Evidence from Folding and Functional Lines of Wings on Inter-ordinal Relationships in Pterygota

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> Abstract

Insects fold their hind wings because of quite simple reasons. With flexed and folded wings, it is easier to hide, to use small crevices and shelters against the impact of weather, e.g. wind and rain, and to escape predators, to name just a few reasons. The fitness advantage is so great that wing folding convergently evolved in many separate insect 'orders' (Heteroptera, Hymenoptera, Lepidoptera amongst others), using superficially different mechanisms. The Dermaptera, Blattodea and Coleoptera were examined in more detail. Included in the comparative study were other, technical and ornamental folded structures such as Origami models. The comparison showed despite very many differences some common features: almost all fold structures consist of Basic Mechanisms, an arrangement of four plates and four folding lines intersecting in one point. In hind wings, resilin is ample; energy is needed to unfold and/or fold the wings and prevents wear at critical locations in the wing. Often the folding lines in the wing are not morphologically differentiated (at least at LM and SEM level), but some specialised structures, typical for taxonomic families and orders do occur. The actual mechanics used in folding and unfolding, respectively, are fundamentally different: Coleoptera use their thoracic muscle to unfold the wing, but the elytra and the abdomen to fold it again. In Dermaptera, the wing is unfolded with the cerci, and folded with intrinsic elasticity stored in the many, strategically placed resilin patches. In Blattodea the wing unfolding is a simple by-product of wing promotion. Technical folded structure such as airplanes' wings are comparatively simple, and take advantage of the option to have additional tools & mechanisms for (un-)folding, as well interrupting the structural integrity for a short period of time. So they become unfunctional for a spell, which is no option for biological structures.

1. Introduction

The wings and flight of insects have fascinated people since long, admiring the colourfulness of wings in butterflies, the delicacy of structure in lacewings, the manoeuvrability of dragonflies and speed of flies. Indeed, wings are one of the key innovations that made the Insecta so successful in species numbers and habitats conquered.

The wings are an essential part in the every-day life of an insect. It goes on the wings when escaping (flies, crickets and grasshoppers), searching for food (beetles) or mates (bees, butterflies and dragonflies). So it is essential to have the wings protected and kept functional during the whole adult life span.

In this contribution, I examine some of the mechanisms how the hind wings are protected and kept functional by folding them underneath the protective fore wings, and I will put these mechanisms in a phylogenetic context. Possibly, this character system proofs helpful in resolving some high-level problems in insect systematics.

2.   Morphology and function

It is beyond the scope of this contribution to give detailed accounts on the morphology of the insect wings. However, some basics, which are essential to understand the function and limitations of insect wings, should be mentioned here.

Insect wings are sac-like extensions of the integument of the meso- and metathorax, which become flattened (and translucent) and sclerotised during the final moult to the imago. In the adult, upper and lower surfaces of this sac lie together firmly connected. Veins with a thickened cuticle are formed by haemolymph lacunae in this sac and altogether stabilize the wing. They usually contain trachea and nerve to supply the sensory setae found all over the wing. In no case, there is musculature within the wing. It is exclusively located in the thorax proper and does not stretch into the wing itself. Corrugation and venation pattern is related so, some veins are always located on ridges (convex, 'mountain fold' or '+'), others in grooves (concave, 'valley fold' or '−').

This structure has a major consequence: all movements, deformations and folding of the wing cannot be achieved by local (intrinsic) musculature but exclusively by some other mechanism. These might be local energy storage in resilin, passive deformations due to aerodynamic forces in flight (WOOTTON 1979) or interferences of cerci, abdomen or elytra with the wing.

The construction of insect wings is thus in sharp contrast to the design of wings of birds, bats and pterosaurs. There, wings are supplied with intrinsic musculature and movements are continuously controlled by the central nervous system. Thus, birds can actively change wing shape at any time in flight (VAZQUEZ 1994), while insects cannot. The intrinsic muscles give a completely new set of options for flight manoeuvres. Nonetheless, also vertebrates fold their wings when at rest, again using the intrinsic musculature. In my view, the convergent evolution indicates some common advantages of wing folding. Furthermore, there is wing reduction in birds (e.g. ostriches, penguins, kiwis) which parallels the frequent reductions in the Pterygota.

The fundamentally different wing morphology reflects the evolutionary history of the two types of wings. In all vertebrates, the wings are always modified fore limbs with its complete set of muscles and nervous control. In insects, the discussion on their origin has not finally settled but all points to a movable appendage of aquatic insect larvae, such as the gills found in Recent Ephemeroptera and Plecoptera. These gills, exactly as Recent wings, have musculature only at their base.

The separate evolutionary history is one explanation why vertebrates have only one wing pair, as there is exactly one pair of fore limbs, while winged insects have two wing pairs and a full set of legs. Three pairs of wings seem to be aerodynamically problematic and are not realised in Recent insects. (The interesting question, why angels are depicted with wings and arms is beyond the scope of this paper.)

