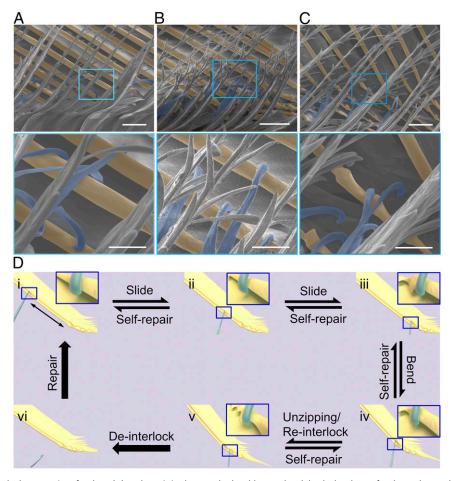


Fig. 4. The cascaded slide-lock system in a feather. (*A*) In the original state, the hooklets on hook barbules droop freely, and some hook the curved margin of bow barbules on adjacent barbs. (*B*) When pulled, the hooklets hook the curved margin of bow barbules and slide along the margin as a slide rail. (*C*) The hooklets slide to the dorsal spines of bow barbules and form interlocking structures. (*D*) Simplified functional model of the cascaded slide-lock system: (i-ii) The hooklets hook and slide reversibly along the curved margin with the increase in the external force. (ii) At a certain force, the hooklets hook the dorsal spine of bow barbules, forming interlocking structures and preventing the hooklet from moving away. (iii-iv) A continuous increase in the external force can cause the bow barbules and hook barbules to bend, and (iv–vi) the interlocking structures are then unzipped when the bend amplitude becomes wide enough, resulting in reinterlocking or unzipping. If the external force were removed before the hooklets moved away from the bow barbules, the hooklets would move back close to the initial position (i–v). (scale bars: *A–C, Top,* 50 µm; *Bottom,* 20 µm.)

barbs to the pan of a balance and lifting the other side with a singleaxis push-and-pull device. With an increase in the spacing of adjacent barbs, the hooklets slid along the curved margin of the bow barbule and hooked the dorsal spines at the distal end, forming interlocking structures with the bending of the barbules. The corresponding force increased almost linearly and finally reached its maximum when the interlocking structures were unzipped with large deformation, defined as the separation force (goshawk feathers, 44.4 ± 8.7 mN) (Fig. 5A and Movie S1). The elongation at separation was $\sim 270\%$ (the ratio of the distance at separation, 1.10 ± 0.10 mm, to the original spacing of adjacent barbs, $0.40 \pm$ 0.02 mm). Then the force curve exhibited a sharp drop, indicating that the barbs were separated. The separation force-lifting distance curves exhibit good consistency and reproducibility (SI Appendix, Fig. S6). When tearing the adjacent barbs from the tip, the tearing force was concentrated on only several couples of hook barbules and bow barbules and ranged from 2 to 5 mN due to the interlocking and unzipping of the hooklets and dorsal spines (Fig. 5B and SI Appendix, Fig. S7). We observed similar structures on the feathers from different birds (magpie, Circus cyaneus, and common buzzard) (SI Appendix, Figs. S8-S10). The separation forces of these barbs vary among birds, likely depending on the barbule density (SI Appendix, Fig. S11 and Table S2).

4 of 6 | www.pnas.org/cgi/doi/10.1073/pnas.1808293115

In flight, the feathers of flapping wings may be pulled with deformation or even be separated by wind or bushes. However, feathers can be self-repaired or repaired with the bill. To evaluate the self-repairing capability and durability of the sample feather's cascaded slide-lock system, we measured the pulling force of two adjacent barbs at different lifting distances: 0.25, 0.4, and 0.5 mm and separated. When the lifting distance was not greater than the distance at separation, the maximum pulling force, defined as the separating force, increased with the lifting distance; repair could be achieved simply by removing the external force, during which the hooklets slid reversibly along the curved margin (Movie S2). This process was repeated, and the maximum separating force of the repaired adjacent barbs was rather close to that of the original adjacent barbs (Fig. 5C). Even when the barbs were separated with the unzipping of the interlocking structure between the hooklets and dorsal spines, the separated feather could be repaired again by stroking. The repaired barbs were separated again to measure the separation force, and this process was repeated. The maximum separation forces were similar, which indicated that the feather was not damaged during separation (Fig. 5D). These results revealed the highly efficient self-repairing capability of the feather's cascaded slide-lock system.

