

Flight adaptations in Palaeozoic Palaeoptera (Insecta)

ROBIN J. WOOTTON¹ and JARMILA KUKALOVÁ-PECK²

¹ School of Biological Sciences, University of Exeter, Devon EX4 4PS, U.K.

² Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada K1S 5B6

(Received 13 January 1999; revised 13 October 1999; accepted 13 October 1999)

ABSTRACT

The use of available morphological characters in the interpretation of the flight of insects known only as fossils is reviewed, and the principles are then applied to elucidating the flight performance and techniques of Palaeozoic palaeopterous insects. Wing-loadings and pterothorax mass/total mass ratios are estimated and aspect ratios and shape-descriptors are derived for a selection of species, and the functional significance of wing characters discussed. Carboniferous and Permian ephemeropteroids ('mayflies') show major differences from modern forms in morphology and presumed flight ability, whereas Palaeozoic odonatoids ('dragonflies') show early adaptation to aerial predation on a wide size-range of prey, closely paralleling modern dragonflies and damselflies in shape and wing design but lacking some performance-related structural refinements. The extensive adaptive radiation in form and flight technique in the haustellate orders Palaeodictyoptera, Megaseoptera, Diaphanopteroidea and Permothemistida is examined and discussed in the context of Palaeozoic ecology.

Key words: Wings, flight, Palaeozoic, Carboniferous, Permian, Ephemeroptera, Odonatoptera, Palaeodictyoptera, Megaseoptera, Diaphanopteroidea, Permothemistida, palaeoecology.

CONTENTS

I. Introduction	130
II. The requirements for flight.....	131
III. Characters reflecting flight performance and technique.....	132
(1) Scale.....	132
(2) Body and appendages	134
(3) Axillae.....	135
(4) Wing shape	135
(5) Wing venation and relief.....	137
IV. Superorder Ephemeroptera – the mayfly clade	138
(1) Introduction.....	138
(2) Flight in modern mayflies.....	139
(3) Palaeozoic ephemeropteroids	141
V. Superorder Odonatoptera – the dragonfly clade	144
(1) Introduction.....	144
(2) Flight in modern Odonata.....	144
(a) The leading-edge spar, and the nodus.....	145
(b) The arculus.....	145
(3) Palaeozoic Odonoptera	146
VI. Palaeodictyopteroid orders: the Palaeozoic haustellate clade.....	150
(1) Introduction.....	150

(2) Palaeodictyoptera: Homiopteridae and Lycocercidae – insect biplanes.....	152
(3) Palaeodictyoptera: Spilapteridae – hind wing expansion.....	154
(4) Palaeodictyoptera: Eugereonidae and Megaptilidae – hind wing reduction.....	154
(5) Palaeodictyoptera: Dictyoneuridae and Eubleptidae – vein reduction in similar wings...	155
(6) Palaeodictyoptera: Breyeriidae and Calvertiellidae – transverse flexibility and distal twisting.....	156
(7) Diaphanopteroidea – the wing-folding Palaeoptera	157
(8) Megasecoptera and Permothemistida – towards hovering flight.....	159
VII. Conclusions: palaeopteran flight patterns and palaeoecology.....	162
VIII. Acknowledgments.....	163
IX. References.....	163

I. INTRODUCTION

Although the circumstances and manner of the origin of insect flight continue to attract widespread – and increasingly informed – interest (Kukalová-Peck, 1983, 1987; Kingsolver & Koehl, 1985, 1994; Ellington, 1991*a*; Wootton & Ellington, 1991; Marden & Kramer, 1994), far less attention has been paid to the subsequent evolution and diversification of insect flight techniques. Early attempts (e.g. Edmunds & Traver, 1954; Wootton, 1976) were hindered by our limited understanding at that time of the aerodynamics involved. Recently, Brodsky (1994) has combined an outstanding knowledge of functional morphology with his own and his colleagues' experimental investigations of wake vorticity to develop a broad view of the history of insect flight. His account makes good use of palaeontological information, but he does not attempt to interpret in detail the striking diversity in the flight apparatus of early flying insects; evidence for a variety in flight habit and technique which is of considerable interest in the broad context of insect evolution and palaeoecology. We now know enough both of insect aerodynamics, and of the functional significance of the wing characters on which insect palaeontology relies so heavily, to attempt such an interpretation.

The long initial phase in flight evolution is quite unknown to us. We do not know when insects developed the power of flight: estimates have ranged from the Upper Silurian to the lower Carboniferous, a spread of some 100 million years. Even if flight arose as late as 350 million years ago, in the late Devonian, nearly 30 million years then elapsed before the Namurian A division of the Lower Carboniferous, wherein the earliest known winged insects are found (Brauckmann, Brauckmann & Gröning, 1996). Not surprisingly the prolific insect beds at Hagen-Vorhalle, Germany (Brauckmann, Koch & Kemper, 1985) and scattered earlier

remains from Germany, Poland and the Low Countries show that significant radiations had by then already taken place. Rich remains from Europe, North America and Siberia show that these radiations continued through the Carboniferous and lower Permian, creating a characteristic, remarkable Palaeozoic fauna, including the stems of various extant orders, together with several major taxa which became extinct by the end of the Permian, approximately 280 million years before the present (MYBP). These taxa show spectacular variety in size and shape, suggesting a wide range of habit and behaviour.

This observation is particularly true of the orders classified together by A. V. Martynov (1923) as the subclass Palaeoptera, the subject of this investigation. Palaeoptera, with the exception of one order, were incapable of folding their wings back over the body, as distinct from the wing-folding Neoptera which include the huge majority of extant insects. The status of these groupings as true clades has often been questioned (Kristensen, 1991, 1997; Whiting *et al.*, 1997). At present we believe the weight of evidence to support their retention.

J. Kukalová-Peck (unpublished observations) divides the Palaeoptera into two taxa, Hydro-palaeoptera, comprising the Ephemeroptera and Odonoptera, and Rostropalaeoptera, comprising the palaeodictyopteroid orders. As so defined, the Palaeoptera comprises three superorders.

The Ephemeroptera include the extant Ephemeropterida (mayflies) and branches of their stem group. The crown group Ephemeropterida, with very unequal fore- and hind wings, may not be represented in the Palaeozoic, although Permian Protereismatidae have been considered to be close to their direct ancestry (Hubbard & Kukalová-Peck, 1980). The Odonoptera comprise the extinct Geroptera and extant Odonopterida, including Odonata (dragonflies) and branches of their stem. Many Palaeozoic forms have traditionally – and

variously – been placed in the paraphyletic Order Protodonata. Bechly (1996) has proposed a new system dividing the superorder Odonoptera into many subgroups.

The remaining clade, the palaeodictyopteroid superorder, is wholly extinct, but was abundant, diverse and spectacular in the Palaeozoic. All known species had elongate, haustellate mouthparts. Four orders are recognized: Palaeodictyoptera, Megasecoptera, Diaphanopteroidea and Permothemistida (= ‘Archodonata’). The first was already established in the Namurian A, approximately 322 MYBP, and the first three were distinct by the end of the Namurian B, approximately 316 MYBP (Brauckmann *et al.*, 1996). Permothemistida have been recognised in the Carboniferous (Rohdendorf *et al.*, 1961; Labandeira, 1994), but are known mainly from the Lower Permian.

Most Palaeozoic Palaeoptera, like modern anisopteran dragonflies, seem to have held their wings outstretched when at rest. Modern mayflies, and Odonata, Sub-order Zygoptera, hold their wings above the body at rest, and since in Zygoptera the thoracic terga are tilted backward the wings appear misleadingly to be folded over the abdomen. In Diaphanopteroidea, the wings could actually be folded, and this ability seems to have been acquired independently of the Neoptera, which are defined by their highly specialised wing-folding capability.

This paper will first review the aerodynamic requirements for flapping flight, and the nature of the evidence available for interpreting the flight adaptations and capabilities of extinct insects. We will then apply these criteria, and our knowledge of flight in modern mayflies and dragonflies, to interpreting that of Palaeozoic Ephemeroptera and Odonoptera. We will examine flight adaptations in Palaeodictyopteroidea, where we have no direct help from recent forms; and will conclude by discussing the flight habits of the Palaeoptera in the context of Palaeozoic ecosystems.

II. THE REQUIREMENTS FOR FLIGHT

If an insect is to fly horizontally level in still air it must elicit a vertically upward reaction force from the air sufficient to support its weight, and a horizontal force (‘thrust’) to balance the drag on its body and appendages. It achieves both these by generating lift with its wings, which are its only propulsive structures. Lift is correctly defined not as

a vertical force, but as that component of the aerodynamic force which acts perpendicularly to the relative airflow, and so to the direction of movement. The body may itself generate some lift, but this is usually small, and is vertically directed since the body is moving horizontally; there is no thrust component. Almost all the thrust, and most of the weight support, comes from the lift of the wings, whose movement is usually oblique to the horizontal, and which by flapping, twisting and changing their cross section generate a net aerodynamic force with a forward as well as a large vertical component. The wings themselves generate drag, but this is small in comparison to the lift.

The insect will also need some physical stability: a tendency automatically to return to its previous attitude and flight path after minor deflections. Stability in roll – ‘lateral stability’ – is provided by the outstretched wings, stroking symmetrically on either side of the body. Stability in pitch – ‘longitudinal stability’ – requires that the insect’s centre of mass is reasonably close to its centre of aerodynamic force. Deflection will tend to be resisted aerodynamically, by asymmetric forces above and below the body, predominantly behind the centre of mass; and by the body’s inertia. Stability in yaw – ‘directional stability’ – will be similarly maintained by body inertia and by laterally asymmetric aerodynamic forces if deflection occurs.

Total stability is undesirable, as it would make voluntary manoeuvres difficult, if not impossible. Manoeuvring involves accelerations – changes in speed, or direction, or both. These need active control; and the same controlling mechanisms serve to correct for any instability. Rolling can be initiated or corrected by asymmetry in the wing stroke, attitude or shape on the two sides of the body. Yawing can be initiated or corrected by stroke asymmetry or by asymmetric movements of the abdomen or appendages, and pitching by changing the wing stroke so as move the centre of aerodynamic force relative to the centre of mass.

The wing kinematics: their movements, and the shifting patterns of wing orientation and shape during the stroke cycle, are clearly crucial in both propulsion and active stabilization. As the wings contain no muscles, all active force generation and control is localised in the thorax, or in the articular sclerites at the extreme wing base. The wings, however, are flexible aerofoils, and their attitude and shape at any instant result from the interaction of these active basal forces, the aerodynamic forces they are receiving, the inertial forces from their

flapping, and the distribution of their own elastic properties. Herein lie many clues to the significance of wing morphology in determining flight performance.

III. CHARACTERS REFLECTING FLIGHT PERFORMANCE AND TECHNIQUE

An insect's flight behavioural repertoire is ultimately limited by its performance capability. Performance has several components. Crucial are: speed, particularly its upper and lower limits; manoeuvrability and agility (usefully distinguished by Norberg & Rayner, 1987); precision, and economy. All are probably influenced by the insect's morphology, although the nature of the influence is not always easy to interpret, even in recent forms. In fossils, where details of the muscles and neurosensory system are unknown, and even some body dimensions can only be crudely estimated, the task is far harder, and it becomes necessary to make the greatest possible use of those features which can clearly be seen and measured.

(1) Scale

The wide size range of Palaeozoic insects, and in particular the large size of many species, raise interesting questions on the effects of scale.

For geometrically similar (isometric) insects flying in a given fluid medium with dynamic similarity (i.e. with the distances moved, velocities reached, and forces exerted by equivalent moving points on the body respectively related by the same constants throughout the scale), orthodox steady-state and quasi-steady aerodynamic theory predicts a relationship between mass, wing-loading, flight speeds and flapping frequency. Characteristic speeds – stalling speed, maximum speed, maximum range speed and minimum power speed – should vary as the square root of wing-loading (weight supported by unit area of lifting-surface). Since wing-loading should vary as $\text{mass}^{1/3}$, speeds should therefore vary as $\text{mass}^{1/6}$. Furthermore, for animals flying with dynamic similarity, flapping frequency will be proportional to forward speed (and hence to the square root of wing-loading) divided by wing length.

Physiological information takes us further. Respirometric studies on a range of insects indicate that metabolic energy utilisation per contraction per unit mass of muscle seems to be more or less constant for a given muscle type, although at different levels for

synchronous and asynchronous muscle. For a given muscle type, therefore, energy consumption per unit mass of insect is directly proportional to frequency, and inversely related to size (Casey, 1989). Furthermore, recent studies (e.g. Casey & Ellington, 1989) indicate that the mass-specific mechanical power output of insect flight muscle is relatively size-independent. If this is generally true, and if the elastic storage in the tissues of the energy required to accelerate and decelerate the wings and attached mass of air is perfect at all frequencies, it follows that the efficiency of the flight muscle is also negatively related to frequency, and positively to body size (Ellington, 1985, 1991*b*).

Summarising, for geometrically similar insects flying with dynamic similarity, an increase in size should bring about an increase in top and other characteristic speeds, a lower wing-beat frequency, increased muscle efficiency, and lower mass-specific energy consumption. Size reduction should reduce characteristic speeds, including top speed; and should increase wing-beat frequency and the mass-specific cost of flying.

Insects as a whole are very far from being geometrically and dynamically similar. Their shape and their flight kinematics vary widely – far more than in flying vertebrates – and it is immediately possible to interpret and predict some aspects of this variation, in adaptive terms. For example, very small size, inescapably associated with high stroke frequency, has only been achieved by the evolution of asynchronous, myogenic flight muscle, since the maximum contraction frequency of neurogenic muscle capable of powering flight seems to be approximately 100 Hz (Pringle, 1976, 1981). While asynchronous muscle has clearly arisen at least ten times (Cullen, 1974; Pringle, 1981; Smith, 1983), stroke frequency in small members of lineages with only synchronous muscle may often have been kept within bounds by an increase in relative wing size and a consequent reduction in wing-loading, or by changes in the kinematic variables of the wing-beat. Conversely, as Dudley (1991) has suggested, some groups of small and medium-sized insects may have used the high-frequency possibilities of asynchronous muscle to increase their wing-loading, and with it their characteristic speeds. Indeed allometric evolutionary change in wing-loading could act to modify the speeds available at any level in the insect size-range.

Empirical analysis of data drawn from a wide range of extant insects shows a predictably complex picture. Byrne, Buchmann & Spengler (1988)

Table 1. Estimated wing-loadings (total estimated weight divided by total wing area) and pterothorax mass/total mass ratios for a selection of Palaeozoic Palaeoptera. The value for *Bojophlebia prokopi* is extremely approximate, as the abdomen is not completely preserved. Those for *Stenodictya* spp. are based on a reconstruction in Kukalová (1970), with details derived from several species. See text for details of measurement techniques

	Wing-loading (N m ⁻²)	Body length (mm)	Pterothorax mass/ total mass	Reference
Ephemeroptera				
<i>Bojophlebia prokopi</i>	1.86	280		Riek & Kukalová-Peck (1984)
<i>Protereisma directum</i>	0.21	35	0.45	Carpenter (1979)
Odonatoptera				
<i>Namurotypus sippelorum</i>	1.25	150	0.37	Brauckmann & Zessin (1989)
Undescribed species	0.35	43	0.37	
Palaeodictyoptera				
<i>Homoioptera vorhallensis</i>	2.28	112	0.38	Brauckmann (1988)
<i>Homaloneura lehmani</i>	0.69	27	0.3	Kukalová (1969)
<i>Dunbaria fasciipennis</i>	0.52	20	0.29	Kukalová-Peck (1971)
<i>Stenodictya</i> spp.	1.46	60	0.29	Kukalová (1970)
<i>Eubleptus danielsi</i>	0.08	18	0.31	Carpenter (1983)
Diaphanopteroidea				
<i>Namurodiapha sippelorum</i>	0.72	33.5	0.33	Kukalová-Peck & Brauckmann (1990)
<i>Uralia maculata</i>	0.4	22	0.32	Kukalová-Peck & Sinichenkova (1992)
<i>Asthenohymen dunbari</i>	0.21	7	0.2	Carpenter (1939)
Megasecoptera				
<i>Mischoptera nigra</i>	0.21	97	0.22	Carpenter (1951)
<i>Protohymen readi</i>	0.39	19	0.44	Carpenter (1933)
<i>Sylvohymen sibiricus</i>	0.63	29	0.4	Kukalová-Peck (1972)

found a significant correlation between frequency and wing-loading only for insects of mass greater than 0.03 g, and conclude that below this size the relationship is confused by the adoption of low-wing-loading strategies and a variety of different, non-steady, aerodynamic techniques. All but one of the species below this mass which they consider have asynchronous muscle, and far more information is needed from small representatives of the orders with only synchronous muscle. Reliable information on top speeds and cruising speeds of insects is far too scarce for the relationship between speed and wing-loading to be tested for the class as a whole, though there is good positive evidence in a few individual groups (Chai and Srygley, 1990, and Dudley, 1990, for neotropical butterflies). For insects as a whole, a few examples hint at the probable scatter. Bumblebees, whose wing loadings generally lie between 15 and 45 N m⁻² (Ellington, 1984*a*; Byrne *et al.*, 1988) seldom fly faster than 5 ms⁻¹ (Heinrich, 1979; Dudley & Ellington, 1990*a*), though some queens have been timed at over 7 m s⁻¹ (Cooper, 1993). Large bumblebees are among the most highly

loaded of all extant insects (Byrne *et al.*, 1988). Anisopterous dragonflies, with wing-loadings between 2 and 5 N m⁻² (Byrne *et al.* 1988), regularly reach similar speeds (Neville, 1960; Rüppell, 1989), and *Libellula depressa*, a lightly loaded species (wing-loading = *c.* 2 N m⁻², Byrne *et al.*, 1988) has been timed at 11 m s⁻¹ in still air (Neville, 1960).

What are the implications of these scaling arguments on the flight patterns of Palaeozoic Palaeoptera? None is small enough for asynchronous flight muscle to have been essential; and indeed asynchronous muscle is unknown in modern Palaeoptera. More interesting are the implications of the remarkably large size of some ephemeropteroids, odonatoids and Palaeodictyoptera; far larger than any actively flying modern forms. How fast and how slowly could they fly? Could the giant Carboniferous and Lower Permian dragonflies hover?

To answer these questions we need some estimates of weights, and hence of wing-loadings for Palaeozoic insects. Table 1 shows estimated wing-loadings for a range of Palaeozoic Palaeoptera whose bodies and wings are well-enough preserved for measurement.

Approximate weights were estimated by modelling the bodies and legs as accurately as possible in water-repellent modelling clay, and immersing each model in a beaker of 50% ethanol with an overflow tube leading into a slender measuring cylinder, or directly in the measuring cylinder itself, and hence finding the volume of the model by displacement. Extant insects – a locust, a cockroach and a dragonfly – were first weighed, then similarly immersed. Their specific gravity was found to be very close to unity, and the same is assumed when calculating the weights of the modelled insects. Small insects were scaled up for modelling, and their estimated weights adjusted accordingly. The wing areas were found by tracing their outlines on paper, scaled up as needed; cutting them out, measuring their areas with a video-planimeter, and adjusting for scale. Wing weight was estimated by measuring the weight per unit area of the hind wing of a freshly dead locust, and multiplying this by the wing area of the fossil species.

The resulting values are no more than best guesses. There are obvious sources of error in modelling three-dimensional bodies from flat impressions, and air sacs or large masses of lipid-filled eggs could significantly influence the mean density of the tissues. Appendages are sometimes incompletely known, and their estimated dimensions are informed guesses. Nonetheless the results are within a plausible range, and help to quantify some visually obvious differences between species. Fig. 1 shows the log of estimated wing-loading plotted against log body length, the latter being chosen as a measure of size which is not directly used in calculating wing-loading. If the insects were geometrically similar all points would lie on a line of gradient 1. They do not, and their positions in the scatter give some useful indications. For example, Palaeodictyoptera, with the exception of one very small species, tend to have high wing-loadings for their size.

In interpreting these results in the context of the Upper Carboniferous and Lower Permian it is necessary to take account of the prevailing atmospheric composition. The calculations of Berner & Canfield (1989) indicate that oxygen levels throughout this time may have been above that at present, reaching 35% around the Carboniferous – Permian boundary, and declining to well below present level in the late Permian. This has physiological and aerodynamic implications (Graham *et al.*, 1995; Dudley & Chai, 1996). The size limits imposed by tracheal respiration would be elevated, allowing the familiar gigantism of many Palaeozoic insects (Dudley, 1998). If one assumes nitrogen and trace

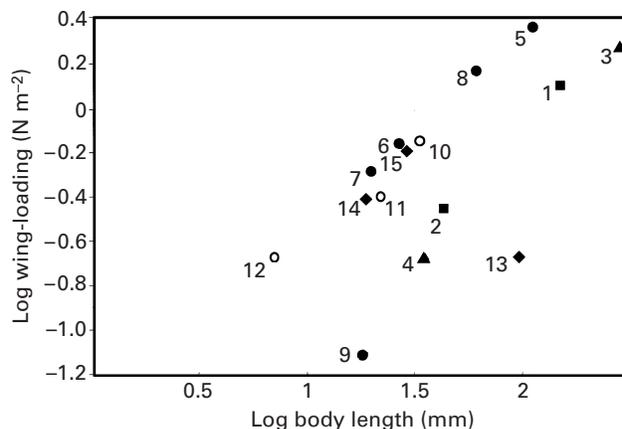


Fig. 1. Logarithmic plot of estimated wing-loadings against body length for a selection of Palaeoptera. 1. *Namurotypus sippelorum*. 2. Unnamed geropterid from Rioja, Argentina. 3. *Bojophlebia prokopi*. 4. *Protereisma permianum*. 5. *Homoioptera vorhallensis*. 6. *Homaloneura lehmani*. 7. *Dunbaria fasciipennis*. 8. *Stenodictya* spp. 9. *Eubleptus danielsi*. 10. *Namurodiapha sippelorum*. 11. *Uralia maculata*. 12. *Asthenohymen dunbari*. 13. *Mischoptera nigra*. 14. *Protohymen permianum*. 15. *Sylvohymen sibiricus*. The estimate for *Bojophlebia prokopi* is extremely approximate, as the abdomen is not completely preserved. That for *Stenodictya* spp. is based on a reconstruction in Kukalová (1970), with details derived from several species. ▲, Ephemeroptera; ■, Odonatoptera; ●, Palaeodictyoptera; ◆, Megasecoptera; ○, Diaphanopteroidea.

gas partial pressures to be more or less as now, air density would reach a peak approximately 21% above the present value, significantly enhancing lift production, so that insects could have flown with relatively smaller wings, and apparent wing-loadings would in effect be lower.

(2) Body and appendages

The form of the body and appendages can be informative. A disproportionately bulky thorax probably indicates a large muscle mass, and hence high available power and potentially speed and speed range; the ratio of flight muscle mass to body mass seems to be the best indicator of flight capability (Marden, 1987; Ellington, 1991*b*). This is unmeasurable in fossils, but a crude estimate of pterothorax mass to total mass can in some cases be made, using the modelling technique described above. Results for a selection of species are shown in Table 1. An elongate body suggests a high moment of inertia about the centre of mass, and a long abdomen would experience aerodynamic restoring

torques if it moved out of alignment with the direction of flight. Both would restrict manoeuvrability, although a long abdomen would provide physical stability in flight.