Returning to insect, we find many functions fulfilled by the wings. Naturally, there is flight in all Pterygota but wings may also serve as heat collectors (Lepidoptera), for stridulation (viz. in Ensifera), as display structures (Mantodea, Lepidoptera) and for camouflage (Caelifera, Heteroptera, Coleoptera, Lepidoptera, etc.). In many taxa (Coleoptera, Blattodea, Dermaptera, Plecoptera to name a few), the fore wings are thickened and stiffened to protect the delicate hind wings. In other groups, the thickening is carried so far that the fore wings form a hard shell around the abdomen and hind wings. Despite their status as key innovation for the Insecta, wings are often reduced either to sensory organs such as the halteres of Diptera or fairly unfunctional flaps as in many Blattodea, Dermaptera and Coleoptera.

3.   Origin and mechanics of folding

The fossil record gives good indication on the presences of wings and their folding. The first winged insects, roughly resembling Recent Odonata, are found in the Early Carboniferous (approx. 320 MYA), suggesting a Devonian (approx. 400 MYA) origin. However, the very transformation of a predecessor structure to wings as we know them today is undocumented by fossils. The first recorded taxa to take discernible steps towards wing folding were the Diaphanopterodea and some Neoptera from the Carboniferous (summary see in KUKALOVÁ-PECK 1991).

Both taxa developed mechanisms to remote the wings from the flight position (about perpendicular to the longitudinal body axis) to a resting position over the abdomen (KUKALOVÁ-PECK & BRAUCKMANN 1990; WOOTTON & KUKALOVÁ-PECK 2000). This had two effects. Firstly, the more compact insect became able to move faster through the vegetation and reach suitable places to hide from predators, rain, and other unfavourable conditions. In addition, it could access new spaces for feeding or egg-laying. Secondly, for geometric reasons the fore wings come to lie over the hind wings (Fig. 1). From this point onwards the fore and hind wings were modified separately to different structures, which had also implications on the flight mechanisms, i.e. if fore or hind wings are the major power source in flight. Here, this aspect cannot be explored further.

However, Dipaphanopterodea and Neoptera are not sister-taxa. The former undoubtedly is a member of

Fig. 1. The fundamental difference between palaeopterous (*Aeshna* sp., Odonata, left) and neopterous (*Perla* sp., Plecoptera, right) Pterygota is exemplified with by two Recent representatives. When sitting, the *Aeshna* sp. needs quite some space, neither fore nor hind wing are protected and its silhouette is perfectly visible from all directions. The plecopteran protects its hind wings with the fore wings and may completely disappear behind a plant stalk. Evidently, neopteran insects need less space when at rest. Both photos by the author.

the Palaeodictyopterida, a sub-taxon of the Palaeoptera (if the latter is monophyletic). Neoptera constitute the sister-taxon to the whole Palaeoptera (or to one of its sub-taxa). Thus, 'neoptery', i.e. the remotion of the wings to a resting position over the abdomen has evolved twice. The assumption of convergent evolution of 'neoptery' is further supported by its very different structural basis in these taxa, which does not allow to conclude that one is the predecessor of the other, or that both were derived from a common ancestral state.

Obviously, wing folding (including vertebrates) evolved at least five times and separated by millions of years, which emphasises its usefulness. Within the Neoptera, the evolution of wing folding went further by including distal hind wing areas as well as basal hind wing areas (e.g. the anal field) into the folding process.

The evolution of the anal area and the fan is not explored here, as it is much too extensive in this context and would need additional experimental and theoretical procedures. Two issues should be mentioned: as necessary when an evolution of an organ is outlined is the agreement on the structure itself. Only then can comparisons and transformations produce the correct result. The great number of nomenclatorial systems from Needham to Kukalová-Peck used for wing venations and areas indicates that this agreement might not be yet reached with the necessary precision and clarity. It also occurred to me that one of the problems is that when 'fan' is said, then fanwise folding is assumed and in the next step, synonymised with the anal area, which is then assumed to be wing area which is fanwise folded. This need not be the case, and is a somewhat circular definition. So the problem of the neopteran fan and anal area will be addressed in separate publications.

The transformations and mechanisms of wing folding have been most extensively studied in the Blattodea, Dermaptera and Coleoptera and these are chosen as case studies. Before describing the characteristics of each of the solutions, some general principles of folding are explained.

