*Acta zoologica cracoviensia*, **46**(suppl.– Fossil Insects): 67-72, Kraków, 15 Oct., 2003

# The evolution of wing folding and flight in the Dermaptera (Insecta)

Fabian HAAS

Received: 30 March, 2002
Accepted for publication: 30 Nov., 2002

HAAS F. 2003. The evolution of wing folding and flight in the Dermaptera (Insecta). *Acta zoologica cracoviensia*, **46**(suppl.– Fossil Insects): 67-72.

Abstract. The structure of the dermapteran hind wings is described and their hind wing folding is compared with other insect taxa with folded wings (i.e. Coleoptera, Hymenoptera and Blattodea). The peculiarities of the dermapteran hind wing folding are pointed out: the wings are unfolded by the cerci, one wing after the other, in a rather slow process. The antagonistic movement, folding the wings, is achieved by intrinsic elasticity and resilin. The stem group representatives of the Dermaptera, the 'Archidermaptera' and the 'Protelytroptera', both taxa probably paraphyletic, do show the step-wise transformation from a simple, unfolded, 'cockroach'-like wing, to the complex wing of Recent Dermaptera.

Key words: Dermaptera, Archidermaptera, Blattodea, Protelytroptera, Coleoptera, wing folding, resilin.

Fabian HAAS, Staatliches Museum für Naturkunde; Rosenstein 1, D-70191 Stuttgart, Germany.
E-mail: haas.smns@naturkundemuseum-bw.de

## I. INTRODUCTION

The wings of insects are of a rather delicate structure and in order to keep them functional over the whole live span of the imago, some protection is certainly helpful. The ancestor of the Neoptera evolved the first mechanism to protect its wings by flexing them over its abdomen. Thus, the wings are carried close to the body, which enables the animal to move through narrow spaces and find shelter there. Using the wing flexion mechanism, the fore wings cover the hind wings and so the latter have an extra layer of protection by the fore wings. In order to increase the efficiency of protection, the fore wings are often thickened and leathery. The hind wings become the major flight organs and so they need to keep some specialised structure and minimum surface area to remain flight-worthy. The surface area is usually much larger than the area of the protective fore wings, and so they need to be folded in order to fit completely under the fore wings. Consequently, 'wing flexion' is defined as the movement of the (fore and hind) wings to their resting position over the abdomen, whereas 'wing folding' is defined as the reversible reduction of surface area of a wing in order to fit into its protective case (usually this applies to the hind wing).

Amongst the Neoptera, wing folding evolved in a number of taxa, such as some Hymenoptera (notably involving the fore wings), the Coleoptera, some Heteroptera, some Blattodea and the Dermaptera (CARPENTER 1992, RASNITSYN & QUICKE 2002). Each of these taxa has evolved mechanically different solutions to fold and unfold their wings according to the morphological structures present. Here, the wing folding and its evolution in the Dermaptera are discussed. This taxon has evolved an extremely complex hind wing folding pattern and mechanics. The Dermaptera are also notable in having morphologically derived cerci, the so-called forceps, and maternal care for eggs and first instar larvae.

A c k n o w l e d g e m e n t s. I would like to thank Prof. Dr. W. KLEINOW, Cologne, Germany, and Mr. C. TIMMINS, Exeter, UK, for permission to use their films and photographs of *Labia minor*.

## II. WING STRUCTURE IN DERMAPTERA

The Dermaptera are one of those taxa which many people consider flightless, because they never saw one on the wing. And indeed about 40 % of the species have reduced wings; the remaining 60 % have wings but not all of them do actually fly (WAGNER & LIEBHERR, 1992). Part of the confusion is that the Dermaptera have densely folded hind wings and so they are hardly visible (Figs 1B, 2C, D). Firstly, the hind wing is folded fan-wise along the folding lines in between anal and intercalar veins. Secondly it is folded transversely along the ring fold. Thirdly, it is folded transversely

