Asymmetric hindwing foldings in rove beetles

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Foldable wings of insects are the ultimate deployable structures and have attracted the interest of aerospace engineering scientists as well as entomologists. Rove beetles are known to fold their wings in the most sophisticated ways that have right–left asymmetric patterns. However, the specific folding process and the reason for this asymmetry remain unclear. This study reveals how these asymmetric patterns emerge as a result of the folding process of rove beetles. A high-speed camera was used to reveal the details of the wing-folding movement. The results show that these characteristic asymmetrical patterns emerge as a result of simultaneous folding of overlapped wings. The revealed folding mechanisms can achieve not only highly compact wing storage but also immediate deployment. In addition, the right and left crease patterns are interchangeable, and thus each wing internalizes two crease patterns and can be folded in two different ways. This two-way folding gives freedom of choice for the folding direction to a rove beetle. The use of asymmetric patterns and the capability of two-way folding are unique features not found in artificial structures. These features have great potential to extend the design possibilities for all deployable structures, from space structures to articles of daily use.

Coleoptera | Staphylinidae | deployable structure | aerospace engineering

Artful wing folding of insects has attracted the interest of aerospace engineering scientists as well as entomologists. Foldable hindwings are the ultimate deployable structures. They have sufficient strength and stiffness to tolerate 20–1,000 beats per second in the flight position, although they can be folded and unfolded instantly, depending on the situation. It is well known that many species of insects are equipped with deployable wings. Simple examples are found in the longitudinally folded forewing of ants and bees (Hymenoptera) (1) and in the fanlike folding of locusts (Orthoptera) and praying mantises (Dictyoptera) (2). These types of deployable wings have simple crease patterns and can be folded and unfolded by relatively easy mechanisms; however, their storage efficiencies are not large. Earwigs (Dermaptera) are known to use advanced fanlike folding (3). Their fan frames have additional bending points, and earwigs achieve more extensive folding by refolding the closed fan. This folding can confer high storage efficiency but requires external support by the cercus for deployment, and the wings cannot be opened quickly. The most highly diverse wing folding patterns and mechanisms are found in beetles (Coleoptera) (4–13) (*SI Text*). Among these examples, the most sophisticated wing folding is found in rove beetles (Coleoptera: Staphylinidae) (7–9, 13), from the perspective of both deployment capability and storage efficiency. In addition to their performance as a deployable structure, the wings have a strange feature that is not observed in other beetles: The right and left wings use different folding patterns. Compared with other typical beetles, elytra of most rove beetles are reduced, and the projecting abdomen is exposed and freely movable (Fig. 1 and Fig. S1). At the expense of protection of the abdomen, rove beetles have highly maneuverable bodies that can move rapidly through narrow and curved spaces and can extend their wide range of microhabitats, especially into leaf litter layer and soil. The most remarkable feature of their survival strategy is that they have never lost their flight wings, despite the reduction of dorsal storage space (with some minor exceptions in soil- and cave-dwelling species). The strategy is achieved by their extraordinary right–left asymmetric wing folding. As a result, rove beetles became highly diverse group, such that they account for 15% (i.e., nearly 60,000 species) of all known species of Coleoptera.

Despite the great potential of the process for engineering applications, few studies have been undertaken revealing the details of this asymmetric wing folding. The wings of a rove beetle have two different crease patterns, but previous studies have described only one side. It is already known that the movement of the abdomen plays a central role in the wing folding (9), but the detailed folding process remains unexplained. A major obstacle to investigation is the difficulty of detailed observation of the folding processes. The wing-folding movement of a rove beetle consists of multiple sequences, and a series of movements is accomplished very smoothly and quickly. The aforementioned problem cannot be solved without careful investigation of this movement. This article is a detailed report on wing folding in rove beetles, including specific crease patterns of respective wings. A high-speed camera was used for the first time to the authors' knowledge to reveal the details of wing folding movements. Specimens were *Cafius vestitus* (Sharp) and were captured in the coastal region of Japan. The results clarify the highly efficient wing-folding mechanism.