4. General principles of folding

Comparing the folding patterns of insects and those of deployed Origami models one finds a surprising similarity. Almost all folding patterns consist of basic mechanisms, in which four folding lines intersect in one point and hinge the four stiff plates between them (as in Fig. 3). Other configurations with three or five folding lines and plates are not foldable at all, or not determined in their movements since they have a degree of freedom greater than 1. The mathematics of this system was treated by a number of authors (e.g. Haas & Wootton 1996, and references therein). Even complex folding patterns, such as those of the Coleoptera and Dermaptera, consist almost exclusively of combinations of such basic mechanisms (Haas 1994, 1998). The second major folding structure is the fan (irrespective of its homology, applies to
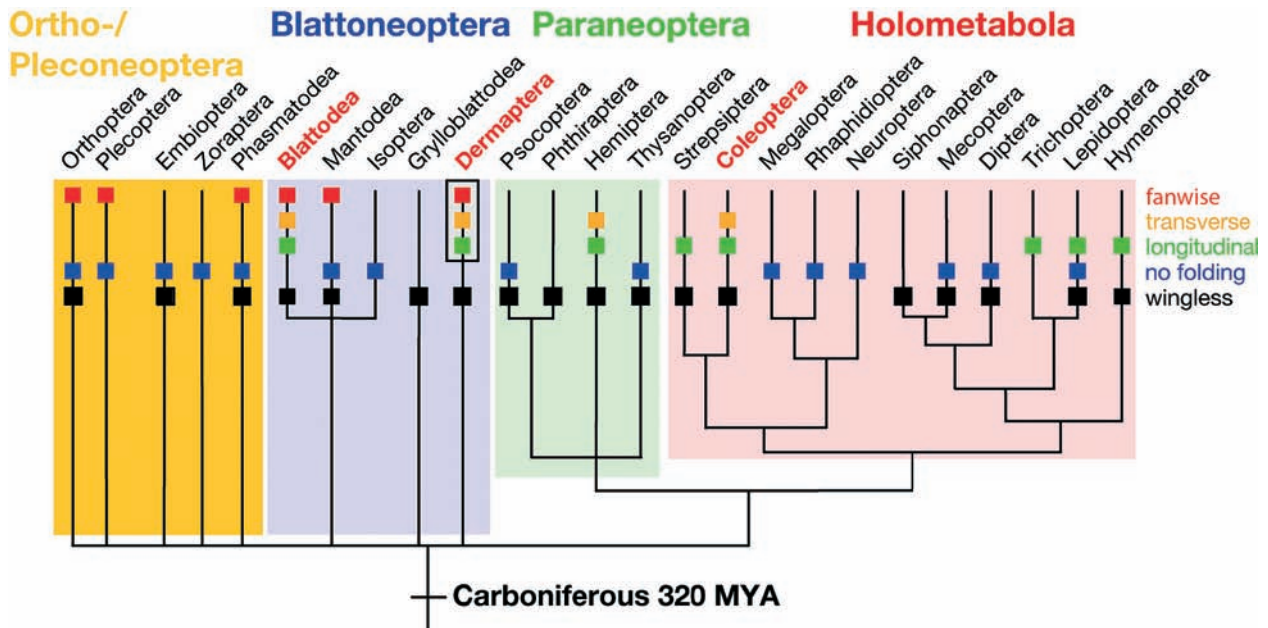
Fig. 2. The mapping of folding characters on a cladogramme for the Neoptera (modified from Kristensen 1991) shows the great diversity in wing folding, including wing reduction. A square indicates that at least one species has a certain folding type; if several types are indicated for a lineage, these do not necessarily co-occur in the same taxon. Naturally, wingless species have no wing folding at all. The box around the squares on the Dermaptera line indicates that the three folding type always occur together. The major lineages are indicated by the coloured backdrop.

Origami, too), in which many folding lines intersect in one point and radiate to the paper (wing) margin. Only a few other folding mechanisms exist (e.g. in Lepidoptera, Hymenoptera, Ensifera: *Gryllotalpa*), which are not treated here. In all cases, veins and folding lines are fairly independent of each other. Even their intersections might be inconspicuous, without specialised hinges in the veins.

5.   Single taxa

The mechanics of hind wing folding in the following taxa was described in a number of publications. Hence, only a short review with special focus on the systematically useful characters is given here. The Blattodea, Coleoptera and Dermaptera are described below (Haas 1999). Before doing so, a short survey of the wing folding occurring in the neopteran taxa is given in Fig. 2 (modified from Haas 1998). A square indicates that at least one species of the taxon has a certain type of folding. The different folding types may occur in single species or whole sub-taxa (genera, subfamilies) and not necessarily together (except Dermaptera). Naturally, wingless species have no wing folding at all.

It is obvious from Fig. 2 that winglessness is common, despite the importance of flight for the diversification of insects. Furthermore, simple and unfolded wings

are common. Longitudinal folding regularly occurs in quite a number of taxa but is less frequent than the other folding types. The most specialised folding is the transverse folding of the wing and it is only the Dermaptera in which all folding types occur always in combination. The Coleoptera are second to this in combining transverse and longitudinal folding in all winged species (i.e., without fan).

5.1.   Blattodea

The cockroaches are interesting not only because of the frequent wing reduction but also because they developed transverse folding several times independently (Rehn 1951; McKittrick 1964). This is the conclusion after mapping the character state 'transverse folding' on several independent cladogrammes for the Blattodea. In no case, this character state is of monophyletic origin and assuming such origin leads to severe conflicts with other character systems.

