New evidence on the mechanics of wing unfolding in Dermaptera (Insecta)

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> Abstract

The wing unfolding in Dermaptera is re-analysed for two species, *Auchenomus* sp. (Spongiphoridae) and *Timomenus lugens* (Bormans, 1894) (Forficulidae), based on several digital movie sequences made in the earwigs' natural environment. The frames were separated and numbered sequentially to establish the time line of unfolding and (where available) folding. It is shown that the steps described earlier in contributions of the first author are confirmed, with the exception of the drivers. It has been assumed that the cerci are essential to unfold the wings. The current contribution clearly shows that this is not the case in all species: the wings can be unfolded without involvement of any other body part. In all examined sequences the wing packages are unfolded without any involvement of the cerci. Thus the Dermaptera are heterogeneous in this respect and this new finding is discussed in a behavioural and phylogenetic context.

> Key words

1. Introduction

Earwigs (Dermaptera) are a well defined group of insects with about 2200 species. They are characterised by fairly uniform morphology and behaviour and their variation in both is only slowly being understood (e.g. Matzke & Klass 2005). The structure of Dermaptera has not changed significantly since the Early Jurassic (Grimaldi & Engel 2005) and there is no difficulty in assigning these fossils correctly. One of the key characteristics of earwigs that evolved early in their evolutionary history (Triassic according to Grimaldi & Engel 2005) is short tegmina and intricately folded hind wings forming a wing package, which protrudes from underneath the tegmina. The hind wing consists essentially of a large fan, which is folded twice transversely, across the fan-wise folding (Haas et al. 2000). This folding pattern is unique within Insecta and is a strong autapomorphy for Dermaptera (Haas & Kukalová-Peck 2001). There is little fossil evidence on how this wing package evolved; however, a fossil protelytropteran gives some clues to the sequence of the origin of folds (Haas 2003).

Within the Dermaptera, the cerci evolved from long, annulated threads into stiff, non-annulated forceps, which clearly is a derived character state (Haas & Kukalová-Peck 2001). In Recent representatives of Dermaptera, the plesiomorphic character state is preserved in the nymphs of Diplatyidae (Shimuzu & Machida 2011; see Haas & Klass 2003 for current state of knowledge on basal relationships in Dermaptera; Jarvis et al. 2005 did not include Diplatyidae
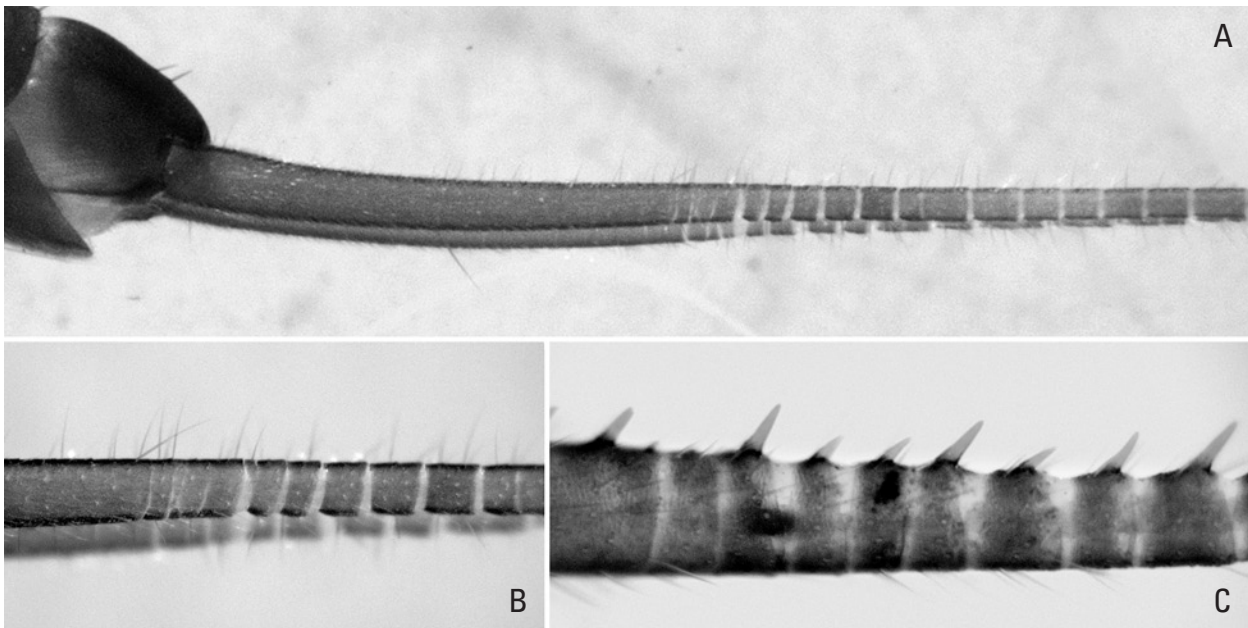
Fig. 1. Basal section of nymphal cerci of *Karschiella* sp. In contrast to a regular annulation of the distal part (right) the cuticle of the basal part appears broken and irregularly annulated. Specimens in the ZMUC collection. **A**: Lateral view on basal portion and following 10 segments of cerci. **B**: Same specimen with annulation enlarged. **C**: Second specimen in dorsal view, denticles point posterio-medially.