Results

By using the high-speed camera, take-off and wing folding movements of *C. vestitus* were filmed from many different angles. Representative movies are available (Movies S1–S3). The results show that the wing folding motion of a rove beetle consists of two types of abdominal movements ("swinging" and "lifting"). With the support of knowledge obtained from these high-speed movies, two different crease patterns of hindwings were investigated by microscopic observations. Our results are summarized in Fig. 2.

Significance

Rove beetles are known to fold their wings in the most complicated and sophisticated ways that have right–left asymmetric patterns. This asymmetric folding can confer both high deployment capability and high storage efficiency, and therefore has a great deal of potential for engineering applications. However, the detailed folding mechanisms have been unclear because of the difficulty of observing of the folding processes. This study used a high-speed camera to observe the wing folding movements of rove beetles. The results show that these characteristic asymmetrical patterns emerge as a result of simultaneous folding of overlapped wings. The specific crease patterns of respective wings and detailed folding motions in each folding sequence are also described here.

APPLIED BIOLOGICAL SCIENCES

ENGINEERING

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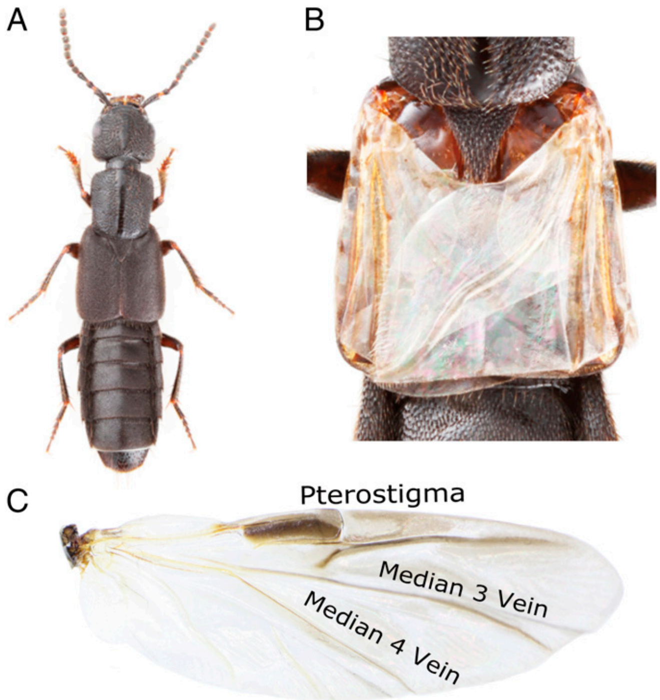

Fig. 1. *Cafius vestitus* (Sharp). (*A*) Overall view (length of body, 6.1 mm). Elytra of most rove beetles are reduced, and the projecting abdomen is exposed and freely movable. (*B*) Wings in the folded position. Elytra are removed in this image. (*C*) Wing venation. The anterior margin (pterostigma) is strongly sclerotized. The wing membrane is supported mainly by two median veins. The terminologies are derived from ref. 7.

Fig. 2*A* shows the crease patterns of unfolded wings. Note that these patterns show the right-wing-overlying case and that wings are folded right to left by the swing movement of the abdomen, as is described in detail here. The right crease pattern consists mainly of a median flexion line (MF) and two transverse fold lines (principal transverse fold and apical transverse fold). The MF folds a wing longitudinally, and the principal transverse fold and apical transverse fold transversely. These terminologies are derived from ref. 7. This pattern is relatively easy to understand because the MF and principal transverse fold are commonly found in hindwing folding in other beetles. In the case of rove beetles, apical folding is also necessitated by truncated elytra. In contrast, the left crease pattern is very characteristic. A fold line (PF) is also found in a similar position of the MF, but another fold line lies just below it (PF′). The wing is pleated at the median 3 vein (Fig. 1*C*) between these lines. As a substitute for the transverse fold lines, the wing is tucked down by fold lines G and H in the base area and by fold lines D, E, and F in the apical area. It is recommended that readers copy and cut these paper models and read the following section while folding them.