The drag of body and appendages ('parasite' drag) of modern insects is generally low (Dudley & Ellington, 1990*b*), but may have been more significant in some large Palaeozoic insects, which were as big as small birds, operating well within the Reynolds number range where some streamlining would be advantageous. Bodies, suitably angled with reference to the airflow, can also provide some lift, especially if dorsoventrally flattened; though measured values in extant insects do not in general exceed 10% of body weight (Dudley & Ellington, 1990*b*).

Segmental appendages – apart from the wings – create only drag, but being movable can help in controlling speed and stability. Many modern insects: Coleoptera, nematoceran Diptera, some Hymenoptera and Lepidoptera, habitually spread their legs when flying slowly, and this must provide some physical stability. At higher speeds the legs are often tucked close to the body, or allowed to trail.

Palaeodictyopteroids and ephemeropteroids have long abdominal cerci, and many Ephemeroptera also retain a long median caudal filament. Brodsky (1973) described how several Ephemeroptera vary the degree to which the cerci are spread in trivial and nuptial flight, closing them against the caudal filament when taking off in windy conditions, spreading them widely when descending during the nuptial dance. The cerci presumably act as physical stabilisers; their drag when spread would tend to oppose body rotation in the pitching, yawing and rolling planes. They probably also detect such rotations, and allow active correction. Whether spread or not, the cerci and caudal filament would tend to limit manoeuvrability.

(3) Axillae

The axillae are complex systems of three-dimensional mechanisms, linking the thorax to the wings and providing the sole route by which muscular forces are transmitted between them. Resting on the fulcrum of the pleural wing process, they form the pivot around which the wings are flapped, and in Neoptera and Diaphanopteroidea folded; and through which the basal angle of attack and camber are actively imposed. The relative movements of the axillary components determine or influence all the kinematic variables of the wing.

However, even in most extant insects the precise mode of operation of the axillary mechanisms is poorly understood, and the conclusions which can at present be gained from fossils are therefore very limited, even when the axillary structure is known. The most obvious variable is apparent mobility. The broad-based, multi-component axillae of some Palaeozoic insects seem to give little scope for basal twisting, placing severe restrictions on their possible modes of flight. Others seem far more compliant, with more degrees of freedom.

(4) Wing shape

The relationships between wing planform and flight performance have been extensively studied in vertebrates (Norberg & Rayner 1987; Rayner, 1987), and have been used in the reconstruction of flight patterns in the extinct Pterosauria (Hazlehurst & Rayner, 1992). The wing shapes of insects are far more varied, and their adaptive significance far less clear. The four-winged condition of many insects, including most Palaeoptera, complicates the interpretation of planform in aerodynamic terms, especially when, like Odonata, the insects beat their fore and hind wings out of phase, inevitably creating highly complex and unsteady flow patterns. Furthermore, most insects are operating at far lower Reynolds numbers than birds and bats, and within a range where minor differences in wing shape and attitude can have marked and often unpredicted aerodynamic effects. The importance of leading-edge vorticity in creating high lift coefficients by delaying stall (Ellington *et al.*, 1996; Willmott, Ellington & Thomas, 1997; Van den Berg & Ellington, 1997) is probably widespread, and the form of these vortices will probably be influenced by wing shape characters.

Some principles, derived from general aerodynamic theory, may be assumed to apply to insects. For a given wing area, a high aspect ratio (span/mean chord) reduces induced drag – the drag incurred in creating the downwash whose momentum flux is necessary to support the insect's weight, and favours a high lift-drag ratio. This is particularly important at low flight speeds and in hovering, when most or all of the downwash has to be created by active flapping. The longer the wings, the larger the area which they sweep out, the greater the volume, and hence mass, of air they encounter per unit time, the less momentum they need to give it, and the lower the energy required. From the Rankine–Froude momentum theory of propellers, the induced

power – the power required to create the downwash – at any given airspeed varies in inverse proportion to the wing span.

In a fossil, therefore, relatively long wings suggest that the insect may have been capable of low speeds, and perhaps of hovering; although other indications are needed. In particular, evidence is required that the wings could twist easily, since most slow flight requires that the insect's weight gains some support on the upstroke as well as the downstroke.

High aspect ratio wings are characteristic of sailplanes and many gliding birds, as they favour shallow glides: the glide angle is the arccotangent of the lift/drag ratio, which is high in slender wings. However, Ennos (1989*b*) has shown theoretically that a high aspect ratio may not be optimal for glide performance in most insects. These operate in a range of Reynolds numbers where narrowing the wing may increase the profile drag to an extent which may eliminate the advantages of reduced induced drag, and may cause the wing to stall at a speed above the theoretical optimal gliding speed, which is never reached. Increasing the aspect ratio may therefore improve the glide angle by less than the conventional analysis would predict. Ennos (1989*b*) suggests that optimal glide performance for insects may come at medium to low aspect ratios. His analysis is based on the lifting line model of the wing, in which the wing is modelled as a line vortex perpendicular to the flight direction, and which is theoretically inappropriate for aspect ratios below 5, but his conclusions are still supported by experience: the insects in which gliding is common are butterflies, Orthoptera and some Odonata, and among the last, the most habitual gliders have unusually broad wings (Corbet, 1962). Some Palaeozoic Palaeoptera, however, are much larger than any living insects, and may well have been in the size and speed range where narrow wings are optimal in gliding.

For fast forward flapping flight in the insect size range, moderately broad wings may also be appropriate, giving high lift, and hence thrust, although with associated high induced drag. Thorax length clearly limits the possible fore wing breadth if significant overlap with the hind wing is to be avoided, so that overall increase in total breadth is normally achieved by enlarging the hind wing. Most of the extra area tends to be concentrated towards the base; distal expansion would increase the wings' moment of inertia, with associated energetic costs.

The distribution of area along the span has other implications. In fast flight the advance ratio (flight velocity/flapping velocity) is high, and the wing

base is moving fast with the body, and is able to provide significant lift. In slow flight, the flapping velocity comes to predominate, and there is a sharp velocity gradient from base to wing tip. A broad wing base would bring little benefit to an insect which habitually flew slowly; and might indeed be a slight disadvantage: any airflow past the base will be directed mainly downwards, and will tend to pull the body down. Not surprisingly, the wings of many habitually slow flying insects – zygopterous Odonata, nematoceran Diptera, myrmeleonid Neuroptera – have narrow, petiolate bases, and the wing area is concentrated distally, where the airflow is fastest, and the aerodynamic forces greatest. Brodsky (1985) has shown in tethered *Tipula paludosa* (Diptera) that the vortex wakes of the two petiolate wings are widely separated from each other and from the body, confirming the predictions of Ellington (1980, 1984*c*). Narrow bases also favour wing twisting. The distribution of wing area along the span is most clearly expressed as the non-dimensional radii of the first, second and third moments of area of the wing about the base – see Ellington (1984*a*) for a detailed discussion. Weis-Fogh (1973) showed that the second moment of wing area is proportional to the mean lift force of the wing as given in the quasi-steady aerodynamic analysis, and that the third moment is proportional to the mean profile power. In the insects which he studied, Ellington (1984*a*) found the radii of these three moments to be closely correlated, and this has since been confirmed in other groups (Betts & Wootton, 1988; Bunker, 1993). Ellington (1984*a*) suggested that wing shape could therefore conveniently be described by a single parameter; the non-dimensional radius of the first moment of area, which is given by the distance of the wing's centroid from the base, divided by the wing length. The centroid of any wing is easily found by computation or by simply suspending a traced shape successively from two points on its perimeter and marking the intersection of the vertical lines below the points of suspension. Values for aspect ratios and non-dimensional radii of the first moments of area of the wings of a range of fossil Palaeoptera are given in Table 2.

A few wings show marked tip sweep-back. Wehl (1945) found that a raked tip in tailless airplanes can reduce induced drag, and Norberg (1973) suggested that the rearward displacement of the centre of pressure which results from swept tips may serve to provide passive pitch-angle control in fast anisopteran dragonflies. Lan (1979) found that an

oscillating swept back wing was much less sensitive than a rectangular one to phase differences in lift and thrust, and always produced positive thrust, while a rectangular one sometimes produced drag. A raked tip is likely also to influence leading-edge vorticity, and hence lift generation by dynamic stalling (C. P. Ellington, personal communication).

Summarising: long, slender wings with narrow bases and the area concentrated distally, giving large radii for the area moments, are probably adapted for relatively slow flight, even for hovering. Wings or wing couples with their area concentrated towards the base, and hence smaller radii for the area moments are predominantly adapted for faster flight, and sometimes for gliding. For information on factors determining the range of available speeds and the manoeuvrability of the insects it is necessary to examine wing morphology in more detail.

(5) Wing venation and relief

Beside providing channels for sensory nerves, tracheae and the transmission of haemolymph, which last is essential in maintaining the compliance and toughness of the cuticle, the veins serve several mechanical functions. They support the wings, and control their three-dimensional shape throughout the stroke cycle by determining how far they are bent and twisted by the aerodynamic and inertial forces of flapping flight. Since shape and attitude themselves strongly influence aerodynamic force production, and since swift controlled changes in shape are involved in many unsteady mechanisms of lift generation (Ellington, 1984*c*, 1995; Wootton, 1992), it is reasonable to assume that much information on the flight techniques and performance of insects is encoded in their venation patterns. The principles involved in the interpretation of these patterns are reviewed by Wootton (1981, 1992) and by Brodsky (1985, 1994). Detailed interpretations will be given group by group in the sections which follow, but some general principles can be introduced here.

It is often possible to recognise areas of the wing which are primarily supporting, and others which are adapted for controlled deformation. Recognisable supporting features include sturdy individual veins, groups of veins linked together by stout transverse or oblique cross-veins into three-dimensional lattice-girders or broader, frame-like structures, and areas of thickened membrane. Features favouring local deformability include slender longitudinal veins, local vein narrowing or

flattening, bands or zones of soft cuticle, annular constrictions, flexible joints between cross- and longitudinal veins, long, slender, curved cross-veins, and low relief.

Four other aspects are particularly relevant to flight in Palaeozoic Palaeoptera: venation 'richness'; the pattern of cross-veins and vein reticulation between the longitudinal branches; the degree of basal juxtaposition and coalescence of the longitudinal vein stems; and the resistance of the wing to transverse bending.

Venation richness varies greatly between insects. It has three components: the number of main longitudinal veins present; the number of branches to each vein; and the relative density of cross-veins and reticulation between the longitudinal veins. The number of longitudinal components can be further increased by the alignment of some reticulate veins into 'intercalary' veins, lying between and parallel to the more distal vein branches. Intercalaries are usually of opposite sense to the veins between which they lie, i.e. they may occupy troughs between a series of veins on ridges or *vice versa*, and so impose corrugation which extends through, and imparts flexural rigidity to, the posterodistal areas of the wing.

Most very small wings have simple venation, but simplicity is certainly not a straightforward function of size. Anisopterous Odonata, for example, have many times more branches and cross-veins than Lepidoptera with similar or greater wing area, and venational richness may vary hugely within a single family. In itself, it tells us little about flight performance or technique. Richness is sometimes associated with cuticular thickening and the modification of the wings into protective tegmina – probably at the expense of flight efficiency. On the other hand Ellington (1984*a*) has shown that some wings with many slender branches are lighter, area for area, than wings with fewer, stouter veins; and some insects with rich venation (e.g. Odonata, many Neuroptera) are spectacular fliers. Flight capability is reflected in venational detail rather than branching complexity *per se* (Wootton, 1992), and such evidence can be sought in fossil forms. Dense venation may have one other significant advantage. By preventing large uninterrupted areas of membrane it can toughen the wing, since any rips would tend to stop at nearby veins.

The form of the cross-veins and reticulate veins can be particularly helpful in identifying the principal functions of particular areas of the wing. A series of short, stout cross-veins joining two longi-

tudinal veins in effect form a two-dimensional lattice-girder. If three longitudinal veins, two on ridges (“convex”) and one in a trough between them (“concave”) are so joined, the resulting girder, with a V- or L-shaped cross-section, is likely to be significant in support.

Wing areas with long, slender, curved, irregular or reticulate cross-venation are probably adapted for flexibility and deformation. Wing deformation in the process of flight almost always involves some shearing of the membrane, and cross-veining of this kind permits this, while still providing some local support and the ‘rip-stop’ advantages discussed above. Palaeoptera, particularly Palaeozoic Palaeoptera, often have large areas of reticulate cross-veining forming irregular polygons. The theoretical ideal for maximum deformability in the plane of the wing is a network of regular hexagons; such a network can be sheared, stretched and compressed. Hexagonal wing reticulation is common in many Palaeoptera. The ‘archedictyon’ of some Palaeodictyoptera, long believed to be a generalized, plesiomorphic reticulation from which true cross-veins evolved, may well be an adaptive feature.

Many Palaeoptera – particularly among zygopterous and similar Permian odonatoids, and some Megasecoptera and Diaphanopteroidea – have narrow, petiolate wings in which the stems of the longitudinal veins are closely juxtaposed, and often fused. Such stems are more compliant in torsion, mass for mass, than are broad bases with more widely spaced veins. Controlled torsional compliance allows the wing to twist to generate useful weight-support in the upstroke as well as the downstroke, and in extant insects petiolate wings are generally associated with slow flight and hovering (Wootton 1991, 1992, and see above). We have seen that wings with broad bases are capable only of limited twisting, and that this is likely to limit their speed range and manoeuvrability. In many modern insects, this limitation is partly overcome by the ability of the wings to flex ventrally and to some extent to twist during the upstroke. This can allow the distal area of the wing to undergo some supinatory twisting and to take up a more favourable angle of attack and section, giving greater control of force direction during the upstroke, and hence of speed and direction of flight. This is exploited by many insects with fore and hind wings coupled together, but is also used by some groups with uncoupled wings: Plecoptera, Megaloptera, Mecoptera (Fig. 2), (Wootton, 1981; Brodsky & Ivanov, 1983; Brodsky, 1986).

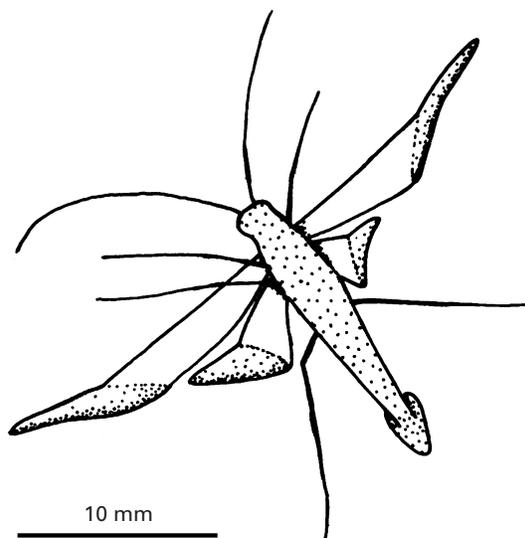


Fig. 2. *Panorpa germanica* (Mecoptera) in mid upstroke, flying freely. Tracing from a high-speed ciné-film, after Ennos & Wootton (1989), with permission. Copyright: Company of Biologists Ltd. Both fore and hind wings are ventrally flexed and partly supinated.

With these principles in mind, we can now proceed to examine the insects.

IV. Superorder EPHEMEROPTERA – THE MAYFLY CLADE.

(1) Introduction

Modern Ephemeroptera have aquatic juveniles and two short-lived, non-feeding winged instars. The penultimate, subimaginal instar is usually capable of flight, but has more opaque wings and shorter tails than the imago. Mayfly adults have markedly unequal fore and hind wings, the much smaller hind wing being closely apposed to the posteroproximal margin of the fore, and beating in the same phase, so that the wing couple acts as a single aerofoil. In Caenidae and some Baetidae, the hind wings are entirely lost. The wings are corrugated throughout, the branches of the main longitudinal veins alternating with secondary intercalary veins of opposite sense, providing a structure which is rigid to transverse bending, while allowing some flexion along axes parallel to the corrugations (Wootton, 1981). The abdomen is slender, and bears two elongate cerci and in many cases a median caudal filament.

Palaeozoic ephemeropterids were very different. Lower Permian species classified in the families

Protereismatidae (Fig. 3A, B) and Misthodotidae had fore and hind wings similar in length, shape and venation, the hind wings in the latter family being slightly broader than the fore. *Palingeniopsis* Martynov, from the Upper Permian, is known only from the hind wing, which is long, but with a concave outline to the anterior margin, and the wing base rather expanded posterobasally, like the hind wings of anisopterous Odonata. None shows the reduced hind wings of the Mesozoic and later families.

The few known Carboniferous ephemeropterids are still less like modern forms. *Triptlosoba pulchella* Brongniart, from the Upper Carboniferous (Stephanian) of France, had rather broad, but essentially similar fore and hind wings (Carpenter, 1963). However the extinct order Syntonopterida Laurentiaux 1953, from the Westphalian D of Illinois, had relatively broader hind wings; those of *Lithoneura lameerei* (Fig. 3C) being particularly expanded posterobasally, contrasting with the basally narrowed fore wings (Carpenter, 1938, 1944). The same is true of the most archaic known ephemeropterid, the giant *Bojophlebia prokopi*, (Fig. 3E) from the Westphalian C of Bohemia (Kukalová-Peck, 1985).

Where the body is known it is slender, as in extant Ephemera. *Triptlosoba*, Protereismatidae and Misthodotidae had elongate cerci and a median filament. The terminalia of adult Syntonopterida: *Lithoneura*, *Syntonoptera* and *Bojophlebia* are unknown, but the probable nymph of a *Bojophlebia* species has elongate cerci and a median filament.

(2) Flight in modern mayflies

It is logical to approach the flight technique of Palaeozoic mayflies by reference to extant species.

Fig. 4A shows the modern mayfly *Ephemera danica*, and Fig. 4B its fore wing base. The condition of the latter and of all modern mayflies is highly derived. The costal and subcostal veins, together with the anterior radius (RA), form a strongly three-dimensional leading-edge spar, stiffened by the strong subcostal brace. Posteriorly to this, and separated from it by a line of flexion, are four veins: the common stem of the posterior radius and anterior media (RP+MA), the posterior media (MP), and the anterior and posterior cubitus (CuA and CuP) radiate almost from a single point, and branch to support most of the wing area. The bases of these are obscured and virtually eliminated by a high-relief, thin-walled area from which the radiating veins are

separated by a band of flexible cuticle. Radiating lines of flexibility lie alongside the most posterior branches of RP and MP and beside CuP. The anal veins support a small, firm convex posterior area. Manipulation shows the main area of the wing to be capable of swinging freely dorsally and ventrally between the relatively rigid leading-edge spar and anal area, bending along the radiating lines of flexure and developing a reversible cambered shape, like part of a cone, which can be changed from dorsally convex to dorsally concave by pressure from below, and *vice versa*. Brodsky (1994) confirms that this radial flexion occurs in flight in *Ephemera vulgata*, and describes 'gradual supination' in which camber development at the start of the upstroke moves progressively backward from the radial flexion line to the posterior cubital.

Radial curvature of this kind in the main area (the 'remigium') of the wing is nearly unique to Ephemeroptera, but is closely paralleled in the expanded anal fans of the hind wings of many neopterous insects, particularly Orthoptera, Dictyoptera and Phasmatodea. These fans are corrugated, and supported by veins radiating from a narrow base, with many adjacent radiating flexion-lines. High-speed film of locusts and phasmids (R. J. Wootton, unpublished data) and high speed flash photographs of Orthoptera and mantids (Brackenbury, 1990, 1992) show that the pronounced radial curvature at the beginning of the downstroke fits the conditions for the 'peel' and 'partial peel' mechanisms of non-steady lift generation identified by Ellington (1984c) and modelled mathematically by Sunada *et al.* (1993). Both mechanisms require wing-strokes of high amplitude, and Brodsky (1971) indeed recorded a stroke amplitude of 160° in tethered *Ephemera vulgata*. It appears highly probable that mayflies too obtain high lift values by these means.

A venational feature which deserves comment is the curvature of CuP of the fore wing of many species. This will tend to hold down the adjacent part of the trailing edge, enhancing the camber, as the wing pronates and supinates about the adjacent flexion line in the downstroke and upstroke (Fig. 5).

Brodsky (1994) describes slight transverse deflection of the distal part of the fore wing at the start of the upstroke in tethered flight. Interestingly, the bending-line which he illustrates does not appear to coincide with the three 'bullae' which interrupt the first three concave veins partway along their length, and which Edmunds & Traver (1954) interpreted as allowing hingewise bending in the

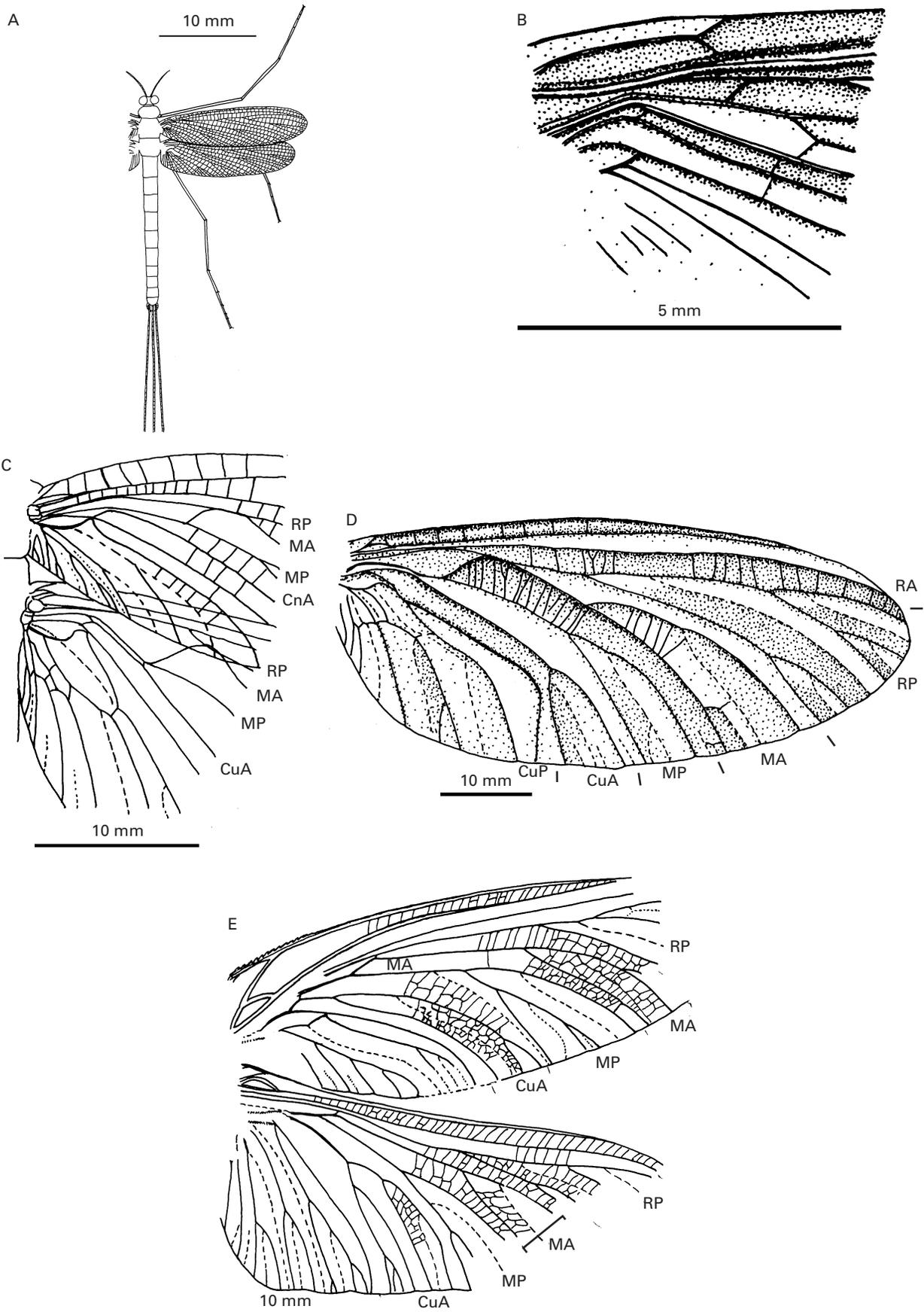


Fig. 3A-E. For legend see facing page.

