

# The Biomechanics and Functional Diversity of Flight

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## Introduction

Insect presence on the earth is ancient, persistent and ubiquitous. Following the initial evolution of wings either in the late Devonian or early Carboniferous, pterygote insects rapidly diversified to become, by the mid- to late Carboniferous, a predominant feature of the terrestrial biota. This role has been retained to the present time, and today pterygote insects can be found in essentially all terrestrial ecosystems and on all continental land masses. The contemporary taxonomic richness of insects is famously high, with the number of described pterygote species exceeding 1 million, and the number of as yet undescribed species ranging potentially as high as 10 million. Among the arthropods, perhaps only mite diversity rivals that of the winged insects (Hammond, 1992; Walter and Behan-Pelletier, 1999), and much of mite species richness may derive from symbiotic associations with insects. Pterygotes today are major consumers of plant productivity and also serve as a nutritional resource for diverse arthropod and vertebrate taxa. A rough indication of the trophic influence exerted by insects is suggested by an estimate for their aggregate biomass. Approximately  $10^{18}$  insects may be alive worldwide at any given time (Williams, 1960). Assuming an average body mass of 1 mg, this number of individuals corresponds to an approximate biomass of  $10^{12}$  kg, a value roughly comparable to the total mass of the contemporary human population (Dudley, 2000). To this day, winged insects thus compete with humans at the level of primary trophic consumption.

Much of the pterygote success story can be ascribed to the initial evolution of flight and subsequent exploitation of the aerial environment. Winged

insects have clearly diversified and exploited a variety of terrestrial habitats far more effectively than have their sister taxon, the wingless apterygotes. Ample testimony to this enhanced diversification is provided by comparison of species richness among the two clades – pterygote insect species outnumber their apterygote counterparts by at least three orders of magnitude. Along with complete metamorphosis and lateral wing flexion, the ability to locomote in three dimensions is regularly cited in entomological textbooks as a causal factor underlying adaptive radiation in winged insects. Monophyly of wing origins (as well as of holometaboly and of the Neoptera) makes it difficult to test such diversification hypotheses directly, but the ability to fly obviously facilitates dispersal to and subsequent evolution within novel environments. Flight also figures prominently in diverse aspects of insect behaviour and ecology, including pollination, phytophagy, haematophagy, aerial predation, escape from predators and mating systems. Understanding of the evolution of functional diversity in flight mechanisms can therefore yield insight into major themes of insect biology.

In order to fly, animals must possess lift-producing structures or wings as well as particular configurations of dedicated muscles that effect wing flapping. Furthermore, a flight-control system based on both extero- and proprioceptive sensory mechanisms is necessary to permit regulation of aerodynamic force output and to enable manoeuvres. Flapping motions of the wings yield time-varying vortex flows over the wings and body that sustain the body mass against gravity and that can propel the body forwards, upwards or laterally. Many features of wing and body motions exhibit strong allometric variation, and in turn the aerodynamics of flight in insects is strongly scale-dependent. Body size itself has undergone substantial evolutionary change in insects, and much of present-day pterygote diversity derives from the process of miniaturization and the correlated acquisition of high wingbeat frequencies during flight. Modification of wings for non-aerodynamic purposes is another major trend underlying morphological diversification of insects. For example, tegminization and elytrization of the forewings for protective purposes is diagnostic of the Orthoptera and Coleoptera, respectively, but related modifications can be found in at least five other orders. Much of the glorious morphological diversity that we see today among the insects derives from transformations of what ancestrally were two pairs of aerodynamically functional wings. Evolutionary origins of such novel structures must therefore be examined if we are to understand their subsequent elaboration for both aerodynamic and non-aerodynamic purposes.

## **The Origins and Elaboration of Flight**

As with other volant animals, the origins and early evolution of winged insects have been the subject of abundant speculation based on a paucity of

empirical observations. Pterygotes are particularly difficult in this regard given that an approximately 45-million-year gap separates the occurrence of the earliest known winged insects (325 Mya) from fossils of their apterygote ancestors (395–390 Mya; Whalley and Jarzembowski, 1981; Shear *et al.*, 1984; Nelson and Tidwell, 1987; Labandeira *et al.*, 1988; Brauckmann and Zessin, 1989; Jeram *et al.*, 1990). Because pterygote insects appear abruptly in the fossil record with no obvious transitional forms, both the anatomical precursors to wings as well as the selective forces promoting their initial evolution remain unresolved. None the less, palaeobiological reconstruction can at least delineate possible scenarios of pterygote evolution. Most indirect evidence suggests that ancestral pterygotes (i.e. propterygotes) were terrestrial animals (Messner, 1988; Pritchard *et al.*, 1993; Dudley, 2000). Apterygote insects, the sister taxon of winged pterygotes, are almost exclusively terrestrial, and in fact the possession of a tracheal system by all hexapods predisposes these animals to life in air. Present-day aquatic habits in some insect taxa, and particularly in the larvae of the palaeopterous Ephemeroptera and Odonata, appear to be secondarily derived (Hinton, 1968; Hennig, 1981; Pritchard *et al.*, 1993). Invasion of either fresh- or saltwater by pterygote ancestors would also have had to surmount the formidable ecological obstacles that confront all metazoan taxa transiting from terrestrial to aquatic habitats (Vermeij and Dudley, 2000). Terrestriality in propterygotes therefore seems the most likely possibility, although only fossil evidence can empirically confirm this inference.

Hypotheses concerning wing origins, as elaborated elsewhere in this volume (Wootton, Chapter 3), distil to two major possibilities: initially fixed paranotal lobes that subsequently acquired mobility in flapping, or pre-existing mobile gills, gill covers or styli that then served aerodynamic purposes. This latter scenario generally presupposes ancestral aquatic habits in propterygotes, together with initially hydrodynamic use for what ultimately became aerodynamic structures. Related hypotheses propose transitional stages of drifting or skimming across the surface of water bodies as a precursor to free flight (Marden and Kramer, 1994, 1995; Kramer and Marden, 1997). In extant taxa, such behaviours appear to be derived rather than retained ancestral characters (Will, 1995; Ruffieux *et al.*, 1998; but see Thomas and Norberg, 1996), and no example exists of an aquatic insect that locomotes via projection of winglike structures across the water–air interface. Any suggestion of protowings operating either completely underwater or partially in air (and against the forces of surface tension) is also biomechanically implausible given the major physical differences between water and air and the correspondingly different flow regimes and patterns of force production in the two media (Denny, 1993; Dudley, 2000).