The detailed folding process is explained by these crease pattern models, as shown in Fig. 2 *B*–*E*. In these figures, the left pictures show the wing folding motions obtained from the high-speed movies, and the right sketches describe the wing shapes in each folding sequence. In the case of Fig. 2, the right wing first settles on the left wing. Then, the underlying left wing is folded slightly longitudinally, as shown in Fig. 2*B*. By this small pleating, folding lines d_1–d_5 lie in a straight line and form fold line D. In such overlapping, the right wing's fold line A meets the left wing's fold line D, and the consequent swinging movement of the abdomen folds wings on these lines (Fig. 2*C*). In the right wing, the anterior margin and the median 4 vein are aligned by folding of the MF, and the whole wing is bent leftward on fold line A. At the same time, the left wing is bent leftward on fold line D. In the next step, these overlapping wings are simultaneously folded into a Z shape by the lifting movement of the abdomen (Fig. 2*D*). In many cases, the lifting movements are observed twice in one folding process. The first movement folds the upper corner of Z, and the second one folds the lower corner. As a result, right and left wings are housed in a compact space beneath elytra (Fig. 1 and Fig. 2*E*). For better understanding, high-speed movies of this folding process are available (Movies S1 and S2).

Discussion

Fig. 2 explains why wing folding is asymmetric. In the wing folding processes of other insects, left and right wings overlap after the folding process. However, in the hindwings of rove beetles, left and right wings first overlap and fold simultaneously. Because of the mirror symmetry of right and left wings, the resulting crease patterns of each wing should be asymmetric. In the housed state, the apexes of right and left wings are aligned to either side. The choice of side depends on which wing was overlying in the first step of wing folding.

In the left-wing-overlying case, the crease patterns show the mirror image of Fig. 2. In fact, specimens with left-overlapped folding wings are not uncommon. Blum (9) pointed out that this right-or-left difference did not depend on interindividual specificity (right-handed or left-handed nature), but each individual rove beetle could fold its wings from both the right and left sides. This assertion can be confirmed easily by continuous observation of a single living rove beetle isolated from other individuals. The investigation of the reason for the two different folding modes is not a subject of this study, but it may be speculated that this right-or-left option confers great advantages for expeditious wing folding and hiding in situations in which obstructions prohibit movement of the abdomen.

Another reason may be aerodynamic: Fixing the folding direction would cause an asymmetric effect on the aerodynamic properties of wings, thus impairing flight. From an engineering perspective, what is so surprising is that one wing internalizes two crease patterns, and then the structure can be folded into two folding modes. In other words, wings are tristable structures with the following three locally stabilized points: completely unfolded, right-overlying folding, and left-overlying folding (Fig. 3).

To achieve this two-way folding in an artificial structure, we have to address problems with manufacturing a vein that is able to correspond to two different folded shapes. The fold lines intersect with the veins at different points in the right and left crease patterns (Fig. 2*A*), such that each vein is expected to have redundant hinges compared with the one-way folding wings. However, adding extra hinges or joints will render the system more complex and negatively affect the mechanical properties of the wing. On this subject, it is noteworthy that microscopic observations revealed no clear joints or hinges in the veins. It was observed in high-speed movies of wing folding that some veins did not bend into sharp angles at defined points, but were bent at various points, and that the bending points traveled in each vein during packing beneath elytra. Nevertheless, wings are finally folded into predetermined shapes. These flexible veins without clear bending points are believed to permit this redundant wing folding. Further investigations, in particular of the microstructures of wing veins, by scanning electron microscopy, Nomarski microscopy, and computed tomography are warranted to elucidate the events that take place at the bending points. Analysis of the distribution of resilin in hindwings that has been performed in studies of other beetles (10) and earwigs (3) will provide useful information about the precise positions of fold lines.

This study revealed the detailed folding processes and crease patterns of one species of rove beetle, which achieved high wing-folding performance. Further entomological studies are required to determine whether the proposed patterns and processes are