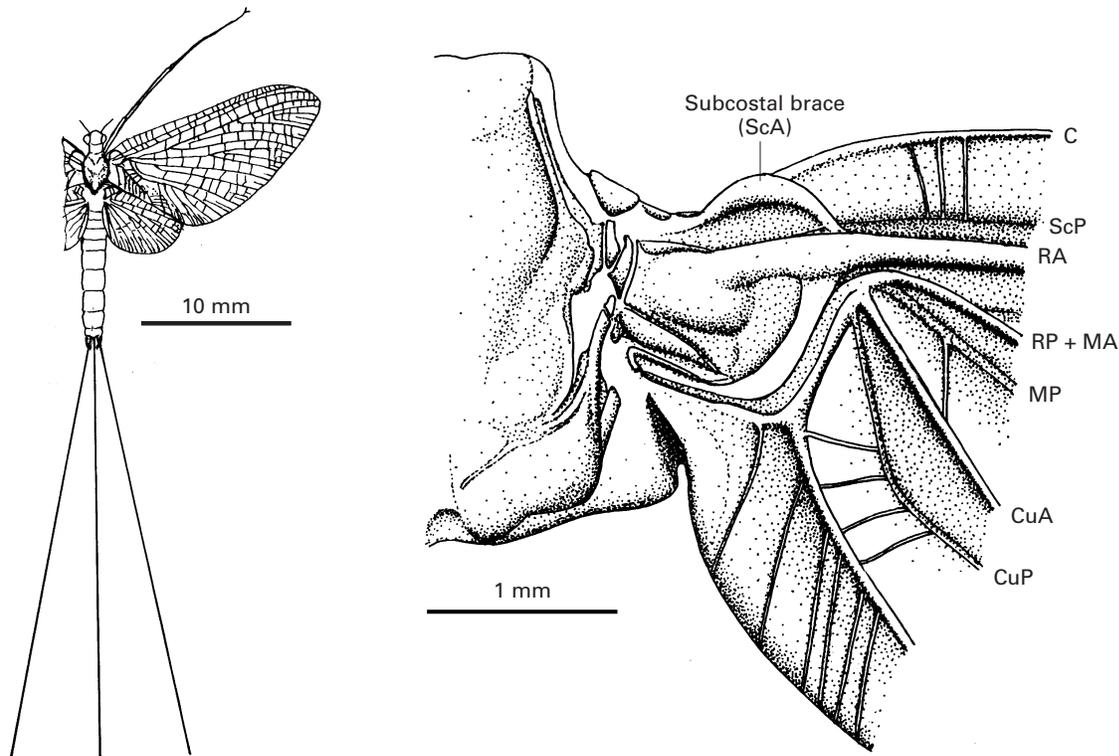


Fig. 4. *Ephemera* sp. (A) Entire insect. (B) Fore wing base. Original. C, costal veins; ScA anterior subcosta, forming the subcostal brace; ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus.

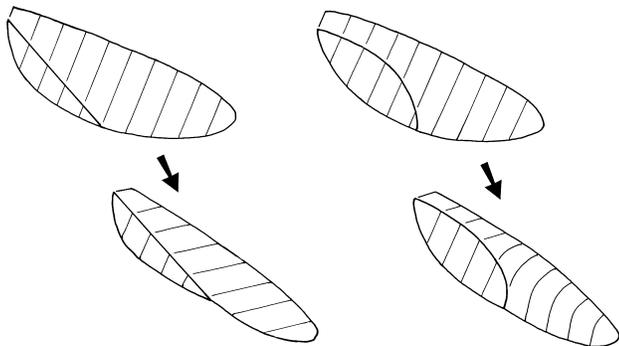


Fig. 5. Diagrammatic representation of the effect on the profile of the wing remigium profile of supinatory flexion in front of a straight (A) and a curved (B) vein. For explanation see text.

upstroke. It seems nonetheless that this must be their function. Strongly corrugated wings can only bend ventrally without permanent damage if the veins in the troughs are able to buckle non-destructively into the plane of the ridge veins (Newman & Wootton

1986), and the bullae would permit this. As described above ventral flexion at supination has been demonstrated in many groups of insects (Wootton, 1981, 1992; Brodsky, 1982, 1994; Ennos & Wootton, 1989). It commonly tends to allow the distal part of the wing to assume a more favourable angle. These kinematic asymmetries between up and downstroke appear to be at odds with Brodsky's (1994) description of a symmetrical vortex wake behind a tethered subimago of *Heptagenia sulphurea*, and indeed wake symmetry, which implies no net lift from flapping, seems unlikely in such evidently specialized wings.

(3) Palaeozoic ephemeropteroids

To what extent can the special adaptations of extant mayfly wings be recognized in Palaeozoic forms?

The common origin of RP+MA, MP, CuA and

Fig. 3. Palaeozoic Ephemeroptera. (A) *Protereisma permianum*, reconstruction. After Carpenter (1933). (B) *Protereisma-directum* fore wing base. Original. (C) *Lithoneura lameerei* wing bases. After Kukalová-Peck (1985). (D) *Lithoneura mirifica* hind wing. Modified after Kukalová-Peck (1985), to show relief. (E) *Bojophlebia prokopi* wings. After Kukalová-Peck (1985). RA, anterior radius; RP, posterior radius; MA, anterior media; MP posterior media; CuA, anterior cubitus; CuP, posterior cubitus.

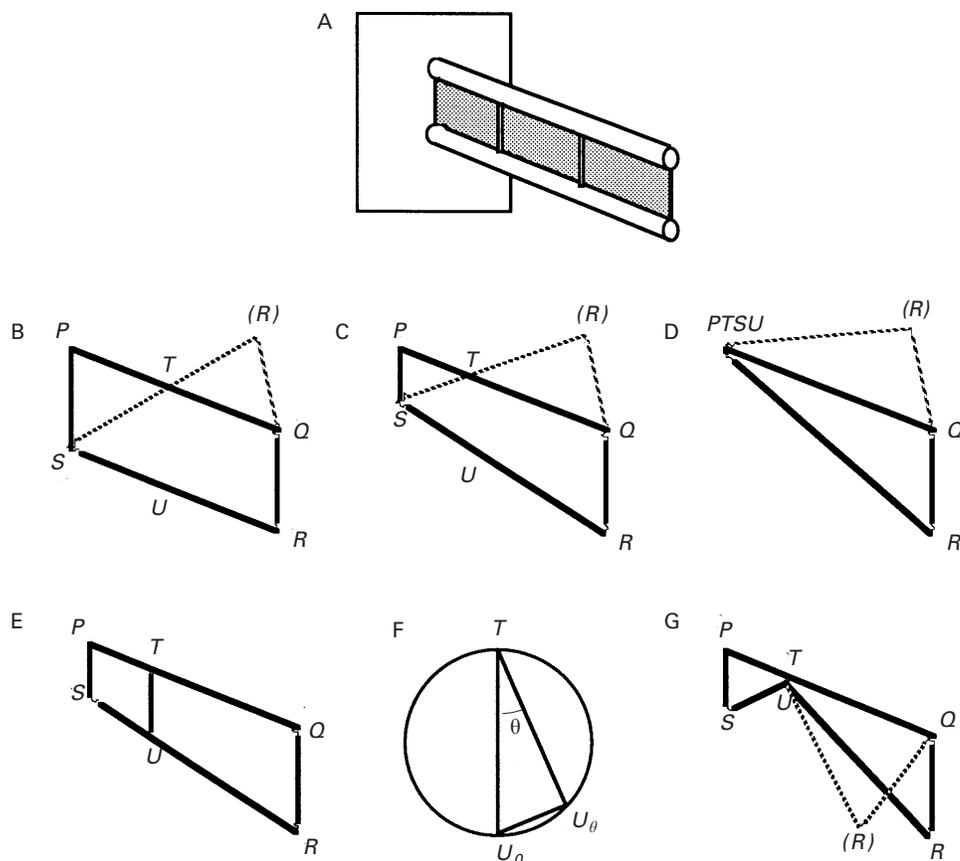


Fig. 6. Diagrammatic representation of the influence of different basal vein conformations on wing torsional properties. For explanation see text.

CuP in modern mayflies has been achieved by the arching of MA near the wing base to fuse briefly with RP, and the arching of CuA to fuse briefly with MP. The progress of these fusions can be followed through the Paleozoic representatives (Kukalová-Peck, 1985). The oldest, *Bojophlebia prokopi* (Fig. 3E), shows MA and CuA both arched, but joined respectively to RP and MP by short cross-veins, rather than fused. In *Lithoneura* spp. (Fig. 3C, D), the only Syntonopterida in which this area of the wing is preserved, MA is briefly fused with RP, but the arched CuA is still linked with MP by a short cross-vein. In *Triplosoba pulchella* the degree of basal fusion is unclear (Carpenter, 1963). In the L. Permian Protereismatidae and Misthodotidae MA and RP are fused, and CuA and MP sometimes fused, sometimes not.

Brief fusion of this kind appears often to be an adaptation to local torsion of part of the wing. The mechanical principles governing torsional rigidity in insect wings have never been formally stated, and it is convenient to do so here.

Consider two longitudinal veins, separated by membrane. If both were rigidly fixed at the base, and the membrane was stiff in compression, or the

longitudinal veins separated by strut-like cross-veins, the structure would resemble a plate-girder with two tubular flanges and a thin web (Fig. 6A). Its torsional rigidity would vary in direct proportion to the distance between the veins, so that a broad base with widely spaced veins would be more resistant to twisting than a narrow one.

In practice there is always some flexibility at the axillary insertion of the veins, and the membrane between them may be soft and easily compressed. A more realistic simplification is shown in Fig. 6B–F. Here the mechanism is modelled as a four-bar framework, with three mobile joints. One short bar, *PS*, represents the wing-base. Two long bars, *PQ* and *RS*, represent two adjacent longitudinal vein stems, one fixed rigidly to the basal bar, the other flexibly jointed to it and free to swing and rotate about the joint. The fourth bar, *QR*, flexibly jointed to the two long bars, represents the distal part of the wing.

The effect of the framework's geometry is shown in Fig. 6B–F. In Fig. 6B–D, *QR* and *RS* are free to rotate about the diagonal, *QS*, of the quadrilateral. *QR*, the distal part of the wing, can rotate through 360°, while *RS* describes the surface of a cone, and *R*

its circular base. As RS rotates in either direction, its movement is ultimately checked by contact with the stationary bar PQ , at a point T on the fixed bar PQ and a point U on RS . Fig. 6F shows the circular path of U relative to T . When U is situated at U_0 the distance TU is maximal; this is the situation illustrated in Fig. 6B and C. As RS swings around QS , TU moves through an angle θ , to a position U_θ on its circular path. The length TU_θ diminishes as the cosine of θ , to zero when T and U coincide.

In Fig. 6B the four bars form a rectangle. In this case T and U will lie at the mid-points of PQ and RS , respectively. In Fig. 6C the framework tapers towards the basal spar PS , and T and U will now lie closer to the PS than to QR . In Fig. 6D, P , S , T and U coincide.

If the framework were filled with membrane, as in a real wing, that in Fig. 6B and C would be compressed, crumpled and probably damaged if the wing underwent significant twisting. This would not be the case in Fig. 6D. It is therefore advantageous for a wing adapted to being extensively twisted in flight to have its longitudinal veins closely apposed at the base. In a wing whose veins are broadly separated basally it is necessary for significant twisting to be prevented. This is readily achieved by bracing the veins apart by strut-like cross-veins. In Fig. 6E a strut is situated at TU , and twisting is effectively eliminated.

It is, however possible to achieve reasonable torsional compliance in a broadly-based wing if the main longitudinal veins first converge and then diverge at a point some distance from the base, as modelled in Fig. 6G. Here, RS converges with PQ , touches it at U , and bends away. If the angle SUR is ϕ , and if RS is free to rotate about the line SU , then R will describe a circle of radius equal to $UR \sin \phi$. However the fixed length of QR prevents this free rotation, so that in theory the model shown in Fig. 6G should be rigid in torsion. In practice a small degree of extensibility in the wing chord represented by QR and some play at S and at UT , all probable in an actual wing, would allow a reasonable amount of torsion to take place.

The following generalizations can therefore be made. (1) A wing with widely spaced vein stems lying parallel or nearly so, braced apart by rigid cross-veins, will be resistant to twisting. Any torsion will result in unacceptable compression and buckling of the cross-veins and the intervening membrane. (2) A narrow wing-base, with closely apposed vein stems, will favour torsional compliance. This is confirmed by the present-day zygopterous Odonata,

myrmeleontid and some ascalaphid Neuroptera and nematoceros and some other Diptera, which make extensive use of wing-twisting in slow flight and hovering (Wootton, 1992). (3) Some local twisting can be achieved in broad-based wings if the vein-stems converge almost to a single point, and subsequently diverge. It is this possibility which is exploited to perfection by extant Ephemeroptera, and progressively demonstrated by Palaeozoic ephemeropteroids as the trunks of the main longitudinal veins become apposed and fuse.

The curvature of CuP mentioned above in connection with camber enhancement in many modern mayflies is particularly marked in *Lithoneura* spp., and again represents a functional advance on *Bojophlebia prokopi*. It is absent, however, from Protereismatidae and Mischopteridae.

Summarising: the available sample of Palaeozoic Ephemeroptera is small, and we do not know how representative it may be. Such as it is, it appears to show a trend from the big, broad-winged Westphalian insects with hind wings larger than the fore, through the smaller Stephanian and Lower Permian forms with subequal wings, towards the Mesozoic and later mayflies whose fore wings are much larger than the hind. It would be naïve to assume that these few insects represent a true lineage, but the general trend may be a real one, and its significance is worth examining.

The earliest ephemeropteroid, *Bojophlebia prokopi* Kukalová-Peck, is by far the largest known, with a wing-span of approximately 450 mm (Kukalová-Peck, 1985); one of a number of gigantic insects from the Carboniferous and Lower Permian whose existence seems to have been permitted by the high oxygen levels then prevailing (Graham *et al.*, 1995; Dudley, 1998). In this and in the smaller, later Syntonopterida, large wings would have been necessary to keep wing-loading within bounds. Wing length is limited by the need to minimise bending moments (proportional to span) and moments of inertia (proportional to span²) about the base. Fore wing breadth is restricted by the length of the mesothorax and the need to limit hind wing overlap, so that hind wing enlargement is the logical route for increasing wing area, and serves also to move the centre of lift posteriorly. The venation of *Bojophlebia* shows few obvious specialisations beyond the minimum requirements of anterior support, a generally deformable remigium whose veins are linked together basally by cross-veins, and some evidence of pronatory/supinatory flexibility along the deeply concave CuP. The wings of *Lithoneura* are similarly

proportioned, and differ from *Bojophlebia prokopi* particularly in the local fusion of MA and RP, with its implication of improved local torsion and camber, and in the camber-enhancing curvature of CuP. These Carboniferous forms would have been unobtrusive, rather clumsy fliers, with a narrow speed range and low manoeuvrability, using the assumed long cerci for physical stabilisation.

Known Permian forms are far smaller, with wing spans between 14 and 70 mm (Carpenter, 1979). Reasonable wing-loadings could be achieved without broad hind wings, and two pairs of high aspect ratio wings would have permitted slow flight, again stabilised aerodynamically by the long cerci, caudal filament and long legs, with the RP/MA fusion allowing considerable torsion between the probably nearly symmetrical half-strokes.

The later development of the modern mayfly form with large rather triangular fore wings and smaller hind wings linked into a single aerofoil is paralleled in Hemiptera, Hymenoptera, and Lepidoptera, where it tends to be associated with versatile flight over a wide speed range. We may interpret its adoption by Ephemeroptera as an adaptation to extend their speed range to embrace both hovering and faster directional flight, appropriate in adults adapted only for nuptial flight and dispersal.

V. SUPERORDER ODONATOPTERA – THE DRAGONFLY CLADE

(1) Introduction

Odonoptera are among the earliest insects to appear in the fossil record and they radiated extensively during the Carboniferous and Permian, giving rise to an array of forms which appears nearly as diverse as today. Their size range indeed was far greater than now. The giant meganeurid proto-donates are the largest known insects from any period. The wing-span of the biggest, *Meganeuropsis permiana* Carpenter, known from a wing base from the Lower Permian of Kansas, has been estimated at 710 mm, and the Upper Carboniferous *Meganeura monyi* was only slightly smaller (Carpenter, 1939). In contrast, *Progoneura minuta* Carpenter, from the same beds as *M. permiana*, had a span of less than 30 mm, comparable with that of the smallest modern zygopterous Odonata (Carpenter, 1931). This represents a span range of approximately 24-fold, compared with approximately sevenfold today. Intriguingly they parallel a wide variety of Mesozoic, Tertiary and extant Odonata in their wing shapes

(Wootton, 1976, and Fig. 7), although differing in detailed structure. The relationship of the Palaeozoic groups within the odonatoid complex is disputed (Pritykina, 1980; Carpenter, 1992; Bechly, 1996), but it is certain that much of this resemblance to later groups is the result of convergence; and the similarities imply that the insects had adopted a similar range of flight techniques, and indeed ways of life. We are therefore ideally placed to compare in detail the wings of Palaeozoic and extant dragonflies, and interpret, group by group, the significance of the differences between them using our extensive knowledge of the flight adaptations of modern forms.

(2) Flight in modern Odonata

All modern Odonata are predatory: skilful, versatile fliers, normally taking their prey on the wing. In this they contrast sharply with the non-feeding Ephemeroptera, as they do in many morphological features. Fore and hind wings are both well developed, with no physical coupling; commonly, though not invariably, beating out of phase. There are no elongate caudal appendages. The functional morphology of the odonatan flight apparatus (see Pfau, 1986, for a detailed review and references to earlier work), and the flight of Odonata (Newman, 1982; Soms & Luttges, 1985; Azuma & Watanabe, 1988; Ruppell, 1989; Wakeling & Ellington, 1997*a-c*) have been extensively studied. Wootton (1991) has discussed the relationship between odonate wing designs and flight techniques, and has drawn attention to a number of characters which contribute to their skilful performance. A key feature of dragonfly flight is their ability to twist each wing along its longitudinal axis though a large angle at the beginning and end of the up- and downstrokes, precisely controlling the direction and velocity of the induced airflow and gaining weight support on both half-strokes. Much of this wing twisting is passively driven by aerodynamic and inertial forces. It allows the insects to operate with great manoeuvrability at a wide range of speeds, including hovering and brief periods of backward and sideways flight.

Several wing characters are identifiable as contributing to this mode of operation, in facilitating and controlling torsion and in limiting the tendency of the wing to swing up to follow the airflow, with loss of aerodynamic efficiency – a possible consequence of the relatively unsupported posterior margin, itself an adaptation to a high degree of torsion (Norberg, 1972).

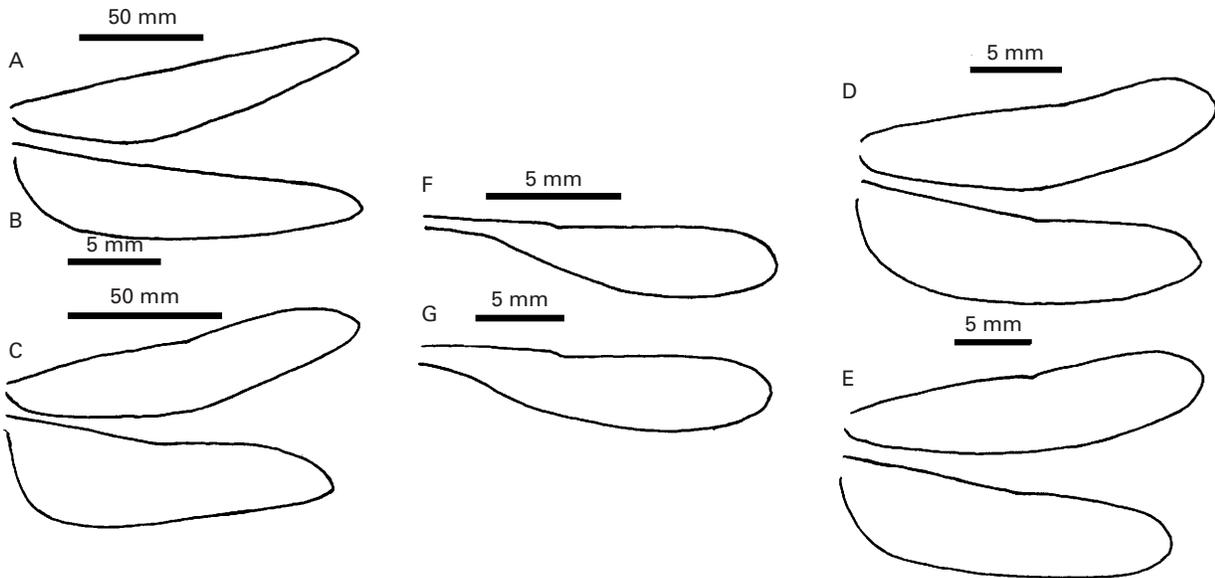


Fig. 7. Comparison of wing planforms of Lower Permian and extant Odonatoptera. (A) *Tupus gracilis* fore wing. (B) *Megatypus schucherti* hind wing. (C) *Uropetala* sp. wing couple. (D) *Ditaxineura anomalostigma* wing couple. (E) *Nannophlebia risi* wing couple. (F) *Progoneura nobilis* wing. (G) *Coenagrion dyeri* wing. After Wootton (1976), with permission.

(a) *The leading-edge spar, and the nodus*

All modern odonatan wings are supported anteriorly by a three-dimensional leading-edge spar, consisting of the costal, subcostal and radial veins with associated cross-veins and membrane. This spar is in two parts, separated by a conspicuous structure, the 'nodus' (Fig. 8 A, B). Here the posterior subcosta (ScP) turns anteriorly to meet the most anterior vein, formed from the fused precosta (PC), costa (C) and anterior subcosta (ScA). Near its end, ScP is braced across to the convex RA and the concave first branch of RP by a sturdy, high-relief cross-vein. Proximally to the end of ScP the composite PC+C+ScA is interrupted by a band of soft, flexible cuticle.