nor Karschiellidae), before all but the basal article is lost in the final moult (Green 1898). The nymphs of Karschiellidae are assumed to have regularly annulated cerci too; however, a closer examination of cerci shows that in contrast to Diplatyidae nymphs, the annulation is clear only in the distal part, while the basal part of the karschiellid cercus is more like a tube that shows an irregular sequence of membranous and sclerotised rings or semi-rings (Fig. 1). In adult earwigs, the cerci serve a variety of functions. They may be used in courtship, specimen interaction, predation and wing unfolding (Briceno & Eberhard 1995).

The mechanics of hind wing folding and unfolding was studied in detail by Kleinow (1966), Haas et al. (2000) and Haas & Kukalová-Peck (2001). The hind wing is equipped with resilin patches which ensure its folding to its resting (= folded) position without muscular activity. Therefore, a mechanism is required to actively unfold the hind wing to its flight position (flat, expanded), as well as a mechanism to keep the hind wing unfolded and stiff enough to counter forces experienced during flight. For the latter, a stiffening fold and an articulation-like structure upon the ulnary area and the radiating vein (around mid-length of the hind wing) snap into position to ensure that the hind wing remains unfolded, and stiff enough to prevent accidental folding in flight. The former, the actual unfolding of the hind wing, was observed on numerous occasions by different observers (Kleinow 1966, see his photos in Haas 2003; Chris Timmins, see his photos in Haas et al. 2001 and Haas 2003) to be achieved by bending

over the cerci craniad, interfering with the erected and slightly opened hind wing package and wiped open in an "unzipping" movement of the cerci (straightening the abdomen). The species examined are representatives of two taxa within the Eudermaptera: *Forficula auricularia* Linnaeus, 1758 (Forficulidae) and *Labia minor* (Linnaeus, 1758) (Spongiphoridae), and observations were conducted in natural as well as laboratory conditions.

So far no observations were known to contradict this understanding of hind wing unfolding and folding, however, it was evident that many species have very long cerci that reach or surpass the length of the abdomen, e.g. members of *Cranopygia* (Pygidicranidae), *Forcipula* (Labiduridae), *Allodahlia*, *Cordax* and *Timomenus* (Forficulidae), and *Auchenomus* and *Spongiphora* (Spongiphoridae). For geometrical reasons it is difficult to conceive how very long and stiff cerci reach into the hind wing package and 'unzip' it in the described way. It was assumed that hind wings are not unfolded at all, though being present and fully developed. Kleinow (1971) and Mercier & Poisson (1923) showed that in Dermaptera the presence of wings is not necessarily correlated with flight capability, i.e. even winged earwig specimens may lack strong dorso-longitudinal thoracic musculature and their phragmata for their attachment. Further, morphometric analyses of winged and flight capable Dermaptera by Kleinow (1971) indicated that in these cases the hind wing surface area is too small for flight, reaching unacceptably high wing loads.

Another observation contradicted this proposed model. Short and densely folded hind wings have evolved in the Jurassic "Archidermaptera" (a grouping including the most primitive true Dermaptera). As far as can be said on the basis of fossil and models, their hind wing folding is similar or identical to Recent dermapterans. However, archidermapterans possess long and annulated cerci. It was concluded by HAAS (2003) that short cerci cannot be an adaptation to hind wing unfolding, and that wing unfolding was achievable with filiform cerci. However, it was not concluded that unfolding was achievable without interference by cerci, mainly based on the observational and structural evidence (resilin) found earlier.

Here, evidence is shown for the first time contradicting the understanding of hind wing unfolding by the mentioned authors (KLEINOW 1966; HAAS et al. 2001; HAAS 2003) and making a re-assessment of the mechanics necessary.

