

WING FOLDING IN INSECTS: A NATURAL, DEPLOYABLE STRUCTURE

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1 Introduction

The hind wings of insects are membranous outgrowths of the integument and they are sensitive to damage. Many insect groups protect their delicate hind wings by leathery or firm forewings, like earwigs (Dermaptera) and beetles (Coleoptera) do. However, the hind wings have to be much larger than the forewings in order to preserve flight capability. Consequently the hind wings need to be folded under the forewings.

So, there is a mechanical problem for beetles. They must be able to unfold their hind wings before flight and to fold them afterwards. This has to be repeatable: the wings would not be of much use for the beetle if unfolding could be done only once. To make things even more complicated, the driving musculature is in the thorax, but, the folded region is at the tip of the wing. There is no musculature in the wing. How do Coleoptera do this?

2 Materials & Methods

Coleoptera have been studied using different techniques. High speed stills using a Nikon camera (0.1 ms exposure time, about life size), high speed video film (500f/s) using Mikromak Camsys and a Sony digital video (25f/s, 0.1 ms exposure time) have been used to analyse the process of unfolding in tethered or free specimens.

The major wing veins and their deformations during folding have been measured by manually digitizing microscopic slides of folded and unfolded wings. The veins have been described mathematically using polynomials. The angle between the two major wing veins has been measured compensating, for elastic deformation. A computer simulation has been developed which is capable of simulating folded structures made of stiff plates.

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Also, the surface area of the whole wing, and parts of it, have been calculated, the calculations and simulations were done with self-designed software based on *Mathematica*TM.

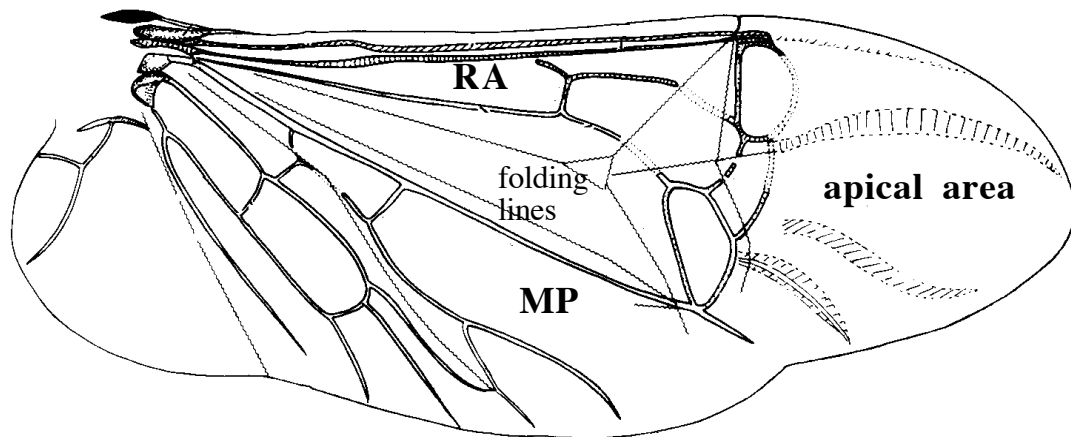


Fig. 1 Right hind wing of *Priacma serrata* (Cupedidae, Archostemata) showing folding pattern and the major veins, Radius anterior (RA) and Media posterior (MP). From Kukulová-Peck & Lawrence (1993), modified.

3 Results

The unfolding of the wing takes at least 20 to 30 ms but may take considerably longer. Wings **do not** unfold instantly when the leathery forewings are lifted; they may be moved from the resting position to the flight position while their apical area is still folded (Fig. 2). Left and right wings unfold independently of each other. Specimens may beat with their wings still folded. Legs are never used to unfold the wings.

Wing folding is done by a combined activity of abdomen and forewings; the abdomen pushes the wings under the forewings, by a brushing movement, and the wings fold according to their pattern.