The assumption of multiple origins of transverse folding is supported by the simplicity in which it is realised (Fig. 3). All wings are folded longitudinally along the shared border of remigium and anal area (which may or may not be folded fanwise). In some species, the apical area is tucked over, so that a small part of the wing tip is actually lying on top of the folded wing. In fact, the tucking generates a basic mechanism in the apical area of the wing. It is unfolded
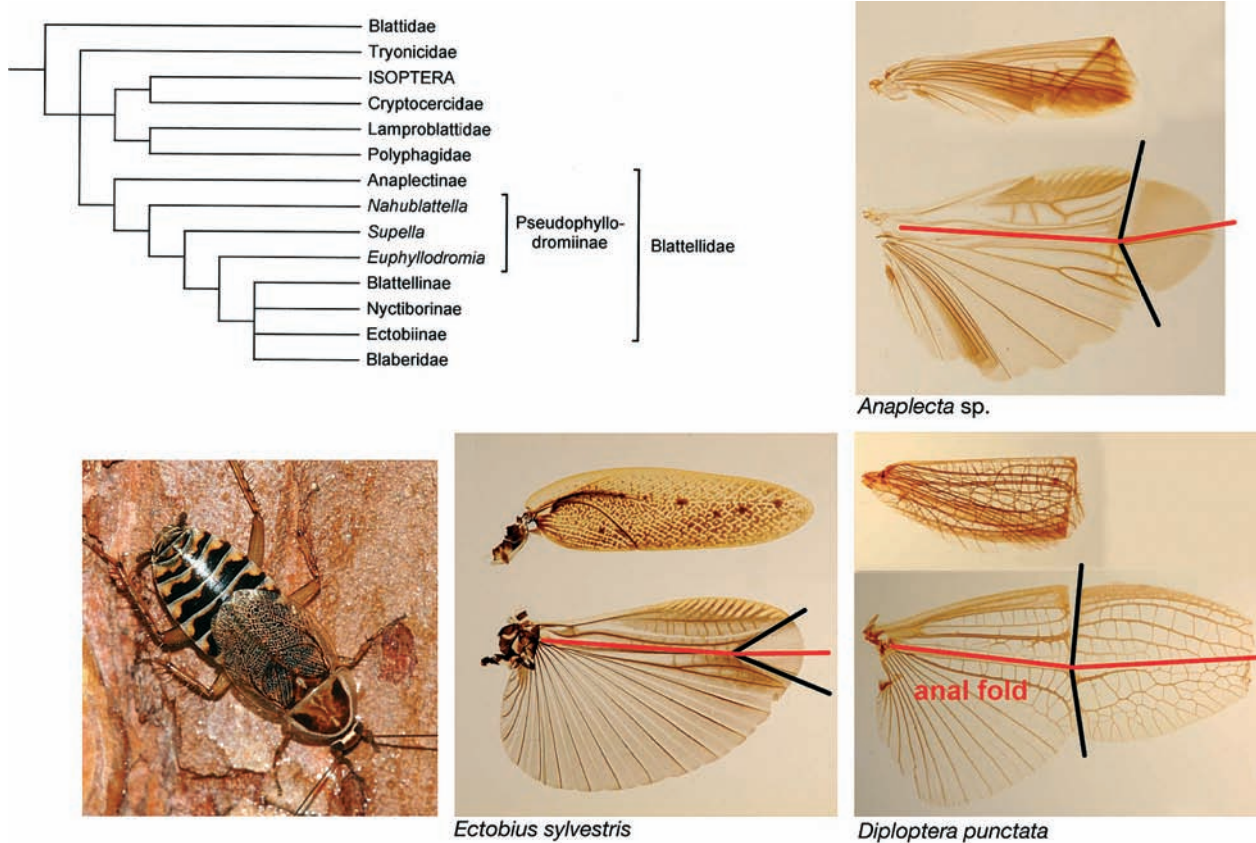
Fig. 3. Transverse hind wing folding in Blattodea evolved several times independently, simply by tucking a smaller or larger apical area of the wing onto its dorsal surface by using a single basic mechanism. For *Ectobius sylvestris*, fore and hind wing is shown, in the other species the folded and unfolded hind wing is shown. The anal fold is roughly marked as red line, while the transverse folding line is black. Cladogramme simplified from KLASS (1997). All photos by the author.

during the wing promotion to the flight position, and folded when remoted to the resting position. Thus, and figuratively speaking, the cockroach does not know when the wing tip is unfolded – and does not even need to know, because it is done automatically when going on the wing. Essential to this unfolding of the wing while promoting it, is the very broad attachement of the hind wing to the thorax, which is much broader than the wing articulation itself. This is very much like a paper fan, which is opened by holding one spar and pulling (= promoting) the other. If this attachment is experimentally destroyed wing unfolding becomes impossible (HAAS 1999).

The folding of a small apical area can be examined in the Central European species of *Ectobius*. The Malaysian species of *Diploptera*, which are reported to fly, brought this mechanism of wing tip folding to an extreme by placing the basic mechanism at about half the wing length (Fig. 3; HAAS & WOOTTON 1996). Consequently, the folded wing 'tip' has about the same length as the base of the wing. However, there is no indication of another specialised mechanism to unfold the wing.

5.2. Dermaptera

The earwigs are prominent among the Pterygota in having either reduced wings (approx. 40 % of the species) or consistently showing a complex folding pattern including both, fanwise and double transverse folding (HAAS et al. 2000; KLEINOW 1966). In no other instance among Recent insects does the fanwise folded area of the wing engage in transverse folding or double transverse folding. A systematic analysis of venation and folding pattern shows extremely low variation among the Dermaptera (HAAS & KUKALOVÁ-PECK 2001; HAAS 2003). This low variation is in sharp contrast to the substantial variation of the two patterns in Coleoptera. Still, this character system is useful for 'family'-level phylogenetic reconstructions in Dermaptera.

