

## Reconstructing insect flight performance from fossil evidence

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**Abstract.** Some structural characters and morphometric variables – size, body shape and proportions, wing shape and structure – that appear in insects to be linked with flight performance, are discussed and evaluated, and methods are described for deriving these from fossil material. Some wing design categories associated with particular flight techniques and capabilities are identified. Their use in reconstructing the flight performance of extinct insects is illustrated with reference to Carboniferous palaeodictyopteroids and Mesozoic palaeontinoid Hemiptera.

**Key words:** Flight, morphology, biomechanics, palaeontology, wings, Palaeodictyoptera, Megasecoptera, Palaeontinidae, Mesogereonidae.

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### I. INTRODUCTION

Flight is arguably the insects' most significant single achievement, and its influence on their evolution is incalculable. Knowledge of the flight capabilities of extinct insects can help in understanding the functioning of ancient communities; can illuminate observed evolutionary trends and phylogenetic events; and can assist cladistic analysis by revealing character correlations and homoplasies.

ROHDENDORF (1949), in a major but seldom-quoted paper which was far ahead of its time, attempted to classify insect wing types in terms of their adaptations to flight, but the mechanisms of insect flight were then very imperfectly known, and few palaeoentomologists have followed his lead. However the last three decades have seen major advances in our understanding both of insect aerodynamics and of the functional principles underlying insect wing design. BRODSKY (1994) and GRODNITSKY (1999) have paid attention to extinct groups in their books on the evolution of insect flight. WOOTTON & BETTS (1986) and WOOTTON & ENNOS (1989) used information both from fossils and from flight studies on modern forms in discussing the evolutionary development and homologies of the wings of Heteroptera and Diptera respectively. WOOTTON et al. (1998) applied our understanding of the wing mechanisms in modern anisopterous Odonata in interpreting a parallel development in a Carboniferous odonate, and WOOTTON & KUKALOVÁ-PECK (2000) published an extensive account of the probable flight adaptations of Palaeozoic Palaeoptera, again based on theoretical principles and on knowledge of the flight of modern insects. This last work reviewed the types of evidence on flight techniques and performance which fossil material may provide. The

present account summarises these, describes how they can be gathered and used, and provides some further examples of their application.

## II. FLIGHT CATEGORIES, FUNCTIONS AND KINEMATICS

Insects have many uses for flight. An incomplete list could include: escape; short journeys from place to place; long-range migration; foraging for slow-moving or static food, whether prey or plant material; feeding at flowers; aerial prey-capture; transporting prey, pollen, nest-materials; seeking mates or oviposition sites; defending territory; manoeuvring within stationary lekking swarms; courtship display; aerial mating. Capabilities vary greatly from group to group. The principal performance variables are: available speeds; breadth of speed range; available flight duration; manoeuvrability; reaction time and precision.

Some modern examples will clarify the relationship between these functions and capabilities. Most flying Orthoptera can only fly fast, jumping to reach flight speed, and landing with a thud. Many fly only short distances in association with escape and trivial movement, but migratory forms fly fast for long periods, covering immense distances, often wind-assisted. Most small insects can only fly slowly, at air speeds below 1 m/s (DUDLEY 2000), though some, voluntarily or involuntarily, may develop significant ground speeds by rising into the wind and staying there. Anisopterous Odonata, many larger Diptera and Hymenoptera, and some Lepidoptera have a wide speed range, enabling them to accelerate to high velocities, but also to fly slowly and hover, often holding station with great precision in moving air in association variously with territory surveillance, and reproductive and feeding behaviour. Muscid and calliphorid Diptera and many butterflies also show spectacular manoeuvrability when avoiding predators, and in sexual interaction and display.

Information on the kinematics – the relative movements of the wings, body and appendages – associated with specific types of free flight, has only become accessible since the 1970s, with the development of high speed cine and still photographic techniques. The same period has seen sweeping advances in our understanding of insect flight mechanics, including the aerodynamics of flapping flight, so that it is now possible to interpret the kinematics in aerodynamic terms, and to recognise associations between an array of morphological characters, the kinematics which they facilitate, and the flight capabilities and behaviour of the insects.

When investigating Tertiary and to some extent Mesozoic insects, it is often possible to draw direct conclusions about flight capability by reference to extant representatives of the same or closely related taxa, but the older the fossils the less practicable this becomes. It is then necessary both to look for interpretable parallels with present-day forms whose flight characteristics are known, and to apply established theoretical principles linking morphological variables with flight performance.