There is elasticity in the wing veins. The veins are long rods in the membrane, formerly assumed to be stiff. This research has shown that they reversibly bend in the process of folding and unfolding. The degree of deformation depends on the species and on the region of the vein. In some species it is restricted to the apical end, in others it is the whole vein that is deformed. The angle between RA and MP is increased when the wing is unfolded. In most species the increase is about 15°.

As there is no musculature in the region where the vein is deformed, it must be brought about by the membrane. So, the membrane cannot be a soft tissue, as assumed before, but is rather stiff and inflexible.

Depending on the species, the surface area of the unfolded wing is, up to 4 times that of the folded wing.

The wing membrane has stiff regions which are connected to other stiff regions by the flexible folding lines. Panels and folding lines are **not** visibly differentiated. Four folding lines most often intersect in one point (Fig. 3).

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Fig. 2. *Lilioceris merdigera* (Chrysomelidae) taking off. In order to increase time resolution the half frames of this digital video sequence have been separated. Time elapsed between frames is 20 ms.

These observations and those on other folded structures show the occurrence of basic mechanisms. A basic mechanism (Haas & Wootton, 1996a, b) consists of four folding lines intersecting in the origin (Fig. 4).

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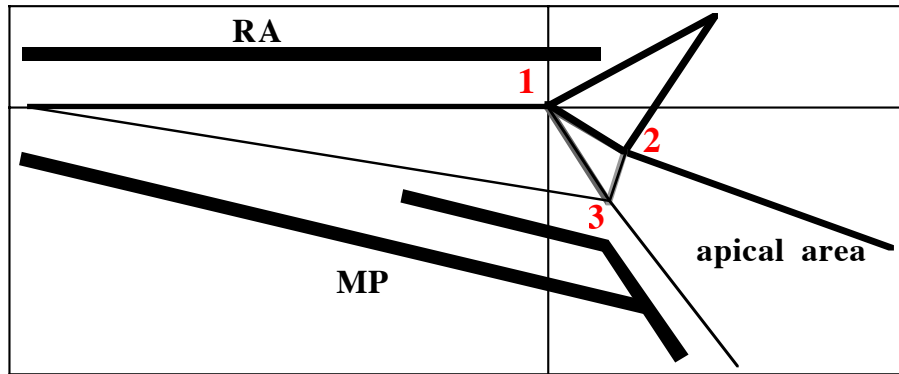


Fig. 3. The digitized folding pattern of *Cantharis livida* (Cantharidae). Each number denotes the point of intersection (origin) of a basic mechanism.

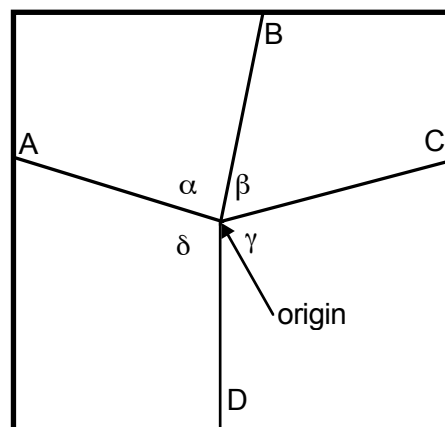


Fig. 4. A basic mechanism consisting of four panels connected by four folding lines, which intersect at one point. Most complex folding patterns, such as hind wings of Coleoptera consist of a combination of several basic mechanisms.

The four folding lines mark the borders of four panels. They are the hinges about which the panels move. The underlying assumption is that the panels are stiff so that the angles between the folding lines and the lengths of the folding lines are constant. A basic mechanism is opened and closed by increasing the angle ϵ between its base panels (Fig. 5). A mathematical model of the basic mechanisms has been developed. More complex folding patterns consist of several such basic mechanisms connected by shared folding lines (Fig. 3). Thus, the complex folding patterns can be modelled by a combination of basic mechanisms.

The simulations of basic mechanisms show that certain geometric rules have to be fulfilled for the mechanism in order to be completely foldable or unfoldable (Haas & Wootton, 1996b). These rules also apply to folding patterns, but additional constraints

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occur. There are folding patterns which are not foldable if their plates are stiff because some deformability is required. Such folding patterns are frequently found in wings, and dissections show that one panel is foil-like in its properties.