A transversely folded fan is otherwise only found among the fossil Protelytroptera. These are assumed to be stem or sister-group to the Dermaptera based on this and other, independent characters (overlapping tergites and sternites etc.; HAAS & KUKALOVÁ-PECK 2001; SHCHERBAKOV 2002). From the fossil record of the Permian in Kansas a specimen was described
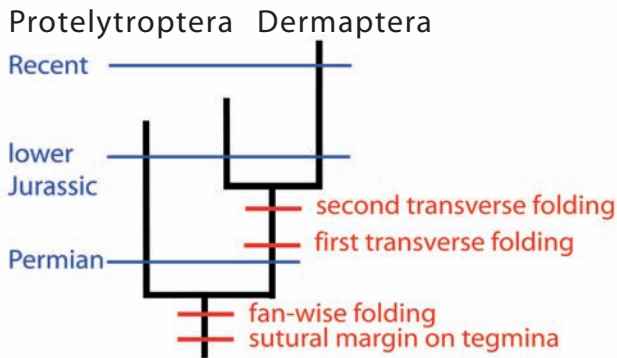
Fig. 4. Rough time scale and sequence for the evolution of hind wing folding in Protelytroptera (partim) and Dermaptera, based on *Protelytron permianum*, an undescribed fossil from Russia, and various dermapteran fossils. Dermaptera and Protelytroptera are occasionally called Forficulida (SHCHERBAKOV 2002), if considered sister-taxa. Modified from HAAS & KUKALOVÁ-PECK (2001) and SHCHERBAKOV (2002).

with a single transverse fold across the fan, as well as the broadened areas at the intersections of radiating veins and transverse fold (HAAS & KUKALOVÁ-PECK 2001 and references therein). From Russia, a yet undescribed protelytropteran actually shows the double transverse folding of the fan we find in Recent Dermaptera (Shcherbakov pers. comm.): a convincing synapomorphy for Dermaptera and Protelytroptera (partim!). This strongly indicates paraphyly of Protelytroptera (Fig. 4).

5.3. Coleoptera

The Coleoptera are the largest insect 'order' and their success is attributed to the evolution of a tight exoskeletal shell leaving only small membranous areas exposed. The stiff elytra have become an integrative part of the shell, inducing the evolution of a complex hind wing folding. Again, for the details of mechanics I refer to the literature (HAAS & BEUTEL 2001 and references therein), and a short description will suffice here.

The hind wings of Coleoptera are promoted and unfolded by separate driving mechanisms. So, the folded wing can be brought to flight position and the unfolded wing can be moved to the resting position (HAAS & BEUTEL 2001). This is unlike the mechanics in Blattodea (HAAS 1995) in which unfolding is strictly linked to promotion and folding to remotion, through the wing's broad attachment to the body. As expected the beetles' wings are only narrowly attached to the body (HAAS & BEUTEL 2001). The wing is promoted, as in all Neoptera, by a contraction of the basalar muscle and unfolded by a remotion of the 3Ax (3rd Axillary or Axillare 3), pulling (rather indirectly) on the Media posterior (MP1+2).

Consequently, the angle between the Radius anterior (RA) and MP1+2 increases visibly by 10°–15° when the wing is unfolded (Fig. 5). Despite the additional function of pulling MP1+2 posteriorly, all other functions, such as wing remotion and functions during flight are maintained (for coleopteran flight, see BRACKENBURY 1994).

The angular increase between RA and MP1+2 triggers the unfolding of the apical area structured with a folding pattern of basic mechanisms. There is some variation in the folding pattern, though they are fairly constant to 'family' or higher taxonomic level (FORBES 1926; KUKALOVÁ-PECK & LAWRENCE 1993). However, this does not exclude inter-generic variation.

The methodical comparison of a large number of coleopteran taxa (HAAS 1998) has shown that there are specialised structures in the coleopteran hind wings related to folding. The 'folding patch' is a morphologically unspecified intersection of folding lines with the wing margin. The 'marginal joint' is an elbow-like articulation of the costal margin found in e.g. scarabaeoids. The 'bending zone' is a smooth bending of the whole costal margin, found in e.g. adephagans. In addition to their presence or absence in certain taxa, these three folding structures are combined along the anterior wing margin. However, the number of actually realised combinations is limited (Figs. 5 and 6): If there is a folding patch at the distal end of the RA, then there never is a bending zone or marginal joint distal to it. If at all, another folding patch is following. To a bending zone, a marginal joint or a folding patch might be added distally. Distal to a marginal joint, one will exclusively find folding patches, but never a bending zone or another marginal joint (Fig. 5).

Thus, a great variety of folding patterns in the apical area are added to a constant and comparatively simple mechanism at the base of the wing, the angular separation of RA and MP1+2. The apical folding determines the actual density of folding, which expressed as folding ratio. The folding ratio, which is the surface area of the unfolded wing divided by that of the folded wing (wings from one specimen), was found to range approx. from 1.3 to 4.5 (HAAS 1998), with no correlation to the absolute hind wing length. It is approx. 10 in Dermaptera and like in Dermaptera (HAAS, GORB & WOOTTON 2000), resilin was found in a number of beetle species (HAAS, GORB & BLICKHAN 2000).