Proximally to the nodus the leading-edge spar is a rigid structure consisting of the convex PC+C+ScA, the concave ScP and the convex first branch of RA, linked by the antenodal cross-veins into a dorsally concave lattice girder with a V-shaped cross-section. Some at least of these cross-veins, the primary antenodals, are high relief angle-brackets which stiffen the spar to both bending and torsional forces. ScP, however, ends at the nodus, and the distal part of the spar consists of the composite PC+C+ScA, the dorsally convex RA, and the dorsally concave RP. Here, the cross-veins are slender and in the plane of the membrane, and the spar is now dorsally convex, and considerably more compliant to twisting and bending than the proximal region. Moreover wings and wing areas with dorsally arched sections

yield more readily to forces from above than from below (Wootton, 1991, 1993; Ennos, 1995). This allows the wings of dragonflies to twist extensively for the upstroke and to provide some upward, weight-supporting force throughout the stroke cycle, allowing versatile helicopter-like flight over a wide speed range. The nodus thus appears to function as a combined brace and shock-absorber, minimising dangerous stresses at the point where the two parts of the leading-edge spar, with their very different mechanical properties, abruptly meet. Wootton (1991) has suggested that the position of the nodus along the span reflects the degree to which the wings can be twisted: the more basal the nodus the twistier the wing. This is supported by the observations and measurements of Ruppell (1989) on a range of Odonata in free flight.

(b) *The arculus*

All modern Odonata have an arculus: a transverse or oblique vein near the base of the fore and hind wings formed from components of RP and MA and linking across from the closely apposed bases of RA and RP to M+Cu (the common base of MA, MP, CuA and CuP). From it RP and MA run towards the wing tip. The mode of action of a similar arculus was explained by Ennos (1989a) in Diptera, and the principle almost certainly applies also to Odonata. In flight, aerodynamic pressure is centred within the area supported by the branches of RP and MA, and would tend to raise these veins, hinging them upward

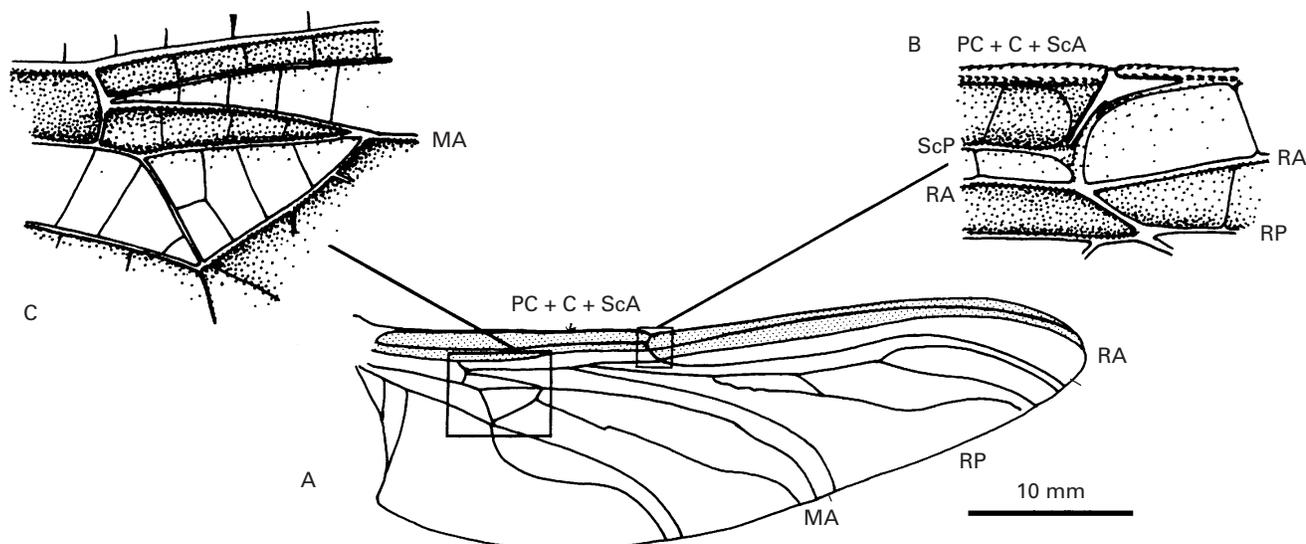


Fig. 8. *Aeshnacyanea*. (A) Hind wing. Shaded area represents the leading edge spar. (B) The nodus. (C) The basal triangle/supratriangle complex. PC, precosta; C, costa (= anterior + posterior costa); ScA, anterior subcosta; ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media. Reproduced with permission from Wootton, R. J., Kukalová-Peck, J., Newman, D. J. S. and Muzon, J. (1998), Smart engineering in the mid-Carboniferous: how well could Palaeozoic dragonflies fly? *Science* **282**, 749–751, Copyright 1998, American Association for the Advancement of Science.

at the arculus. This in turn tends to pronate the wing's leading-edge, although to a limited extent because it is rather rigid in torsion, and more effectively to lever down the trailing edge of the wing, cambering the wing and maintaining its aerodynamic effectiveness. In coenagrionid and lestid damselflies, the downward leverage is assisted by a short, rigid cell, the 'quadrilateral', projecting posterodistally from the arculus and transmitting the supinatory torque to the posterior part of the wing. In Anisoptera and Anisozygoptera the arculus forms part of a high-relief basal complex of vein, the triangle and supratriangle (Fig. 8C, and see Fig. 11A), which themselves appear to act as a further mechanism which automatically lowers the trailing edge and enhances the camber under aerodynamic loading (Wootton, 1991; Wootton *et al.*, 1998).

(3) Palaeozoic Odonatoptera

As with modern forms, two general categories of wing planform are found in the Palaeozoic: those, like Anisoptera today, with relatively broad bases, the hind wings markedly broader than the fore; and those, like modern Zygoptera and Anisozygoptera, with narrow-based, similar fore and hind wings. Most of the latter category have strongly petiolate wing bases, like present-day Coenagrionoidea and Lestoidea.

The Meganeuridae were large to gigantic in size,

with associated very rich venation – many branches, many cells. They had no nodus: ScP was long and straight, converging gradually with the fused ScA and costal veins to join them three quarters or more of the wing length from the base. No high, angle-bracket-like cross-veins, comparable to the primary antenodal cross-veins of modern dragonflies, are recognisable: the anterior supporting spar tapers evenly towards the tip, and its compliance to bending and torsion would have increased along the span, with no sharp discontinuity. The many branches of the median, cubital and anal veins curve sharply to the trailing edge, most meeting it at an angle approaching 90°. Newman (1982) has shown that a series of curved corrugations of this kind serves to create a cambered section when the wing experiences lift, and Ennos (1988) has shown theoretically that it would tend automatically to depress the trailing edge; essential for a wing with no rigid posterior support (Wootton, 1991). It is the only apparent such mechanism in Meganeuridae, which had no arculus, but it would have been enough to maintain an effectively cambered profile in a wing capable of twisting extensively between the up- and down-strokes, and probably gaining some weight-support on both half-strokes. It has often been suggested that Meganeuridae were capable only of gliding flight, but there is no reason to suppose that this was the case. Indeed, the wings appear well-adapted for versatile flapping flight over a significant speed

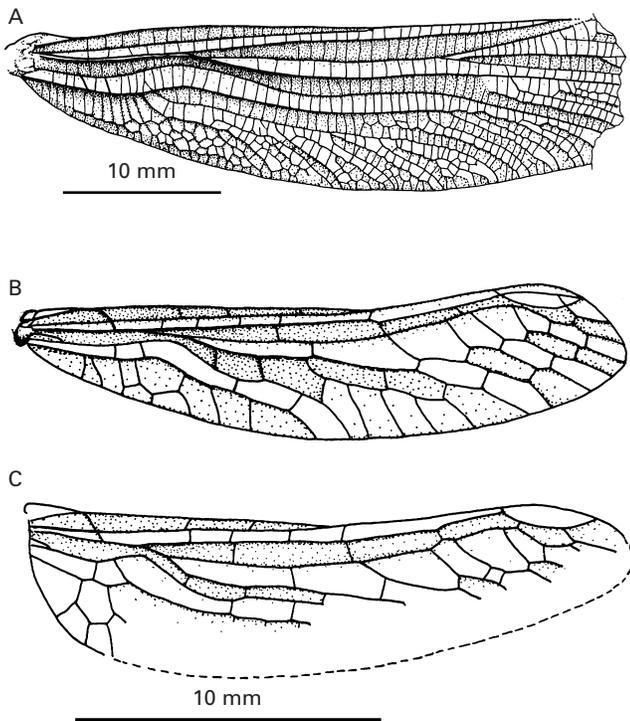


Fig. 9. Lower Permian Odonatoptera. (A) *Oligotypus tillyardi* fore wing. (B) *Ditaxineura anomalostigma* fore (upper) and hind wing (lower). *Oligotypus tillyardi* and *Ditaxineura anomalostigma* fore wing, original drawings; *Ditaxineura anomalostigma* hind wing modified after Carpenter (1939).

range; remarkably so for a family already well-established in the Namurian (Brauckmann & Zessin, 1989). *Namurotypus sippelorum* Brauckmann & Zessin, a relatively small (wing span 320 mm) species from Hagen Vorhalle provides our best information on the body. This was slender, and rather small relative to the wings, as would be necessary in large insects if the wing-loading were to be kept within reasonable limits. Our wing-loading estimates (Fig. 1, Table 1) suggest that this was indeed so. The bodies of the far larger *Meganeura* species and their relatives from the late Carboniferous and early Permian are poorly known. The only relatively complete body, of *Meganeurula selysii* (Carpentier & Lejeune-Carpentier, 1949; Laurentiaux, 1953) is crushed and spread, and its wings are not preserved. *Meganeurula* was regarded by Carpenter (1992) as a synonym of the genus *Tupus*, and hence not a meganeurid.

Other Paleozoic odonatoids were far smaller. *Paralogus aeschnoides* Scudder, from the Upper Carboniferous, and *Oligotypus tillyardi* Carpenter (Fig. 9A), from the Lower Permian of the USA, classed together by Carpenter (1992) in the family Para-

logidae, are within the size-range of modern Anisoptera. Their wings resemble those of Meganeuridae, but ScP is relatively much shorter, meeting the anterior vein complex approximately half-way along the wing, although with no recognisable nodus. The effect of this would nonetheless have been as described above for modern dragonflies, allowing significant supinatory twisting of the distal half of the wing, and thus aiding the generation of some weight-supporting force in the upstroke. The shorter subcosta may simply be a function of size; the longer wings of the larger Meganeuridae would probably have undergone enough passive torsion without this device.

The remaining broad-based odonatoids form two very different groupings, each showing striking adaptations. The little Ditaxineuridae (Fig. 9B) and Permaeschnidae are Permian, and closely related. Their bodies are unknown. Their wings have no arculus, although the stems of the radial, median and cubital veins lie close together proximally and may have provided some of the rigidity which is the role of the arculus in trailing-edge depression. A true nodus, however, is present, between half and two-thirds the wing length from the base. Furthermore, the veins of the antenodal part of the leading-edge spar are strongly braced together by distinctive cross-veins. These insects superficially parallel small modern libellulid Anisoptera, and it is reasonable to suppose that they were already competent, versatile fliers, adapted to pursue and feed on the small insect prey now available in the Permian, although still falling well short of the supreme skills of the behaviourally complex libellulids today.

The Eugeroteridae and Erasipteridae are known from the Namurian and Westphalian of Europe and Argentina: geographically remote sites which show clearly how widely and well established the Odonatoptera already were when pterygote insects first appear. These have been placed by Brodsky (1994) in a new order, the Geroptera. These insects had wing spans between 80 and 100 mm, well within the size-range of modern dragonflies. New, undescribed material shows them to have been proportioned rather like modern Libellulidae, but with relatively smaller bodies, and with winglets on the prothorax – a not uncommon feature in Carboniferous insects, but previously unknown in odonatoids (Fig. 10). As in modern Anisoptera the hind wings were broader than the fore. The venation is in most respects the most archaic in any known odonatoids, and assisted Riek & Kukalová-Peck (1984) in reinterpreting the venation of the super-

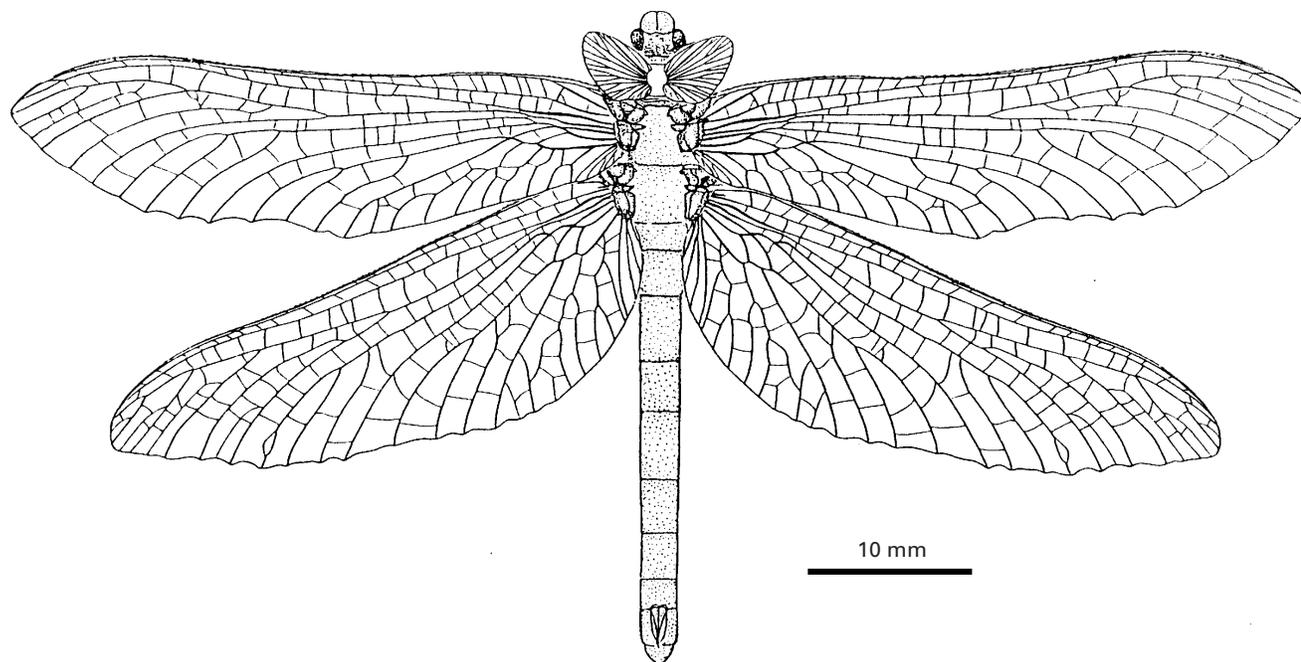


Fig. 10. Undescribed geropterid from Westphalian of Rioja, Argentina. Original drawing.

order, but they nonetheless already have some remarkable derived characteristics. In particular, both wings show a high-relief alignment of veins in the cubital fork, which we interpret as a mechanism which would have automatically lowered the trailing edge in response to aerodynamic loading. This strikingly resembles the functioning of the triangle/supratriangle mechanism of extant Anisoptera, although involving quite different veins (Wootton *et al.*, 1998). The two mechanisms are shown diagrammatically in Fig. 11. The mechanism in Anisoptera is easily demonstrated by manipulation of a fresh wing, and can also be modelled in thin card. A force applied to the lower side of the wing in the region where aerodynamic pressure is expected to be centred, levers the trailing edge down about this basal complex, cambering the wing and increasing its angle of pitch. In Fig. 11A, the broad arrow at *X* represents an upward aerodynamic force applied to the median vein. Raising this vein applies a downward torque to the regions *Y* and *Z*, respectively anterior and posterior to the modelled triangle/supratriangle basal complex, and causes them to be lowered. In the actual wing, the area anterior to the complex is relatively rigid, so that downward deflection of the more flexible posterior zone is enhanced. In flight, this would hold down the trailing edge, increase the wing's camber and maintain a positive angle of attack, in direct response to aerodynamic loading. The mechanism works only in the downstroke; in the upstroke the wing is

twisted along its span, and there is no danger of the proximal trailing edge swinging up into the airflow.

Fig. 11B shows the proximal part of the hind wing of *Eugeropteron lunatum* Riek, from the mid-Carboniferous of Argentina, and Fig. 11C shows the functioning of the basal mechanism as we interpret it, with the basal complex shown as a double, three-dimensional parallelogram with a v-shaped cross-section. An upward force applied at *X* – here representing the anterior cubital vein – flexes the parallelogram about its diagonal, and applies depressing torques to the wing both anteriorly and posteriorly, at *Y* and *Z*. In the actual wing, the diagonal flexion of the complex would slightly bend three veins, and their elastic recovery may have aided the reversal of the mechanism when the aerodynamic load was removed.

If our interpretation of this mechanism is correct, these early dragonflies had already developed efficient 'smart' wings capable of maintaining a favourable camber and angle of attack while undergoing significant torsion between half-strokes, allowing manoeuvrable flight over a fairly wide speed range (Wootton *et al.*, 1998).

The remaining Palaeozoic odonopterans resemble modern Zygoptera in their slender, more or less identical fore and hind wings, and their relatively simple venation. Modern coenagrionoid and lestinoïd damselflies are perhaps the most helicopter-like of all insects: hovering, and flying and hunting at relatively low speeds, with their bodies horizontal

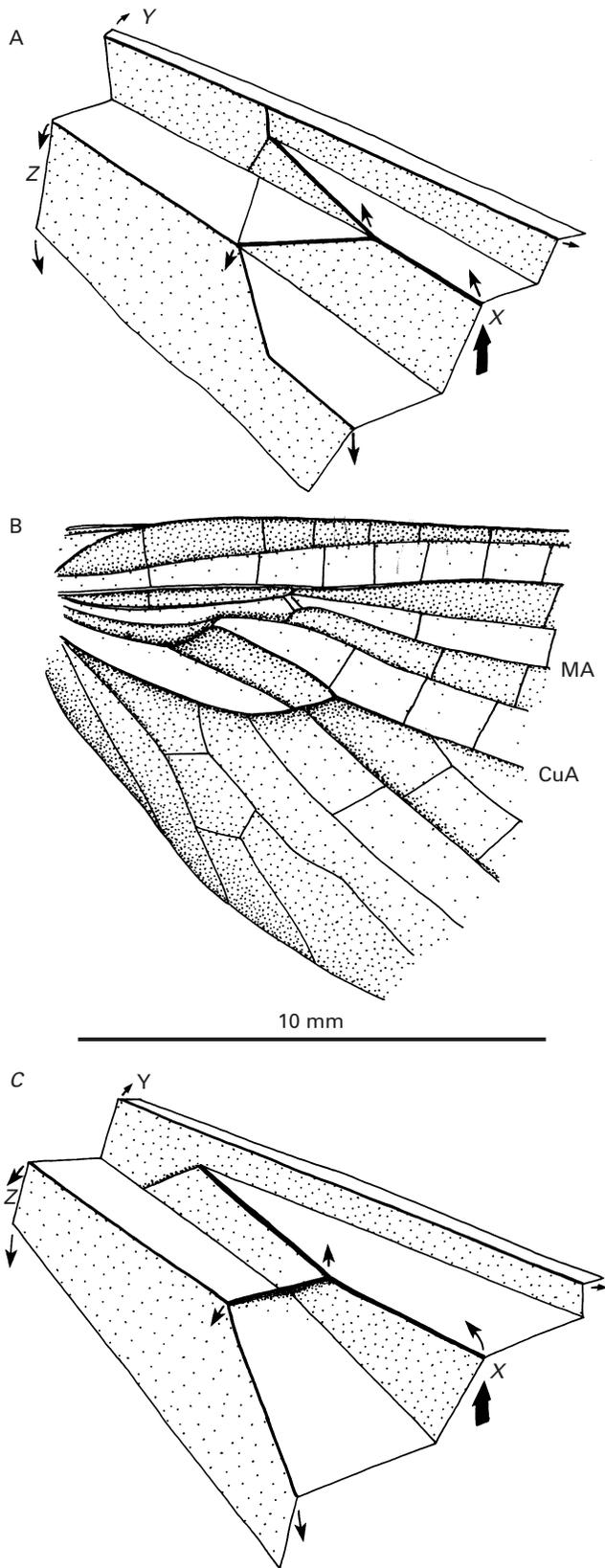


Fig. 11. Trailing edge depression mechanisms in modern and Carboniferous dragonflies. (A) Diagram of the mode of operation of the basal complex of *Aeshna* sp. (B) Hind

and their wing-strokes nearly so. Their narrow-based wings, with their rather proximally-situated nodus, are adapted to twist extensively between the morphological downstroke and upstroke, and the arculus and posterodistally-directed quadrilateral cell serve to hold down the trailing edge and to maintain a cambered section in the downstroke. The petiolate shape is again associated with slow and hovering flight: a broad wing base has limited value in slow flight since the airspeed of the base will be low and the lift negligible. Furthermore the petioles serve to separate the vortex wakes on the two sides of the wing, with some probable aerodynamic advantage. The Permian Kennedyidae, Permolestidae, Permagrionidae and Permepallagidae are very similar to these in wing shape, and we may reasonably assume them to have flown similarly, and be similarly adapted to feed on small, relatively slow-moving prey. Tillyard (1925) and Fraser (1957) believed them close to the stem of modern Zygoptera, and indeed of all modern Odonata, and demonstrated how the progressive evolution of the nodus and arculus could be traced among them. Pritykina (1980) by contrast, believed them to be offshoots of the protodonate stem, which would imply that the nodus and arculus arose independently in these and in the true Zygoptera.

Summarising: the Odonatoptera seem to have adopted their present adult habit of aerial predation at a surprisingly early stage in winged insect evolution. The loss of caudal appendages, and consequent improved manoeuvrability, was accompanied by the development of torsionally compliant wings. This allowed the generation of useful forces, including some weight support, in both up and down strokes; and a consequent widening of the range of available speeds, with the possibility of slow, near-hovering flight. They diversified early, and their great size range reflects their exploitation of a correspondingly wide range of prey – medium to very large insects in the Carboniferous, progressively smaller in the Permian. Particularly remarkable are

wing base of *Eugeopteron lunatum* Riek. MA, anterior media; CuA, anterior cubitus; (C) Diagram of the mode of operation of the basal complex of *Eugeopteron lunatum*. For further details see text. In (A) and (B) the broad arrow represents an upward force applied at X. Other arrows, at Y, Z and elsewhere, represent local deflections. Reproduced with permission from Wootton, R. J., *et al.* (1998), *Science* **282**, 749–751, Copyright 1998, American Association for the Advancement of Science.

the early development of 'smart' mechanisms for the automatic control of profile under aerodynamic loading; and the striking similarity between the various wing planforms of Palaeozoic and modern species, reflecting fundamental similarities in their respective flight techniques.