2.   Material and methods

A visual identification of the two species was conducted based on the recorded clips; the specimens have not been available for morphological examination. Two species are recorded: *Auchenomus* sp. female (Eudermaptera: Spongiphoridae) and *Timomenus lugens* (Bormans, 1894) (Eudermaptera: Forficulidae).

Clip 1 in Fig. 2 shows *Auchenomus* sp. and was recorded using a Casio EX-FH100 (www.casio-intl.com) digital camera with a Raynox macroscopic lens (www.raynox.co.jp), model M-250. Exposure metering was camera's auto mode, the resolution 640×480 pixels at 120 fps (frames per second). This produced an AVI video file (13 MB) showing at 30 fps and resulting in a four times slower motion than the real process. Playing time is 8 seconds, while the actual process took 2.2 seconds. The movie was shot by Hung Bun Tang on the 25th March 2011 at about 12:30 hrs local time near Venus Drive in Singapore.

Clip 2 in Fig. 3 shows *Auchenomus* sp. and was recorded (AVI video file, 4.4 MB at 448×336 pixels) on 24th Oct 2011 at 11:46 am at the same location as Clip 1, with same equipment as Clip 1 and at 240 fps (playing time 5 seconds, actual process 0.71 seconds).

Clip 3 in Figs. 4–6 shows *Timomenus lugens* and was recorded with a Sanyo Digital Movie Camera VPC-CG65 in MPEG-4 format at 30 fps, and a resolution of 640×480 pixels. This produced a MPEG-4 file of 8.8 MB and 49 seconds duration. The movie was recorded by Arlo Pelegrin in Nan, Thailand on the 04th May 2008 at about 14:00 hrs.

All figures show continuous frame sequences. The frames of the movies were separated using Apple Mac OS 10.6.8 (www.apple.com) with GraphicConverter 7.5 (www.lemkesoft.de) and saved as TIFF image files. Estimates of the duration of a particular process were done counting the frames on which the process was visible, using the following formula:

$$ t \quad = (n-1)/\text{fps} $$

with
$$ t \quad = \text{elapsed time [seconds] for the process} $$
$$ n \quad = \text{number of consecutive frames on which process is visible} $$
$$ \text{fps} = \text{frames per second of recording} $$

3.   Results

Clip 1

The clip (Fig. 2) shows an *Auchenomus* sp. and has 265 separate frames (sequential numbers 001–265; 2200 ms). All relevant body parts are visible; the specimen is freely moving on a leaf.