Independent of anatomical origins and ecological context, fossil as well as neontological evidence suggests that both larvae and adults of ancestral winged insects expressed winglets or winglike structures on thoracic as well as abdominal segments (Kukalová-Peck, 1978; Carroll *et al.*, 1995). In

addition to a possible aerodynamic role, a variety of other functional possibilities have been ascribed to these structures, including epigamic display during courtship (Alexander and Brown, 1963; Alexander, 1964) and thermoregulation (Whalley, 1979; Douglas, 1981; Kingsolver and Koehl, 1985, 1994). None of these roles are mutually exclusive. However, the most parsimonious hypothesis for the evolution of winglike structures is aerodynamic utility, possibly but not necessarily in concert with other functions. If terrestriality can be assumed for protopterygotes, then lift on the body as well as on winglets or protowings would have advantageously facilitated gliding performance (Ellington, 1991a). Escape from predators is the behavioural context classically presumed for jumping and gliding in protopterygotes, particularly given the ancestral nature of jumping and startle responses in hexapods, if not all arthropods (Edwards and Reddy, 1986; Kutsch and Breidbach, 1994; Edwards, 1997). Predatory pressures on protopterygotes within late Palaeozoic ecosystems were likely substantial, and the increasing spatial complexity of contemporaneous vegetation provided further advantages to escape strategies that facilitated movement in all three spatial directions (Dudley, 2000).

Once the aerodynamic utility of winglets was established, then winglet mobility (either acquired ancestrally or subsequently derived) would have facilitated greater aerial manoeuvrability and/or enhanced flight performance. Greater mobility in the air would obviously have been advantageous for purposes other than escape from predators, in particular for mate location and for resource acquisition from the rapidly diversifying terrestrial flora. Wings on the prothoracic segment, as well as on abdominal segments, appear to have been lost early in pterygote evolution, possibly because of deleterious aerodynamic interaction among winglets of adjacent segments (Grodnitsky, 1995). Instead, wings of the two posterior thoracic segments increased in size and became aerodynamically dominant. This locomotor dedication of the meso- and metathoracic segments would have been accompanied by hypertrophy in pterothoracic musculature, elaboration of the axillary apparatus, and systematic increases in aerodynamic force production mediated by changes in stroke amplitude and wingbeat frequency (Dudley, 2000). By the middle of the Carboniferous, pterygotes are impressively diversified into about 15 orders, some with seemingly modern morphologies (Wootton, 1990; Kukalová-Peck, 1991; Labandeira and Sepkoski, 1993). Major ordinal-level differentiation of pterygotes thus occurred in the Lower Carboniferous over a time period spanning 30–40 Mya.

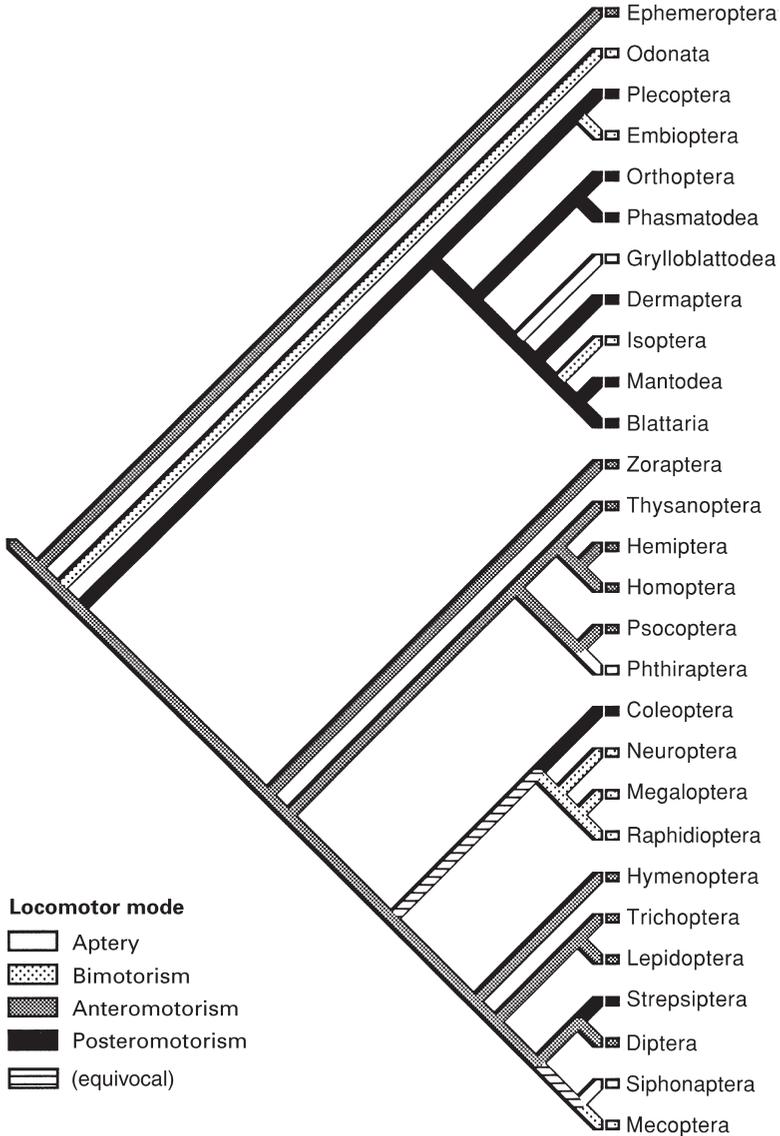
Many Carboniferous insects possessed homonomous wings (i.e. wings of approximately equivalent size, shape and function) that were probably limited to low-amplitude flapping (e.g. Diaphanopteroidea, Megasecoptera, many Palaeodictyoptera; Carpenter, 1992). However, morphological differentiation in the size of meso- and metathoracic wings is equally evident in this fauna. Differences in relative wing size in turn suggest varying aerodynamic roles of the fore- and hindwings. Schwanwitsch (1943, 1958)