VI. PALAEOICTYOPTEROID ORDERS: THE PALAEOZOIC HAUSTELLATE CLADE

(1) Introduction

The palaeodictyopteroids are the most spectacular extinct insect clade, and the only one of superordinal ranking known to have vanished without descendants. They are a remarkable group which became extremely numerous and diverse in the Carboniferous and Lower Permian, and sharply declined and departed in the Upper Permian. The presence of prothoracic winglets in many members of the largest order, the Palaeodictyoptera, led Handlirsch (1906–8) to the belief that these were the stem group of the entire Class Insecta, and they were long believed to have included the ancestors of all other Pterygota. It is now clear, however, that the entire superorder had highly derived elongate probing/sucking mouthparts, and they are now considered by most authors to be a specialised clade of liquid and spore-feeding Palaeoptera, with a mosaic of primitive and derived characters. Rasnitsyn & Novokshonov (1997) have made a case for their being ancestral to the hemipteroid Neoptera; for reasons given elsewhere (Kukalová-Peck, 1992, 1997) we do not share this view.

They were a varied group. The largest Palaeodictyoptera were second in size only to the meganeurid odonatoids. A thoracic tergum, all that is known of *Mazothairos enormis* Kukalová-Peck and Richardson, a probable homoiopterid from the Westphalian of Illinois, is 40 mm across; and comparison with smaller, more complete species suggests that its wing span may have been as much as 560 mm (Kukalová-Peck & Richardson, 1983). At the other end of the scale the palaeodictyopteran *Eubleptus danielsi* Handlirsch, from the same beds, had a span of approximately 30 mm, and the smallest known diaphanopterodean, *Asthenohymen parvulus* Carpenter, from the Lower Permian of Kansas, a span of no more than 10 mm, the size of a large mosquito.

All palaeodictyopteroids whose bodies we know had elongate, mayfly-like cerci, sometimes more than twice as long as the body. We have seen that

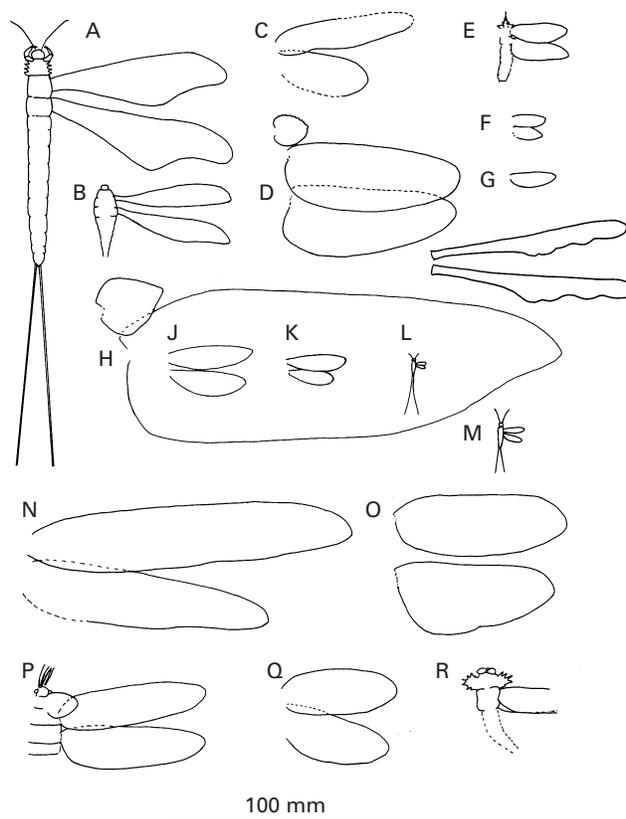


Fig. 12. Outlines of paleodictyopteroids, to the same scale, modified after Wootton (1976). (A) *Mischoptera nigra* (Megasecoptera). (B) *Sylvohymen sibiricus* (Megasecoptera). (C) *Peromaptera filholi* (Palaeodictyoptera). (D) *Homoioptera woodwardi* (Palaeodictyoptera). (E) *Homaloneura lehmani*. (Palaeodictyoptera). (F) *Madera mamayi*. (Palaeodictyoptera). (G) *Permothemis libelluloides* (Permothemistida). (H) *Homoioptera gigantea* (Palaeodictyoptera). (I) *Hana lineata* (Megasecoptera). (J) *Namurodiapha sippelorum* (Diaphanopterodea). (K) *Elmoa trisecta* (Diaphanopterodea). (L) *Asthenohymen dunbari* (Diaphanopterodea). (M) *Eubleptus danielsi* (Palaeodictyoptera). (N) *Dictyoptilus peromapteroides* (Palaeodictyoptera). (O) *Lamproptilia grandeurii* (Palaeodictyoptera). (P) *Dictyoneura laurentiaxi*. (Palaeodictyoptera). (Q) *Mecynostomata dohrni* (Palaeodictyoptera). (R) *Notorhachis wolfforum*. (Palaeodictyoptera). A modified from Carpenter (1951); B from Kukalová-Peck (1972); C, D, H, N from Kukalová (1969b); E, O, Q from Kukalová-Peck (1969a); F from Carpenter (1970); I from Kukalová-Peck (1975); J from Kukalová-Peck and Brauckmann (1990); K from Carpenter (1943); L from Carpenter (1939); M from Carpenter (1983); P from Kukalová (1970); P from Carpenter and Richardson (1971).

these are likely to be associated with low manoeuvrability; but any implication that palaeodictyopteroids were therefore poor fliers is at odds with the quite remarkable variety of their wings

Fig. 12 shows in outline a range of these insects, to

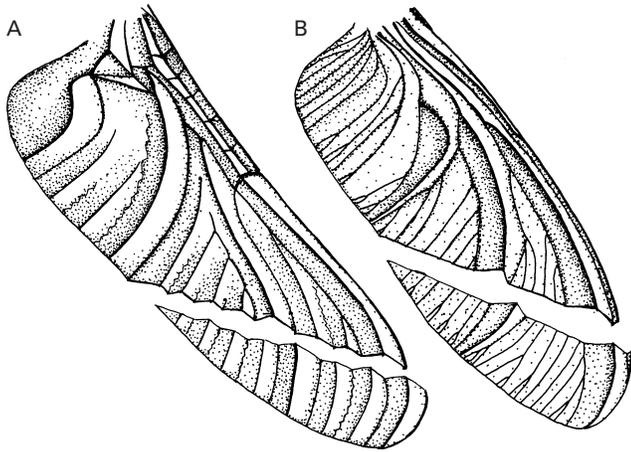


Fig. 13. Comparison of the wing relief of an anisopteran dragonfly (A), and a homiopterid palaeodictyopteran (based on *Mazonopterus wolfforum*) (B).

the same scale, and illustrates the diversity of wing shapes. Some have no parallel among modern insects, and the same is true of many venational and other flight-related characters. The lack of modern representatives or obvious parallels presents a real challenge to our deductive skills.

The shapes of some of the outstretched wings variously recall dragonflies and damselflies. However, their wings differ from odonatoids, and also from ephemeropteroids in one respect, of fundamental functional significance. While retaining the primitive, mechanically stiffening alternation of convex and concave true veins in an essentially corrugated wing: with the exception of one unusual family they have no regular intercalary veins. In existing and fossil dragonflies and mayflies these pseudoveins, formed secondarily by alignment of elements of the network of cross-veins, lie between the longitudinal principal vein branches. They are of opposite sense to the adjacent principal branches – concave between convex branches, convex between concave branches, so that the entire wing is corrugated, and stiffened to bending across the veins (Fig. 13A). In palaeodictyopteroids, all the branches of each main vein have the same sense, so that in the absence of intercalaries the areas supported by these branches are essentially flat, or in very large Homiopteridae evenly convexly raised (Fig. 13B).

The consequences are interesting. In species with many branches to each vein, the posterodistal part of the wing consists of a sequence of flat, more or less triangular areas, supported alternately by all convex and all concave veins. This is found, for example, in the large family Spilapteridae of the Palaeodictyoptera. In most families of Palaeodictyoptera,

however, the convex veins on the ridges of the corrugations – RA, MA and CuA – are unbranched, or have just a few small distal branches. The result is a series of narrow, stiff, convex ridges, providing major support for the wing, alternating with broader, lower-lying, more flexible areas around the branches of RP, MP and CuP. This situation has no exact parallel elsewhere in the insects, although the loss of relief from the vein branches in many Neoptera has something of the same effect.

Such a wing is dorsoventrally asymmetrical in both its structure and its mechanical properties. In particular, the narrow convex ridges would, like all arched shells, be more rigid to forces from the ventral side than from the dorsal (Wootton, 1981). The wing would hence be far stiffer and more aerodynamically effective in the downstroke than the upstroke, and it is in the downstroke that most if not all of the useful force would be generated. The same is true of most modern Orthoptera, and places serious limits on their flight performance. They can only gain sufficient lift by flying fast; slow flight and hovering are beyond their capabilities. By contrast the complete corrugation of odonatoid and ephemeropteroid wings renders them more or less equally aerodynamically effective either way up. The wings twist extensively, and both downstroke and upstroke generate lift.

Were all palaeodictyopteroids therefore restricted to fast forward flight? Clearly not. Most Megaseoptera have narrow, often stalked wings, recalling those of zygopteran Odonata, and we have seen that wings of this kind usually generate lift on both half-strokes, and are associated with slow, near hovering flight. The dorsoventral asymmetry characteristic of Palaeodictyoptera is here minimised by a reduction in the number of branches to each vein and by adopting a pectinate arrangement of veins, recalling that of many hovering Neoptera, which will be discussed below. The wings of Diaphanopteroidea are rather diverse, but some at least are strikingly convergent with those of Megaseoptera.

What function, if any, was served by the prothoracic winglets? These are reduced or absent in Megaseoptera, Diaphanopteroidea and Permthemistida, but common in Palaeodictyoptera, though variable in relative size. They were borne high on the prothorax. Well-developed examples, as in *Dictyonera laurentiauxi* (Fig. 12P) and *Stenodictya lobata* (see Fig. 16a), were membranous and supported by veins, like orthodox wings. They had narrow bases, and appear from this and from the often complex relief of the pronota to have been

actively movable, although not necessarily flappable. Each was almost symmetrical about a line from the base to the tip, unlike the meso and metathoracic wings, all of which show some concentration of veins towards the leading-edge as would be expected from fully functional aerofoils. Although they may have generated some lift, they never form more than 5% of the total wing area, and their role in weight support will have been trivial, although it is possible that their downwash may have helped delay stalling at the wing roots at low speeds and high angles of attack. By far their most plausible function is control of stability in pitch, in the manner of canard aerofoils on some aircraft. We have seen that pitch control in insects is usually achieved by adjusting the wing stroke so as to move the line of action of the net aerodynamic force relative to the centre of mass. The broad, relatively inflexible axillae of many Palaeodictyoptera may have limited the extent to which this was possible. Anteriorly situated winglets with adjustable angle of attack and perhaps camber may have provided valuable fine adjustment. Canard-like aerofoils would only function if the insect was flying fast enough for them to be generating significant lift. It is no accident that fully developed prothoracic winglets are only retained in broad-winged, fast flying types.

In his incomparable survey of fossil insects Carpenter (1992) listed 20 families of Palaeodictyoptera (including Permothemistidae, here treated as a distinct order, and Syntonopteridae, which we believe to be ephemeropteroid); 21 families of Megasecoptera; and nine families of Diaphanopteroidea. Readers are referred to this work for a fully illustrated resumé of these orders; in the present account, we can only select examples to indicate variation and some trends.

In the following discussion, families are grouped together according to their apparent adaptations. The groups do not necessarily reflect systematic relationships.

(2) Palaeodictyoptera: Homiopteridae and Lycocercidae – insect biplanes

The Homiopteridae are an ancient group of large, sometimes gigantic insects, represented in the oldest Carboniferous insect beds, and extending throughout the period. Their venation is quite varied, and it may be that the family will eventually require splitting. Most had unusually large wings; a predictable result of large size and the need to keep wing-loading within reasonable bounds. They none-

theless appear to have been among the most highly loaded of all Palaeozoic Palaeoptera (Table 1, Fig. 1) The hind wings were usually broader-based than the fore, but the latter were sometimes themselves so broad that they overlapped extensively with the hind wings, to an extent unknown in modern insects (Fig. 12D, H). The same appears to have been true of some members of the family Lycocercidae. *Lycocercus goldenbergi* Brongniart, from the Stephanian of Commentry, France shows extensive wing overlap, and an even more biplane-like conformation is found in *Notorhachis wolfforum* Carpenter and Richardson (Fig. 12R), in which the wings appear to have overlapped almost completely.

Flapping flight would have been entirely possible in these forms provided that the wings beat in the same phase, or their fields of vertical movement did not significantly overlap. However the arrangement would have had some of the disadvantages of biplanes: the pressure distribution around the two wings on either side preventing each from reaching the lift of which it would have been capable alone. As a means of achieving a large wing area without the excessive mechanical problems associated with large span, this solution would appear to be less effective than hind wing expansion. It is not surprising that there are no modern parallels.

The wings themselves are of the classic dorso-ventrally asymmetric type described above, although the convex MA and CuA may have more than one branch in broad-winged forms. The more narrow-winged types tend to have these veins unbranched. Fig. 14 shows the hind wing of *Mazonopterus wolfforum*, from the Westphalian of Mazon Creek, Illinois (Kukalová-Peck & Richardson, 1983); a relatively high aspect ratio homiopterid species. The long convex veins RA, MA and CuA and their adjacent strut-like cross-veins form high, narrow supporting girders, with the many branches of the concave RP, MP and CuP filled with an array of irregular, reticulate cross-veins occupying wide, flat and deformable areas between them. The wing base is very broad, with a massive, multicomponent, inflexible axilla. The anal veins are linked together into a single functioning unit by a curved brace of thickened cuticle which is usual in Palaeodictyoptera. The wing shows almost no adaptation for twisting. The wing-loading would have been relatively high, and the insect could only have been capable of fast forward flight, gaining stability and some control from the elongate cerci characteristic of the family, and probably also from the prothoracic winglets.

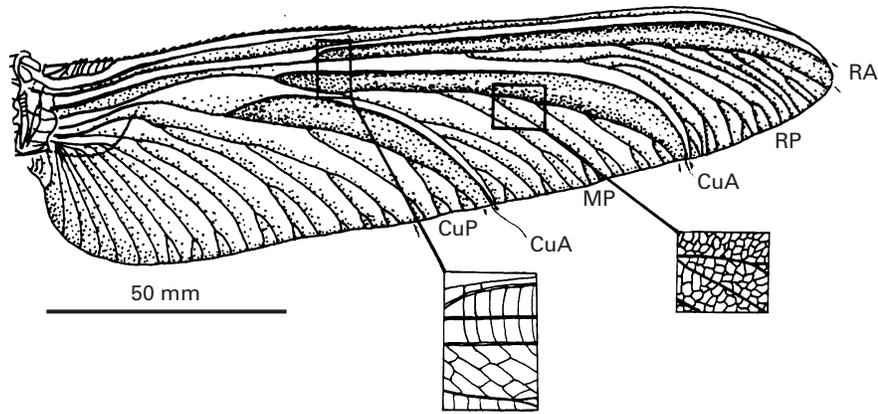


Fig. 14. Wings of Palaeodictyoptera: Homiopteridae. *Mazonopterus wolfforum* hind wing. Modified after Kukulová-Peck and Richardson (1983), to show relief and details of cross-veining. RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus.

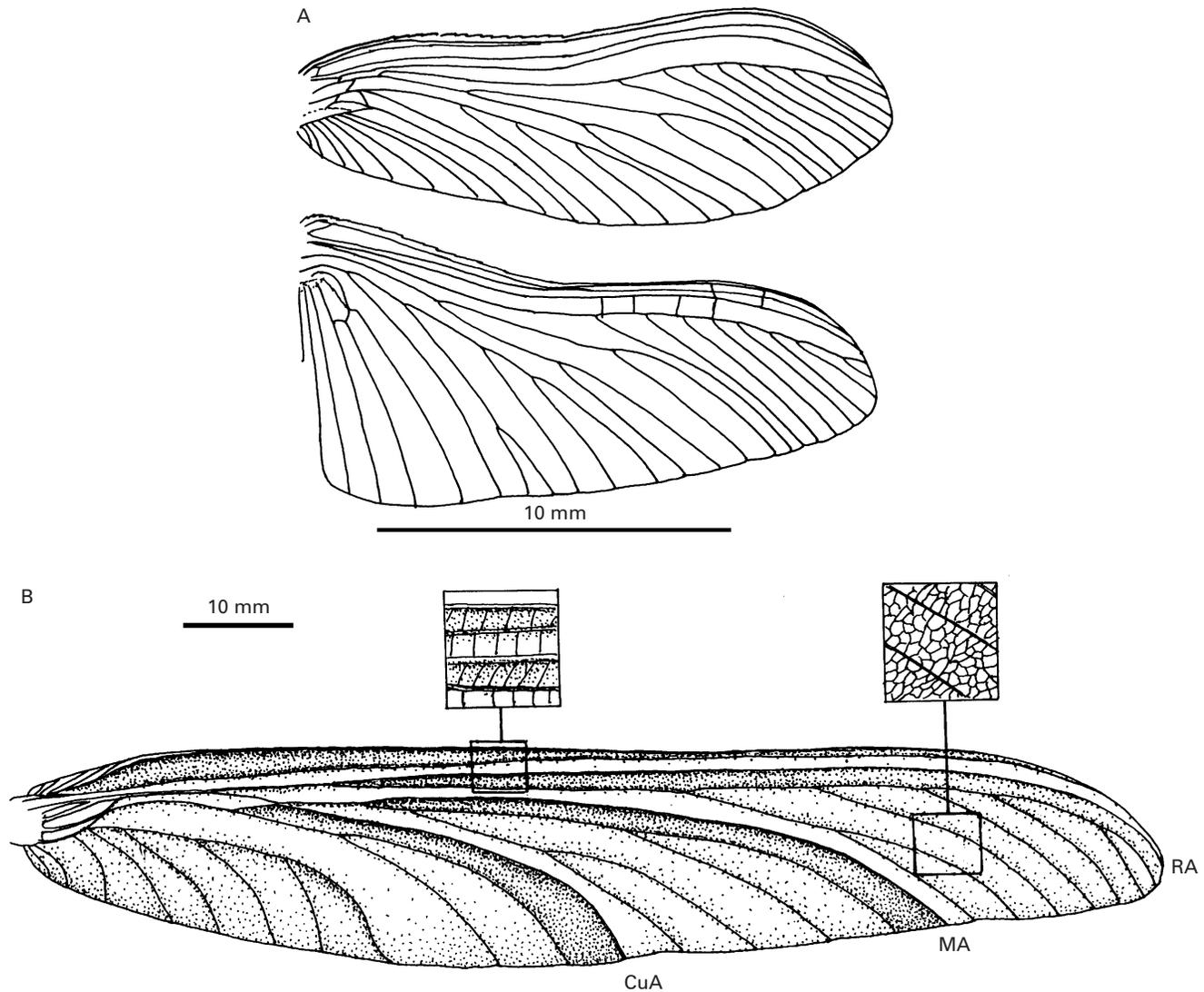


Fig. 15. Wings of Palaeodictyoptera: Spilapteridae and Eugereonidae. (A) *Dunbaria fasciipennis*, after Kukulová-Peck (1971). (B) *Dictyoptilus sepultus*. fore wing, modified after Kukulová (1969b). RA, anterior radius; MA, anterior media; CuA, anterior cubitus.

These conclusions probably apply generally to the members of these two families. One lycocercid, however – *Madera mamayi* Carpenter (Fig. 12F) from the Upper Carboniferous of New Mexico – was relatively tiny, with a wing span of perhaps 35 mm, and correspondingly lower wing-loading and presumed flight speeds.

(3) Palaeodictyoptera: Spilapteridae – hind wing expansion

The Spilapteridae were a large, varied family, with the longest fossil record of any Palaeodictyoptera; the earliest winged insect so far recorded appears to be a spilapterid (Brauckmann *et al.*, 1996), and they were probably the last of the Order to survive. Wing spans ranged from 37 to 190 mm. Prothoracic winglets were usually present, but small.

Most of the Carboniferous species were bulky insects, with stout bodies and large wings. Permian forms like *Dunbaria fasciipennis* and its relatives (Fig. 15A) were generally much smaller, but their wings were relatively large, and wing-loadings must have been unusually low for the Order. The hind wings were generally larger than the fore – some markedly so – and the family in general adopted the aerodynamically preferable route to wing enlargement, by hind wing expansion. Many species indeed have a distinctly Orthoptera-like planform, and even venation. Fore- and hind wing overlap is considerable in some Carboniferous species, and these must have been subject to the same kinematic restrictions as Homiopteridae, but many hind wings show a tendency to a concave outline to the leading-edge which when fully developed as in *Dunbaria fasciipennis* would have allowed the hind wing to clear the fore during the stroke, and the two wings to beat out of phase, like orthopteroid and dictyopteroid insects today. The family venation is characteristic. The leading-edge composite vein, ScP and RA are the only unbranched veins, and form the primary support for the wing. All other veins are branched, so that the convex as well as the concave veins support broad planar areas of membrane, and the wings benefit only basally from the stiffening effect of corrugation.

How did they fly? In later forms the parallels with Orthoptera are again informative. There is no evidence of adaptation for significant torsion or transverse flexion. The most obvious evidence of a special adaptation for flight efficiency is in the fan-like anal area of the hind wing, where a series of radiating anal veins meeting the trailing edge at a

slightly acute angle recalls the ‘umbrella effect’ of orthopteroids, by which the promotion of the wing during the downstroke compresses and curves these veins, giving camber to the wing section and holding down the trailing edge (Wootton, 1990, 1995). The high insertion of the wings on the terga makes it probable also that they were able to beat with a high amplitude, and to make use of the ‘near clap and partial peel’ mechanism for gaining extra lift by bringing the wings close together at the top of the stroke and peeling them apart (Ellington, 1984*b, c*; Brackenbury, 1990, 1991, 1992). Most useful aerodynamic force would come from the downstroke, and the flight would not have been particularly versatile, but aerodynamic efficiency would have been high – far higher than the homiopterid/lycocercid pattern, and indeed that of the earlier Spilapteridae.

(4) Palaeodictyoptera: Eugereonidae and Megaptilidae – hind wing reduction

The Eugereonidae, known from the later Carboniferous and Lower Permian, have much in common with the *Mazonopterus wolfforum* type of Homiopteridae, but show several interesting derived characters (Fig. 15B). As in *Mazonopterus wolfforum* the wings are supported by long, curved, convex girders crested by RA, MA and CuA, linked by predominantly strut-like cross-veins to the adjacent multi-branched concave veins, which occupy broad, flat areas with reticulate cross-venation. All veins curve posteriorly, those behind RA meeting the trailing edge. The fore-wings of both species show significant proximal linkage of the main longitudinal veins, with the common stem of MA and MP stem closely approximate or fused to that of RA and RP, and the base of CuA close or fused to MA+MP. The result is rather dragonfly-like, or more specifically like the meganeurid and paraligid stem Odonatoptera: high aspect ratio wings with strong basal and anterior support; their length allowing a reasonable degree of even passive torsion along the span, with the curved vein branches holding down the trailing edge and maintaining a functional profile.