In a phylogenetic context, the wing folding provides an interesting character system for intra-Coleoptera systematics (Fig. 7) but offers no information on the sister-taxon. The most basal Coleoptera as well as the possible sister-taxa have hind wings without any trace of folding. It is probable that the basal mechanism of the wing folding, the angular separation of RA and MP1+2 driven by the 3Ax, is derived from the
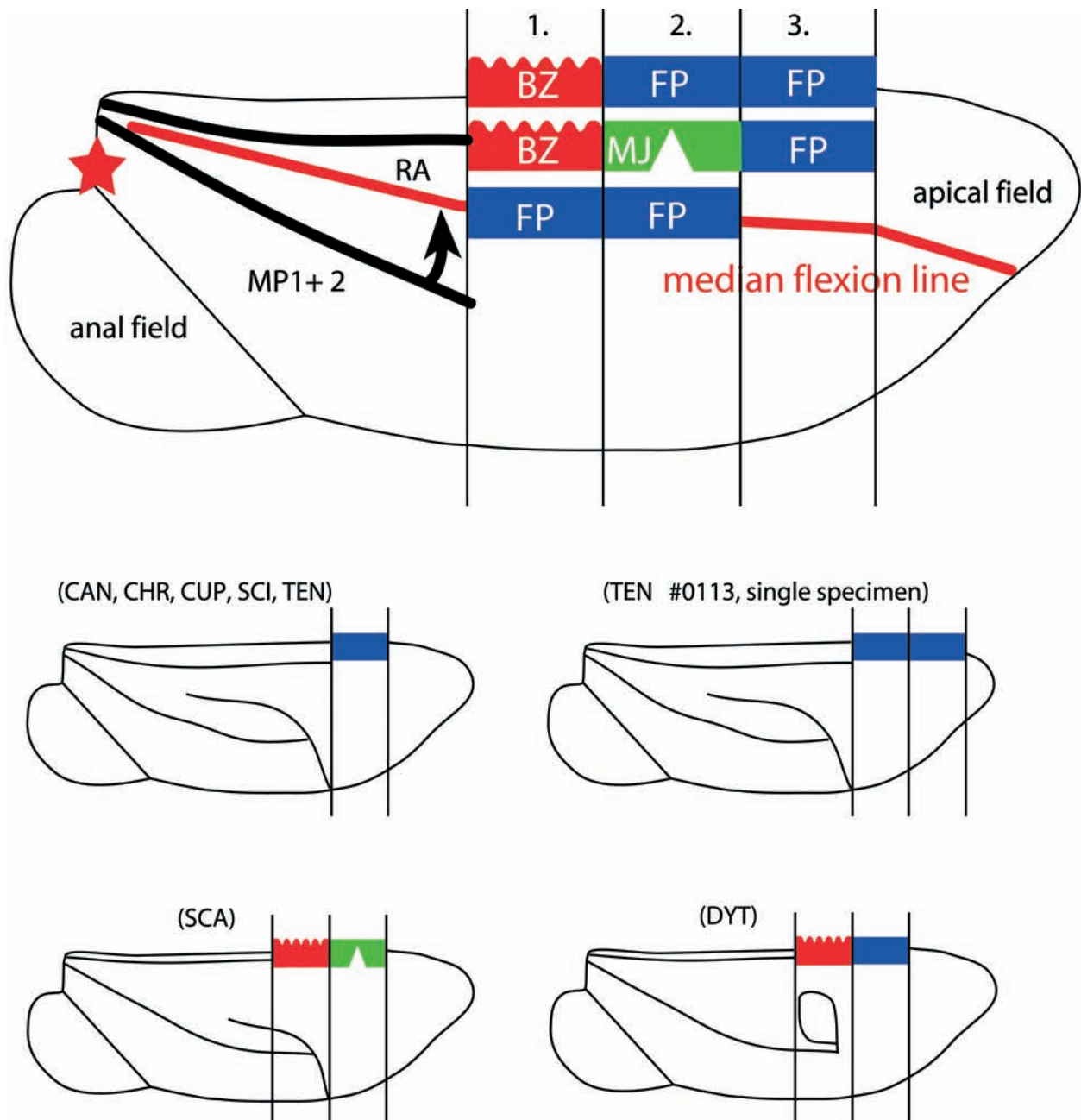
Fig. 5. Schematic view of the arrangement of folding structures in the coleopteran hind wings. BZ: bending zone, FP: folding patch, MJ: marginal joint, MP1+2: Media posterior, median flexion line shown in red, RA: Radius anterior, star indicates the position of the wing articulation, arrow on MP1+2 inidcates folding movement of MP1+2. CAN: Cantharidae, CHR: Chrysomelidae, CUP: Cupedidae, DYT: Dytiscidae, SCA: Scarabaeidae, SCI: Scirtidae, TEN: Tenebrionidae, TEN #0113 refers to a single specimen which had two FPs instead of one, which is usual for this species *Zophobas rugipes*. 1, 2, 3 refers to the first, second and third folding structure in the wing. Modified from HAAS (1998).

median flexion line, which is present in all Neoptera (WOOTTON 1979). This flexion line is essential for the proper deformation of the wing in flight but has, with exception of the Coleoptera, no function in folding. The mapping of the wing folding characters on a cladogramme including Megaloptera as outgroup and fossil stem-group Coleoptera, however, nicely shows the sequence of innovations leading to the complex folding pattern and mechanism of Recent Coleoptera (BEUTEL & HAAS 2000; HAAS 1998).