applied to pterygotes the terms of anteromotorism, posteromotorism and bimotorism to describe the conditions of enlarged forewings, enlarged hindwings or homonomous wings, respectively. Because force production in flapping flight depends not only on wing area but also on the particulars of wing motion, relative size alone does not necessarily indicate the extent of aerodynamic contribution. In the contemporary fauna, however, these two measures are broadly congruent (Dudley, 2000). Ipsilateral wing differentiation and expression of heteronomous wings were well underway by the Upper Carboniferous. For example, some Palaeodictyoptera possessed hindwings only half the area of the forewings, whereas expanded hindwings of the contemporaneous Protorthoptera are characteristic of posteromotorism. Hindwings were also much reduced or absent in the palaeodictyopteroid lineage Permothemistida (Carpenter, 1992).

Among extant orders, antero- and posteromotorism occur at approximately equal frequencies, although posteromotorism is (with the exceptions of the Coleoptera and Strepsiptera) mostly confined to the exopterygotes (Fig. 2.1). The most parsimonious reconstruction of the ancestral locomotor mode in extant pterygotes suggests anteromotorism rather than homonomous bimotorism (Dudley, 2000; see also Fig. 2.1), although this result may in part derive from exclusion of extinct Palaeozoic taxa from the analysis. For example, Ephemeroptera of the Carboniferous were characterized by equally sized fore- and hindwings (Carpenter, 1992), in contrast to the anteromotoric condition of extant mayflies. If bimotorism is assumed for the Ephemeroptera, parsimonious reconstruction of the ancestral locomotor mode in pterygotes yields bimotorism rather than anteromotorism. Bimotorism persists to this day in at least seven orders (Fig. 2.1), and the salient example of dragonfly manoeuvrability indicates no necessary correlation between flight performance and this particular locomotor mode. Evolution of heteronomous wing pairs has been, however, a major theme in ordinal-level innovation. Subsequent to the great Carboniferous radiations, the species-rich and posteromotoric Coleoptera appeared with fully elytrized forewings by the mid- to late Permian. Similarly, the major orders Hymenoptera and Diptera originated in the Triassic, with the hindwings relegated to either a reduced or no direct aerodynamic role, respectively.

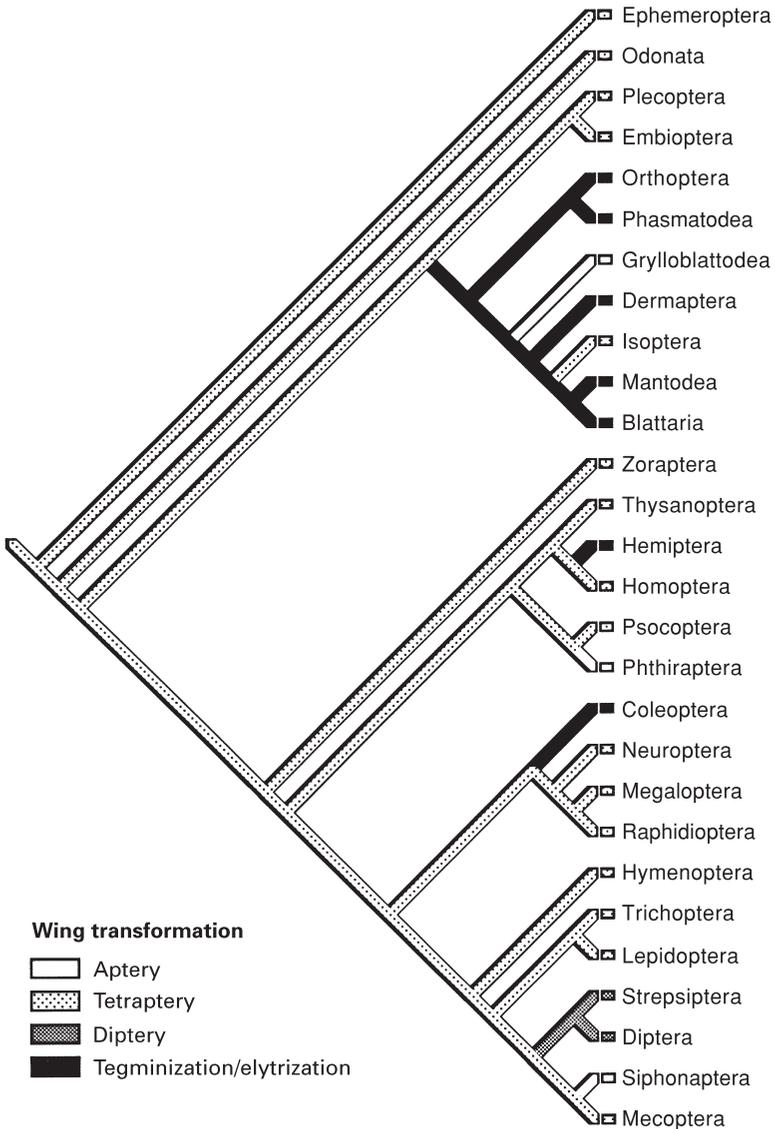
Parallel with locomotor dedication of either the fore- or hindwings, wing transformation for non-aerodynamic purposes has been widespread in pterygote evolution (Fig. 2.2). True diptery characterizes the Strepsiptera and the eponymous Diptera, with the fore- and hindwings, respectively, being miniaturized and used for purposes of flight control (Pix *et al.*, 1993; Dickinson, 1999). Dipterous anteromotorism is, however, a rare outcome among pterygotes. Much more common has been the assumption of a protective role by the forewings. Forewings in many insects tend to be slightly thickened relative to the hindwings. Also, tegminization and elytrization have occurred at least three times at the ordinal level, and possibly many more times if tetraaptery in the Isoptera is a retained ancestral trait (Fig. 2.2).