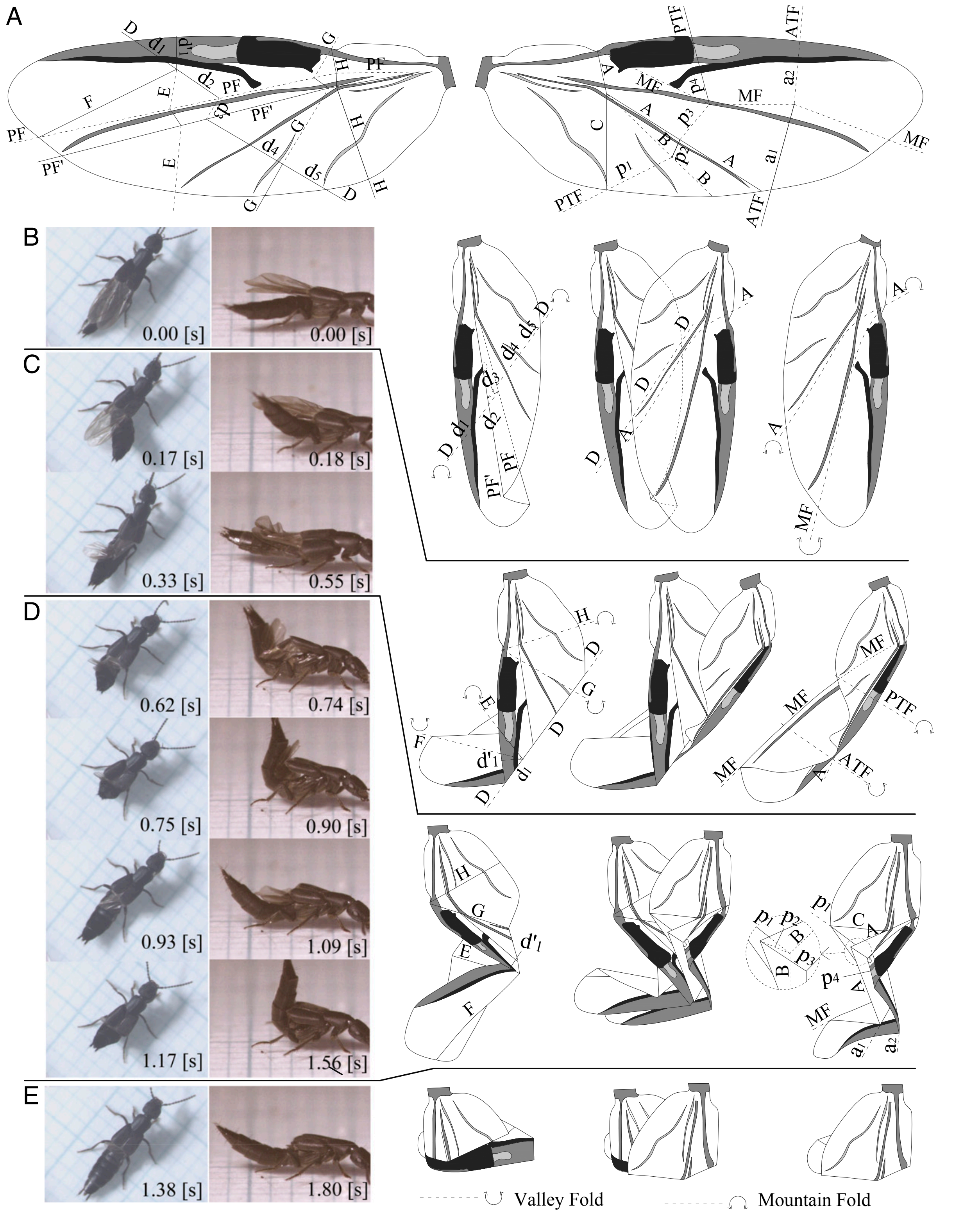

Fig. 2. Crease patterns and detailed wing folding process of the rove beetle. (*A*) (*Right*) Crease pattern of the right (overlying) wing. (*Left*) Crease pattern of the left (underlying) wing. This figure shows the right-wing-overlying case. In the left-wing-overlying case, the crease patterns show the mirror-reversed image. Fine lines: mountain folding lines. Dashed lines: valley folding lines. (*B–E*), Wing-folding process of rove beetles. Unlike other insects, rove beetles fold their left and right wings simultaneously. This folding process is driven by the freely movable abdomen. (*B*) Hindwings are aligned backward along the abdomen and overlapped at the resting position. The right wing overlaps the left wing in this case. The left (underlying) wing is folded slightly at the folding lines PF and PF′, and the emerging fold line D fits the right wing's folding line A. (*C*) Overlapped wings are folded into a perpendicular direction on the folding lines D and A by the swinging movement of the abdomen from the side of the overlying wing to that of the underlying wing (right to left in this figure). In the right wing, the anterior margin and the median 4 vein are aligned by the folding line MF. (*D*) Wings are folded into a Z shape simultaneously by the lifting movement of the abdomen and tucked beneath elytra. (*E*) Completely folded state (see also Fig. 1*B*).