## III. SIZE AND BODY SHAPE

Some flight capabilities are directly linked to size. Insects of the same shape but different sizes flying with dynamic similarity (i.e. with distances moved, velocities reached, and forces exerted, by equivalent moving points on the body respectively related by the same constants throughout the size range) should according to conventional aerodynamic theory and known physiology show predictable relationships between mass, wing-loading (weight/wing area), flight speeds, flapping frequency, muscle efficiency and energy consumption per unit muscle mass. Larger insects would be expected to have higher maximum and minimum speeds, lower wing-beat frequencies, higher muscle efficiency and lower mass-specific oxygen consumption than smaller insects (WOOTTON & KUKALOVÁ-PECK 2000).

In fact the situation is much more complex. Insects are far from being the same shape; they do not necessarily fly with dynamic similarity; and insect aerodynamics are often unconventional. On

available evidence, correlations between wing-loading and flight speeds are too imprecise to justify much effort in calculating body masses from flattened insect impressions – certainly of small insects where such calculations would be very imprecise. Nonetheless WOOTTON & KUKALOVÁ-PECK (2000) made approximate estimates of body masses of a range of Palaeozoic Palaeoptera by modelling them in waterproof modelling clay, finding their volume by displacement of water in a measuring cylinder, and assuming a specific gravity of unity for insect tissue. A logarithmic plot of calculated wing-loadings against body length served to draw attention to species whose wing-loadings were unusually high or low for their size, and these results were used with other evidence in reconstructing the insects' probable flight capabilities. The mass of the thorax alone was also estimated, and the ratio of thorax mass to total mass used to give some comparative indication of the degree of flight muscle development, and hence of available power.

Large insects have relatively high inertia, and this will affect their manoeuvrability, particularly at high speeds. More important at low speeds is the distribution of body mass about the centre of aerodynamic force. Long bodies give physical stability in flight, but at the expense of manoeuvrability. Shorter, more compact bodies and appendages may favour rapid manoeuvres, but require a greater degree of active neurosensory control. The size and form of appendages also influence manoeuvrability and stability, both by their mass and by their drag. Elongate cerci, like those of Ephemeroptera and Palaeodictyopteroidea, and long legs, like those of many Nematocera, give physical stability and some active control when spread at low speeds, but can seriously limit manoeuvrability.

#### IV. WING CHARACTERS

##### Shape

The relationship between flight performance and wing shape, in the sense of planform, is far from simple, and in many respects far from clear. Wing shape is hard to quantify. Most widely used, and easily derived, is the Aspect Ratio (AR), a measure of relative breadth: high AR wings are narrow, low AR wings broad. Fossils often consist of single wings, and it is essential to clarify whether a given value refers to an individual wing, or to coupled wings on one side only, or to the wings of both sides. The last is preferable for comparison with published values in the flight literature, and is most easily found by:

$$AR = 4(\text{wing length})^2/\text{wing area}$$

As it is dimensionless it can be calculated from the actual wing, or from accurate photographs or drawings without rescaling.

Although widely used in vertebrate flight studies, in insects the aspect ratio by itself is rather uninformative. High AR wings are typical of sailplanes and many gliding birds. At these scales, it provides a high ratio of lift to drag, and hence a shallow glide angle. However, this may not apply to insects. The relatively few that make much use of gliding – some dragonflies, butterflies and Orthoptera – have rather broad wings. ENNOS (1989b) has discussed why this may be so. Low AR wings and wing couples are widespread, and generalisations are hard to find. In many heavy bodied Orthoptera they are associated with fast, straightforward flight; and we can assume similar flight characteristics in many structurally similar extinct forms. By contrast in butterflies, with relatively small bodies, low AR wings allow extremely low wing-loadings and low wing-beat frequencies, and can provide remarkable manoeuvrability, with tight turns happening within a single wing-stroke. Other low AR types – some Trichoptera, Neuroptera, Hemiptera, other Lepidoptera, do not easily fit either description, and we need to seek other wing characters to interpret their flight techniques.