The tegmina are being erected in 6 frames (frames 153–158, 41.66 ms), which is almost simultaneous to the erection of the hind wing package (frames 154–157, 25.00 ms). The tegmina assume an approx. V-shaped position perpendicular to the longitudinal body axis. The hind wing package stays in the erect position for about four frames (frames 157–160, 25.00 ms), showing little motion blur, just before strong flapping of the hind wing package starts (frames 159–160, 8.33 ms). After 12 frames (frames 159–170, 91.66 ms) the hind wing is expanded, and after another 7 frames with significant motion blur, the hind wing appears to be fully expanded and standing still (at frame 177). Both left and right hind wing are moved synchronously, the left one with better visibility due to the perspective. The fully unfolded hind wings are held still over, for about 39 frames (frames 177–215, 316.66 ms). Afterwards, strong flapping occurs as if the specimen was going to take off, but it hardly loses contact with the substrate (possibly for few frames 218–221, 16.67 ms). The exact posture of the legs and tarsal contacts are not visible due to motion blur. The cerci are lifted upright to about 90° to the longitudinal body axis (frames 188–217, 241.66 ms) only after complete unfolding of the hind wings, and never interfere with the hind
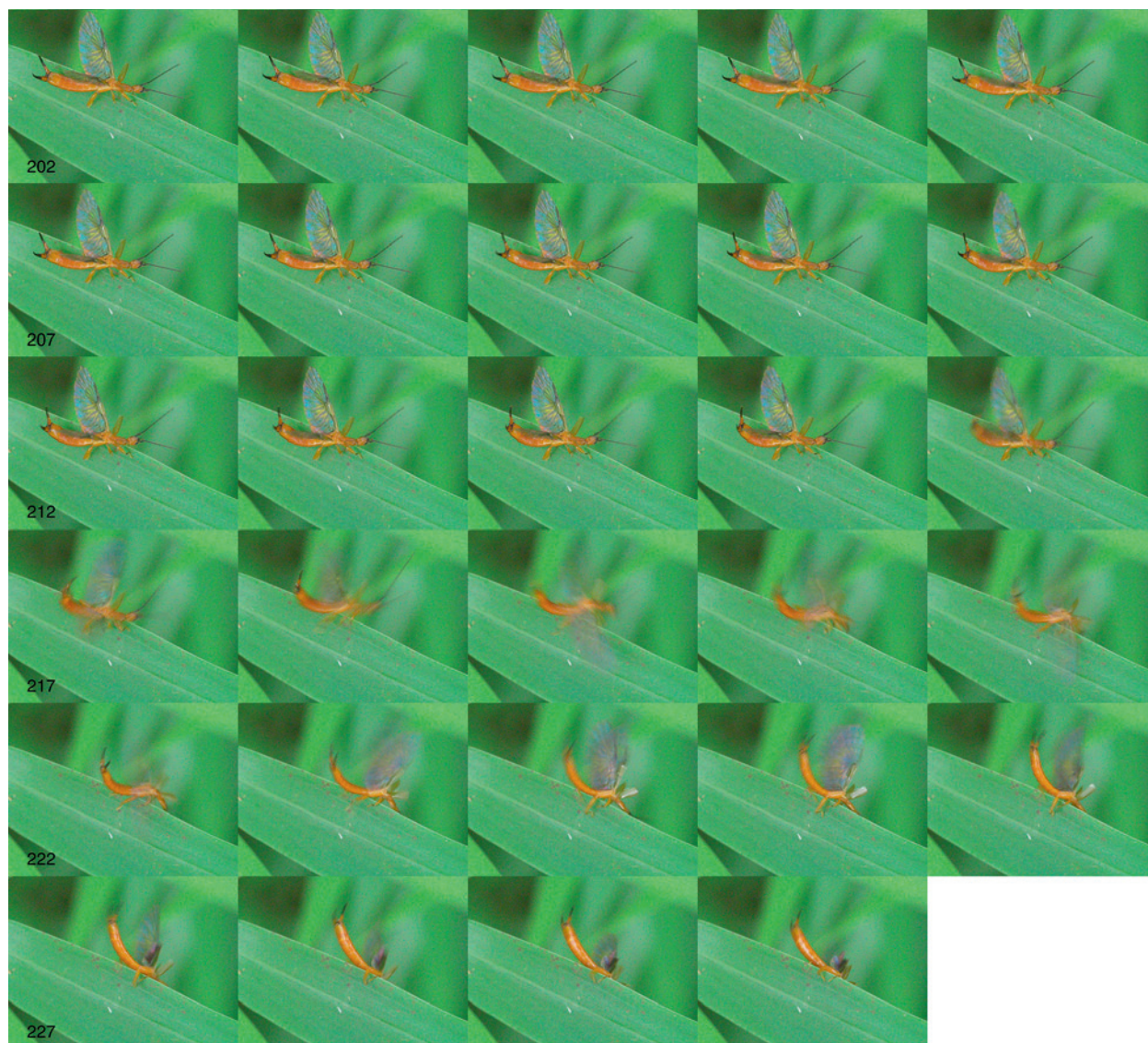
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Fig. 2. Wing unfolding of female *Auchenomus* sp. (Spongiphoridae) showing continous frames 152−230 (316.67 ms) of Clip 1. Frame rate 120 fps.

Clip 2

The clip (Fig. 3) shows an *Auchenomus* sp. and has 172 consecutive frames (sequential numbers 001−172; 712.5 ms). The wing unfolding procedure starts in frame 068. Tegmina reach the final position, perpendicularly erected over the throrax in frame 077. They remain there until frame 125 when they start moving to a position more on the side of the thorax, and remain in the new position until take off (frame 137). The hind wing package is being erected from frame 069 to 075 (25 ms) and continues to move vigorously during frames 076 to 094, during which time the wings are fully unfolded. The wings are kept unfolded and motionless from frame 095 to 133 (158 ms). In the time to take off (137) the wings start flapping, and

wings. The right hind wing folds in 2 frames (frames 226−227, 8.33 ms) to form a wing package, while the left one appears to remain open.