Coriaceous tegmina are characteristic of the Blattaria, Dermaptera, Mantodea, Orthoptera, Phasmatodea, and of some Homoptera. In some Phasmatodea, the remigium of the hindwing is also thickened and serves to protect the vannus (R. Wootton, personal communication). Elytra of the



**Fig. 2.1.** Phylogenetic distribution of locomotor mode among extant pterygote orders (tree topology from Kristensen, 1991, 1997; Pashley *et al.*, 1993; Whiting *et al.*, 1997). MacClade 3.0 (Maddison and Maddison, 1992) was used to generate the most parsimonious reconstruction of ancestral character states.

Coleoptera have much reduced aerodynamic roles relative to the hindwings, and provide for greater mechanical resistance to crushing in conjunction with increased sclerotization of the body as a whole (Dudley, 2000). A similar functional role may be hypothesized for tegmina and for hemipteran



**Fig. 2.2.** Phylogenetic patterns of wing transformation among pterygote orders. These designations describe only the general trend within each order; further details as well as exceptions to ordinal-level characterizations can be found in Dudley (2000).

hemelytra; all such cases of mesothoracic specialization are necessarily associated with posteromotorism (Fig. 2.1).

By contrast, anteromotorism is typically characterized by the retention of aerodynamically functional hindwings, albeit with reduced surface area. Diptera are exceptional in this regard given their miniaturized halteres. In other anteromotoric orders, hindwings are only somewhat reduced in relative size and tend to operate in phase with the forewings. Such orders are functionally dipterous while retaining four wings, although some exceptions exist to this characterization (e.g. the miniaturized hamulohalteres of male Coccidae). In most anteromotoric groups, however, the hindwings are either mechanically coupled to or physically overlapped by the forewings. Physical overlap of ipsilateral wings is termed amplexiform coupling, and is characteristic of mayflies (Ephemeroptera) and butterflies. Alternatively, direct mechanical coupling between wings (e.g. hamuli of Hymenoptera, frenulum and jugum of moths) may be associated with the evolution of high wingbeat frequencies and with further reduction in relative hindwing area (Dudley, 2000). Evolutionary modifications of potentially ancestral wing homonomy have thus been functionally diverse. In addition to the roles of aerodynamic force production and possibly physical protection by the forewings, insect wings may also serve a variety of behavioural roles, including sound production and visual communication. None of these functions are mutually exclusive, although the role of aerodynamic force production must remain paramount for at least one wing pair. Having broadly delineated the range of pterothoracic diversification evident among extant orders, we now turn to the biomechanical specifics of aerodynamic force production through wing flapping.

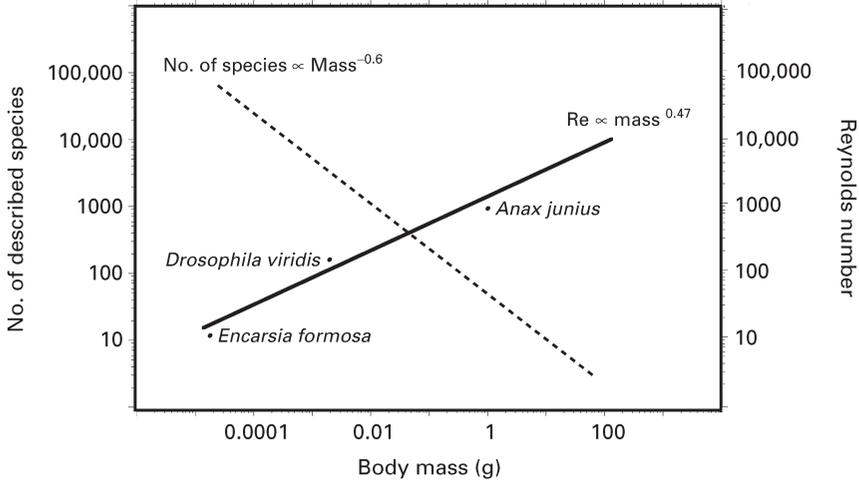
## Kinematics and Aerodynamics

Diversity in wing shape and form is matched by functional divergence in wingbeat motions (i.e. kinematics) and in the underlying aerodynamics of flight. Two of the most important kinematic features of flight are the frequency of flapping motions and the speed of the entire body relative to the surrounding air (i.e. the airspeed). Much variation in these parameters is associated with differences in body mass ( $m$ ), a quantity which in the extant fauna ranges over seven orders of magnitude. Such variation in body mass in turn yields major differences in wingbeat kinematics among different taxa. For example, large butterflies exhibit wingbeat frequencies as low as 5 Hz, whereas some small flies have frequencies as high as 1000 Hz. For the extant fauna, wingbeat frequencies span approximately three orders of magnitude and vary with  $m^{-0.24}$  (Dudley, 2000). Insect flight speeds are also allometrically dependent, varying theoretically in proportion to  $m^{0.17}$ . Empirical results demonstrate that larger insects fly faster, and insect airspeeds in general range from 0.5 to 10 m s<sup>-1</sup>. Steady forward flight requires the

maintenance of a constant force balance to offset gravity and to create thrust that offsets drag on the body. Also, the transient generation of aerodynamic forces and rotational torques can yield near-instantaneous turns, accelerations, and directional changes that form the basis of aerial manoeuvrability in insects. Hovering, backward and even sideways flight are also common in many taxa.