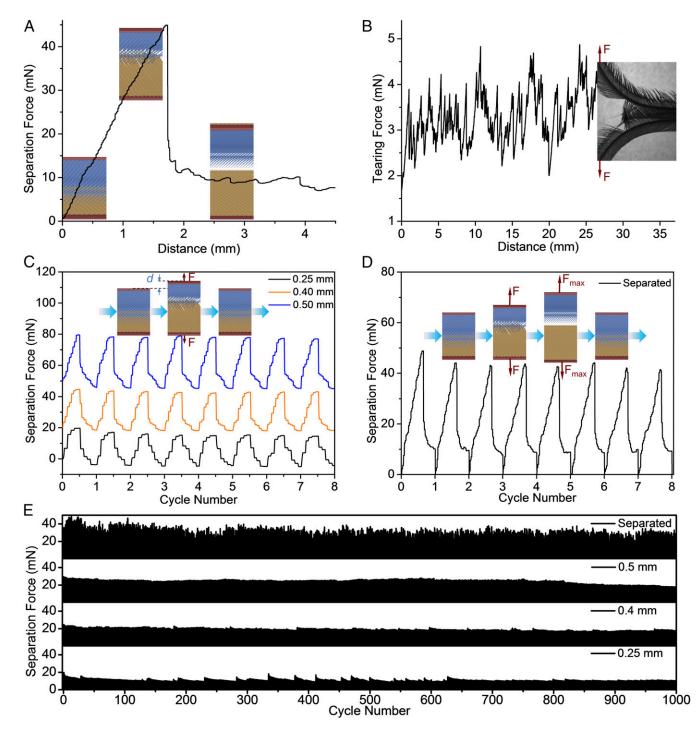


Fig. 5. The superdurability of the feather's cascaded slide-lock system confirmed by the separation force. (A) The separation force of two adjacent barbs as a function of lifting distance. The separation force increased with the distance between two barbs and declined sharply when the barbs were separated. (*B*) Plot of tearing force of adjacent barbs versus lifting distance from the tip of the barbs. (C) Highly efficient self-repair within the elongation at separation. The separating forces were measured repeatedly before the adjacent barbs were separated (*Insets*). Lifting speed: 30 mm/min; lifting distances: *d*, 0.25, 0.4, and 0.5 mm. (*D*) Highly efficient self-repairing capability of the adjacent barbs after separation. The adjacent barbs were stretched to separation at 30 mm/min and then returned to the original position (as illustrated in the *Insets*). The next cycle of separation force measurement was conducted after the separated barbs were repaired by hand. The separating forces and separation forces demonstrated excellent repeatability, indicating the highly efficient self-repairing capability of the feathers' cascaded slide-lock system. (*E*) Superdurability of the feathers' cascaded slide-lock system. The above-mentioned separation-repair process was repeated more than 1,000 times. The separating forces and separation forces remained nearly unchanged after 1,000 cycles of separation and repair, which verified the high self-repairing stability of the feathers' cascaded slide-lock system.

The feather exhibited not only an excellent self-repairing capability but also superdurability. The pulling forces of the repaired feather within the distance at separation or when being separated were measured repeatedly. As shown in Fig. 5E, the separating forces and separation forces remained nearly unchanged, with only a slight decline over 1,000 cycles. The one-thousandth

separation force of the repaired feather after separation was still 80% of the first separation force, which demonstrates the high self-repairing stability of the feather's cascaded slide-lock system.

Conclusion. A cascaded slide-lock system has been demonstrated in feathers via 3D X-ray microscopy and microscopy with a micronano manipulating system. The cascaded slide-lock system of feathers ensures their superdurability and high self-repairing capability and helps birds survive in hostile environments. Our findings provide insight into the design of smart textiles and flexible devices.

Materials and Methods

Cleaning of the Feathers. Before characterization, the feathers were cleaned with water and alcohol successively by an ultrasonic method. Then, the cleaned feathers were air-dried at room temperature.

Scanning Electron Microscopy. The samples were sputtered with a thin layer of platinum. Field-emission scanning electron microscopy (JSM-7500F; JEOL) was performed to investigate the morphology of feathers at an acceleration voltage of 5.0 kV.

- Nachtigall W (1974) Biological Mechanisms of Attachment: The Comparative Morphology and Bioengineering of Organs for Linkage, Suction, and Adhesion (Springer, Berlin), pp 74–76.
- Hooke R (1665) Micrographia, or, Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries Thereupon (The Royal Society, London).
- 3. Wray RS (1887) On the structure of the barbs, barbules, and barbicels of a typical pennaceous feather. *Ibis* 29:420–423.
- 4. Stubbs F (1910) An undescribed feather element. Nature 84:329.
- 5. Getty R (1948) Feather morphology in biological research. *Iowa State Univ Vet* 10: 19–23.

X-Ray Tomography. To observe the spatial site distribution of the micro/ nanostructures on adjacent barbs, an X-ray microscopy (Xradia 510 Versa system, Carl Zeiss) was used (performed by Chunjie Cao at Carl Zeiss, Inc.) at a resolution of 0.8 μ m with an X-ray source voltage and power of 50 kV and 4 W, respectively.

Mechanical Measurement. The separation force of adjacent barbs was measured by sticking one side (~6 mm wide) of the closed two adjacent barbs to the pan of a sensitive balance (with an accuracy of 0.01 mg, Mettler Toledo XSI05 DualRange) and lifting the other side with a single-axis push-and-pull device at a pulling speed of 30 mm/min. Weight loss was recorded in real time; multiplied by gravitational acceleration, the weight loss was exactly the separation force.

ACKNOWLEDGMENTS. This research was supported by the National Natural Science Foundation of China Grants 21425314 and 21421061; the Top-Notch Young Talents Program of China; the National Research Fund for Fundamental Key Projects Grant 2012CB933800; the Key Research Program of the Chinese Academy of Sciences Grant KJZD-EW-M03; and the 111 Project Grant B14009.

- Jing S, Hang F, Li Y, Liu J, Wang X (1995) Microstructure of feather of red crowned crane (Grus japonensis). J For Res 6:71–76.
- Gorb SN (2001) Biological Micro-and Nanotribology: Nature's Solutions (Springer Science Business Media, New York).
- Kovalev A, Filippov AE, Gorb SN (2013) Unzipping bird feathers. J R Soc Interface 11:20130988.
 Sullivan TN, et al. (2016) A lightweight, biological structure with tailored stiffness: The
- feather vane. Acta Biomater 41:27–39.
- Sullivan TN, Wang B, Espinosa HD, Meyers MA (2017) Extreme lightweight structures: Avian feathers and bones. *Mater Today* 20:377–391.
- 11. Sullivan TN, et al. (2017) Reversible attachment with tailored permeability: The feather vane and bioinspired designs. Adv Funct Mater 27:1702954.