During their unfolded and non-flapping phase, the hind wings show all corrugation expected and induced by folding pattern and stiffening mechanisms (e.g. frame 203).
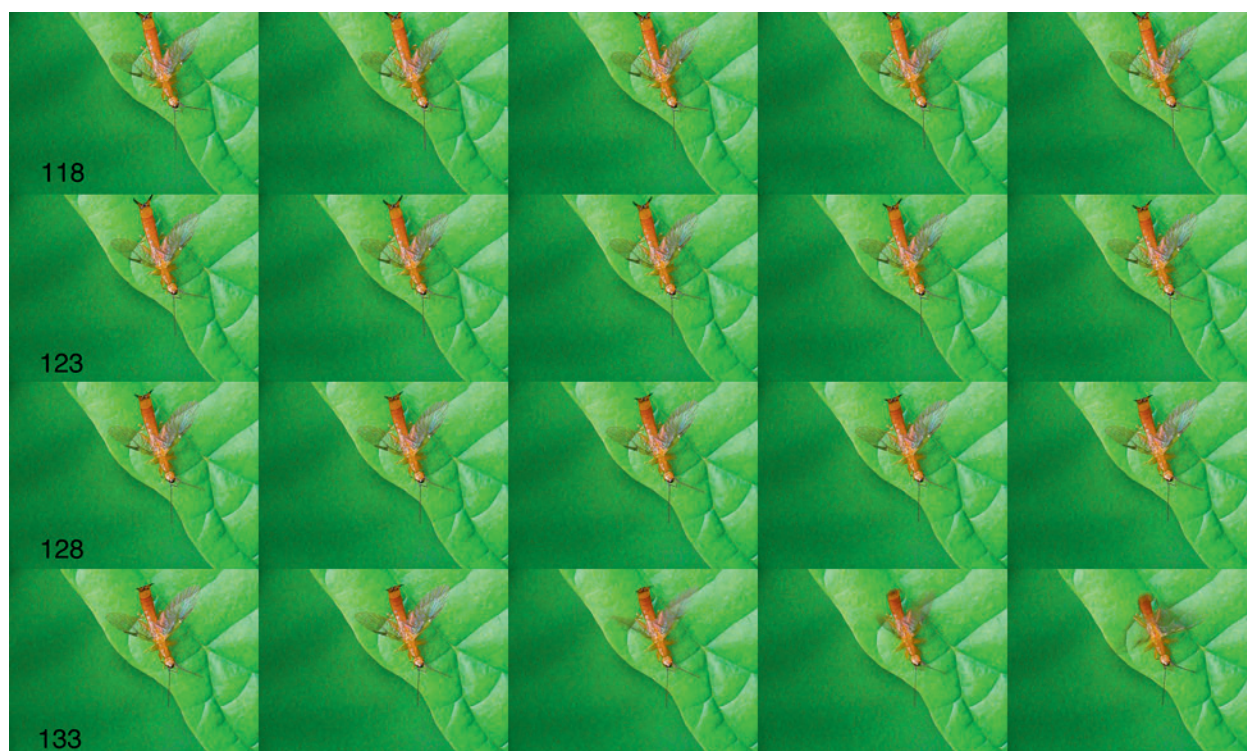
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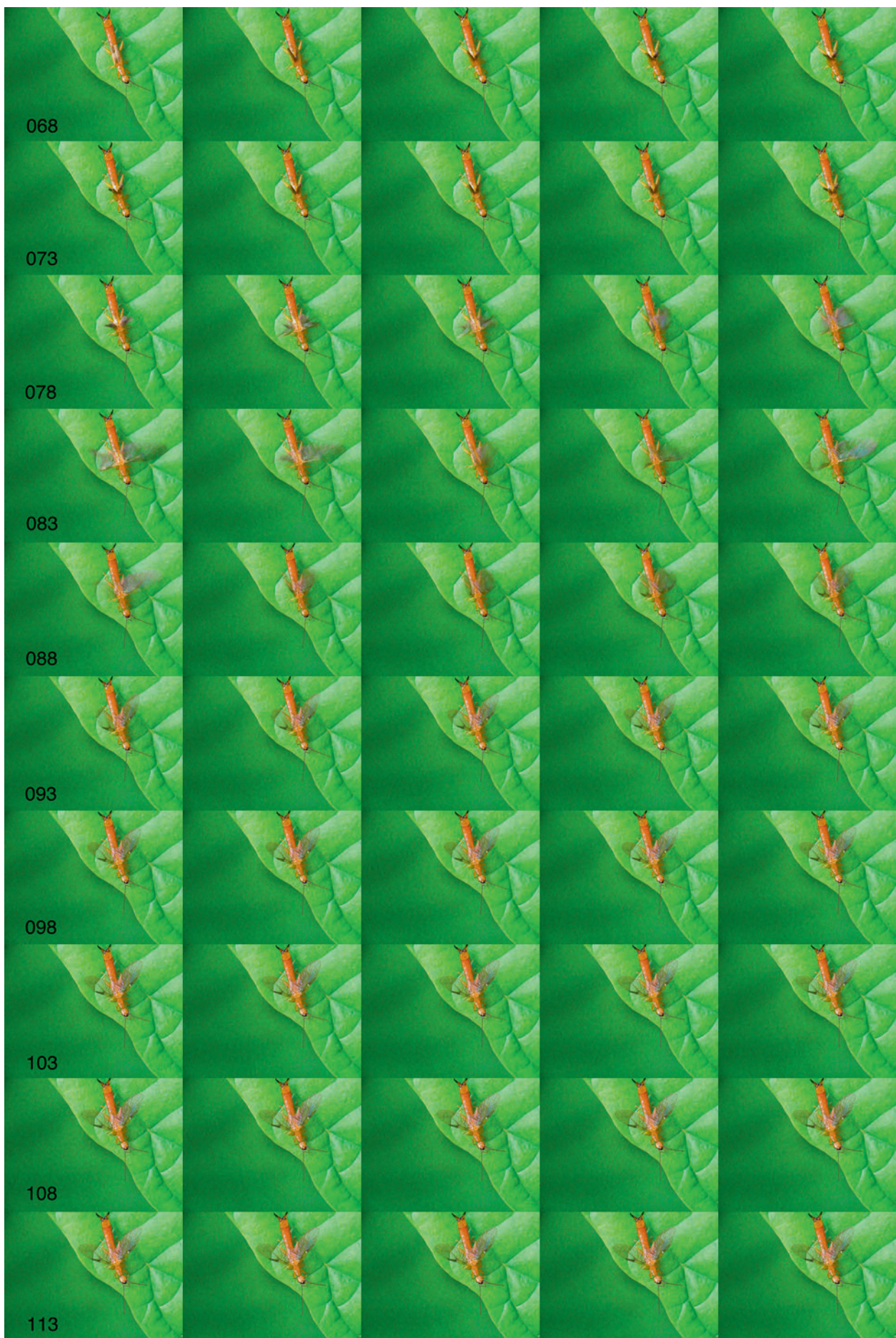
Fig. 3. Wing unfolding of female *Auchenomus* sp. (Spongiphoridae) showing continous frames 068–137 (308.33 ms) of Clip 2. Frame rate 240 fps.