Aerodynamically, the forces generated by flapping wings vary with wing morphology, with the kinematic details of motion, and with the density and viscosity of the surrounding air. For any object moving within a fluid, density of the fluid influences the inertial characteristics of the flow field around the object, whereas fluid viscosity determines the magnitude of shear forces exerted over the object's surface. The ratio of inertial to viscous forces thus varies with the ratio of fluid density and viscosity, and is also linearly proportional to the object's dimensions and to its velocity relative to the fluid. The four variables of density, viscosity, linear dimension and the relative velocity can be combined to yield a dimensionless parameter termed the Reynolds number ( $Re$ ) that broadly characterizes the nature of forces within moving fluids (Vogel, 1994). At low  $Re$ , flow is highly viscous and shear forces within the fluid exert a predominant influence. Flow is usually laminar below  $Re$  of  $10^3$ – $10^4$ , whereas turbulence and inertially driven flows become more pronounced at higher  $Re$ . Values of the  $Re$  for large insects typically range from  $10^2$  to  $10^4$  (Dudley, 2000). Most insects, however, are fairly small by anthropomorphic standards, and the  $Re$  for the majority of these taxa is in the range of  $10^0$ – $10^2$  (Fig. 2.3). A quantitative comparison of the two allometries indicated in Fig. 2.3 suggests that approximately 85% of the fauna hovers with  $Re$  for the wings below 1000, and that nearly one-half of the fauna (47%) hovers at  $Re$  below 100. Flight at such low Reynolds numbers is aerodynamically challenging – viscosity exerts a predominant influence on moving appendages, and wing flapping is often analogized to swimming in molasses.

Given that most insects fly in fairly low  $Re$  regimes, one basic question in biomechanical analysis concerns the magnitude of aerodynamic forces on the flapping wings, as well as the associated expenditure of mechanical power. In both hovering and forward flight, flapping of wings results in continuous changes in the speed and orientation of the wings relative to the surrounding fluid. These conditions violate many assumptions of traditional aerodynamic analysis, and the application of conventional aerodynamics to wing flapping by insects typically yields force balances inconsistent with those known to apply in free flight (Ellington, 1984; Dudley and Ellington, 1990; Dudley, 2000). Instead, unsteady aerodynamic mechanisms pertain that include such effects as wing acceleration, wing rotation and airflow along the length of the wing (Ellington, 1995). At  $Re$  corresponding to the hovering flight of the hawkmoth *Manduca sexta* (L.) ( $Re \sim 1000$ ), direct visualization of flow around mechanically flapping wings together with computational modelling have revealed the presence of a leading-edge vortex attached dorsally to the



**Fig. 2.3.** Allometry of insect species diversity and of the Reynolds number ( $Re$ ) during hovering flight. Values of body mass and the corresponding  $Re$  are indicated for three representative species. Species numbers are approximate worldwide values and do not reflect the reduced number of insect species at very small body masses. The  $Re$  refers to values for the wing chord in hovering flight; see Dudley (2000) for derivation of the associated allometry.

surface of the wing (Ellington *et al.*, 1996; van den Berg and Ellington, 1997a,b; Liu *et al.*, 1998). High-speed rotation of the leading-edge vortex creates a low-pressure zone above the wing, and transiently increases lift production above that feasible through linear translation at a constant velocity. At lower  $Re$  corresponding to the flight of smaller insects the size of *Drosophila* ( $Re \sim 100$ ), leading-edge vortices also predominate, but supplemental unsteady forces derive from wing rotation about the longitudinal axis at the ends of the half-stroke (Dickinson *et al.*, 1999). The high flapping velocities associated with small body size also yield high rotational velocities of the wings during pronation and supination at the ends of the up- and downstrokes, respectively. Thus, rotational circulation and associated force production are likely to be more pronounced in small insects. At such low  $Re$ , the presence of vortices shed previously from the flapping wings also appears to advantageously influence unsteady force production (Dickinson *et al.*, 1999). A diversity of unsteady aerodynamic mechanisms characterizes the flight of insects, and body size plays a major role in determining the relative importance of different kinds of aerodynamic forces.

Independent of the physical nature of these mechanisms, the predominant force produced by flying insects is directed vertically to offset gravity acting on the body mass. Regulation of forward airspeed is attained primarily by changes in the direction but not magnitude of the net aerodynamic forces on the wings. Except at very high forward speeds, thrust is small relative to

vertical force production and the magnitude of the resultant aerodynamic vector remains approximately constant. Reorientation of the resultant force vector, however, is most simply attained by altering the angle of inclination between the plane of wing motions and the horizontal plane. Given the generally fixed dorsoventral nature of wing flapping motions, vertical and horizontal partitioning of total force output is effected through changes in body angle, a parameter which usually shows an inverse relationship with forward airspeed (Dudley, 2000). In turn, changes in more subtle kinematic features such as the mean positional angle of the wings and in rotational velocities during pronation and supination contribute to the regulation of body angle. Wing motions are bilaterally symmetric in forward and hovering flight. During manoeuvres, however, even small asymmetries in contralateral wing motions at different stages of the wingbeat have major implications for generation of roll, yaw and pitching moments. Relative body elongation, wing flexibility and the use of four rather than two wings (as characterizes the highly manoeuvrable dragonflies) also influence the extent of rotational and axial agility in the air (Dudley, 2000).

Application of aerodynamic models to known wingbeat kinematics allows calculation of the associated energetic costs of flapping flight. Insect flight represents an extreme of metabolic expenditure among animals, with rates of oxygen consumption during flight exceeding resting metabolic rates by a factor of 50–200 (Kammer and Heinrich, 1978; Casey, 1989). Also, flight in insects is powered exclusively through aerobic pathways. Metabolic power input and the actual expenditure of mechanical power for useful aerodynamic work (the mechanical power requirements) are related by the overall efficiency of the flight muscle. Because flight is so energetically expensive, selection has presumably acted to minimize mechanical power expenditure and to maximize flight muscle efficiency. Comparative studies of flapping energetics thus permit analysis of evolutionary optimization at the level of biomechanical performance. The variation in mechanical and metabolic power requirements with forward airspeed, the so-called power curve, is also of interest because of implications for optimal strategies of airspeed selection. Aerodynamic theories that evaluate the power curve quantitatively have been extensively applied to volant vertebrates (Norberg, 1990), but have received much less application to the flight of insects. Existing aerodynamic theories are also inadequate to incorporate the aforementioned unsteady aerodynamic effects now known to be pervasive in insect flight, but none the less provide a useful baseline estimate for the costs of flight.