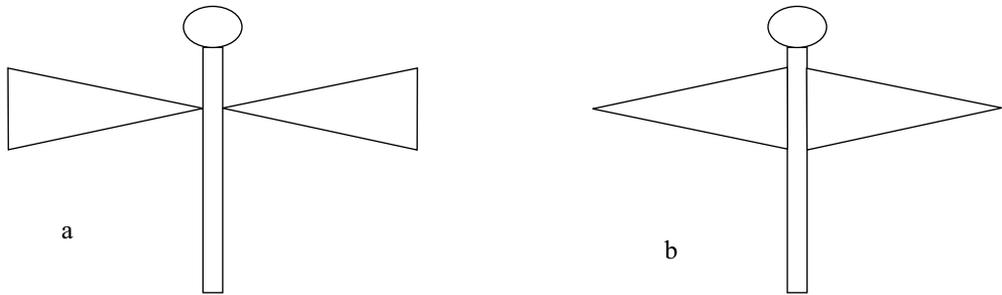


Fig. 1. Diagrammatic insects to demonstrate that wings may have the same aspect ratio, but very different distributions of area, quantifiable by the moments of area of area about the wing hinge. Explanation in the text.

Aspect ratio alone gives no indication of the distribution of wing area along the span. The wings of the two highly diagrammatic insects in Fig. 1 both have an aspect ratio of 9.5, but are clearly different, and would have very different aerodynamic characteristics. The distribution of area along the span is conveniently expressed by the moments of area about the wing hinge (WEIS-FOGH 1973; ELLINGTON 1984a). The first, second and third moments of area all have aerodynamic significance. Their derivation is fully explained by ELLINGTON (1984a). Conveniently, ELLINGTON also found, in the wide range of wings which he studied, that these three moments were closely correlated. The spanwise distribution of area can apparently be described by a single variable: the dimensionless radius,  $\hat{r}_1 S$ , of the first moment of area of the wing about the base. This is easily calculated by finding the position of the centroid, or geometric centre of the wing, or wing couple as appropriate; measuring its distance from the base; and expressing this as a decimal fraction of the wing length. The centroid can be computed, or found practically by accurately tracing the outline of the wing, scaled up as needed, onto stiff paper or thin card; cutting around it; suspending the model wing from a vertical surface by a pin, located as close as possible to the perimeter, so that it can swing freely; drawing a vertical line from the pin, with the help of a weighted thread (Fig. 2); and repeating the entire process with the pin through another suspension point on the perimeter. The centroid is the point of intersection of the two lines.

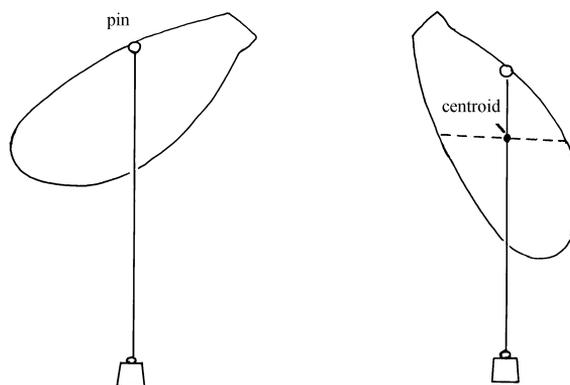


Fig. 2. The method of finding the geometric centre (centroid) of a wing. Explanation in the text.

The two wings in Fig.1 are now clearly distinguished.  $\hat{r}_1 S$  for 1a is 0.7, for 1b is 0.3. A low value indicates that the wing area is concentrated towards the base, a high value shows concentration towards the tip, with a narrow, perhaps petiolate base.

The nature of the airflow around wings of different sizes and shapes, and the relative contributions of steady-state and unsteady mechanisms, are still under active investigation (ELLINGTON et al. 1996; DICKINSON et al. 1999; BIRCH & DICKINSON 2001; USHERWOOD & ELLINGTON in press), but some consequences of area distribution can be predicted, and are confirmed by experience of extant forms. Flapping creates a gradient of airflow velocity from the wing base to the tip. In a hovering insect the velocity at the extreme base will be close to zero. The useful aerodynamic forces will be generated further out along the span, and it is logical for hovering and habitually slow-flying insects to have concentrated the wing area away from the base. In a habitually fast flying insect the airspeed at the base will approximate to the flying speed, and breadth in the proximal part of the wing will be useful, particularly in insects with a relatively low flapping frequency. A high value of  $\hat{r}_1 S$ , and indeed its consequent visible shape, suggest a habit of slow flight, close to hovering. A low value suggests that the insect is adapted for faster flight; and is either limited to this, or is capable of flying over a wide speed range. How wide will be influenced by size, wing-beat frequency, and other aspects of wing design.

### Relief, venation and flexion-lines

Understanding the functional morphology of insect wings requires some knowledge of the way they operate in flight.