the cerci bend cranially. The cerci are not involved in unfolding tegmina or wing package.

Clip 3

The clip (Figs. 4–6) shows a male of *Timomenus lugens* and has been saved as 1474 separate images (sequential numbers 0001–1474; 49100 ms). Clip 3 contains three separate unfolding events of the same specimen taking off and landing on Mr Pelegrin's hand. Besides moving his hand so that the specimen is in the field of view he did not interfere with the specimen. Each unfolding process is described separately, and the respective sequences are named Clip 3.1, 3.2 and 3.3.

Clip 3.1

It comprises frames 0001–0279 (9266 ms, Fig. 4), in which the specimen walks on the hand in explorative movements with erect, spread cerci. The opening of the tegmina is achieved in 3 frames (0268, tegmina close, 0269 tegmina blurred, and 0270) and they assume a position perpendicular to the longitudinal body axis, apparently on the sides of, but not over, the body. The unfolding of the hind wings follows and is syn-chronous between left and right wing. In frame 0268, tegmina and hind wings are clearly in the resting position while 0269 shows the hind wing packages diverging, and in 0270 the hind wing packages appear to be erected over the body and held motionless, as inferred from the lack of motion blur. In the next frame, 0271, the hind wing packages start flapping, with an increased blur over a wider area in 0272, which indicates a fast flapping movement inducing an unfolding of the hind wings. Frames 0273–0275 (66.66 ms) show the brown-ochre hind wings fully unfolded and standing still over the body. The following 3 frames (66.67 ms) show take off and disappearing of the animal from the image frame. Legs or cerci were never involved in the unfolding process.