6.   Conclusion

The following pattern becomes evident. Wing folding is advantageous for insects and increases the fitness as it evolved several times independently. The capability to remote the wings over the abdomen evolved in Neoptera and in the Diaphanopterodea (Palaeoptera), though on a different structural basis. Both mechanisms, however, provided protection of the hind wings by covering them with the fore wings. This enabled the
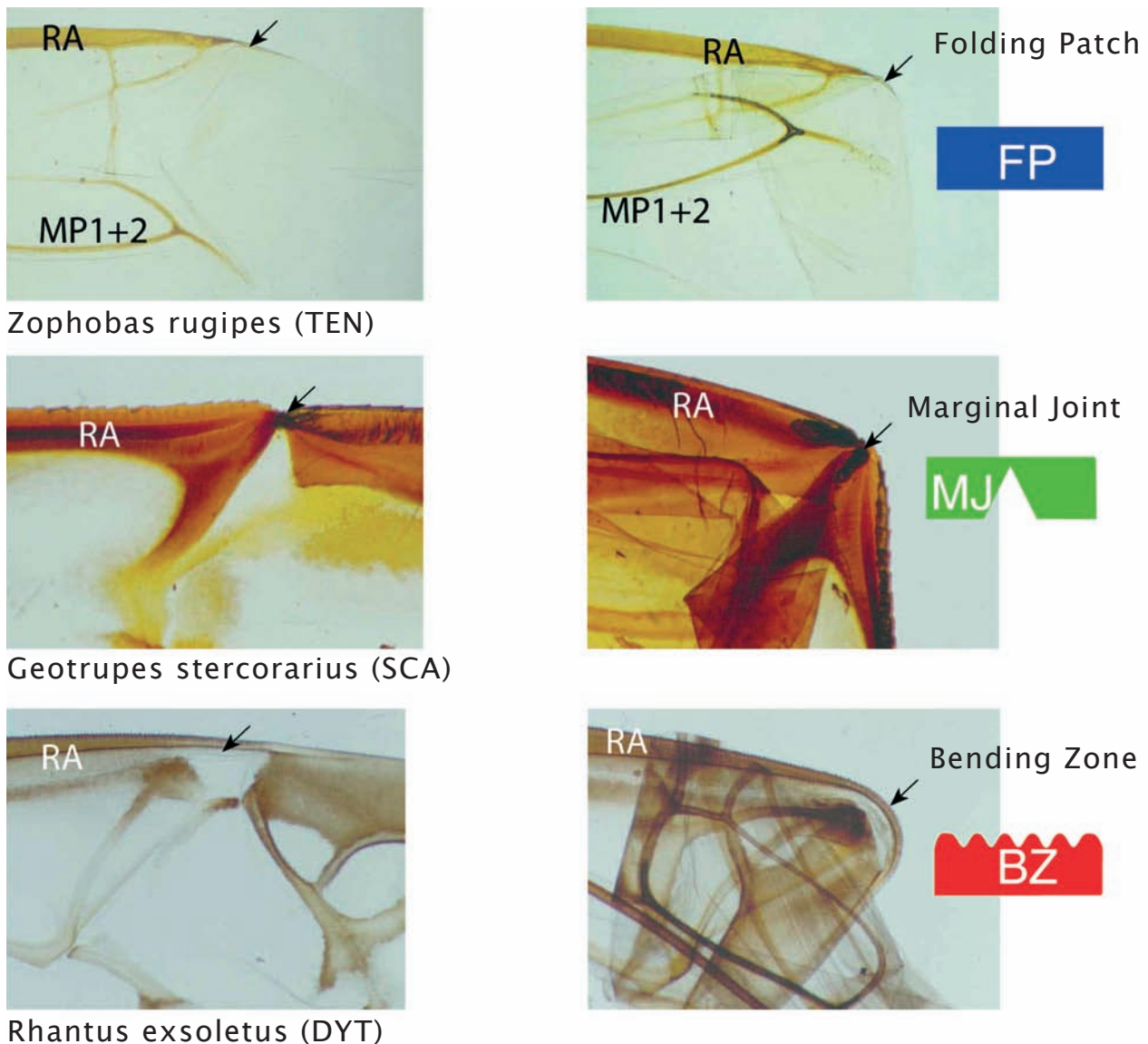
Zophobas rugipes (TEN)

Geotrupes stercorarius (SCA)

Rhantus exsoletus (DYT)

Fig. 6. Macro-photographs of the folding structures in the Coleoptera; for abbreviations see Fig. 5. Modified from HAAS (1998). All photos by the author.

individuals to hide in spaces or behind stalks from predators and unfavourable conditions.

Later in evolution, the wing folding was further refined by adding folds. This mainly concerns the hind wings since they are covered by the fore wings and need to be large to provide sufficiently large aerofoil for flight. More folds and more complicated folding patterns allow for wings with higher folding ratios and for the development of stiff and short tegmina or elytra. This developement occurred in several taxa independently and is often an autapomorphic character for the so-called 'orders', e.g. Coleoptera and Dermaptera. In Blattodea, Heteroptera and Lepidoptera (e.g. Ptero-phoridae, Alucitidae, Sessiidae), on the other hand, hind wing folding evolved at lower taxonomic levels, such as 'family', and may constitute an autapomorphic character state there.

An exception to the rule of folding only the hind wings are the Hymenoptera, the Vespidae in particular which fold their fore plus hind wings. A detailed description of the mechanisms and folding patterns is given by DANFORTH & MICHENER (1988) and the interested reader is referred to this contribution. However, as in Blattodea and Heteroptera, the wing folding evolved at a lower taxonomic level, since the last common ancestor of the Hymenoptera had no wing folding.