Such aerodynamic modelling of bumblebees in forward flight suggests that mechanical power requirements are approximately constant over an airspeed of 0–4.5 m s<sup>-1</sup> (Dudley and Ellington, 1990). By contrast, two moth species as well as various odonates exhibit substantial increases in mechanical power expenditure with forward airspeed (Dudley and DeVries, 1990; Wakeling and Ellington, 1997; Willmott and Ellington, 1997). Power requirements at hovering and intermediate airspeeds are nominally similar,

but then increase substantially at higher speeds, yielding a 'J'-shaped power curve (Ellington, 1991b). The precise shape of the power curve, however, derives from trends in individual components of power expenditure. The power required to overcome drag forces on the body (the parasite power) increases approximately with the cube of forward airspeed. Also, the power to overcome drag forces on the wing (the profile power) is strongly dependent on airspeed (Dudley, 2000), and a steep overall rise in mechanical power requirements is evident when insects fly faster. The power curve for most taxa is positively curvilinear under such circumstances, and the choice of airspeed during flight will accordingly have major energetic implications. Also, the relative costs of three-dimensional mobility may be reduced for small insects. Mass-specific power expenditure in forward flight increases with  $m^{0.05-0.19}$ , suggesting reduced relative costs of horizontal movement for smaller taxa (Dudley, 2000). Body size alone thus exerts a major influence on the kinematics, energetics and aerodynamics of flight in insects.

## Gigantism and Miniaturization

A major feature of pterygote evolution with important flight-related consequences has been historical change in body size. Although direct palaeontological evidence is not available, ancestral body lengths of pterygotes were probably in the range of 2–4 cm (Flower, 1964; Wootton, 1976; Labandeira *et al.*, 1988). Following pterygote emergence and the diversification of the Palaeoptera and the exopterygote Neoptera, various endopterygote Neoptera appeared by the Upper Carboniferous and radiated extensively through the remainder of the Palaeozoic. Quantitative information of body-size distributions is not available for the late Palaeozoic fauna, but substantial increases in body length appear to have occurred by the mid-Carboniferous. Gigantism relative to today's forms was typical of many Carboniferous and Permian insects as well as of other contemporaneous arthropods (Briggs, 1985; Graham *et al.*, 1995; Dudley, 1998). Giant forms were characteristic of at least three entire orders (Megasecoptera, Palaeodictyoptera, Protodonata), and also occurred among other pterygote as well as apterygote hexapods.

The most parsimonious explanation for late Palaeozoic gigantism is an increased oxygen concentration of the late Palaeozoic atmosphere, possibly to values as high as 35% relative to today's value of 20.9% (Berner and Canfield, 1989; Berner, 1997, 1998). For arthropods with tracheal respiratory systems, diffusional limits on oxygen supply probably constrain maximum body size. Greater partial pressures of oxygen, together with higher diffusion constants associated with an increased total pressure of the atmosphere, would relax these diffusional constraints and permit evolution of giant forms (Dudley, 1998). Furthermore, all giant arthropod taxa of the late Palaeozoic were extinct by the mid- to end-Permian (Carpenter, 1992; Graham *et al.*,

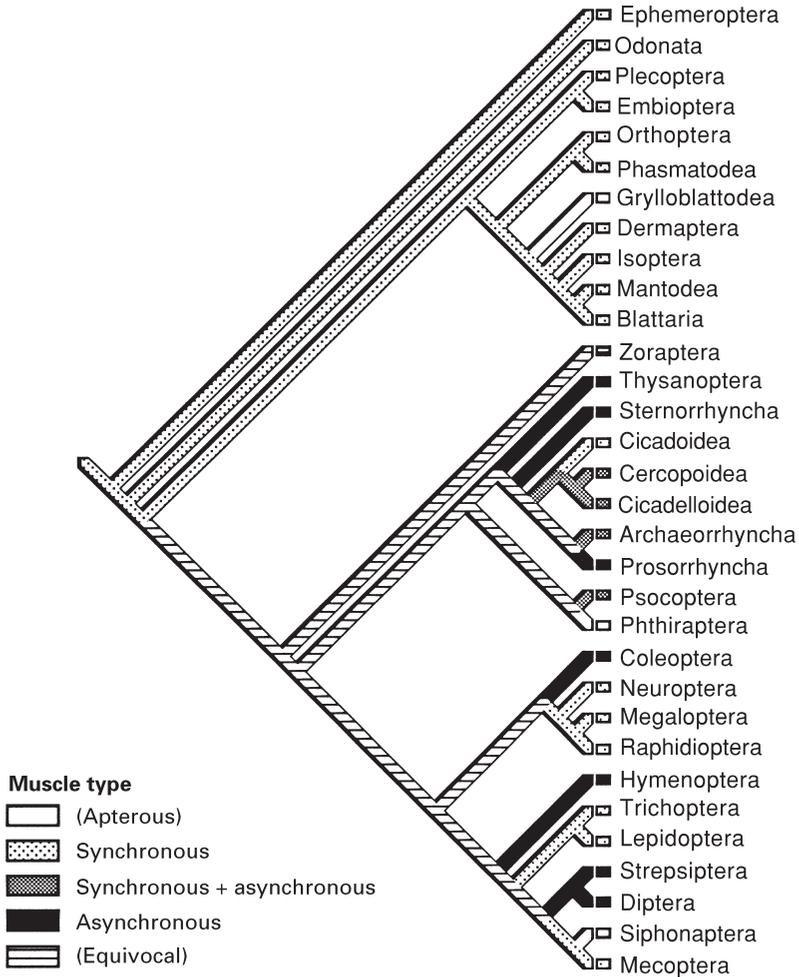
1995; Dudley, 1998), exactly as would be predicted by a decline in atmospheric oxygen concentration and concomitant asphyxiation of giant forms (Berner and Canfield, 1989; Graham *et al.*, 1995). Detailed analysis of phyletic size change within diffusion-limited taxa thus represents an important bioassay for effects of atmospheric hyperoxia in the late Palaeozoic, as well as for a secondary hyperoxic episode in the Cretaceous/Tertiary (Dudley, 1998).