Clip 3.2

It comprises frames 0617–0858 (8000 ms, Fig. 5), in which the specimen walks again on the hand in explorative movements and with upright, spread cerci. From their resting position over the thorax (frame 0847), tegmina opened within two frames (0848–0849, 33.33 ms) and they assume a position perpendicular to the longitudinal body axis, apparently on the sides. The hind wings follow immediately, but no erect and immobile hind wing packages are apparent here. Legs or cerci were not involved in the unfolding process. Flapping, indicated by significant motion

Fig. 4. Wing unfolding of male *Timomenus lugens* (Bormans, 1894) (Forficulidae) showing continous frames 0267–0278 (333.33 ms) of Clip 3.1. Frame rate 30 fps.
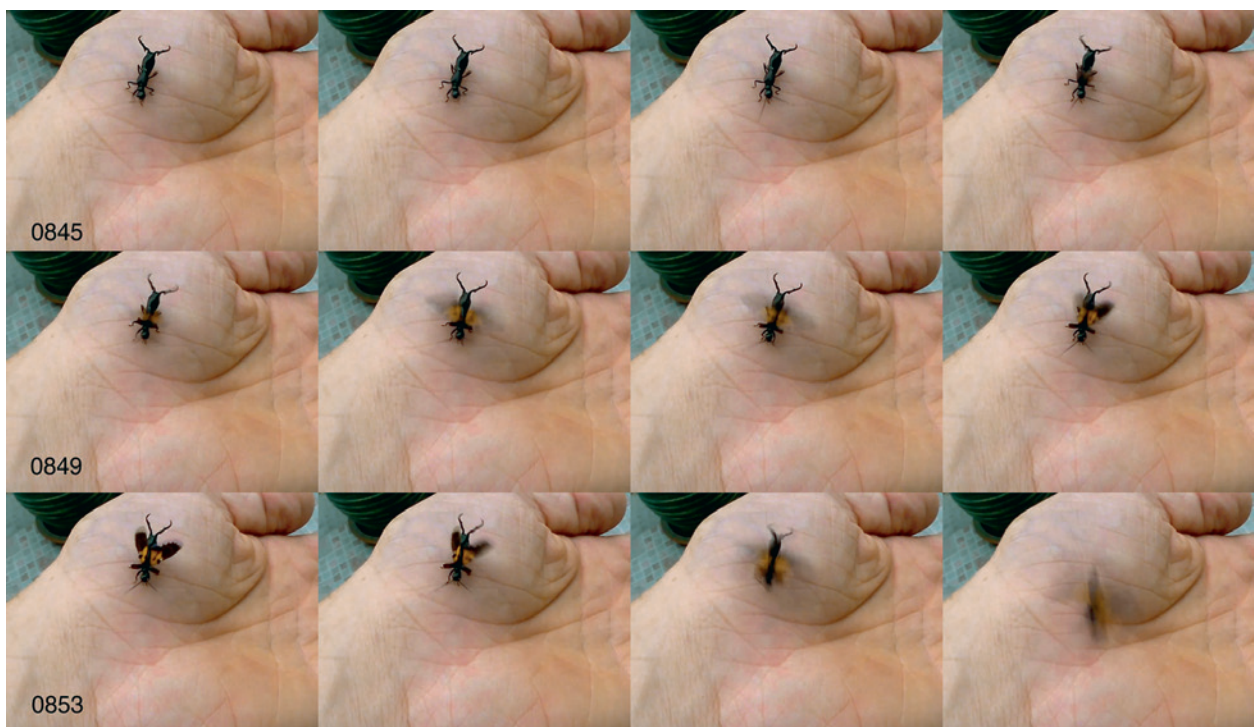

Fig. 5. Wing unfolding of male *Timomenus lugens* (Bormans, 1894) (Forficulidae) showing continous frames 0845–0856 (366.67 ms) of Clip 3.2. Frame rate 30 fps.

blur, starts immediately after lifting the hind wings and continues for 4 frames (frames 0849–0852, 100 ms). They seem to be held still in one frame (0853) but take off follows immediately (frames 0854–0856, 66.66 ms).

Clip 3.3

It comprises frames 1265–1392 (4200 ms, Fig. 6), in which the specimen walks on the wrist in explorative movements and with upright, spread cerci. The un-

Fig. 6. Wing unfolding of male *Timomenus lugens* (Bormans, 1894) (Forficulidae) showing continous frames 01381–01392 (366.67 ms) of Clip 3.3. Frame rate 30 fps.

folding sequence starts at frame 1383. At 1385 the tegima are opened and assume a position perpendicular to the longitudinal body axis. The hind wing packages are being erected and seem to move. Hind wings start flapping immediately (frame 1385) and are soon fully unfolded (frame 1386). They are possibly held almost motionless (frames 1387–1389, 66.66 ms) and take off follows immediately (1390–1391, 33.33 ms), the animal leaving the field of view (frame 1392). Legs or cerci were never involved in the unfolding process.