A wing beat cycle consists of a downstroke, where the wings beat ventrally relative to the body; a supinatory (leading edge upward) rotation around the bottom of the stroke; an upstroke; and a pronatory (leading edge downward) rotation into the position for the next downstroke. The shape and attitude of the wings in the downstroke is fairly uniform: relatively flat, with a slightly arched profile, and often a slight nose-down, propellor-like twist from the base to the tip. The shapes which the wings assume at the top and bottom of the stroke, and during the upstroke, are far more variable, and these strongly influence the overall magnitude and direction of the force generated in the stroke as a whole. Crucially the stroke must generate an adequate net upward force component to support the weight of the insect, and this requires asymmetry between the two half-strokes. The wing may twist, bend, alter in camber or effective area, or any combination of these in the translational part of the upstroke, so that the aerodynamic force developed at least does not oppose that of the downstroke, and may well augment it. In addition the wings may develop brief, useful “unsteady” forces when changing shape and attitude at stroke reversal, e.g. by clapping together and ‘flinging’ or ‘peeling’ apart, leading edge foremost (ELLINGTON 1984b), or by rotating while still decelerating for the next half-stroke (BIRCH & DICKINSON 2001).

Although syrphid Diptera at least apparently rely on downstroke forces only, in most insects the ability to fly slowly and to hover requires useful, weight-supporting force to be contributed by the upstroke. This capability is closely associated with the capacity of the wings at least in part to rotate and/or twist within their length into an appropriate angle of attack. This capacity in turn is associated with recognisable morphological characteristics. Uncoupled, high aspect ratio wings with narrow bases, like those of zygopterous Odonata and many Diptera, often permit a high degree of passive supinatory twist along the span, driven by inertial and aerodynamic torques; as well as active basal rotation. Wings of this kind usually have a fairly straight leading edge spar, from which arise a series of parallel, usually pinnately arranged branches of the radial sector and median veins, directed posterodistally towards the trailing edge. This arrangement tends automatically to create a cambered section in the wing under aerodynamic loading in both the upstroke and the downstroke (ENNOS 1988). The clavus, if present, is often short, frequently with low relief, so that the posterior edge of the wing has relatively weak static support, and in flight is actively depressed by automatic internal mechanisms driven by the inertial and aerodynamic forces which the wing is receiving (ENNOS 1989a; ENNOS & WOOTTON 1989; WOOTTON 1991).

Broader wings with broader bases can usually twist far less. However this is often to some extent overcome by the presence of a transverse line of flexibility that allows some ventral bending of the distal part of the wing in the upstroke. Dorsal bending on the downstroke is normally prevented by the wing's dorsally convex cross-section. If, as is commonly the case, this flexion line is to some extent oblique (see Fig. 4f), the distal part of the wing twists as well as bends, so that it can assume a more favourable angle of attack than the rest of the wing, and is more capable of producing weight-support in the upstroke as well as the downstroke. There is evidence from some forms – *Panorpa germanica* LINNAEUS 1758 (Mecoptera) (ENNOS & WOOTTON 1989) and some Heteroptera (BETTS 1986) – that the degree of flexion may be controllable from the base, by actively altering the height of the cambered section of the proximal part of the wing through hingewise bending along a longitudinal flexion line, found in the majority of neopterous insects. It seems probable that the presence of both these flexion lines allows a wider range of speeds than would be possible if the flexion line were absent.

In the interest of flight versatility, transverse ventral bending in the upstroke may become still more useful in insects where fore and hind wings are coupled into a single functional aerofoil. The broad insertion of a wing couple on two thoracic segments seriously limits the degree of basal twisting, and some oblique flexion seems often to assist the wing tip to assume a more favourable angle of attack in the upstroke. The most versatile fliers with coupled wings, e.g. aculeate Hymenoptera, sphingid Lepidoptera (WILLMOTT & ELLINGTON 1997), alydid Heteroptera (BETTS 1986) and those, like aphids, which habitually fly slowly and hover (WOOTTON 1996, 2002) have substantially reduced the area of their hind wings relative to the fore wings, and achieve a high degree of distal torsion with negligible bending.

How far can these characters be recognised in fossil wings? In fossils the presence of a longitudinal flexion line may be suggested by the absence of cross-veins from, or the presence of weakened or thinned cross-veins in, an area between two longitudinal vein systems. A transverse flexion-line may be apparent as a line in the membrane, as for example in cicadoid and palaeontinoid Homoptera, and Palaeozoic blattinopsid 'protorthopterans', or may be visible as a transversely-aligned series of local weakenings or interruptions of the longitudinal veins. A tendency for ventral bending can also be indicated by a transverse alignment of cross-veins, or by an abbreviated subcosta, especially if it ends more or less level with the end of the clavus. In *Panorpa germanica*, ENNOS & WOOTTON (1989) found the orientation of the transverse line of ventral flexion, clearly visible in their high-speed film of free flight, to be significantly different in the fore and hind wings, and determined by the respective lengths of the subcosta in the two wings (Fig. 3).