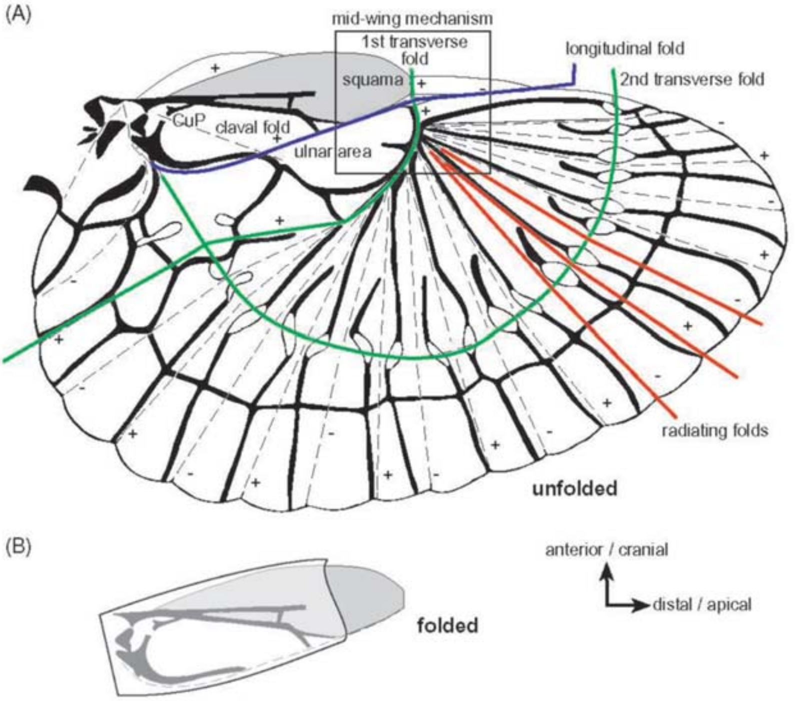
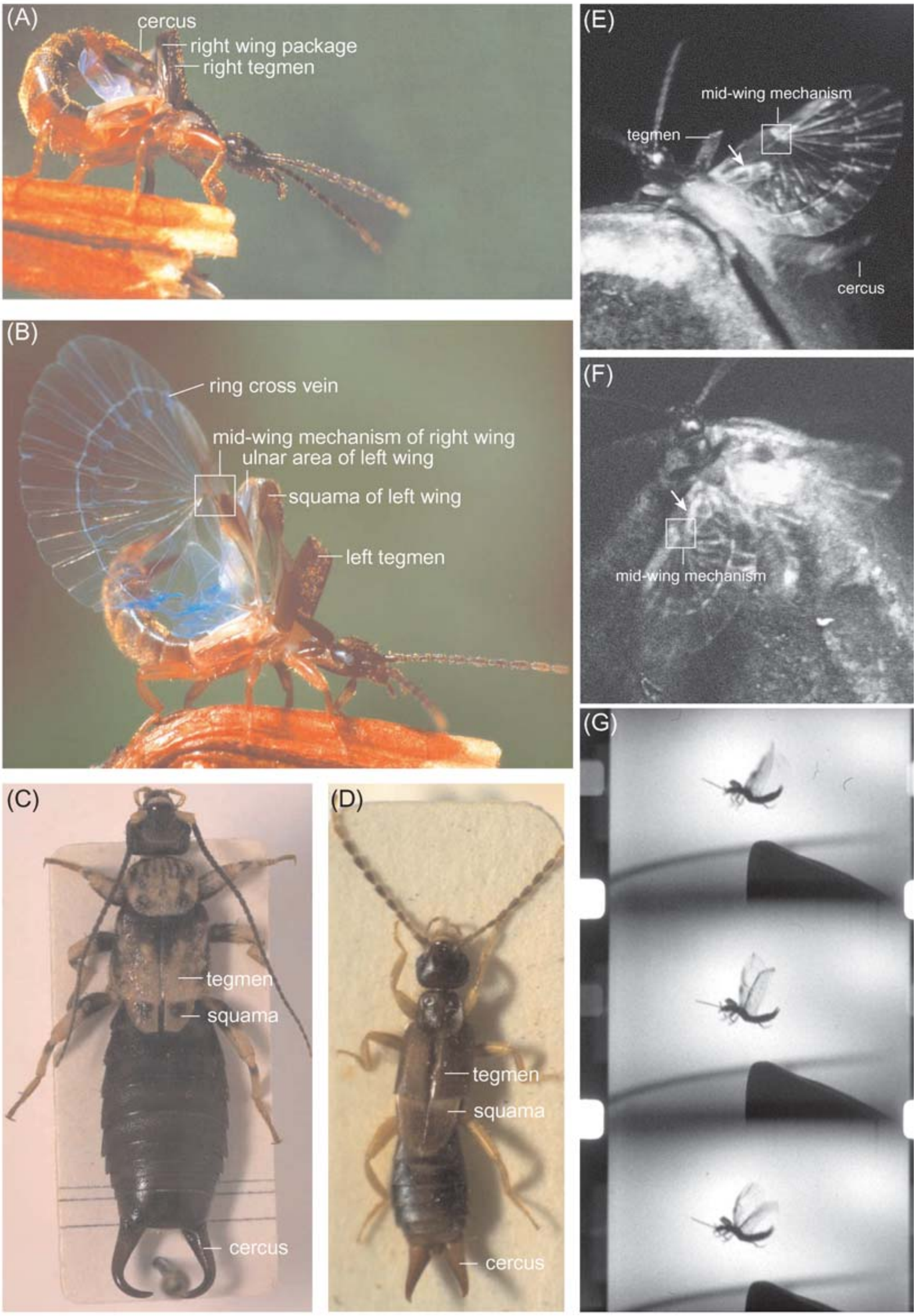