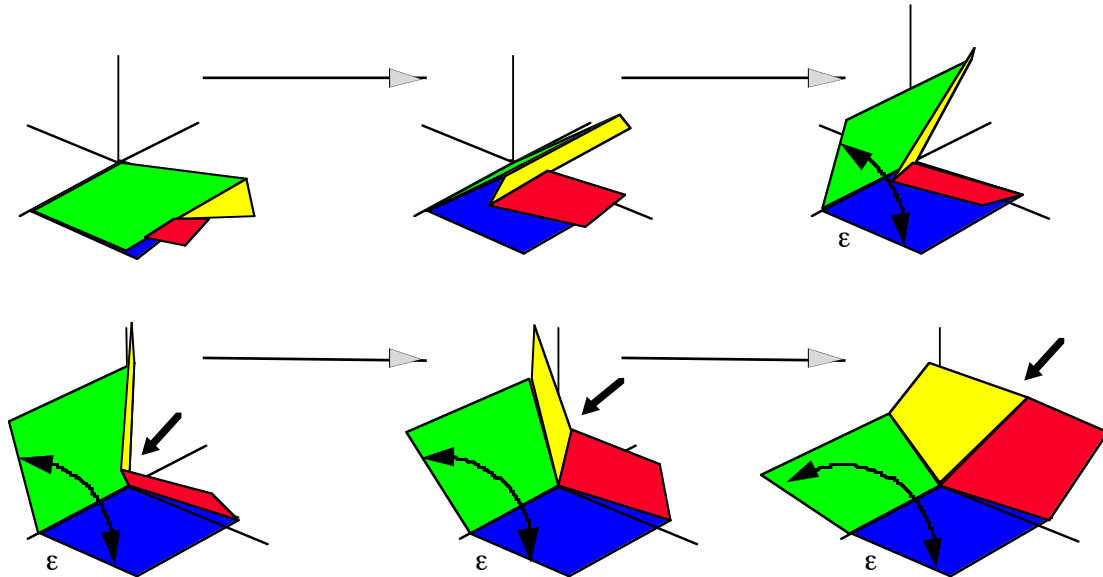


Fig. 5. The opening sequence of a basic mechanism (type -INT) showing the path of point B (arrow) when opening angle ϵ is increase. The path is a function of ϵ , α , β , γ , δ .

4 Discussion

The evidence presented has major implications for the understanding of the mechanics of folding. In the old model the veins were stiff rods transmitting the forces from the body to the folded region of the wing. Folding was completely controlled by the base. In the new model presented here the membrane assumes a much more active role. It is elastic, so that it generates forces, possibly driving the unfolding from the wing tip. The veins do separate suggesting that they activate the mechanisms in the tip. The stiff membrane forms basic mechanisms which work as levers. Thus, a bent region in the wing margin can be straightened by the backward pull of a vein.

In contrast to the computer simulation, unfolding and folding of wings is done using different mechanics. Unfolding is basically achieved and controlled from the wing base, whereas folding is possible only by using additional structures, like forewings and abdomen.

Wing folding and unfolding is, to my knowledge, the only mechanism in animals in which the antagonistic movements are not only achieved by different mechanisms — *thoracic musculature* vs. *abdomen plus forewings* — but where the mechanisms are located in different body parts. In all other systems using different mechanism for the reverse movements, the mechanisms are located in the same body parts. This is true, for example, for spider legs and butterfly proboscis which extend hydraulically and are flexed by muscles.

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The solutions and principles used by the Coleoptera to fold their wings may also be transferred to technical problems. Shields or umbrellas may be built completely driven from one point. Platforms with measuring instruments might be moved into a medium and uncovered simultaneously with a single remote motor. Also, the hind wings of the Coleoptera are an example of a smart structure: a remote motor, stiff plates and elastic rods create a defined and repeatable movement.

5 References

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