Wing torsion, and flight versatility, seem least apparent in groups like Orthoptera, Dictyoptera and Phasmida, where the fore wings show limited bending, and the anojugal area of the hind wing is expanded into a fan, with radiating veins. The functioning of the fan has been studied in detail in locusts (WOOTTON et al. 2000) and modelled generally (WOOTTON 1995) and for the desert locust (HERBERT et al. 2000). The typical geometry results in the generation of unsteady lift by the 'clap and peel' or 'near clap and partial peel' effects (ELLINGTON 1984b) at the start of the downstroke, and in the development of a cambered section with a lowered trailing edge for the downstroke itself.

## V. WING CATEGORIES AND FLIGHT TECHNIQUES

In summary, we can recognise in fossils several broad categories of wing, associated in extant forms with some particular flight characteristics. These are illustrated in Fig. 4.

### **Where the wings are uncoupled:**

(a) a broad-based fore wing with a long, rigid-seeming posterior supporting clavus, and no evidence of transverse bending, combined with a hind wing which is either similar or has an expanded anal fan, suggests a limited range of flight speeds, with little or no capability for slow flight or hovering, and low manoeuvrability (Fig. 4a);

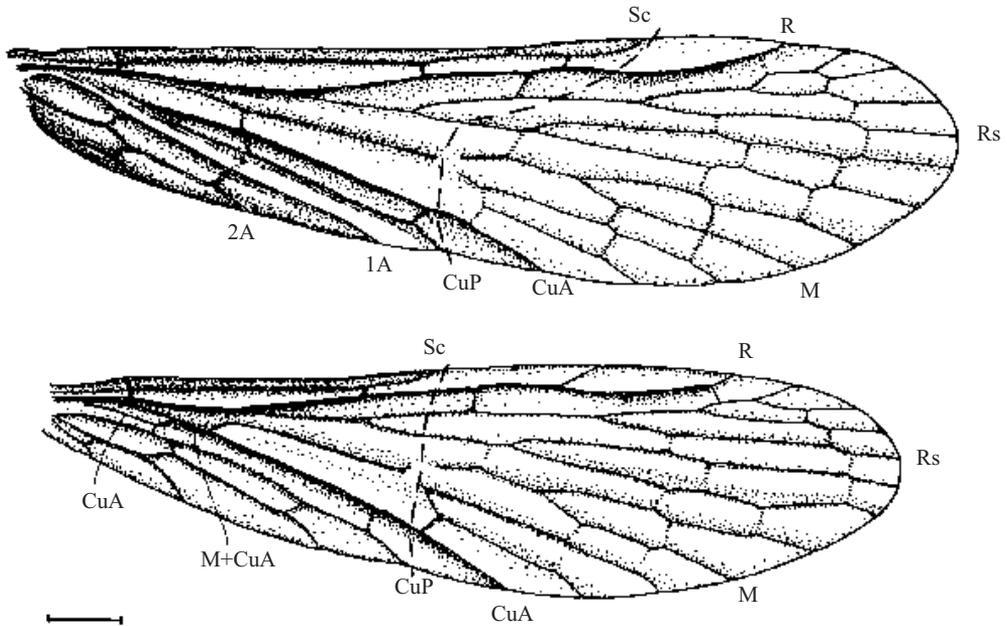


Fig. 3. The fore and hind wings of *Panorpa communis* LINNAEUS 1758 (Mecoptera). Venation is similar in the two wings, but the subcostal vein (Sc) is longer in the fore wing. High speed film of the similar *P. germanica* shows that the wings flex ventrally in free flight, along a line (here dashed) running from the end of Sc to the end of the posterior cubital vein CuP. The longer Sc in the fore wing causes the flexion line to be more oblique than in the hind, so that the distal area twists as it bends. Modified after WOOTTON & ENNOS (1989). Sc: subcosta. R: radius. M: media. CuA: anterior cubitus. CuP: posterior cubitus. 1A and 2A: first and second anal veins. Scale bar: 1mm.