Fig. 1. Schematic view of the unfolded (A) and folded (B) wing of *Forficula auricularia* (LINNAEUS, 1758). (A) shows the major folding line, along which the wing is folded into the small wing package (B) with only about a tenth of the surface area of the unfolded wing. Most of this package is covered by the tegmen, leaving only the apical part of the squama visible. +: convex fold; – concave fold.

---

Fig. 2. Different species of Dermaptera at rest, during flight preparation, and during flight. (A, B) for unfolding the wing, the wing package is erected over the abdomen, so that the cercal tip can interfere with it and unfold one wing after another. (C, D) shows two mounted species of Dermaptera at rest. Only the tip of the squama surpasses the tegmen, which leads to the often heard erroneous conclusion that Dermaptera are wingless. In species capable of flight, such as *Labia minor* (D), the visible part of the squama is longer than in those not capable, such as *Echinosoma micropteryx* GÜNTHER, 1929 (D). In the unfolded wing of *Labia minor* (LINNAEUS, 1758) (E, F) the two stiffening mechanisms are locked to keep the wing deployed (white arrow points to claval fold). (G) *Labia minor* on the wing. (A, B) are kindly provided by C. TIMMINS, Exeter; (E, F, G) were kindly provided by W. KLEINOW. All pictures used with permission. Not to scale.


(A)
cercus
right wing package
right tegmen
(B)
ring cross vein
mid-wing mechanism of right wing
ulnar area of left wing
squama of left wing
left tegmen
(C)
tegmen
squama
cercus
(D)
tegmen
squama
cercus
(E)
mid-wing mechanism
tegmen
cercus
(F)
mid-wing mechanism
(G)

along the anal fold. And fourthly, longitudinally along a fold between squama and ulnar area (Fig. 1A). The folding is actually done in one movement and results in a small wing package of about 10% the surface area of the unfolded wing. This small wing package makes many people believe that earwigs are either wingless or cannot fly. Both assumptions are not true (Fig. 2C, D, G). The venation and folding pattern is unique amongst insects especially in two aspects: the veins radiate from the centre of the hind wing, rather than from its base, and the large fan is folded three times, once radially and twice transversely (Fig. 1).

## III. MECHANICS OF WING FOLDING

Mechanical experiments have shown that the dermapteran hind wing is actually folded by intrinsic elasticity, stored by resilin in well-defined patches in the wing veins (KLEINOW 1966; HAAS et al. 2000). If the Dermaptera have densely folded hind wings and yet can fly, then the wing package must be unfolded during the flight preparation and folded again after flight. Unfolding is done by a unique mechanism: both hind wings, one after the other, are unfolded by the cerci (Fig. 2A, B). The abdomen bends over cranially, interferes with the cerci in the erected wing package and 'wipes' them out (i.e. unfolds the hind wings). This is done with one hind wing after another and may fail in the first trial. Consequently, wing unfolding does need quite some time (about 300 ms each wing, KLEINOW 1966), which probably is the reason why flight is not an escape reaction in Dermaptera.

If the hind wing folds automatically due to intrinsic elasticity, then it must be kept unfolded during flight by some mechanism capable to withstand the aerodynamic forces, otherwise the hind wing would fold. The dermapteran hind wings are locked in an unfolded position by two stiffening mechanisms, the mid-wing mechanism and the claval fold, which keep the wings deployed and stable in flight (Figs 1A, 2E, F, 3A, B). Some movement in the wing articulation probably unlocks them in order to fold the hind wing again.

Apart from a superficial similarity, the wing folding in Coleoptera relies on a completely different mechanics. All unfolding movements are driven from the wing base and no other body part is involved. In contrast to the Dermaptera, the coleopteran hind wing folding is achieved with the help of the elytra and the abdomen, and is largely non-automatic (HAAS & BEUTEL 2001). Resilin has been found but its functional importance in folding or unfolding remains unknown (HAAS et al. 2000).

## IV. EVOLUTION OF WING FOLDING AND THE FOSSIL RECORD

The complex system of hind wing folding in Dermaptera (i.e. location of veins and resilin; bending of abdomen; wing stiffening mechanisms) certainly did not evolve in one step. A detailed study of the wing articulation and venation in 25 representative of all Recent dermapteran families shows that venation and folding pattern is virtually identical, with some but relatively slight and phylogenetically useful variation (HAAS & KUKALOVÁ-PECK 2001).