4. Discussion

Erection of tegmina

Almost all Dermaptera possess a locking device that consists of a row of macro-setae on each tegmen (termed spiny crest) and two such rows on the metascutellum (tegmina locking device; both terms from Haas 1995). They interlock when the tegmina are at rest and need to separate before the wings can be erected and unfolded. The systematic distribution has been examined by Haas (1995) and Haas & Kukalová-Peck (2001), and all examined members of the

Spongiphoridae and Forficulidae possess such a locking device. It is thus safe to assume that such a device is present in the two species observed, too, but it is too small (an estimated $1/10–1/15$ of the body length) to observe its function in any detail. It appears, however, that the tegmina are erected 'effortless', without deformation or discernable time delay, suggesting a simple opening procedure for the locking device.

Hind wing unfolding

No kinematic or statistical analyses can be conducted here due to the low spatial and temporal resolution, and the fact that only one (Clips 1 and 2; Figs. 2, 3) or three (Clip 3; Figs. 4, 5, 6) repetitions have been recorded from three different specimens. However, some general statements can be derived from the observations on the process of opening the tegmina and unfolding as well as folding the hind wings. The two tegmina move synchronously to their flight position, which is approx. perpendicular to the longitudinal body axis. They are held in a V-shaped position and do not vibrate (as indicated by lack of motion blur of tegmina). Both left and right hind wing package move synchronously to a fully erected position, standing essentially parallel to each other. The erection of hind wing packages follows the erection of tegmina with a slight delay. Sequences of images in Clips 1 and 3

demonstrate that hind wing packages do not automatically unfold, when released from below the tegmina. Indications of their unfolding (increase in size) are always related to their flapping, which starts when they are fully erected. No details can be recovered for the high degree of motion blur, however, they do increase in size during this flapping. Since no other structure, such as legs or cerci, is involved, this appears to be a dynamic process relying on the flapping.

The movies clearly show that in the species here examined the cerci have no function in unfolding the hind wings: both earwig species we have studied can unfold their hind wings without any interference of the cerci, by muscle-driven mechanisms based in the thorax and transmitted by the wing articulation. This is in contrast to the experiments and results obtained in a previous study on another species of Dermaptera, *Labia minor* (Spongiphoridae) (KLEINOW 1966; HAAS et al. 2001): in this species the cerci are required to open the hind wings. Cutting of cerci results in their inability to unfold the hindwings. This means that the mechanism of hindwing unfolding is heterogeneous among the Eudermaptera.

Hind wing folding and stiffening

The hind wings are stiffened through instrinsic mechanisms, and it could be suggested that the hind wings keep unfolded simply by aerodynamic forces. The recordings give some evidence on this question. Clip 1 shows that the hind wing has stiffening mechanisms, although these are vaguely visible in the frames. The lack of motion blur in the hind wing provides a clear view on its venation and other structures, strongly suggesting that the hind wing is not moved at all. Consequently, there are no aerodynamic forces which could prevent folding of the wing, supporting the earlier findings of stiffening mechanisms in the wing (KLEINOW 1966; HAAS et al. 2000). Clip 3 supports these findings, however, evidence in the form of clear views of non-moving hind wings is more limited due to the recording rate being lower by four times (30 fps vs. 120 fps).

The folding of a single hind wing is captured in Clip 1, and is done in between two frames (0226–0227) without the interference of any body part. The extreme short duration (approx. 8 ms) supports eralier findings that it is not a muscular process, but rather one that relies on stored energy, presumably in the patches of resilin found earlier (KLEINOW 1966; HAAS et al. 2000). It remains unclear how the stiffening mechanisms are released. However, it appears that this can be done separately for each hind wing.

Phylogeny and evolution

In a phylogenetic perspective the situation found in *Forficula auricularia* and *Labia minor* (unfolding of hind wing packages using cerci) appears to be a derived character state: An out-group comparison (to establish character polarity) is difficult here, since the hind wing folding in Dermaptera is highly derived with no intermediate state present in any possible out-group. Taxa with large fans, such as Caelifera and Blattodea did not evolve transverse folding of the fan, with exception of *Diploptera punctata* (Eschscholtz, 1822) (Blattodea: Blaberidae), which has so-called basic mechanism in the centre of the hind wing (HAAS & WOOTTON 1996). The unfolding mechanics is unknown, however, the cerci appear unspecialised. This situation and that found in fossil Archidermaptera (hind wing package and filiform cerci) suggest that unfolding without cerci is the ancestral character state, while those taxa using cerci are derived in this character.

5. Acknowledgements

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