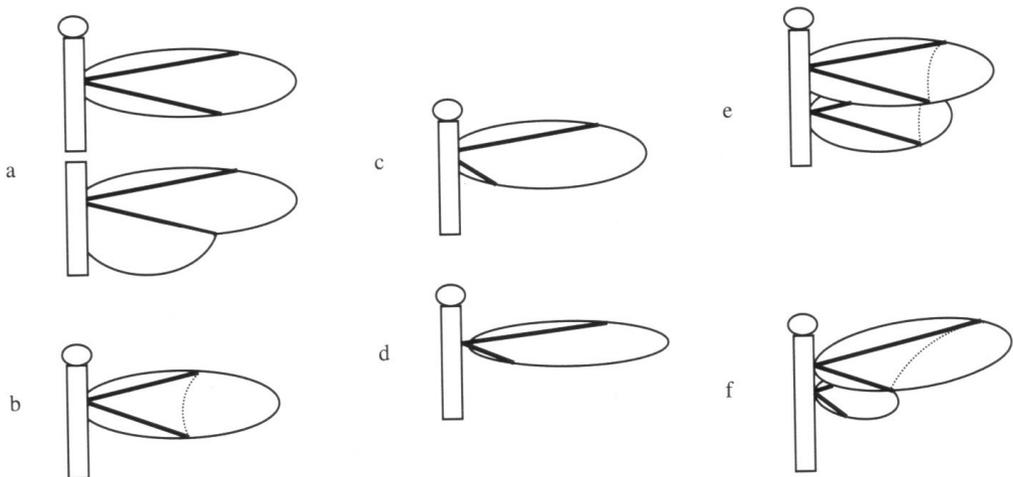


Fig. 4. Diagrams of a range of widely-occurring wing categories, showing the principal zones of support (thick lines) and transverse flexion lines (dashed) where present. a-d represent uncoupled wing designs, e and f are wing couples. Explanation in the text.

(b) similar wings with evidence of adaptation for transverse ventral bending, particularly if oblique, indicate a greater capacity for slow flight, with or without greater overall versatility (Fig. 4b);

(c) a broad-based wing with a fairly high aspect ratio and short posterior support, allowing greater torsion, suggests a capacity for slow flight, and possibly hovering, but with a reasonably broad speed range (Fig. 4c);

(d) a narrow-based, high aspect ratio, possibly petiolate wing with a short posterior support indicates habitual slow flight, probably hovering, and reasonable manoeuvrability at low speeds (Fig. 4d).

#### Where the wings are coupled:

(a) fore and hind wings subequal in length, or the forewings rather longer than the hind, with evidence of transverse flexion, suggest moderately versatile flight (Fig. 4e);

(b) fore wings significantly longer than the relatively small hind wings, with shortened posterior support, a rather triangular form, with or without evidence of transverse or oblique flexion: in small insects suggests slow and hovering capabilities, in larger insects versatile, agile flight over a wide speed range (Fig. 4f).

We may expect the actual speed range to have been significantly influenced by other factors, discussed earlier: overall size, wing-loading, relative mass of thoracic muscle.

## VI. SOME EXAMPLES

### Carboniferous Palaeodictyopteroidea

Fig. 5 shows reconstructions of two Carboniferous palaeodictyopteroids: *Homoioptera vorhallensis* BRAUCKMANN & KOCH 1982, and *Mischoptera nigra* BRONGNIART 1885. Both were large insects, each with a wing span around 150 mm. Both had long, stabilising cerci. The palaeodictyopteran *H. vorhallensis* (Fig. 5a) had broad-based wings, each with an aspect ratio of 6.0 for the wing pair, and values of  $\hat{r}_1S$  at 0.46 (fore wing) and 0.44 (hind wing). Fore and hind wings overlapped to a remarkable extent, so that they could only have been flapped in same phase, with negligible twisting. There is no evidence of transverse flexion. Estimated wing-loading was around  $2.3 \text{ N m}^{-2}$ . These can be interpreted as fast, straightforward fliers with little versatility, using flight mainly to get from place to place, and limited to rigid, supportive parts of the plants on which they fed.

The megasecopteran *M. nigra* (Fig. 5b) was very differently adapted. The narrow-based wings have aspect ratios of 10.7 and 11.9 for the fore and hind wing pairs respectively, and  $\hat{r}_1S$  values of 0.53 and 0.54. Their shape and venation are characteristic of high-twist wings adapted for slow flight and hovering. The estimated wing-loading is an order of magnitude lower than *H. vorhallensis*, at  $0.21 \text{ N m}^{-2}$ . This species, like most Megasecoptera, was evidently adapted for slow, near hovering flight, which would have given them access to sporangia on the periphery of plants, and to confined spaces between the fronds (WOOTTON & KUKALOVÁ-PECK 2000, from which all quoted values are taken).