In sharp contrast to these Palaeozoic giants, the contemporary insect fauna is characterized by a remarkable diversity of miniaturized forms. For example, mean adult beetle body length lies between 4 and 5 mm (May, 1978; Crowson, 1981). Much of the wealth of dipteran and hymenopteran diversity is similarly associated with small body sizes, particularly among the parasitoid and hyperparasitoid taxa. No global estimate of insect body size distribution is presently available. However, existing data can be used at least to approximate body-length distributions for the North American fauna. Arnett (1985) provided species counts together with minimum and maximum body lengths (or in some cases, wing length) for each family present in the continental fauna. If the number of species within a family can be assumed to be inversely proportional to the square of body length (May, 1978), then mean body length within families and for the entire fauna can be calculated. This exercise suggests that the average interspecific body length for the North American insect fauna is about 7 mm. Note also that taxa composed of smaller insects are less likely to be well sampled than are those with more massive species. What are the historical origins and biomechanical correlates of such pronounced body miniaturization among pterygotes?

As mentioned previously, wingbeat frequencies are inversely proportional to body size. Insects less than 1 cm in body length typically fly with wingbeat frequencies and thus with contraction frequencies of the flight muscle in excess of 100 Hz (Dudley, 2000). Such rapid oscillations can only be attained using the specialized asynchronous flight muscle unique to particular lineages of pterygote insects. Asynchronous flight muscle contracts repeatedly in response to only one nervous impulse through a biophysical mechanism termed stretch-activation (Pringle, 1949, 1978). Contraction strains tend to be lower in asynchronous muscle relative to those of synchronous muscles characterized by only one contraction per activational nervous impulse. However, the higher oscillation frequencies of the former muscle type yield substantially higher power output during repetitive contraction. Energetic savings may also be associated with asynchronous flight muscle because of a much reduced need for calcium cycling that provides the molecular signal for myofibrillar activation (Josephson and Young, 1985).

Although phylogenetically basal pterygote orders possess synchronous flight muscles, asynchronous flight muscle has evolved repeatedly within and among more derived pterygote lineages (Fig. 2.4). The paraphyletic assemblage Homoptera is particularly characterized by a complex representation of synchronous and asynchronous muscle types (Cullen, 1974; Dudley,

2000). Asynchronous flight muscle is phylogenetically derived relative to synchronous muscle, although the exact nature of transitional forms remains unclear. Also, reversion from asynchronous to synchronous flight muscle is physiologically unlikely, but systematic phylogenetic analysis is not possible because muscle types are not well-resolved for key taxa (e.g. Zoraptera;



**Fig. 2.4.** Phylogenetic distribution of asynchronous flight muscle following TiegS (1955), Boettiger (1960), Cullen (1974), Smith (1984), and Smith and Kathirithamby (1984). Note that the paraphyletic taxon Homoptera is here represented at the lower taxonomic levels of suborders and superfamilies. Relatedness of homopteran and hemipteran lineages follows Campbell *et al.* (1994, 1995), Sorensen *et al.* (1995), von Dohlen and Moran (1995), and Schaefer (1996). Equivocal branch designations indicate either an unknown (e.g. Zoraptera) or an unresolved character state.

Fig. 2.4). Most muscle type designations have also been made using morphological inference (i.e. reduced sarcoplasmic reticulum) rather than by direct physiological measurement. Furthermore, asynchronous flight muscle may be present in a number of insect taxa supplemental to those indicated in Fig. 2.4, most importantly in certain mayfly lineages (Dudley, 2000).

Because of the obligate association between elevated wingbeat frequencies and small body size, the taxonomic and numerical preponderance of small insects may have been facilitated by the acquisition of asynchronous flight muscle (Dudley, 1991, 2000). For example, three of the four largest orders (Coleoptera, Diptera and Hymenoptera) possess asynchronous flight muscle. Similarly, comparison of sister taxa that differ in flight muscle type suggests a decrease in body size and an increase in species number following acquisition of asynchronous flight muscle, at least for the North American fauna (Table 2.1). This association can be rigorously tested using an independent contrast analysis that controls for phylogenetic relatedness among taxa. Application of such a method to the character distribution portrayed in Fig. 2.4 demonstrates a statistically significant relationship between possession of asynchronous flight muscle and species richness (one-tailed sign test,  $n = 6$ ,  $P = 0.016$ ; Dudley, 2000). Higher wingbeat frequencies are furthermore associated with greater force production that enables a reduction in effective wing area relative to body mass.

**Table 2.1.** Number of species and mean body length for lineages in the North American fauna possessing only synchronous flight muscle, and for their sister clades characterized either partially or exclusively by possession of asynchronous flight muscle.

Clade possessing synchronous flight muscle:	No. of species	Mean body length (mm)	Sister clade either partially or exclusively possessing asynchronous flight muscle:	No. of species	Mean body length (mm)
Cicadoidea	166	34.5	[Cercopoidea + Cicadelloidea]	2,820	5.8
Archaeorrhyncha (=Fulgoromorpha)	530	6.7	Prosorrhyncha (= Hemiptera)	3,587	6.1
[Neuroptera + Megaloptera + Raphidioptera]	349	17.9	Coleoptera	23,592	6.0
[Mecoptera + Siphonaptera] <sup>a</sup>	393	3.3	[Diptera + Strepsiptera]	17,023	7.0

<sup>a</sup>The Mecoptera alone comprise 68 species with an estimated mean body length of 7.7 mm.

Species numbers are taken from Arnett (1985); calculations of mean body length are described in the text.

Correspondingly, one wing pair can be used in non-aerodynamic roles, as in the hemelytra of Hemiptera, the elytra of Coleoptera and the halteres of Diptera. Acquisition of asynchronous flight muscle has thus played a major role in ordinal-level insect diversification.