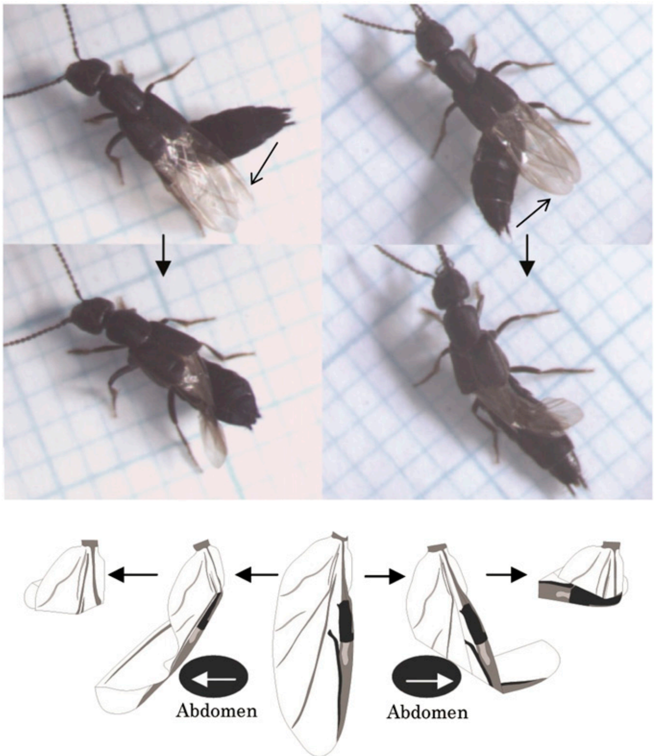

Fig. 3. Two possible folding movements. Each individual rove beetle can fold its wing from both sides. Thus, each wing internalizes two crease patterns and can be folded in two different ways.

common in other rove beetle species, but they seem to have a certain level of generality, in view of their agreement with the observations of previous studies. With regard to wing actuation mechanisms, previous studies have shown that the skeletomuscular apparatus of the metathorax plays a major role in other beetles (11–13). Because the wings of rove beetles have exclusive properties such as the right–left asymmetry in the crease patterns, the sequential wing-folding process using the abdomen, and the capability of two-way folding, further investigations are required to determine whether their hindwings can be actuated with the same apparatus. The high-speed movies on wing folding clearly show that the wings possess elastic forces for deployment and become stable when completely unfolded. This elasticity is thought to provide the main force for deployment (*SI Text* and Movie S3). Further investigation on the hold-down and release mechanisms is required to elucidate the mechanisms underlying this elastic deployment. Obviously, for *C. vestitus*, flight is the first choice for emergency avoidance of dangerous situations. The speed-up of wing unfolding requires larger elastic forces to morph the structures, implying that wings should store higher elastic energy in the folding process. In addition, the wings of rove beetles are obligatorily folded into a more compact space than those of other beetles. These challenging problems about high-standard wing folding are solved by their movable abdomens. It is noteworthy that this wing folding mechanism can achieve two different objectives at the same time, as follows: one is compact and quick wing folding and the other is efficiently storing elastic energy for subsequent wing deployment.

The mechanisms underlying folding have a large application potential in various engineering fields. Immediate applications include space-deployable structures represented by solar array paddles and antenna reflectors of satellites. Because self-deployment by intrinsic elasticity requires no mechanical actuators, it will contribute to reducing the weight of the satellite body and to improving the reliability of the deployment system. Furthermore, it is worth emphasizing that the hindwings of rove beetles provide two innovative ideas about deployable structures. The first is the use of asymmetric patterns in folding symmetrically shaped structures. The resulting simultaneous folding cannot only confer high storage efficiency but also must enable consolidation of the folding systems. It will accordingly advance the design of symmetrically shaped deployable structures such as solar array paddles and wings of carrier-based aircrafts. The second idea is that of a deployable structure that can be folded into two different shapes. Although further investigations of the veins and their tristable properties are required, this capability will provide new possibilities for how to use deployable structures. Moreover, these innovative ideas are expected to broaden the design possibilities for articles of daily use, such as umbrellas and fans. More direct applications will be established in the field of insect robots. Rove beetles have highly maneuverable bodies and can run rapidly on the ground and crawl through small gaps. This is the ideal model for a search robot that could search for signs of life trapped under wreckage resulting from disasters such as earthquakes and tsunamis. Deployable wings on these robots will enable the expansion of the search area in the same manner they enable the expansion of habitat in rove beetles.