### Mesozoic Palaeontinoidea (Homoptera)

Fig. 6 shows reconstructed wings of the Palaeontinidae *Fletcheriana triassica* EVANS 1956, *Eocicada lameerei* HANDLIRSCH 1906 and *Wonnacottella pulcherrima* WHALLEY & JARZEMBOWSKI 1985; and the Mesogereonidae *Mesogereon superbum* TILLYARD 1921 and *M. shepherdii* TILLYARD 1921.

The Upper Triassic *Fletcheriana* (Fig. 6a), here reconstructed from two dissociated specimens, shows what seems to be a plesiomorphic wing form for the Palaeontinidae. Fore wings are elliptical, and crossed by a clear flexion line, slightly proximal to the midpoint of the wing length. The high-relief wing base is principally supported by a three-pronged fork formed by the common base of the subcostal (Sc), radial (R) and radial sector (RS) veins; the median vein (M); and the anterior cubitus

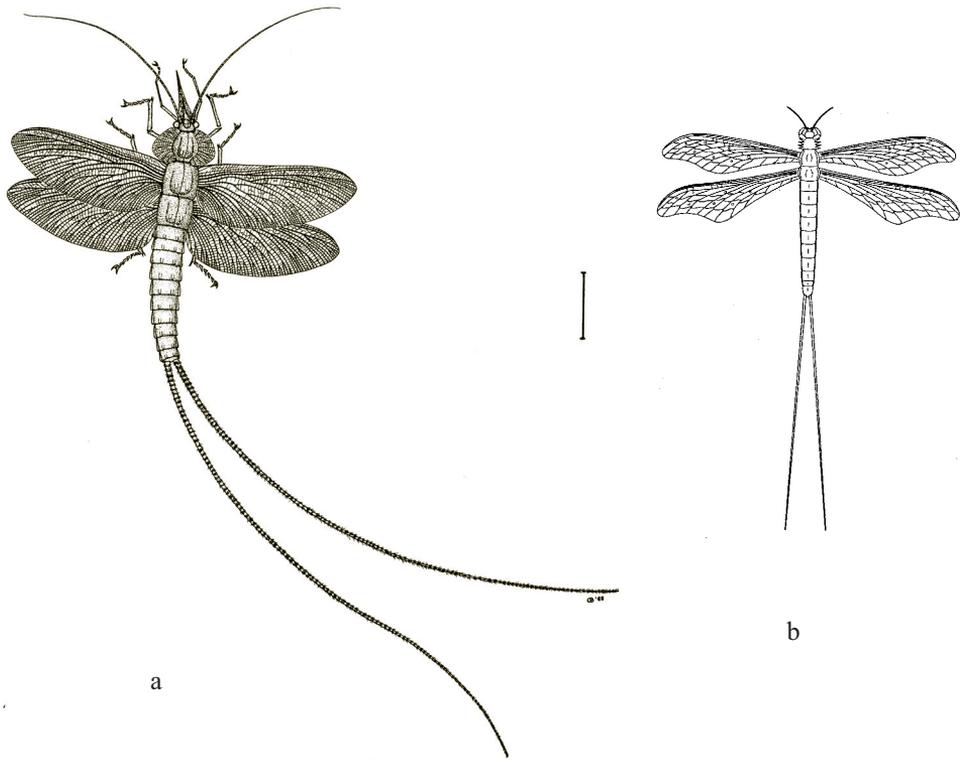


Fig. 5. Reconstructions of contrasting Carboniferous Palaeodictyopteroidea. a. *Homioptera vorhallensis* (Palaeodictyoptera), from BRAUCKMANN (1991); b. *Mischoptera nigra* (Megaseoptera), from CARPENTER (1951). Abbreviations as in Fig. 3. Scale bar: 30 mm.