Another important consequence of miniaturization concerns a necessary reduction in flight speeds and a correspondingly increased influence of ambient winds on the flight trajectory. Most small insects cannot fly faster than typical wind speeds, and the majority of the extant fauna must accordingly fly close to the ground or within vegetation if intentionally directed flight is to be attained (Dudley, 1994). Conversely, long-distance dispersal in miniaturized taxa derives primarily if not exclusively from entrainment by ambient winds. The difficulty of measuring simultaneously the airspeed of small insects and their local wind speed precludes detailed analysis of endogenous contributions to wind-assisted displacement. However, even 'passive' drifting with winds must involve considerable energetic expenditure in order to stay aloft. Small insects being convectively dispersed must offset their body weight aerodynamically, either while maintaining a forward airspeed or while hovering within a moving air volume. If the goal of dispersal is to maximize the horizontal distance travelled, then flight at the minimum power speed maximizes time aloft and thus the extent of wind-assisted displacement. Given preceding arguments that power curves for the majority of insect taxa are strongly curvilinear, this speed is likely to be relatively low for 'J'-shaped power curves, and could be very close to the minimum power speed. A general rule for small insects maximizing long-distance displacement might then be to hover and simply to maintain vertical position in the moving air. Logistically, the measurement of airspeeds on minute insects flying under natural conditions hundreds of metres from the earth's surface remains a challenging problem. Systematic reduction in body size, however, must profoundly influence long-distance strategies of dispersal and resource location in insects.

## The Evolutionary Escalation of Flight Performance

Flight plays a central role in the lives of most pterygotes. A partial list of important insect behaviours mediated or facilitated by flight includes pollination, phytophagy, haematophagy, escape from predators and mate acquisition. In such various contexts, both natural and sexual selection have probably demanded ever-increasing flight performance through evolutionary time, whereas various agents of selection are often mutually reinforcing. Moreover, forces of both intra- and intersexual selection often act synergistically on manoeuvrability and flight capacity, thereby promoting rapid evolution in these traits. For example, dragonflies defend territories and chase out male conspecifics (intrasexual selection), pursue females (intersexual selection), capture prey items in the air (natural selection for aerial

attack), and evade both aerial and terrestrial predators via flight (natural selection for aerial escape). Multiple modes of selection have thus probably acted to enhance flight performance in this famously manoeuvrable taxon.

Such an evolutionary outcome may be general for volant taxa. Flying insects are regularly the subject of attack by insectivorous birds and bats, escape from which requires increased manoeuvrability and/or greater flight speeds. Males of many insect species also attempt to capture females during chases, thus selecting for manoeuvrability in the context of mate choice (Thornhill and Alcock, 1983). Because performance traits that are under sexual selection can evolve rapidly (Andersson, 1994), synergistic interaction between reproductive behaviour and overall flight performance is likely to have been pronounced for those insects with aerial components to their mating systems. In contrast, sexual selection can potentially exaggerate secondary male characters at the expense of flight-related morphological investment (e.g. Kawano, 1997). For winged insects generally, however, intense selection on aerodynamic performance and the underlying biomechanics of flight is imposed in a variety of con- and heterospecific contexts. Such diverse evolutionary forces can, in general, result in reciprocal escalation between biotic selective agents and the target of selection (Vermeij, 1987), yielding ever-increasing levels of performance. Among all animal taxa, flying insects may best exemplify the extent of behavioural and physiological diversification that can arise as a consequence of such evolutionary escalation.

One of the major co-evolutionary interactions of the terrestrial biosphere concerns relationships between insects and plants. Phytophagy and pollination by insects are particularly influenced by three-dimensional aerial mobility, the capacity for which dramatically increases access to nutritional resources and suitable oviposition sites. The relative importance of phytophagy is difficult to overestimate for the present-day fauna, as approximately 85% of extant insect species feed on plants at some stage in their life cycle (Strong *et al.*, 1984). Such interactions probably began at the very outset of flight in pterygotes, given that the fossil record demonstrates feeding on plants by insects in the Upper Carboniferous and early Permian (Labandeira and Phillips, 1996a,b; Rasnitsyn and Krassilov, 1996). Similarly, angiosperms are pollinated primarily by flying insects, in particular by the Coleoptera, Diptera, Hymenoptera, Lepidoptera and Thysanoptera (Kevan and Baker, 1983; Proctor *et al.*, 1996). With the exception of the Lepidoptera, insects from these orders possess asynchronous flight muscle and are often miniaturized forms that hover at flowers either prior to or during pollination. Small insects can also act as wind-dispersed pollen vectors that become aeri-ally entrained by prevailing winds, but also that exert some measure of behavioural choice once in the vicinity of nectar-bearing plants. In contexts both of phytophagy and pollination, selection for improved flight efficiency and capacity has probably been complementary to modes of selection for greater flight performance over much shorter time scales.

## Conclusions

The evolution of wings in the late Palaeozoic was a defining event for subsequent hexapod radiations on (and above) the surface of the earth. Equally important to the evolutionary diversification of insects have been repeated events of miniaturization, a process enabled by acquisition of asynchronous flight muscle and elevated wingbeat frequencies during flight. Ordinal-level patterns of wing transformation for non-aerodynamic purposes have similarly been influenced by high flapping frequencies, an effect most clearly evidenced by the elytra of Coleoptera and the halteres of Diptera. Most insects are fairly small and fly in Reynolds-number regimes strongly influenced by the viscosity of air. The combined effects of wing flapping and rotation at the ends of half-strokes yield strongly unsteady airflows, leading-edge vortices, and aerodynamic forces well in excess of those associated with steady-state wing translation. Flight has been an essential underpinning to diverse features of insect ecology and behaviour, including aerial mating systems, phytophagy and the pollination of angiosperms. Low flight speeds derived biomechanically from small body sizes, however, indicate that ambient flight trajectories are often dominated by ambient winds. Forces of both natural and sexual selection have contributed synergistically to the evolution of insect flight performance and manoeuvrability, yielding the wonderfully agile taxa that to this day compete with *Homo sapiens* for dominance of the terrestrial biosphere.

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