However, where both are known, as in the Carboniferous *Dictyoptilus peromapteroides* (Meunier) (Fig. 12N) and the Permian *Eugereon boeckingi* Dohrn, fore and hind wings were distinctly different in both size and venation. The fore wings are long and slender, the hind wings both broader-based and distinctly shorter. The hind-wings moreover show

spectacular curvature in the cubital veins. In *Peromaptera filholi* Brongniart, also from Commeny, hind wing shortening is taken further (Fig. 12C). It is perhaps two-thirds the length of the slender fore wing, but nearly twice as broad. The trailing edge of the fore wing is slightly emarginated, as if to accommodate the hind wing leading-edge. The cubitus does not have the same marked curvature as in the other species.

One other Carboniferous family, the Megaptilidae, shows hind wing reduction – in huge insects: the incomplete fore wing of *Megaptilus blanchardi* Brongniart is 144 mm long, suggesting a span of perhaps 340 mm in the whole insect. The only known fore wing is far broader than in Eugereonidae but has rather similar venation. The known hind wings were shorter and also broad.

Hind wing shortening is of course a common feature of many insect groups, particularly Ephemeroptera, Hemiptera, Hymenoptera and many Lepidoptera. In these forms, the wings invariably beat in the same phase, and they are commonly coupled together, acting in effect as a single aerofoil. Since both wings have their own musculature the insect has considerable control of the section of the composite aerofoil, and the hind wing can act as a flap-like controlling surface as well as in lift-generation. In wasp-like or hawkmoth-like species where the hind wing is greatly reduced and its trailing edge almost aligned with that of the fore wing, the flight tends to be complex, manoeuvrable and versatile, operating over a wide speed range. It seems probable that Eugereonidae and Megaptilidae were beginning to exploit these possibilities, beating fore and hind wings in the same phase and gaining some of the new advantages of a single, adaptable aerofoil. The long, high aspect ratio fore wings of Eugereonidae would have minimised induced drag, and allowed enough passive distal torsion for slower flight, while the broad base provided by the hind wing would have given extra lift and so thrust in faster flight, and perhaps extra lift in gliding. The Megaptilidae are by far the largest insects known to have had hind wing reduction.

(5) Palaeodictyoptera: Dictyoneuridae and Eubleptidae – vein reduction in similar wings.

The Dictyoneuridae have always posed problems. Regarded by Handlirsch (1906–8) and other early workers as the most primitive Palaeodictyoptera – and indeed insects – because of their large pro-

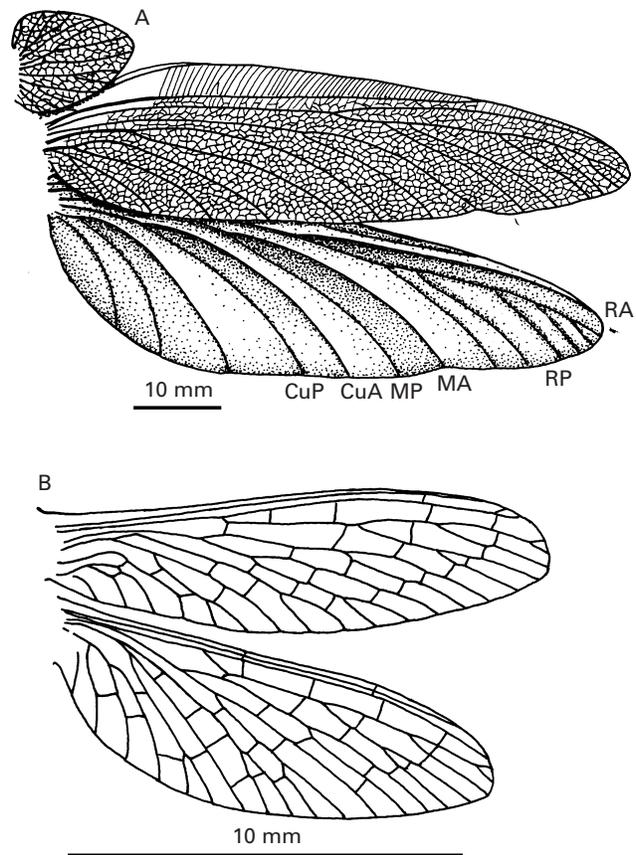


Fig. 16. Wings of Palaeodictyoptera: Dictyoneuridae and Eubleptidae. (A) *Stenodictya lobata*, modified after Kukulová (1970). The fore wing is drawn to illustrate the fine reticulation, the hind wing shaded to show relief. RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus. (B) *Eubleptus danielsi*. Modified after Carpenter (1983).

thoracic winglets, lobed abdominal segments and fine, reticulate cross-venation, the so-called arche-dictyon, they now appear in many respects derived. Their wings are fairly slender, rather elliptical and fairly similar in size, the fore wings tending to have a curved, convex leading-edge, the hind wings being slightly broader-based. They do not overlap significantly, and could have flapped in the same or out of phase – or both.

The venation is of the now familiar unbranched convex/branched concave pattern, with high ridges alternating with low, broader areas, but the number of branches to RP and MP tends to be small, and the branching rather distally-situated (Fig. 16A) The result is a rigid leading-edge spar, and a series of obliquely, posterolaterally-directed, rather curved veins. The cross-veins in the leading-edge spar are slender and linear, but throughout the rest of the

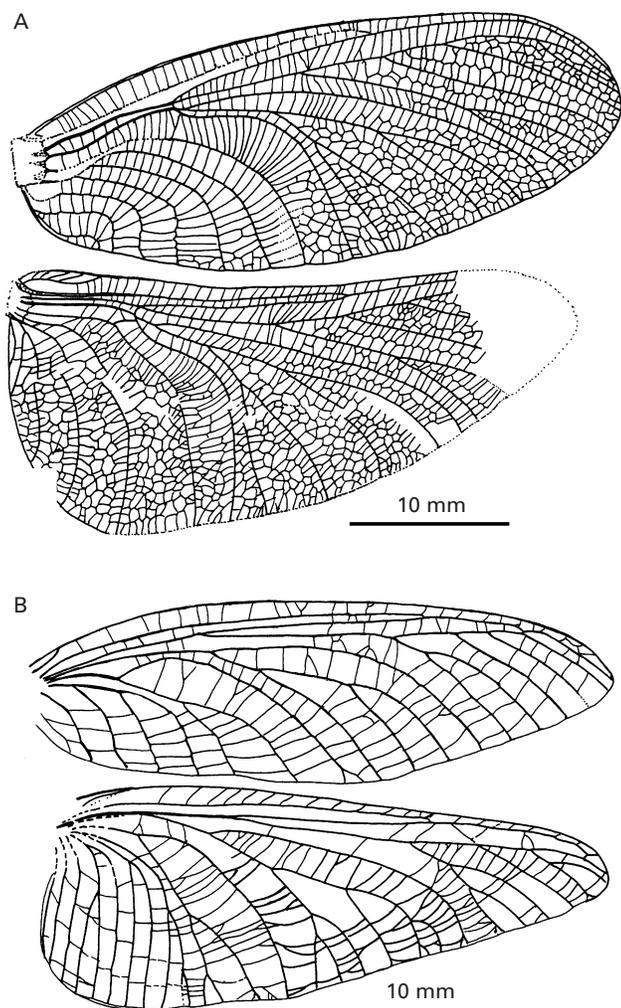


Fig. 17. Wings of Palaeodictyoptera: Calvertiellidae and Breyeriidae. (A) *Moravia convergens*, after Kukalová 1964. (B) *Breyeria rappi* fore wing, after Carpenter (1967); *Breyeria barborae* hind wing, after Kukalová (1959).

wing form a very dense meshwork of polygonal cells, with no more substantial cross-veins. Is this an archaic feature, with no functional significance, or is it an adaptation to minimise tearing in a membrane which necessarily undergoes appreciable stretching in flight? We cannot be sure. A polygonal network can undergo shearing and stretching distortion in any direction without damage, and any rips which developed under tension in the membrane would tend to stop at the next vein.

Their flight technique is also rather unclear. Their wings are perhaps best interpreted as refined, structurally 'tidy' versions of the pattern which we have seen in Homiopteridae, with the biplane-like overlap eliminated, and planform optimised. They show no particular adaptations to twisting or bending, although some spanwise passive torsion is

probable. Their estimated wing-loading was relatively high (Table 1, Fig. 1). On balance they appear adapted to straightforward directional flight: basic, but effective.

Comparison may be drawn with a less well-known family of much smaller insects, the Eubleptidae. Two species only are known. With a span of only 30 mm, *Eubleptus danielsi* Handlirsch, from the Carboniferous (Westphalian) of Illinois (Fig. 16B), is the smallest known palaeodictyopteran, and may be close to the Spilapteridae (Carpenter, 1983). Nonetheless some of the characteristics of Dictyoneuridae also apply here: elliptical wings, the hind wing slightly broader; support primarily from the anterior spar, with the rest of the wing occupied by posterodistally directed slightly curved, late-branching veins. Instead of the characteristic reticulation of dictyoneurids the wings have neat, straight cross-veins, rather Mecoptera-like in appearance. Although probably remote from Dictyoneuridae, they may have been adapted to rather similar flight. Being far smaller, however, their wing-loading was inevitably low – by far the lowest of those which we have estimated (Table 1, Fig. 1), and drag coefficients would have been relatively high. Their speed would necessarily have been low, and the narrower wing bases and absence of prothoracic winglets hint at a slow, drifting flight transitional to the pattern which we will see to be characteristic of Megaseoptera.

(6) Palaeodictyoptera: Breyeriidae and Calvertiellidae – transverse flexibility and distal twisting

These two families – the former Carboniferous, the latter Carboniferous and Lower Permian – have not usually been thought closely related, but they show very similar adaptations (Fig. 17). Both have the now familiar arrangement of RA, MA, and CuA unbranched and supporting high convex spars, alternating with broad low fields occupied by the many branches of RP and MP. Both have elliptical fore wings, and hind wings with significant postero-basal broadening. In both, ScP does not extend the full length of the wing, but stops well short, usually by fusion with RA. In both the cubital and anal veins are strongly arched – spectacularly so in Calvertiellidae. In both, the separation of RA and RP, and that of MA and MP, lie close together, almost at the same point along the span.

This condition is clearly derived, and several of the characters appear, sometimes in combination,

elsewhere in the insects. We have already seen in discussing Odonoptera that an abbreviated ScP increases the flexibility and the torsional compliance of the distal part of the wing; and in the section on Ephemeroptera that closely apposed vein bases assist torsional mobility of the distal area which the branches of these veins support, and that strong curvature in the cubital and anal veins serves to hold down the trailing edge when the distal part of the wing undergoes pronatory (leading-edge down) twisting. Together, these characters indicate that both fore and hind wings could undergo appreciable beneficial deformation in flight. In the downstroke, the whole radial and median areas would twist slightly nose down, and assume a cambered section enhanced by the depression of the trailing edge by the curved cubital and anal veins. In the upstroke, the distal part of the wing could twist and flex, taking up a more favourable section and angle of attack than would be allowed in a more rigid wing design. We have seen (see Section III. 5) that this combination of limited tip torsion and bending to enhance force production in the upstroke has many parallels, e.g. in Hemiptera (Betts, 1986; Betts and Wootton, 1988; Wootton, 1992) and in Plecoptera, Megaloptera, Trichoptera and Mecoptera (Wootton, 1992; Ennos & Wootton, 1989; Dalton 1975; Dalton & Bailey, 1989; Brackenbury, 1992). In Breyeriidae and Calvertiellidae, with their broad hind wing bases, these correlated characters suggest the development of enhanced manoeuvrability and versatility in essentially rapid-flying forms.

(7) Diaphanopteroidea: the wing-folding Palaeoptera

Diaphanopteroidea, like Palaeodictyoptera and Megasecoptera, are present among the earliest known winged insects in the Namurian division of the Carboniferous, and continue well into the Permian; a life of at least 80 million years. Their diversity, although appreciable, is far less than that of Palaeodictyoptera. Wing-spans vary between approximately 80 mm in *Namurodiapha sippelorum* Brauckmann and Kukalová-Peck, from the Namurian of Hagen-Vorhalle, Germany, and approximately 10 mm in *Asthenohymen parvulus* from the Lower Permian of Oklahoma, USA. Venation varies from the fairly complex to the extremely simple, to some extent following diminishing wing size.

Although nine families are recognised (Carpenter, 1992) the group can be discussed as a whole, since

their evolution shows certain clear trends. Their wings are more or less elliptical, without the petiolate base which characterises many Megasecoptera – see below. The hind wings are essentially similar to the fore, with no significant posterobasal expansion. With a few exceptions aspect ratios are moderate, as are the dimensionless radii of the first area moments (Table 2). Calculated values of the latter are close to 0.5, as one would expect from nearly elliptical wings.

Diaphanopteroidea are often preserved with their wings folded over the abdomen, and seem remarkably to have developed this capability independently of the true Neoptera. Interestingly many wing characters also recall some Neoptera, and names like *Asthenohymen* and *Rhaphidiopsis* reflect incorrect early assignments to neopterous orders. A particularly Neoptera-like feature is the effective division of the wing into two areas, equivalent to the remigium and clavus. This was brought about at an early stage by the partial fusion, near the wing base, of major longitudinal veins: MA with RP, and CuA with the common stem of MA and MP and the proximal part of MP (Kukalová-Peck & Brauckmann, 1990). All the pre-anal veins are hence functionally linked, leaving the anal veins as a separate unit, separated from the remainder by a strip of membrane traversed by a few slender cross-veins. There is every likelihood that this strip functioned like the claval flexion-line in Neoptera as a long hinge, allowing the main part of the wing to become pronated and supinated relative to the anal area. Significantly, the anal veins of all but the earliest forms do not show the strong curvature which characterises so many Palaeodictyoptera, but is rare in Neoptera; in most orders – Orthoptera, Plecoptera, Hemiptera, Psocoptera, Megaloptera, Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Hymenoptera – they form a firm posterior support to the fore- and sometimes the hind wing. In these orders the angle of attack and basal camber of the wing are controlled by flexion along the claval line, and between the 2nd and 3rd axillary sclerites. The axilla of Diaphanopteroidea was quite differently formed (Kukalová-Peck & Brauckmann, 1990), but flexion between the bases of CuA + CuP and the first anal vein, AA, appears wholly possible.

As in many Neoptera, and in the calvertiellid and breyeriid Palaeodictyoptera discussed above, ScP ends well short of the wing tip, on either the leading-edge vein or on RA. We have seen that this favours both flexion and supinatory twisting of the wing tip relative to the rest of the wing. In many of the neopterous orders listed above some transverse

Table 2. Aspect ratios (AR) and dimensionless radii of first area moments, $\hat{r}_1(S)$, of fore (FW) and hind (HW) wings of selected Palaeozoic Palaeoptera. Aspect ratios are calculated as: $4(\text{wing length})^2/\text{area of wing pair}$. $r_1(S)$ is the distance of the wing's centroid (geometric centre) along the length of the wing, divided by the wing length. The values for *Meganeura spp.* are based mainly on *M. monyi* Brongniart, but completed with reference to related species

		Aspect ratio	$\hat{r}_1(S)$	Reference
Ephemeroptera				
<i>Bojophlebia prokopi</i>	FW	7.3	0.475	Riek & Kukalová-Peck (1984)
	HW	6.6	0.432	
<i>Protereisma permianum</i>	FW	10.5	0.514	Carpenter (1933)
	HW	8.8	0.471	
Odonatoptera				
Undescribed geropterid	FW	9.2	0.489	
	HW	7.8	0.450	
<i>Meganeura spp.</i>	FW	11.9		
	HW	10.8		
<i>Namurotypus sippelorum</i>	FW	14.2	0.461	Brauckmann & Zessin (1989)
	HW	13.1	0.440	
Palaeodictyoptera				
<i>Stenodictya lobata</i>	FW	10.0	0.466	Kukalová (1970)
	HW	9.3	0.459	
<i>Homoioptera woodwardi</i>	FW	6.2	0.462	Kukalová (1969 <i>b</i>)
	HW	6.2	0.443	
<i>Homoioptera vorhallensis</i>	FW	6.0	0.457	Brauckmann (1988)
	HW	6.0	0.443	
<i>Homaloneura lehmani</i>	FW	8.0	0.500	Kukalová (1969 <i>a</i>)
	HW	6.9	0.438	
<i>Dunbaria fasciipennis</i>	FW	7.8	0.520	Kukalová-Peck (1971)
	HW	6.0	0.453	
<i>Lamproptilia grandeurii</i>	FW	6.5	0.495	Kukalová (1969 <i>b</i>)
	HW	5.5	0.464	
<i>Eubleptus danielsi</i>	FW	7.7	0.513	Carpenter (1983)
	HW	7.5	0.478	
Megasecoptera				
<i>Mischoptera nigra</i>	FW	10.7	0.531	Carpenter (1951)
	HW	11.9	0.542	
<i>Sylvahymen sibiricus</i>	FW	15.6	0.568	Kukalová-Peck (1972)
	HW	15.6	0.552	
<i>Protohymen readi</i>	FW	14.4	0.542	Carpenter (1933)
	HW	13.1	0.549	
<i>Hana lineata</i>	FW	24.5	0.563	Kukalová-Peck (1975)
	HW	23.2	0.551	
Diaphanopterodea				
<i>Namurodiapha sippelorum</i>	FW	9.1	0.491	Kukalová-Peck & Brauckmann (1990)
	HW	8.1	0.503	
<i>Uralia maculata</i>	FW	8.9	0.512	Kukalová-Peck & Sinichenkova (1992)
	HW	8.0	0.516	
<i>Asthenohymen dunbari</i>	FW	10.1	0.542	Carpenter (1939)
	HW	9.8	0.542	

ventral bending occurs during the upstroke, and this can allow the development of usefully-directed lift by this part of the wing (Wootton, 1981, 1992), and

with it improved control of flight speed and direction. Bending is often localised along a clearly visible flexible line, but in many insects in which it

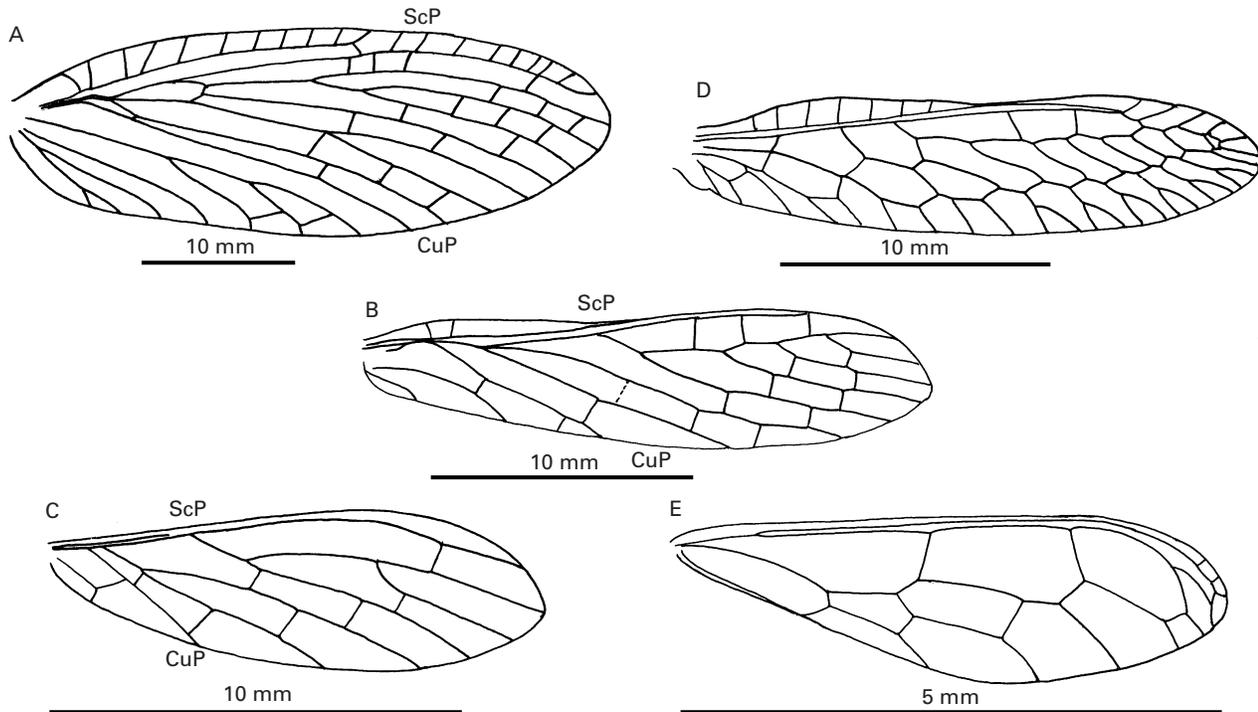


Fig. 18. Fore wings of Diaphanopteroidea (A-C) and Neoptera (D,E). (A) *Parelmoa revelata*, after Carpenter (1947). (B) *Eumartynovia raaschi*, after Carpenter (1947). (C) *Asthenohymen apicalis*, after Carpenter (1947). (D) *Mantispa* sp. (order Neuroptera, family Mantispidae). (E) *Miuria palauana* Fennah (order Hemiptera, family Derbidae), after Fennah (1956). ScP, posterior subcosta; CuP, posterior cubitus.

occurs no line is apparent in the stationary wing. No line is visible in Diaphanopteroidea, but it is highly probable that some ventral bending occurred in the upstroke, approximately along the line between the ends of ScP and CuP. Ennos & Wootton (1989) have shown that in *Panorpa germanica* (Mecoptera) the positions of the ends of these veins, which are different in the fore- and hind wings, determine the alignment of this bending, and hence the directions of the forces generated in the upstroke (Fig. 2).

Fig. 18 illustrates the similarity between the wings of some Diaphanopteroidea and some neuropteroid and hemipteran Neoptera. It is wholly due to convergence, presumably towards similar modes of flight.

The presence of a long, firm posteriorly-supporting anal area tends to inhibit overall torsion, and several neopterous groups show progressive reduction of this area in association with greater upstroke twisting, and improved slow and hovering flight capabilities (Wootton and Ennos, 1989; Wootton 1992). This is clearly also to be seen in some Diaphanopteroidea: compare the positions of CuP in Fig. 18A, B and C. Fig. 18C shows the fore wing of

Asthenohymen apicalis Carpenter. Here, ScP is very reduced, and lies close to RA, giving rigidity in the narrow basal part of the leading-edge spar. Distally, the anterior support for the wing is provided by the broad girder formed by the costal margin, RA and RP, which has the inverted V section which as we have seen in Odonata provides rigidity to dorsal bending in the downstroke but allows some bending and supinatory twisting in the upstroke. The tiny anal area would allow considerable supinatory twisting of the whole wing. This kind of wing has several parallels elsewhere, but two are particularly striking. Fig. 18E is the fore wing of *Miuria palauana* Fennah 1956, a modern derbid homopteran. In contrast to Diaphanopteroidea the hind wing is tiny and coupled to the fore, but it is similarly adapted for extreme torsion and for hovering or near hovering flight (Wootton 1996). The other parallel, one of the most remarkable in the Insecta, is with the megasecopteran family Protohymenidae (Fig. 19C). The venation in this family appears almost identical to *Asthenohymen* spp., but as Carpenter (1947) demonstrated is differently derived. Both are highly and convergently adapted for a similar mode of flight.