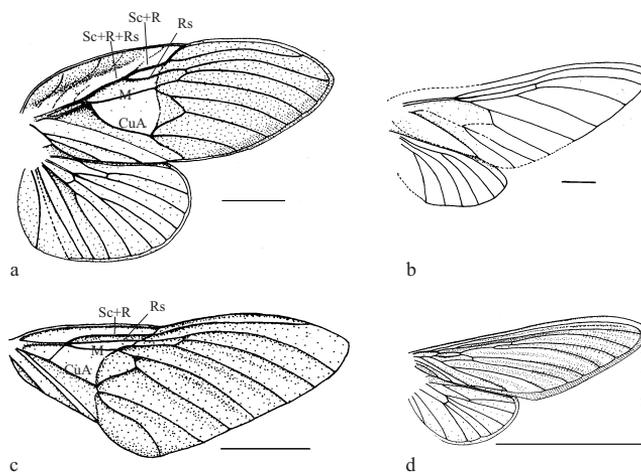


Fig. 6. Reconstructed wings of Mesozoic palaeontinoids (Homoptera). a. *Fletcheriana triassica* (Palaeontinidae). b. *Eocicada lameeri* (Palaeontinidae). c. *Wonnacottella pulcherrima* fore wing (Palaeontinidae). d. *Mesogereon* (Mesogereonidae) composite reconstruction combining the fore wing of *Mesogereon superbum* and the hind wing of *M. shepherdi*. Original, from the holotype counterparts. Abbreviations as in Fig. 3. Scale bar: 10 mm.

(CuA), which is arched to meet the media. The hind wing is shorter and broad. The wings seem to have been coupled, if only by a butterfly-like overlap of the fore and hind wing bases. They conform reasonably well with the category illustrated in Fig. 4e, and, being large insects, can be taken as fast, but moderately versatile fliers.

The Upper Jurassic *Eocicada* (Fig. 6b) and slightly later *Wonnacottella* (Fig. 6c) are of a different type. The fore wings have a high aspect ratio, and are relatively triangular in form. The transverse flexion line is oblique, and significantly closer to the wing base, so that the distal area is relatively enlarged, and the posterior supporting clavus is short. The base is supported now by a narrower, more anterior three-pronged fork formed by Sc+R, Rs and M, with CuA some distance away. The hind wing of *Eocicada* (that of *Wonnacottella* is unknown, but the short fore wing clavus indicates that it was probably similar) is small and narrow and its posterior margin is more or less aligned with that of the fore wing. These species conform in every respect with the type illustrated in Fig. 4f, and seem to have been highly versatile insects capable, like modern wasps and sphingid moths, of agile flight over a wide speed range.

*Mesogereon* (Fig. 6d), in a separate but related family is, like *Fletcheriana*, Upper Triassic in age, but shows the trends seen in *Eocicada* and *Wonnacottella* to an even more extreme degree. The slender fore wing is even more expanded distally, with a tiny posterior, supporting clavus. The wing plan is still more triangular, with a straight leading edge. There is no transverse flexion line: the elongate distal area would have been capable of considerable torsion without one. The hind wing of *M. superbum* is probably unknown, but *M. shepherdi* shows its probable shape, and perhaps size. It again conforms with Fig. 4f, and among modern insects is perhaps most reminiscent of some derbid Homoptera, whose wings again seem adapted to agile flight over a wide speed range.

## VII. CONCLUSION

Our understanding of the relationships between morphology and flight performance and behaviour is still very imperfect. The many morphological variables interact in ways that are only partly predictable. Broadly similar wing plans and designs appear in insects of widely similar sizes, and scaling effects will certainly influence performance: particularly top speeds and manoeuvrability. Furthermore the flight of only a handful of modern species, from a limited range of higher taxa, has been studied in real detail, and the few comparative investigations that have been carried out within single orders raise many unanswered questions. Butterflies with nearly identical venation and similar wing shapes and dimensions may differ strikingly in their flight behaviour, and these differences appear to result from differences in stroke amplitude, symmetry and timing which could not be predicted from morphology (BUNKER 1993). This makes any attempt to apply observations on butterfly flight to some superficially butterfly-like Palaeontinidae a very uncertain enterprise; particularly as the latter had much broader bodies and presumably different thoracic and axillary morphology. The degree to which minor morphological differences may influence performance is very unclear. Small bumblebees (*Bombus* spp.) are effective hoverers, but appear clumsy compared with some Anthophoridae, whose morphology is very similar but which hover with spectacular precision, and can instantly be distinguished from bumblebees by flight alone. The contribution of the neurosensory system to the behaviour patterns of complex fliers should never be underestimated – and it does not fossilise.

Nonetheless, with these qualifications, the present state of our knowledge does allow us to draw broad and fairly confident conclusions about the probable flight techniques of many extinct insects from preserved morphology alone. These in turn can be really valuable in interpreting both their roles in ancient ecosystems, and the ecological and behavioural trends that accompanied and governed their evolution.

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