Materials and Methods

Specimens were of *C. vestitus* (Sharp) and were captured in the coastal region of Japan (Fukuoka Prefecture, Kyushu). A high-speed camera (HAS-L2, DITECT Co., Ltd.) was used to acquire slow-motion movies (Movies S1–S3) at 500–800 frames per second. The specimens were put in an acrylic box and were kept in focus by simultaneously moving the box on the table to keep them in frame.

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1. Danforth BN, Michener CN (1988) Wing folding in Hymenoptera. *Ann Entomol Soc Am* 81:342–349.
2. Wootton RJ (1995) Geometry and mechanics of insect hindwing fans: A modelling approach. *Proc R Soc B* 262:181–187.
3. Haas F, Gorb S, Wootton RJ (2000) Elastic joints in dermapteran hind wings: Materials and wing folding. *Arthropod Struct Dev* 29(2):137–146.
4. Forbes WTM (1924) How a beetle folds its wings. *Psyche (Stuttg)* 31:254–258.
5. Forbes WTM (1926) The wing folding pattern of the Coleoptera. *J NY Entomol Soc* 24:42–68, 91–139.
6. Hammond PM (1979) Wing-folding mechanisms of beetles, with special reference to investigations of adephagan phylogeny (Coleoptera). *Wing-Folding Mechanisms of Beetles, with Special Reference to Investigations of Adephagan Phylogeny (Coleoptera)*, eds Erwin TL, Ball GE, Whitehead DR, Halpern AL (Dr W. Junk, The Hague), pp 113–180.
7. Brackenbury JH (1994) Wing folding and free-flight kinematics in Coleoptera (Insecta): A comparative study. *J Zool (Lond)* 232:253–283.
8. Schneider VP (1978) Flight types and hing wing folding in Coleoptera. *Zool Jahrb Abt Anat Ontogenie Tiere* 99:174–210.
9. Blum VP (1979) Phylogeny and ecological significance of elytrareduction and abdomen-mobility of the Staphylinidae (Coleoptera): Comparative and functional morphological studies. *Zool Jahrb, Abt Syst Okol Geogr Tiere* 102:533–582.
10. Haas F, Gorb S, Blickhan R (2000) The function of resilin in beetle wings. *Proc R Soc B* 267(1451):1375–1381.
11. Haas F, Wootton RJ (1996) Two basic mechanisms in insect wing folding. *Proc R Soc B* 263:1651–1658.
12. Haas F, Beutel RG (2001) Wing folding and the functional morphology of the wing base in Coleoptera. *Zoology (Jena)* 104(2):123–141.
13. Fedorenko DN (2009) *Evolution of the Beetle Hind Wing, With Special Reference to Folding (Insects, Coleoptera)* (Pensoft Publishers, Bulgaria).

Supporting Information

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SI Text

Wing Folding Mechanisms of Beetles. Compared with wing venation, an important characteristic for taxonomy and phylogeny, the ways of wing folding have tended to be neglected by entomologists, and few studies have been devoted to this subject. This field was explored by the pioneering work of Forbes in the 1920s (1, 2). He illustrated some 125 wing-folding patterns of beetles and attempted to establish phyletic grouping. Studies by entomologists also included investigation of the mechanisms used in wing folding/unfolding, as well as crease patterns. Unlike animal limbs, the wing folding and unfolding processes of insects cannot be actuated only by muscular driving for arthro-jointed veins. They are the result of a number of mechanisms involving the elastic behaviors of structures, internal forces driven by muscle or blood pressure, and external forces from other body parts.