Thus, wing folding is in almost all cases (maybe except Neoptera, Diaphanopterodea, Dermaptera-Pro-telytroptera), an 'order' or lower level character and is therefore hardly suitable to establish inter-'ordinal' relationships. Often, the fan or anal area is discussed as a synapomorphy for a number of pterygote 'orders'. However, the problems with the fan and anal area are shortly outlined in 'Origin and mechanics of folding'
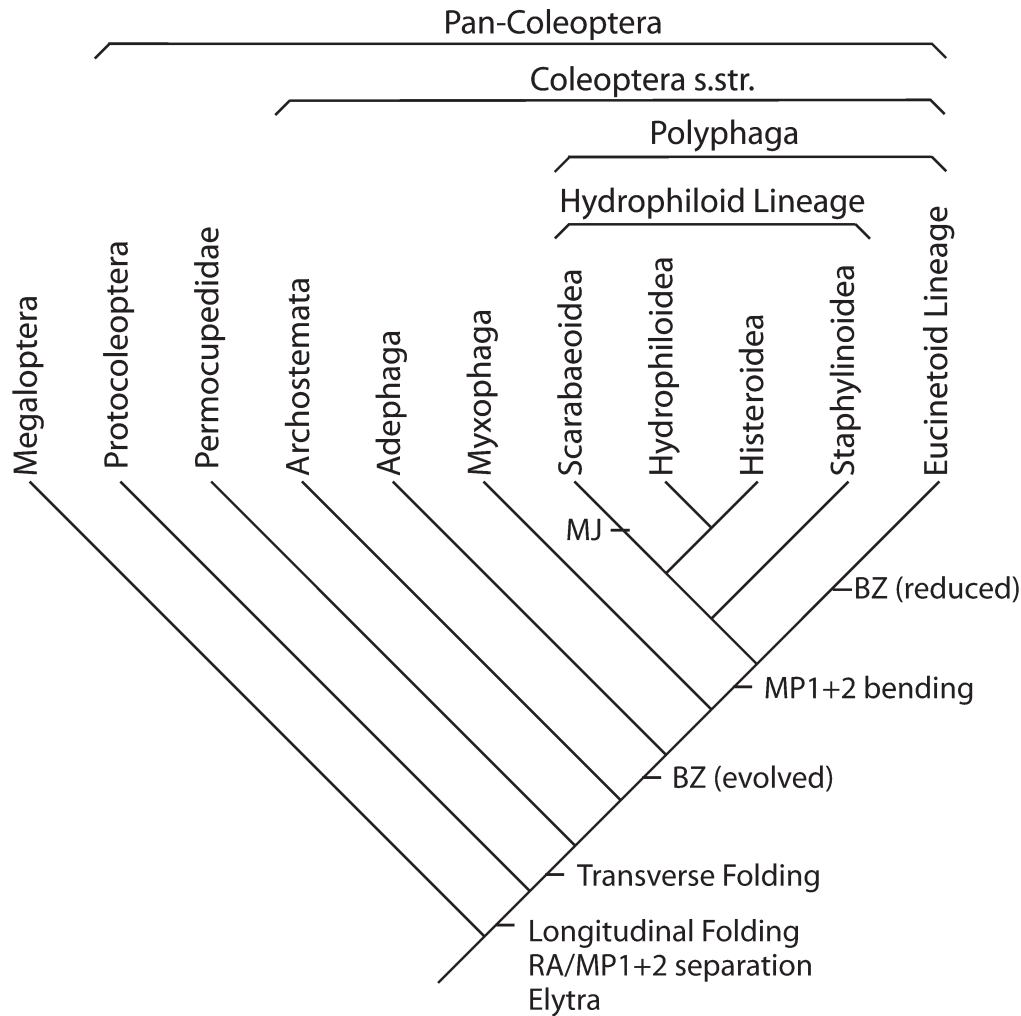
Fig. 7. Cladogramme showing the sequence of evolution of the folding structures and characters in Coleoptera. Abbreviations see above; it is assumed that the BZ is secondarily reduced in the Eucinetoid Lineage. Modified from HAAS (1998).

of this paper and so I refrain to make a clear statement on such a problematic factual base.

Another character system worthwile to explore especially in this context might be the width of the wing attachment to the thorax. Is it broad, as broad as the whole notum, or narrow, just about the width of the wing articulation and much narrower than the notum. The former is, at least, present in the Plecoptera, Dermaptera and Blattodea, the latter in Diptera, Coleoptera and other Holometabola (HAAS 1998). This character system might hold valuable information, also in the context of the fan and anal area.

Mechanically speaking, wing folding uses pre-existing structures such as flexion and folding lines caused by the remotion of the wing, broad (Blattodea, Dermaptera) or narrow attachments (Coleoptera, Hymenoptera) to the body, the median flexion line, or the motility of the 3Ax, to fold apical wing areas.

It also became evident that there is no 'Resilinoptera'. Resilin is present in all taxa and, at best, belongs to the ground pattern of the Insecta (if not higher systematic

level). It should also be stressed that some taxa (Diptera, Hymenoptera: Apidae) have no protective devices or wing folding, but nonetheless, live on decaying materials or dig in the soil. In these cases, frequent cleaning compensates for the lack of protection.

7. Acknowledgements

8.   References

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