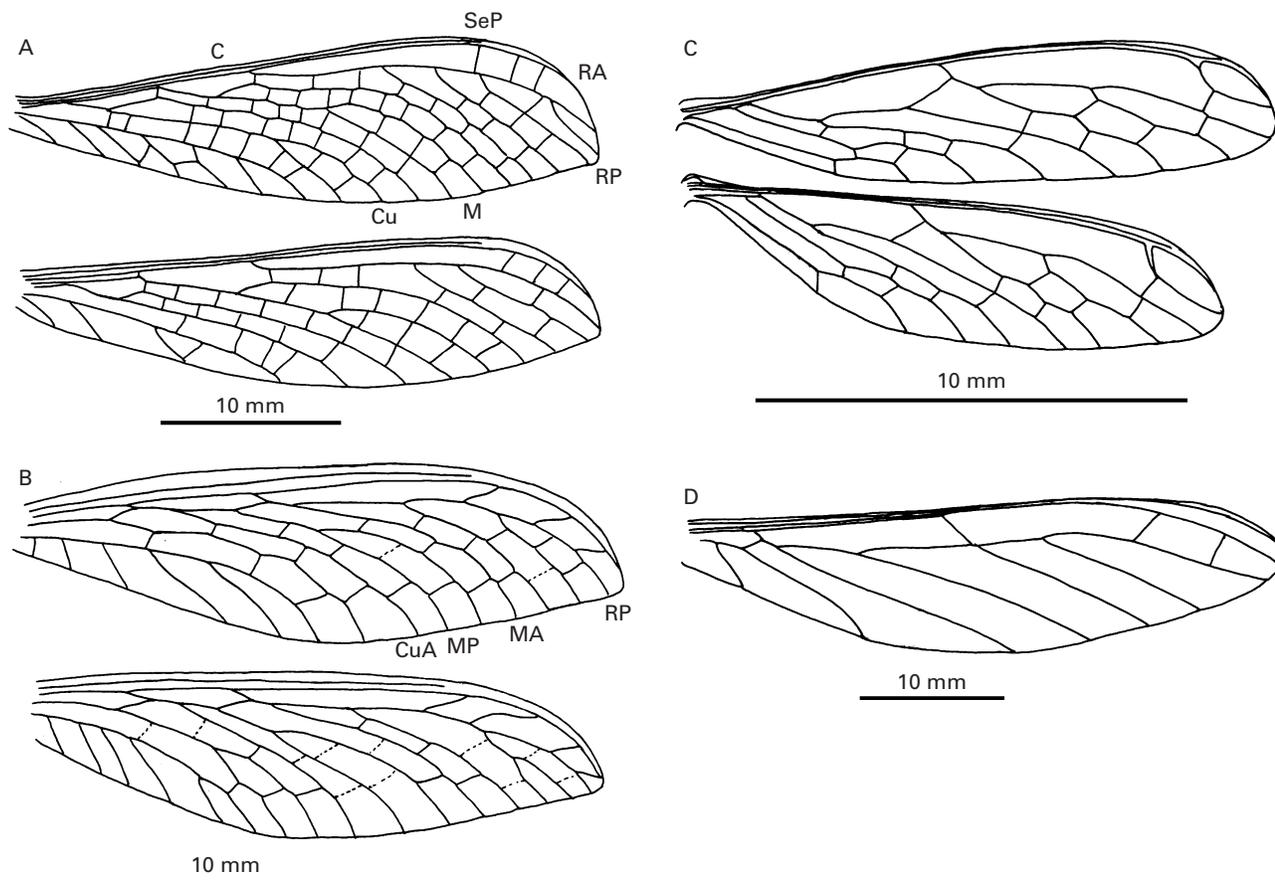


Fig. 19. Wings of Megasecoptera. (A) *Aspidothorax triangularis*. (B) *Corydaloides scudderii*. (C) *Protohymen permianus*. (D) *Scytohymen extremus*. A, B after Carpenter (1951); C after Carpenter (1947); D from Carpenter (1992), after Martynov (1937). C, costa; ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; M, anterior + posterior media; CuA, anterior cubitus; Cu, anterior + posterior cubitus.

(8) Megasecoptera and Permothemistida: towards hovering flight.

From their first appearance in the Namurian, Megasecoptera are clearly adapted to slow flight, and their evolution during the next 80 million years can be seen as experiment in, and refinement of these adaptations. They are characterised by narrow-based, often stalked wings, with the area concentrated distally (see Table 2 for the high values of the aspect ratio and the dimensionless radii of the first area moments); by the approximation and in due course virtual coalescence of ScP and RA with the leading-edge vein; and by a tendency for the bases of MA and CuA to become arched towards and sometime briefly fused with RP and MP. The convex (ridge) veins are always unbranched, and the branches of the concave (trough) veins few. The cross-veins are seldom reticulate, although *Eubrodia dabasinskii* Carpenter from the Carboniferous of Illinois, had the fine 'archedictyon' network in the membrane, together with slender cross-veins

(Carpenter, 1967). Cross-veins are often aligned or arranged in a step-like formation across the wing. There was probably a good deal of parallel evolution within the order; in particular the coalescence of MA and CuA with adjacent veins may have happened several times (Carpenter, 1992).

Fig. 12 A, B, I shows several species in outline, and Fig. 19 illustrates four species in detail, and demonstrates an important trend – though there is no reason to suppose that these species are part of a linear evolutionary series. In *Aspidothorax triangularis* Brongniart, from the late Carboniferous of Commeny (Fig. 19A), the approximation of the costal and subcostal veins and RA, and basally in this species the stems of M and Cu, would give a rigid support to the leading-edge. Behind this, RP is pectinately branched, with its main axis parallel to the leading-edge, and separated from it by a band of membrane, which is aligned with two more proximal cells behind the stems of R and M, together forming a broader, lower, posterior component of an anterior spar. The remaining branches of RP, those of the

median and cubital veins, and the main axis of the pectinate anal veins, run more or less parallel, obliquely towards the trailing edge. This conformation is a familiar one. Ennos (1988) showed that wings with a straight leading-edge, rigid to bending but less so to torsion, from which arise a series of parallel, posterodistally directed veins, automatically develop a cambered section in flight in response to aerodynamic loading from either the dorsal or ventral side. If such a wing is capable of significant twisting, as a narrow wing base permits, it can generate lift on both the up- and downstroke. If the wings are beating in a plane which is horizontal or nearly so, they will develop vertical, weight-supporting force on both half-strokes and the insect will be capable of slow flight and even hovering. We can envisage these insects flying with the body steeply inclined and the long cerci spread, beating their wings horizontally and hovering, rising, falling and drifting with the wind, or manoeuvring slowly around the branches of the plants on which they fed. In *Corydaloides scudderi* Brongniart (Fig. 19B), brief fusion of MA with RP and CuA with MP has strengthened the wing base and emphasised the leading-edge spar as a functional unit. In *Protohymen permianus* Tillyard (Fig. 19C), from the Lower Permian of Kansas, the wing is further neatened and refined, and this is taken still further in the later Lower Permian *Scytohymen extremus* Martynov (Fig. 19D). It is these Permian forms which are so strongly convergent with the diaphanopterodean *Asthenohymen* spp (Fig. 18C, 12L) Most Permian species are variants on these latter designs, with more or fewer cross-veins, and with greater or less fusion between the bases of the veins.

Exceptions, however, are a range of unusual species with rich, irregular cross-venation, from the Lower Permian of Obora, in the Czech Republic (Kukalová-Peck, 1975). Most curious of these are *Hana filia* and *H. lineata*, known only from incomplete wings which are the most slender of any known insects (Fig. 12I). These forms may not be true Megaseoptera, but aberrant palaeodictyopteroids which have independently developed some of the same slow-flight adaptations.

Our measurements and dimensional calculations throw more light on the diversity of this fascinating Order. A few species are completely-enough known for their wing-loadings and pterothorax/total mass ratios to be estimated (Table 1). *Mischoptera nigra* Brongniart (Fig. 12A), from the Upper Carboniferous of France was a large species (wing span 158 mm), but the body and particularly the

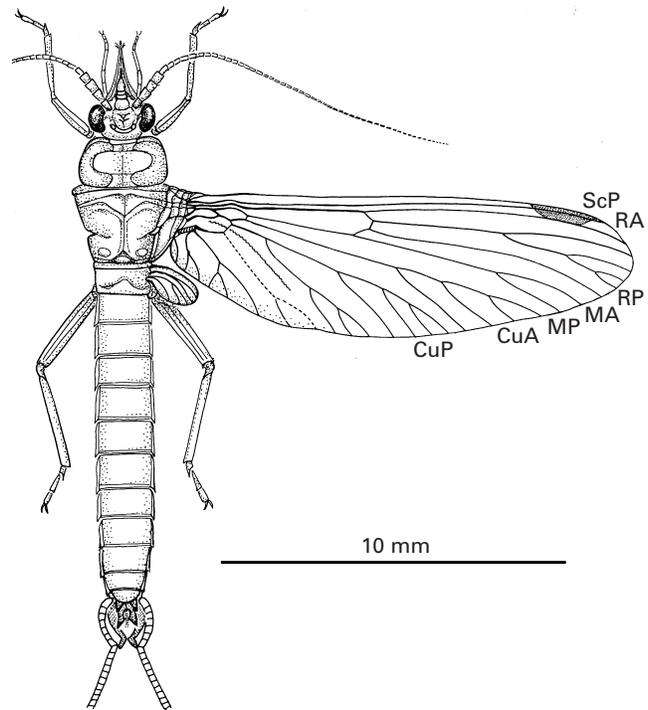


Fig. 20. Permian Palaeoptera. Reconstruction of *Diathema tenerum* Sinichenkova 1980. Lower Permian of Tsherkarda, Russia. Original, based mainly on the holotype, 1700/369, Palaeontological Institute, Russian Academy of Sciences. Head, mouthparts and wing base details are based on *Diathemidia monstrosa* Sinichenkova 1980, 1700/367 and 1700/368. Note that only the bases of the long cerci are shown. ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus.

pterothorax were relatively small, and the wing-loading and pterothorax/body mass ratios are both notably low. The curiously-shaped wings are distally expanded and clearly adapted as usual for slow flight and hovering, and the low wing-loading and evidently limited flight muscle mass indicate that they would have been capable of no more than this, although they may have benefited from the greater mass-specific muscle efficiency associated with large size, and the lower power requirements for flight in the dense Upper Carboniferous atmosphere. By contrast the smaller, Permian protohymenid *Protohymen readi* Carpenter and the much larger, and rather later *Sylvohymen sibiricus* Kukalová-Peck (Fig. 12B) have relatively higher wing-loadings and relatively larger pterothorax segments. The long, high aspect ratio wings, with high radii of area moments (Table 2) appear ideally adapted to hovering, but these would have been capable of operating over a far greater range of flight speeds.

By the Kungurian division of the Permian, where *S. sibiricus* is found, atmospheric oxygen levels would already have been declining (Berner & Canfield, 1989), and relatively larger flight muscles would have become necessary.

Finally, to the Permothemistida (Fig. 20), a poorly known, mainly late group which appear also to have developed a slow flying/hovering habit, but via a different route. These are Permian palaeodictyopteroid parallels to the modern caenid and some baetid Ephemeroptera, whose hind wings are extremely reduced or in some cases entirely lost. Their fore wings are moderately elongate, with a straight leading-edge and a curved trailing edge. There is no fusion between the stems of ScA + ScP, RA + RP, MA + MP and CuA + CuP, but cross-veins join the bases of MA + MP and CuA + CuP, and CuA + CuP and AA, forming a double cell which will have given some rigidity to the wing base. The veins and their branches effectively radiate from the base, in a rather mayfly-like manner, and it seems probable that they flew rather similarly.

VII. CONCLUSIONS: PALAEOPTERAN FLIGHT PATTERNS AND PALAEOECOLOGY

How far does knowledge of the flight adaptations and capabilities of these insects assist our understanding of their ecology?

The great majority of known Carboniferous Palaeoptera come from a broad, warm and humid tropical belt of the then equatorial regions of Europe, North America and eastern Asia. There is a lesser record from the temperate zones of Angara, in the Kuznetsk Basin of Siberia; and of Argentina, Zimbabwe and Tasmania. The dominant Carboniferous insect taxa persisted well into the Permian, mainly in lowland forests, but progressive aridity in the Northern Hemisphere and glaciation in the Southern Hemisphere induced well-defined climatic zones and major changes in ecosystem structure. Large lycopods become extinct, and ferns, pteridosperms and Cordaitales were progressively replaced by gymnosperms. With these climatic and floristic changes came the decline and eventual disappearance of the haustellate, plant-reliant palaeodictyopteroids. However, Odonoptera and Ephemeroptera with their aquatic larvae and predatory or non-feeding adults continued to diversify, alongside a rapid, spectacular radiation of Neoptera, many of which would have provided them with food.

The flight adaptations of the Neoptera are beyond

the scope of this paper, but the morphology of the Carboniferous forms, at least, does not suggest particular versatility. No doubt, like most modern Orthoptera, they flew when necessary, but without subtlety, relying extensively on hiding, jumping and protective patterning (Carpenter, 1969) for predator evasion. Palaeoptera relied far more on flight; necessarily, since outstretched wings seriously hamper substrate locomotion, whether across windswept open spaces or in trees, and also make hiding difficult. Wing-folding allowed the Neoptera to readopt substrate, as well as aerial, mobility, and to hide away. Of Palaeoptera, the Diaphanopteroidea alone had this option, and some at least had long, stout legs (Kukalová-Peck & Brauckmann, 1990). Ephemeropteroids, odonatoids and other palaeodictyopteroids would have been effectively restricted to flight, in open situations and around the outside of plants, although smaller species would have been able to fly in correspondingly smaller spaces.

Palaeozoic ephemeropteroids and odonatoids contrast sharply in their degree of similarity to later forms. The wing shapes and venation patterns of the earliest odonatoids are already close enough to modern dragonflies to be instantly recognisable, and this is still more true of the relatively diverse Permian species. Clearly Palaeozoic odonatoids, like modern forms, were already adapted for versatile flight, associated with aerial predation on a variety of prey in a miscellany of habitats. Thereafter, their flight technique would diversify and their performance progressively improve keeping pace with the radiation and increasing agility of their potential prey; their size range would shift as falling oxygen levels made gigantism impracticable, and with the massive Permian and Mesozoic expansion of smaller insects on which they fed; but their overall design would remain essentially the same.

The handful of known Carboniferous ephemeropteroids, on the other hand, are so different from today that their assignment is still disputable (Carpenter, 1987, 1992), and even the Permian species are quite different in general form from later mayflies. So must have been their flight, and this may represent a major change of use. The non-feeding adults and subadults of modern mayflies use flight only for mating, oviposition and limited dispersal, but there is evidence that this was not always so. Tshernova (1965) found large biting mandibles on some Permian *Misthodotidae*, suggesting that they were active, probably predatory feeders as adults, and we can suppose that the same was true of earlier forms. The winged stages would

have lived longer and had a wider range of flight activities than today. It may be, however, that the only mayflies to survive the Permian, in the face of better-adapted competitors, were a lineage in which the vulnerable winged stages were brief, and feeding was concentrated into the aquatic juvenile stages. The wings would then have become optimised for nuptial and short-range trivial flight alone.

To interpret the diverse flight adaptations of Palaeodictyopteroidea we need to examine both evolutionary change and resource partitioning. Their ecology and feeding adaptations have been reviewed by Scott & Taylor (1983), Scott, Stephenson & Chaloner (1992), Shear & Kukalová-Peck (1990), Labandeira and Phillips (1996) and Labandeira (1998). Their elongate beaks varied considerably in both absolute and relative length and breadth, and it is clear that their diet was far from uniform. There is direct evidence for sap-sucking (Labandeira & Phillips, 1996), and for feeding on microspores (Kukalová-Peck, 1987) and the semi-liquid endosperm of cordaitalan megaspores (Sharov 1973). Beaks of many Palaeodictyoptera and Megasecoptera were massive (Labandeira & Phillips, 1996; Shear & Kukalová-Peck, 1990) and may have been adapted to feed on fruiting bodies, rather than to penetrate the thick cortices of Early and Middle Pennsylvanian trees (Smart & Hughes, 1973). Others were long and slender, and Labandeira & Phillips (1996) have associated long, curving punctures in late Pennsylvanian tree ferns of the genus *Psaronius* with the slender probosces of eugereonid and mecynostomatid Palaeodictyoptera. Most known Diaphanopteroidea, late spilapterid Palaeodictyoptera of *Dunbaria* type, and Permothemistida had short beaks, and it is probable that they could only have fed on microspores and/or the sap of frond rachises and young tissues of trees, and on the smaller herbaceous pteridophytes which latter became progressively available from the late Pennsylvanian onwards.

These feeding habits on the whole accord with our interpretations of flight techniques. Large Palaeodictyoptera of the homiopterid type would only have been capable of flying directly from tree to tree – and landing with a thud. Spilapteridae, Dictyoneuridae, and particularly Eugereonidae, Breyeriidae, Calvertiellidae and early Diaphanopteroidea were developing greater control of flight speed and direction, and would have been capable of reaching and exploiting less rigid plant structures. Megasecoptera would from the first have been able to fly slowly around the periphery of the plants, and

manoeuvre into confined spaces to feed on less accessible structures. The later, smaller Megasecoptera, Diaphanopteroidea and Permothemistida would have exploited their hovering skills to reach and probe for spores on flexible structures which would not have supported the weight of their more robust relatives, perhaps partly supporting their weight by flapping, in the manner of many flower-visiting butterflies today.

Beside their contribution to our understanding of their ecology, the flight adaptations of these insects have broader evolutionary implications. A fascinating aspect is the impression which one gains of experimentation with designs and techniques. Examples include the biplane flight of Homiopteridae and Lycocercidae, apparently abandoned by the end of the Carboniferous and never seen again; and the wide range of wing planforms found in Megasecoptera, including the steeply raked design of *Aspidothorax* spp., the lobed trailing edge of *Mischoptera* spp., and the extraordinary, virtually unparalleled high-aspect-ratio wings of *Hana* spp. The Palaeoptera also provide excellent examples of directional trends and refinement and improvement of design, particularly in the Odonata, the Diaphanopteroidea and the Megasecoptera; of mosaic evolution, particularly in Megasecoptera; and of spectacular convergence in the Lower Permian Megasecoptera and asthenohymenid Diaphanopteroidea.

VIII. ACKNOWLEDGEMENTS

This collaboration was made possible by a grant from the National Research Council of Canada. We are grateful to Dr C. P. Ellington for his comments on part of an earlier draft, and to Dr R. Dudley in his capacity as referee.

IX. REFERENCES

- AZUMA, A. & WATANABE, I. (1988). Flight performance of a dragonfly. *Journal of experimental Biology* **137**, 221–252.
- BECHLY, O. (1996). Morphologische Untersuchungen an Flügelgädder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata). *Petalura* **2**, 1–402.
- BERNER, R. A. & CANFIELD, D. E. (1989). A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science* **289**, 333–361.
- BETTS, C. R. (1986). Functioning of the wings and axillary sclerites of Heteroptera during flight. *Journal of Zoology (B)* **1**, 283–301.
- BETTS, C. R. & WOOTTON, R. J. (1988). Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidea and

- Hesperioidea): a preliminary analysis. *Journal of experimental Biology* **138**, 271–88.
- BRACKENBURY, J. (1990). Wing movements in the bush-cricket *Tettigonia viridissima* and the mantis *Ameles spallanziana* during natural leaping. *Journal of Zoology, London* **220**, 593–602.
- BRACKENBURY, J. (1991). Wing kinematics during natural leaping in the mantids *Mantis religiosa* and *Iris oratorio*. *Journal of Zoology, London* **223**, 341–56.
- BRACKENBURY, J. (1992). *Insects in Flight*. Blandford, London.
- BRAUCKMANN, C. (1988). Hagen-Vorhalle, a new important Namurian insect-bearing locality (Upper Carboniferous; FR Germany). *Entomologia generalis* **14**, 73–79.
- BRAUCKMANN, C., BRAUCKMANN, B., & GRÖNING, E. (1996). The stratigraphical position of the oldest known Pterygota (Insecta. Carboniferous, Namurian). *Annales de la Société Géologique de Belgique* **117**, 47–56.
- BRAUCKMANN, C., KOCH, L. & KEMPER, M. (1985) Spinnentiere (Arachnida) und Insekten aus den Vorhalle-Schichten (Namurium B; Ober-Karbon) von Hagen-Vorhalle (West-Deutschland). *Geologie und Paläontologie Westfalen* **3**, 1–131.
- BRAUCKMANN, C. & ZESSIN, W. (1989). Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BRD) und die Phylogenie der Meganisoptera (Insecta, Odonata). *Deutsche entomologische Zeitschrift* **36**, 177–215, pl 3–8.
- BRODSKY, A. K. (1971). Experimental studies of the flight of the mayfly *Ephemera vulgata* L. (Ephemeroptera). *Entomological Reviews* **50**, 25–29.
- BRODSKY, A. K. (1973). The swarming behaviour of mayflies (Ephemeroptera). *Entomological Reviews* **52**, 33–39.
- BRODSKY, A. K. (1982). Evolution of the wing apparatus in stoneflies (Plecoptera). Part 4. Wing kinematics and general conclusion. *Entomological Reviews* **61**, 34–43.
- BRODSKY, A. K. (1985). Some new principles of the flight of insects. *Doklady Akademii Nauk SSSR* **283**, 1491–95 (In Russian).
- BRODSKY, A. K. (1986). Flight of a gigantic stonefly *Allonarcys sachalina* (Plecoptera, Pteronarcyidae) and analysis of the mechanism of supination of insect wings. *Zoologicheskii Zhurnal* **65**: 349–60 (In Russian)
- BRODSKY, A. K. (1994). *The Evolution of Insect Flight*. Oxford University Press, Oxford.
- BRODSKY, A. K. & IVANOV, V. D. (1983). Functional assessment of wing structure in insects. *Entomological Reviews* **62**, 32–51
- BUNKER, S. J. (1993). Form, flight pattern and performance in butterflies (Lepidoptera: Papilionoidea and Hesperioidea). PhD thesis, University of Exeter, Exeter.
- BYRNE, D. N., BUCHMANN, S. L. & SPANGLER, H. G. (1988). Relationship between wingloading, wingbeat frequency and body mass in homopterous insects. *Journal of experimental Biology* **135**, 9–23.
- CARPENTER, F. M. (1931). The Lower Permian insects of Kansas. Part 2. The orders Palaeodictyoptera, Protodonata and Odonata. *American Journal of Science* **21**, 97–139.
- CARPENTER, F. M. (1933). The Lower Permian insects of Kansas. Part 6. Delopteridae, Protelytroptera, Plectoptera, and a new collection of Protodonata, Odonata, Megasecoptera, Homoptera and Psocoptera. *Proceedings of the American Academy of Arts and Sciences* **68**, 411–505.
- CARPENTER, F. M. (1938). Two Carboniferous insects from the vicinity of Mazon Creek, Illinois. *American Journal of Science* **36**, 445–452.
- CARPENTER, F. M. (1939). The Lower Permian insects of Kansas. Part 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plectoptera and Protopterlaria. *Proceedings of the American Academy of Arts and Sciences* **73**, 29–70.
- CARPENTER, F. M. (1943). The Lower Permian insects of Kansas. Part 9. The orders Neuroptera, Raphidioidea, Caloneuroidea and Protorthoptera (Probnisidae), with additional Protodonata and Megasecoptera. *Proceedings of the American Academy of Arts and Sciences* **75**, 55–84.
- CARPENTER, F. M. (1944). Carboniferous insects from the vicinity of Mazon Creek Illinois. *Illinois State Museum, Scientific Papers* **3**, 1–20.
- CARPENTER, F. M. (1947). Lower Permian insects from Oklahoma. Part 1. Introduction, and the Orders Megasecoptera, Protodonata and Odonata. *Proceedings of the American Academy of Arts and Sciences* **76**, 25–54.
- CARPENTER, F. M. (1951). Studies on Carboniferous insects from Commentry, France: Part II. The Megasecoptera. *Journal of Palaeontology* **25**, 336–355.
- CARPENTER, F. M. (1963). Studies on Carboniferous insects from Commentry, France: Part IV. The genus *Triplosoba*. *Psyche, Cambridge* **70**, 120–128.
- CARPENTER, F. M. (1967). Studies on North American Carboniferous insects. 5. Palaeodictyoptera and Megasecoptera from Illinois and Tennessee, with a discussion of the Order Sypharopteroidea. *Psyche, Cambridge* **74**, 58–84.
- CARPENTER, F. M. (1969). Adaptations among Palaeozoic insects. *Proceedings of the North American palaeontological Convention. Part 1*, 1236–1251.
- CARPENTER, F. M. (1970). Fossil insects from New Mexico. *Psyche, Cambridge* **77**, 400–412.
- CARPENTER, F. M. (1979). Lower Permian insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. *Psyche, Cambridge* **86**, 261–290.
- CARPENTER, F. M. (1983). Studies on North American Carboniferous insects. 7. The structure and relationships of *Eubleptus danielsi* (Palaeodictyoptera). *Psyche, Cambridge* **90**, 81–95.
- CARPENTER, F. M. (1987). Review of the extinct family Syntonopteridae (order uncertain) *Psyche, Cambridge* **94**, 373–388.
- CARPENTER, F. M. (1992). *Treatise on Invertebrate Palaeontology. Volume 3: Superclass Hexapoda*. Geological Society of America and University of Kansas.
- CARPENTER, F. M. & RICHARDSON, E. S. JR. (1971). Additional insects in Pennsylvanian concretions from Illinois. *Psyche, Cambridge* **78**, 267–295.
- CARPENTIER, F. & LEJEUNE-CARPENTIER, M. (1949). Conformation de l'abdomen d'un insecte Protodonate du Stéphannien de Commentry (Allier, France). *Annales de la Société Géologique de Belgique* **72**, 317–327.
- CASEY, T. M. (1989). Oxygen consumption during flight. In *Insect Flight* (ed. G. Goldsworthy and C. Wheeler), pp. 257–272. CRC Press, Boca Raton.
- CASEY, T. M. & ELLINGTON, T. P. (1989). Energetics of insect flight. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 200–210. Georg Thieme Verlag, Stuttgart.
- CHAI, P. & SRYGLEY, R. B. (1990). Predation and the flight, morphology and temperature of Neotropical rain-forest butterflies. *American Naturalist* **135**, 748–765.
- COOPER, A. J. (1993). *Limitations on Bumblebee Flight Performance*. PhD. thesis, Cambridge University.