Hammond (3) attempted a classification based on grade of mechanism of wing folding and unfolding without direct reference to accompanying folding patterns. This classification focused on differences in the spring mechanism and the presence or absence of external agents supporting wing folding. Hammond also summarized other anecdotal descriptions of folding mechanisms. In his classification, the most important mechanism is the intrinsic elasticity of the wing. In previous studies, Forbes also pointed out that the wings of certain beetles relax into the folded position at rest (2). In the same way, the wings of another species of beetles show relaxation to unfolded shapes. These elastic behaviors are observed in wings cut from living or freshly killed specimens. With respect to wing materials, Haas and colleagues investigated the distribution of resilin, a rubber-like protein that contributes to the elasticity of the wings of beetles (4). Brackenbury (5) classified the wing-folding mechanism of beetles into two categories, depending on the direction of their "spring back." In category A, wings are folded automatically and become stable at the resting position as a result of the elastic force. In contrast, wings in category B are unfolded automatically.

Discussions regarding these elastically stable points observed in insect wings were rephrased into more technical words in the studies of Haas and colleagues (6), which indicated that the wings of earwigs may be considered as bistable structures having two local stabilization points in both folding and unfolding processes, rather than a simple spring system with a single stable point. This model considers Brackenbury's two categories as states possessing lower elastic energy, rather than states possessing a stable point. This proposal explains well why folding-stable wings can maintain unfolded shapes in the flight position (or vice versa) and describes clearly the relationship between intrinsic elasticity and other folding/unfolding mechanisms such as muscle actuations from the perspective of elastic energy; they are needed only to overcome the critical point of elastic energy.

It has also been proposed that the skeletomuscular apparatus of the metathorax plays a major role in wing unfolding in some beetles (7–9). Quantitative evaluation of the contributions of each mechanism requires further engineering studies, but it is well accepted that insect wings may be classified into the following two groups based on structural characteristics: folding (most)-stable type and unfolding (most)-stable type. In each group, the movement toward a stable point is easy to achieve because it can be triggered by a small force and progresses automatically by elastic force. Naturally, problems are observed mainly in reverse-directed movements that require a larger force to cross the peak of elastic energy. Some insects address these problems by unique and somewhat heavy-handed methods. One example is found in earwigs, which use the cercus for wing unfolding, as mentioned in the main text. It is also known that ladybird beetles, which are categorized into the second group, fold their wings by "pumping" movements of the abdomen (3, 5). In this process, elytra and the tragal spicule patch are estimated to play an important role. One of the best examples of these unique techniques is found in rove beetles, which are discussed here.

Wing Unfolding in Rove Beetles. The wings of rove beetles possess elastic forces for deployment and become stable when completely unfolded. It is confirmed that the wings of anesthetized or freshly killed specimens spring back to the unfolded state with mild stimulation. Rove beetles can deploy their hindwings and take off in a moment by virtue of this elasticity. Movie S3 shows the take-off process of *C. vestitus*. As mentioned in main text, different crease patterns may be observed in the left and right wings. The unfolding process is completed within ∼0.1 s, corresponding to approximately one-tenth of the folding process. This spring back is activated not only by opening elytra; therefore, it is assumed that the folding state also confers local stability and that some supporting mechanisms trigger expansion. Such a mechanism was suggested by Brackenbury (5) and Schneider (10) to be a hydraulic mechanism that straightens the wing veins. In addition to this dynamic deployment, *C. vestitus* can also unfold their wings in a nonurgent way. Before grooming hindwings, they withdraw their hindwings from beneath their elytra, using their middle legs. In imminently dangerous situations, they use a dynamic unfolding mechanism and take off quickly to escape. After landing on the ground, wings are aligned backward along the abdomen. In this position, wings are still unfolded but do not interfere with locomotion, and these insects can walk around at a speed about equal to that of completely folded wings. It is also easy to take off again and escape in this configuration. After confirming the safety, the rove beetle begins the characteristic folding process.