To examine the ancestral state, we need to turn to the probable stem line of the extant Dermaptera, the Jurassic 'Archidermaptera' (Fig. 4). These ancestors clearly bore small wing packages implying they had the same wing folding pattern and mechanics as extant earwigs. However, they also had long and filiform cerci, implying that hind wing unfolding must have been possible with long, annulated cerci. Short and non-annulated cerci in the Dermaptera are clearly no adaptation to hind wing unfolding.

The interesting question whether the forceps-like cerci are required to unfold the wing or whether they constitute a separate adaptation can be answered. The Protelytroptera bore short, i.e. 'cockroach'-like, annulated cerci, and there is no case reported that Recent Blattodea would unfold their wing with the help of the cerci. However, the fossil 'Archidermaptera', which could fold their hind wings into small packages, bear relatively long and annulated cerci. Assuming the same folding pattern, these annulated cerci must have been useable to unfold the wings, as this cannot be done

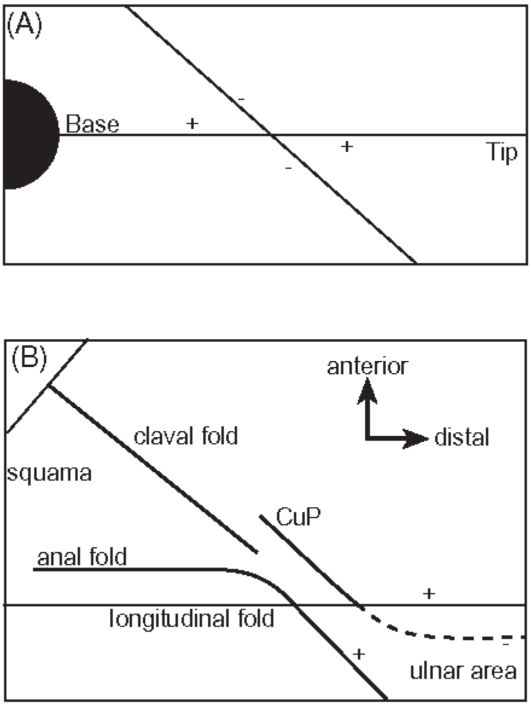



Fig. 3. Schematic view of the stiffening mechanisms present in the Dermaptera hind wing. (A) once the oblique fold is active, the area becomes stiff and prevents flapping or folding along the line from base to tip. (B) shows a detailed model of the wing base. The reader is encourage to xerox and enlarge this figure and fold it according to the instructions. +: convex fold; - concave fold. For details see HAAS & KUKALOVÁ-PECK (2001).

by the wing base. Thus, forceps-like cerci, which lost annulation, very probably constitute an adaptation not related to wing unfolding. In extant Dermaptera long and annulated cerci are still found in the larvae of 'Diplatyidae' and Karschiellidae (Fig. 4) (HAAS 1995; HAAS & KUKALOVÁ-PECK 2001).

Another representative of the dermapteran stem line, the 'Protelytroptera', gives some indication to the evolution of hind wing folding. Apart from a large number of fossils with no wing folding, such as *Acosmelytron delicatum* TILLYARD, 1931, fossil hind wings of *Protelytron permianum* TILLYARD, 1931 (Fig. 4) bear some resemblance to extant Dermaptera. The common characters, apart from similarities in the venation, are the transversely folded fan and the chitinous patches (or broadenings). These characters occur elsewhere in the Neoptera only in Dermaptera and thus strongly support close relationship (HAAS & KUKALOVÁ-PECK 2001). However, in the fossil the fan is transversely folded only once, instead of twice as in extant Dermaptera. During the 2$^{nd}$ International Congress on Palaeoentomology, Cracow, Poland, for which this volume has been produced, Dr. D. E. SHCHERBAKOV, Moscow, Russia, has shown slides of a yet undescribed representative of the 'Protelytroptera' with two transverse folds crossing the fan. The habitus of this specimen is utterly 'cockroach'-like: tegmina long with distinct venation, hind wings as long as the abdomen, coxae long and cerci short. According to our present knowledge, this specimen is a 'missing link' in the evolution of the complex folding pattern in dermapteran hind wing. It shows one of the intermediate steps between the unfolded hind wing to dermapteran triple folded hind wing. A detailed description of this fossil is extremely desirable.