- CORBET, P. S. (1962). *A biology of dragonflies*. London: Witherby.
- CULLEN, M. J. (1974). The distribution of asynchronous muscle in insects with particular reference to the Hemiptera. *Journal of Entomology (A)* **49**, 17–41.
- DALTON, S. 1975. *Borne on the Wind*. London: Chatto and Windus. 160 pp.
- DALTON, S. & BAILEY, J. (1989). *At the Water's Edge*. Century Hutchinson, London, Melbourne, Auckland, Johannesburg.
- DUDLEY, R. (1990). Biomechanics of flight in Neotropical butterflies: morphometrics and kinematics. *Journal of experimental Biology* **150**, 37–53.
- DUDLEY, R. (1991). Comparative biomechanics and the evolutionary diversification of flying insect morphology. In *The Unity of Evolutionary Biology; Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology* (ed. E. Dudley), pp. 503–514.
- DUDLEY, R. (1998). Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *Journal of experimental Biology* **201**, 1043–1050.
- DUDLEY, R. & CHAI, P. (1996). Animal flight mechanics in physically variable mixtures. *Journal of experimental Biology* **199**, 1881–1885.
- DUDLEY, R. & ELLINGTON, C. P. (1990a). Mechanics of forward flight in bumblebees. I. Kinematics and morphology. *Journal of experimental Biology* **148**, 19–52.
- DUDLEY, R. & ELLINGTON, C. P. (1990b). Mechanics of forward flight in bumblebees. II. Quasi-steady lift and power requirements. *Journal of experimental Biology* **148**, 53–88.
- EDMUNDS, G. F. JR. & TRAVER, J. R. (1954). The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. *Journal of the Washington Academy of Science* **44**, 390–400.
- ELLINGTON, C. P. (1980). Vortices and hovering flight. In *Instationäre Effekte on Schwingenden Tierflügeln* (ed. W. Nachtigall), pp. 64–101. Franz Steiner Verlag, Wiesbaden.
- ELLINGTON, C. P. (1984a). The aerodynamics of hovering insect flight. II. Morphological parameters. *Philosophical Transactions of the Royal Society of London. Ser. B* **305**, 17–40.
- ELLINGTON, C. P. (1984b). The aerodynamics of hovering insect flight. III. Kinematics. *Philosophical Transactions of the Royal Society of London. Ser. B* **305**, 41–78.
- ELLINGTON, C. P. (1984c). The aerodynamics of hovering insect flight. IV. Aerodynamic mechanisms. *Philosophical Transactions of the Royal Society of London. Ser. B* **305**, 79–113.
- ELLINGTON, C. P. (1985). Power and efficiency in insect flight muscle. *Journal of experimental Biology* **115**, 293–304.
- ELLINGTON, C. P. (1991a). Aerodynamics and the origin of insect flight. *Advances in Insect Physiology* **23**, 171–210.
- ELLINGTON, C. P. (1991b). Limitations on animal flight performance. *Journal of experimental Biology* **160**, 71–91.
- ELLINGTON, C. P. (1995). Unsteady aerodynamics of insect flight. In *Biological Fluid Dynamics. Symposia of the Society for Experimental Biology XLIX* (ed. C. P. Ellington and T. J. Pedley). Company of Biologists Ltd., Cambridge.
- ELLINGTON, C. P., VAN DEN BERG, C., WILLMOTT, A. P. & THOMAS, A. L. R. (1996). Leading-edge vortices in insect flight. *Nature* **284**, 628–630.
- ENNOS, A. R. (1988). The importance of torsion in the design of insect wings. *Journal of experimental Biology* **140**, 137–160.
- ENNOS, A. R. (1989a). The comparative functional morphology of the wings of Diptera. *Zoological Journal of the Linnean Society* **96**, 27–47.
- ENNOS, A. R. (1989b). The effect of size on the optimal shapes of gliding insects and seeds. *Journal of Zoology* **219**, 61–69.
- ENNOS, A. R. (1995). Mechanical behaviour in torsion of insect wings, blades of grass and other cambered structures. *Proceeding of the Royal Society of London, series B* **259**, 15–18.
- ENNOS, A. R. & WOOTTON, R. J. (1989). Functional wing morphology and aerodynamics of *Panorpa germanica* (Insecta: Mecoptera). *Journal of experimental Biology* **143**, 267–284.
- FENNAH, R. G. (1956). Homoptera: Fulgoroidea. *Insects of Micronesia* **6** (3), 39–211. Bernice P. Bishop Museum, Honolulu, Hawaii.
- FRASER, F. C. (1957). *A Reclassification of the Order Odonata*. Royal Zoological Society of New South Wales, Sydney.
- GRAHAM, J. B., DUDLEY, R., AGUILAR, N. & GANS, C. (1995). Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature* **375**, 117–120.
- HANDLIRSCH, A. (1906–8). *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Fischer, Leipzig.
- HAZLEHURST, G. A. & RAYNER, J. M. V. (1992). Flight characteristics of Triassic and Jurassic Pterosauria: an appraisal based on wing shape. *Paleobiology* **18**, 447–463.
- HEINRICH, B. (1979). *Bumblebee Economics*. Harvard University Press, Cambridge, Mass.
- HUBBARD, M. D. & KUKALOVÁ-PECK, J. (1980). Permian mayfly nymphs: new taxa and systematic characters. In *Advances in Ephemeroptera Biology* (ed. J. F. Flannagan and K. E. Marshall), pp. 19–31.
- KINGSOLVER, J. G. & KOEHL, M. A. R. (1985). Aerodynamics, thermoregulation and the evolution of insect wings: differential scaling and evolutionary change. *Evolution* **39**, 488–504.
- KINGSOLVER, J. G. & KOEHL, M. A. R. (1994). Selective factors in the evolution of insect wings. *Annual Review of Entomology* **39**, 425–451.
- KRISTENSEN, N. P. (1991). Phylogeny of extant hexapods. In *The Insects of Australia*. Vol. 1. 2nd edn., ed. CSIRO. pp. 125–140. Melbourne University Press, Melbourne.
- KRISTENSEN, N. P. (1997). The groundplan and basal diversification of the hexapods. In *Arthropod Relationships* (ed. R. A. Fortey and R. H. Thomas), pp. 281–293. Chapman & Hall, London.
- KUKALOVÁ, J. (1959). *Breyeria barborae* n. sp. (Insecta, Palaeodictyoptera) of Upper Silesian Coal basin (Westphalian). *Vestník Ústředního Ústavu Geologického* **34**, 310–313.
- KUKALOVÁ, J. (1964). Review of the Calvertiellidae, with description of a new genus from Permian strata of Moravia (Palaeodictyoptera). *Psyche, Cambridge* **71**, 153–168.
- KUKALOVÁ, J. (1969a). Revisional study of the Order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France, Part I. *Psyche, Cambridge* **76**, 163–215.
- KUKALOVÁ, J. (1969b). Revisional study of the Order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France, Part II. *Psyche, Cambridge* **76**, 439–486.
- KUKALOVÁ, J. (1970). Revisional study of the Order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France, Part III. *Psyche, Cambridge* **77**, 1–44.
- KUKALOVÁ-PECK, J. (1971). The structure of *Dumbaria* (Palaeodictyoptera). *Psyche, Cambridge* **78**, 306–318.
- KUKALOVÁ-PECK, J. (1972). Unusual structures in the Palaeozoic insect orders Megasecoptera and Palaeodictyoptera, with a description of a new family. *Psyche, Cambridge* **79**, 243–268.
- KUKALOVÁ-PECK, J. (1975). Megasecoptera from the Lower Permian of Moravia. *Psyche, Cambridge* **82**, 1–19.

- KUKALOVÁ-PECK, J. (1978). Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *Journal of Morphology* **156**, 53–126.
- KUKALOVÁ-PECK, J. (1983). Origin of the insect wing and wing articulation from the arthropodan leg. *Canadian Journal of Zoology* **61**, 1618–1669.
- KUKALOVÁ-PECK, J. (1985). Ephemeroïd wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). *Canadian Journal of Zoology* **63**, 993–955.
- KUKALOVÁ-PECK, J. (1987). New Carboniferous Diplura, Monura, and Thysanura, the hexapod ground plan, and the role of thoracic lobes in the origin of wings (Insecta). *Canadian Journal of Zoology* **65**, 2327–2345.
- KUKALOVÁ-PECK, J. (1991). Fossil history and the evolution of hexapod structures. In *The Insects of Australia*. Vol. 1. 2nd edn., ed. CSIRO. pp. 141–179. Melbourne University Press, Melbourne. pp. 141–179.
- KUKALOVÁ-PECK, J. (1992). The ‘Uniramia’ do not exist: the groundplan of Pterygota as revealed by the Permian Diaphanopteroidea from Russia (Insecta: Paleodictyopteroidea). *Canadian Journal of Zoology* **70**, 236–255.
- KUKALOVÁ-PECK, J. (1997). Arthropod phylogeny and ‘basal’ morphological structures. In *Arthropod Relationships. Systematic Association Special Volume Series 55* (ed. R. A. Fortey and R. H. Thomas), pp. 249–268. Chapman and Hall, London.
- KUKALOVÁ-PECK, J. & BRAUCKMANN, C. (1990). Wing folding in pterygote insects, and the oldest Diaphanopteroidea from the early Late Carboniferous of West Germany. *Canadian Journal of Zoology* **68**, 1104–1111.
- KUKALOVÁ-PECK, J. & RICHARDSON, E. S. JR. (1983). New Homiopteridae (Insecta: Paleodictyoptera) with wing articulation from Upper Carboniferous strata of Mazon Creek, Illinois. *Canadian Journal of Zoology* **61**, 1670–87.
- KUKALOVÁ-PECK, J. & SINICHENKOVA, N. D. (1992). The wing venation and systematics of Lower Permian Diaphanopteroidea from Russia (Insecta: Paleodictyoptera). *Canadian Journal of Zoology* **70**, 229–235.
- LABANDEIRA, C. C. (1994). A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology* **88**, 1–71.
- LABANDEIRA, C. C. (1998). Early history of arthropod and vascular plant associations. *Annual Review of earth and planetary Sciences* **26**, 329–377.
- LABANDEIRA, C. C. & PHILLIPS, T. L. (1996). Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing and sucking functional feeding group. *Annals of the Entomological Society of America* **89**, 157–183.
- LAN, C. E. (1979). The unsteady quasi-vortex-lattice method with applications to animal propulsion. *Journal of Fluid Mechanics* **93**, 747–765.
- LAURENTIAUX, D. (1953). Classe des insectes (Insecta Linné 1758). In *Traité de Paléontologie*, **3**, ed. J. Piveteau, pp. 397–527. Paul Masson, Paris.
- MARDEN, J. H. (1987). Maximum lift-production during take-off in flying animals. *Journal of experimental Biology* **130**, 235–258.
- MARDEN, J. H. & KRAMER, M. G. (1994). Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. *Science* **266**, 427–430.
- MARTYNOV, A. V. (1923). On two basic types of insect wings and their significance for the general classification of insects. *Trudy Pervogo Vserossijskogo S'ezda Zoologov, Anatomov i Gistologov* **1**, 88–89. (In Russian.)
- MARTYNOV, A. V. (1937). Permian fossil insects of Kargala and their relationships. *Trudy paleontologičeskogo Instituta Akademii Nauk SSSR* **7**, 1–91. (In Russian.)
- NEVILLE, A. C. (1960). The function of the flight muscles, axillary sclerites and associated structures during the wing-stroke cycle of Odonata. PhD thesis, University of London.
- NEWMAN, D. J. S. (1982). The functional wing morphology of some Odonata. PhD thesis, University of Exeter. Exeter.
- NEWMAN, D. J. S. & WOOTTON, R. J. (1986). An approach to the mechanics of pleating in dragonfly wings. *Journal of experimental Biology* **125**, 361–72.
- NORBERG, R. A. (1972). The pterostigma of insect wings, an inertial regulator of wing pitch. *Journal of comparative Physiology* **81**, 9–22.
- NORBERG, R. A. (1973). Autorotation, self-stability and structure of single-winged fruits and seeds (samaras) with comparative remarks on animal flights. *Biological Reviews* **48**, 561–596.
- NORBERG, U. & RAYNER, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia, Chiroptera): wing adaptations, flight performance, foraging strategies and echolocation. *Phil. Trans. R. Soc. London Ser. B* **316**, 335–427.
- PFAU, H. K. (1986). Untersuchungen zur Konstruktion, Funktion und Evolution des Flügelapparates der Libellen. *Tijdschrift voor Entomologie* **129**, 35–123.
- PRINGLE, J. W. S. (1976). The muscles and sense organs involved in insect flight. In *Insect Flight. Symposia of the Royal Entomological Society of London No. 7* (ed. R. C. Rainey), pp. 3–15. Blackwell, Oxford, London, Edinburgh, Melbourne.
- PRINGLE, J. W. S. (1981). The evolution of fibrillar muscle in insects. *Journal of experimental Biology* **94**, 1–14.
- PRITYKINA, L. N. (1980). Order Libellulida Laicharting 1781. In: *Historical Development of the Class Insecta* (ed. B. B. Rohdendorf & A. P. Rasnitsyn). *Trudy Palaeontologičeskogo Instituta Akademii Nauk SSSR* **175**, 128–134. (In Russian.)
- RASNITSYN, A. P. & NOVOKHSHONOV, V. G. (1997). On the morphology of *Uralia maculata* (Insecta: Diaphanoptera) from the Early Permian (Kungurian) of Ural (Russia). *Entomologica Scandinavica* **28**, 27–38.
- RAYNER, J. M. V. (1987). Form and function in avian flight. In *Current Ornithology* (ed. R. F. Johnston), pp. 1–66. Plenum Press, New York.
- RIEK, E. F. & KUKALOVÁ-PECK, J. (1984). A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology* **62**, 1150–1166.
- ROHDENDORF, B. B. (1992). Order Archodonata. In *Osnovy Paleontologii* (ed. B. B. Rohdendorf), p. 55. Akademii Nauk SSSR, Moscow.
- ROHDENDORF, B. B., BECKER-MIGDISOVA, E. E., MARTYNOVA, O. M. & SHAROV, A. G. (1961). Paleozoic insects of the Kuznetsk Basin. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* **85**, 1–705. (In Russian.)
- RÜPPELL, G. (1989). Kinematic analysis of symmetrical flight manoeuvres of Odonata. *Journal of experimental Biology* **144**, 13–42.
- SCOTT, A. C., STEPHENSON, J. & CHALONER, W. G. (1992).

- Interaction and coevolution of plants and arthropods during the palaeozoic and Mesozoic. *Philosophical Transactions of the Royal Society of London. Ser. B.* **335**, 129–165.
- SCOTT, A. C. & TAYLOR, T. N. (1983). Plant-animal interactions during the Upper Carboniferous. *Botanical Review* **49**, 259–307.
- SHAROV, A. G. (1973). Morphological features and mode of life of Paleodictyoptera. In *Chteniya pamyati Nikolaya Aleksandrovicha Kholodkovskogo*, pp. 45–63. Nauka, Leningrad. (In Russian).
- SHEAR, W. A. & KUKALOVÁ-PECK, J. (1990). The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology* **68**, 1807–1834.
- SINICHENKOVA, N. D. (1980). Revision of the Order Permothemistida (Insecta). *Paleontologicheskii Zhurnal* **1980** (4), 91–106. (In Russian).
- SMART, J. & HUGHES, N. F. (1973). The insect and the plant: progressive palaeoecological integration. In *Insect-plant Relationships, Symposia of the Royal Entomological Society of London No. 6* (ed. H. F. Van Emden), pp. 143–155.
- SMITH, D. S. (1983). 100 Hz remains the upper limit of synchronous muscle contraction: an anomaly resolved. *Nature* **183**, 539.
- SOMPS, C. & LUTTGES, M. (1985). Dragonfly flight: novel uses of unsteady separated flows. *Science* **228**, 1236–1238.
- SUNADA, S., KAWACHI, K., WATANABE, I. & AZUMA, A. (1993). Fundamental analysis of three-dimensional ‘near fling’. *Journal of experimental Biology* **183**, 217–248.
- TILLYARD, R. J. (1925). Kansas Permian insects. Part V. The orders Protodonata and Odonata. *American Journal of Science* **10**, 41–73.
- TSHERNOVA, O. A. (1965). Some fossil mayflies (Ephemeroptera, Misthodotidae) found in Permian deposits in the Ural Mountains. *Entomological Reviews* **44**, 202–207.
- VAN DEN BERG, C. & ELLINGTON, C. P. (1997). The three-dimensional leading-edge vortex of a ‘hovering’ model hawkmoth. *Philosophical Transactions of the Royal Society of London. Ser. B* **352**, 329–340.
- WAKELING, J. M. & ELLINGTON, C. P. (1997a). Dragonfly flight. I. Gliding flight and steady-state aerodynamic forces. *Journal of experimental Biology* **200**, 543–556.
- WAKELING, J. M. & ELLINGTON, C. P. (1997b). Dragonfly flight. II. Velocities, accelerations and kinematics of flapping flight. *Journal of experimental Biology* **200**, 557–582.
- WAKELING, J. M. & ELLINGTON, C. P. (1997c). Dragonfly flight. III. Quasi-steady lift and power requirements. *Journal of experimental Biology* **200**, 583–600.
- WEHL, A. R. (1945). Wing tips for tailless aeroplanes. *Aircraft Engineering* **17**, 259–266.
- WEIS-FOGH, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *Journal of experimental Biology* **59**, 169–230.
- WHITING, M. F., CARPENTER, J. C., WHEELER, Q. D. & WHEELER, W. C. (1997). The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences. *Systematic Biology* **46**, 1–68.
- WILLMOTT, A. P., ELLINGTON, C. P. & THOMAS, A. R. (1997). Flow visualization and unsteady aerodynamics in the flight of the hawkmoth, *Manduca sexta*. *Philosophical Transactions of the Royal Society of London. Ser. B* **352**, 303–316.
- WOOTTON, R. J. (1976). The fossil record and insect flight. In *Insect Flight. Symposia of the Royal Entomological Society of London No. 7* (ed. R. C. Rainey), pp. 235–254. Blackwell, Oxford, London, Edinburgh, Melbourne.
- WOOTTON, R. J. (1981). Support and deformability in insect wings. *Journal of Zoology, London* **193**, 447–68.
- WOOTTON, R. J. (1990). The mechanical design of insect wings. *Scientific American* **262**, 114–120.
- WOOTTON, R. J. (1991). The functional morphology of the wings of Odonata. *Advances in Odonatology* **5**, 153–169.
- WOOTTON, R. J. (1992). Functional morphology of insect wings. *Annual Review of Entomology* **37**, 113–140.
- WOOTTON, R. J. (1993). Leading-edge section and asymmetric twisting in the wings of flying butterflies (Insecta, Papilionoidea). *Journal of experimental Biology* **180**, 105–119.
- WOOTTON, R. J. (1995). Geometry and mechanics of insect hind wing fans: a modelling approach. *Proceedings of the Royal Society of London B* **262**, 181–187.
- WOOTTON, R. J. (1996). Functional wing morphology in Hemiptera systematics. In *Studies on Hemipteran Phylogeny* (ed. C. W. Schaefer), pp. 179–198. Entomological Society of America, Lanham, Maryland.
- WOOTTON, R. J. & ELLINGTON, C. P. (1991). Biomechanics and the origin of insect flight. In *Biomechanics and Evolution* (ed. J. M. V. Rayner and R. J. Wootton), pp. 99–112. Cambridge University Press, Cambridge.
- WOOTTON, R. J. & ENNOS, A. R. (1989). The implications of function on the origin and homologies of the dipterous wing. *Systematic Entomology* **14**, 507–520.
- WOOTTON, R. J., KUKALOVÁ-PECK, J., NEWMAN, D. J. S. & MUZÓN, J. (1998). Smart engineering in the mid-Carboniferous: how well could Palaeozoic dragonflies fly? *Science* **282**, 749–751.