1. Forbes WTM (1924) How a beetle folds its wings. *Psyche (Stuttg)* 31:254–258.
2. Forbes WTM (1926) The wing folding pattern of the Coleoptera. *J NY Entomol Soc* 24: 42–68, 91–139.
3. Hammond PM (1979) Wing-folding mechanisms of beetles, with special reference to investigations of adephagan phylogeny (Coleoptera). *Wing-Folding Mechanisms of Beetles, with Special Reference to Investigations of Adephagan Phylogeny (Coleoptera)*, eds Erwin TL, Ball GE, Whitehead DR, Halpern AL (Dr W. Junk, The Hague), pp 113–180.
4. Haas F, Gorb S, Blickhan R (2000) The function of resilin in beetle wings. *Proc R Soc B* 267(1451):1375–1381.
5. Brackenbury JH (1994) Wing folding and free-flight kinematics in Coleoptera (Insecta): A comparative study. *J Zool (Lond)* 232:253–283.
6. Haas F, Gorb S, Wootton RJ (2000) Elastic joints in dermapteran hind wings: Materials and wing folding. *Arthropod Struct Dev* 29(2):137–146.
7. Haas F, Wootton RJ (1996) Two basic mechanisms in insect wing folding. *Proc R Soc B* 263:1651–1658.
8. Haas F, Beutel RG (2001) Wing folding and the functional morphology of the wing base in Coleoptera. *Zoology (Jena)* 104(2):123–141.
9. Fedorenko DN (2009) *Evolution of the Beetle Hind Wing, With Special Reference to Folding (Insects, Coleoptera)* (Pensoft Publishers, Bulgaria).
10. Schneider VP (1978) Flight types and hing wing folding in Coleoptera. *Zool Jahrb Abt Anat Ontogenie Tiere* 99:174–210.

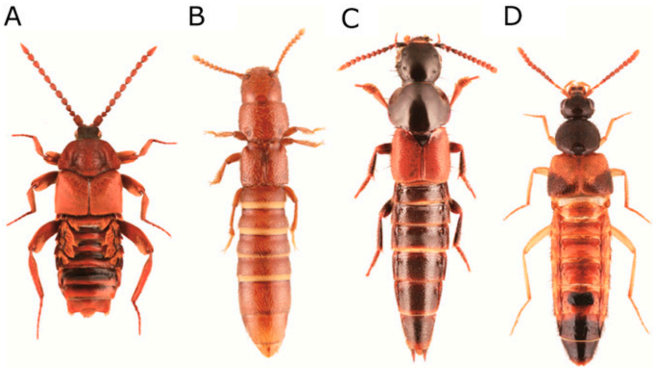
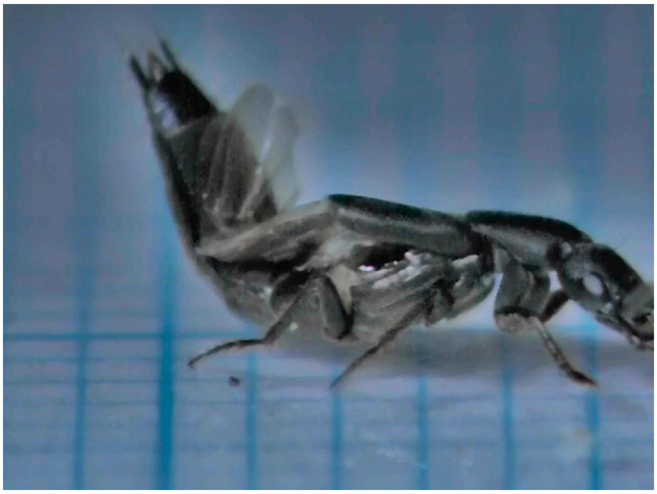


Fig. S1. Representative species of rove beetles (Staphylinidae). (*A*) *Lomechusoides suensoni* (Bernhauer, 1936) (4.7 mm). (*B*) *Mimogonus microps* (Sharp, 1889) (3.3 mm). (*C*) *Quedius hirticornis* (Sharp, 1889) (12.0 mm). (*D*) *Zyras* sp. (8.3 mm).

Movie S1. Wing-folding motion of a rove beetle imaged with a high-speed camera (top-down view).

Movie S1



Movie S2. Wing-folding motion of a rove beetle imaged with a high-speed camera (sideways view).

Movie S2

Movie S3. Take-off motion of a rove beetle imaged with a high-speed camera. Rove beetles have unfolding-stable-type wings and can deploy them very quickly with the help of the intrinsic elastic force. Different folding patterns are observed in left and right wings.

Movie S3