The evolution of the wing folding and cerci is summarised in Fig. 4. The evolution of highly derived and complex systems can be traced, once the structure and its function is understood and the

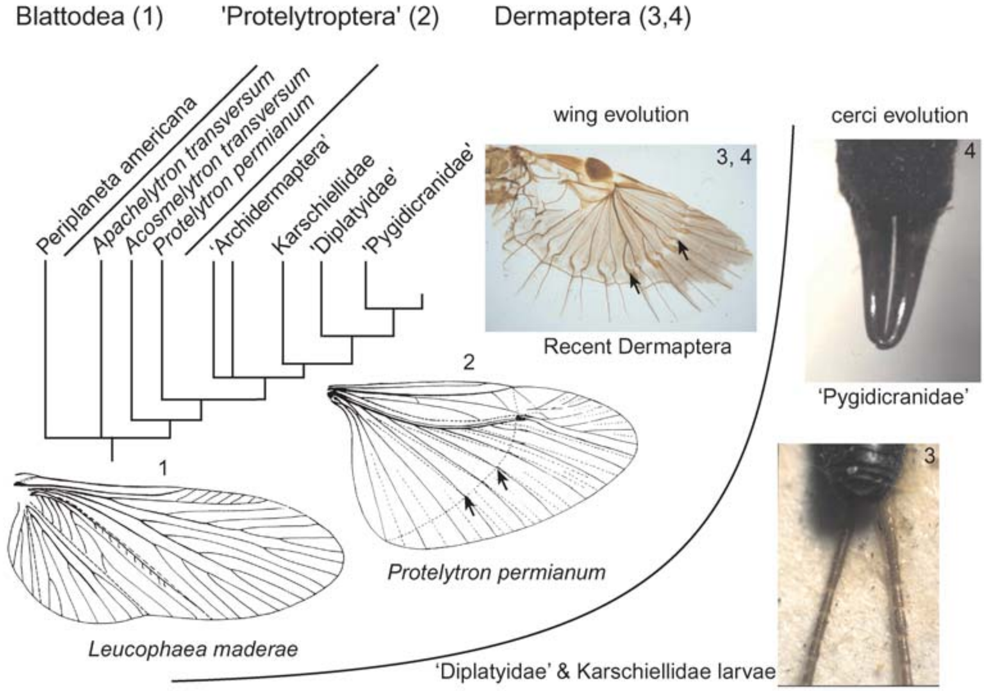



Fig. 4. The relationships of 'Protelytroptera', 'Archidermaptera' and Dermaptera and the evolution of hind wing folding as well as cerci. Recent Blattodea constitute the outgroup in the analysis conducted by HAAS & KUKALOVÁ-PECK (2001). Clade modified.

relationships between fossil and living taxa are known. The fossils also indicate when the wing folding evolved: it must have taken place between the Permian (245 mya), when the dermapteran stem group was 'cockroach'-like, and the Jurassic (200 mya), from which we know specimens already very similar to Recent Dermaptera.

## REFERENCES


CARPENTER F. M. 1992. Superclass Hexapoda. Treatise on Invertebrate Paleontology, Part R, *Arthropoda*, **4**: 143-153.

HAAS F. 1995. The phylogeny of the Forficulina, a suborder of the Dermaptera. *Systematic Entomology*, 2**0**: 85-98.

HAAS F., GORB S., WOOTTON R. J. 2000. Elastic joints in dermapteran hind wings: materials and wing folding. *Arthropod Structure & Development*, **29**: 137-146.

HAAS F., GORB S., BLICKHAN R. 2000. The function of resilin in beetle wings. *Proceedings of the Royal Society of London*, Series B, **267**: 1375-1381.

HAAS F., BEUTEL R.G. 2001. Wing folding and the functional morphology of the wing base in Coleoptera. *Zoology*, **104**: 123-141.

HAAS F., KUKALOVÁ-PECK J. 2001. Dermaptera hind wing structure and folding: New evidence for familial, ordinal and supraordinal relationships within Neoptera (Insecta). European *Journal of Entomology*, **98**: 445-509.

KLEINOW W. 1966. Untersuchungen zum Flügelmechanismus der Dermapteren. *Zeitschrift für Morphologie und Ökologie der Tiere*, **56**: 363-416.

RASNITSYN A. P., QUICKE D.L. J. 2002. History of Insects. Kluwer Academic Publisher, Dordrecht, Boston, London. 517 pp.

TILLYARD R. J. 1931. Kansas Permian Insects Pt. 13. The new order Protelytroptera, with a discussion of its relationships. *American Journal of Science*, **21**: 232-266.

WAGNER D. L., LIEBHERR J. K. 1992. Flightlessness in Insects. *Trends in Ecology and Evolution*, **7**: 216-219.