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SELECTIVE FACTORS IN THE EVOLUTION OF INSECT WINGS

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PERSPECTIVES AND OVERVIEW

The evolution of wings and flight undoubtedly contributed to the unparalleled success and diversity of insects. In the fossil evidence, the appearance of pterygotes coincides with the remarkable diversification of insects beginning in the Paleozoic (7, 79). Understanding the evolutionary origins of insect wings and flight is thus a key to understanding this diversification.

The study of flight's evolutionary origins is also of general interest. Flight represents a major innovation that has evolved independently in several different animal groups. How such key innovations can evolve has been one of the major questions in evolutionary biology since the time of Darwin. Many of Darwin's early critics argued that natural selection was not adequate to explain the many transitional steps required for the evolution of these complex structures and functions: What good is half an eye, or a nub of a wing (24, 49)? This challenge required that natural selection act directionally to favor a series of intermediate, transitional forms. In response to it, Darwin proposed the notion that the functional factors selecting for changes in the

trait may in fact change during the evolution of that trait. This idea—functional shift with structural continuity—remains a cornerstone for our ideas on the evolution of key innovations (46).

The problem, however, with a key innovation is that it typically represents a singular evolutionary event and is therefore difficult to study. Comparative methods are unhelpful, and we have no means of testing hypotheses except in a post hoc fashion (45). This situation is especially vexing for insect wings because of the lack of an adequate fossil record from the crucial time period (see below). Consequently, many of the basic ideas about both the morphological origins of wings and the selective factors in the evolution of flight have been around for some time and regularly are in and out of vogue. How can we ensure that these changes represent scientific progress rather than mere fashion?

The approach taken in this review might best be termed bounded ignorance. Rather than attempt to identify a profile for the most likely protopterygote, we describe a range of possible morphologies that seem consistent with available evidence. Instead of constructing a specific scenario for the selective factors involved in the evolution of flight, we explore a variety of plausible functions of which we ask: Do small changes in wing morphology result in functional changes (that is, would selection on wing morphology result)? As we shall see, in many cases our conclusions about selective factors depend crucially on aspects of size and morphology of which we remain largely ignorant.

ORIGINS OF INSECT WINGS

Neontological Evidence

The anatomical origin of insect wings has been controversial since pre-Darwinian times (50, 54). Most of the discussion has focused on two alternatives. One view advocates a pleural origin for protowinglets that were primitively articulated and moveable (37, 38, 77, 78). Kukalova-Peck and coworkers (38–41) recently argued that these structures were derived from outer appendages [exite (38) or exite plus endite (70)] of the arthropod leg above the subcoxa and that they occurred on both thoracic and abdominal segments (Figure 1*b*). The other view argues that winglets were derived from extensions of tergal paranotal lobes, and were primitively immobile (27, 58, 59). The paranotal hypothesis thus suggests that the wing articulation is derived secondarily. The current evidence seems to more strongly support the pleural hypothesis. First, the juveniles of Paleoptera from the Paleozoic have thoracic and abdominal winglets that are articulated; in contrast, extant Paleopterous nymphs have thoracic winglets that are fused with the terga (8, 37–39). The latter suggests that fusion with the terga, as in paranotal lobes, is the derived condition. Second, recent neurophysiological studies show that interneurons

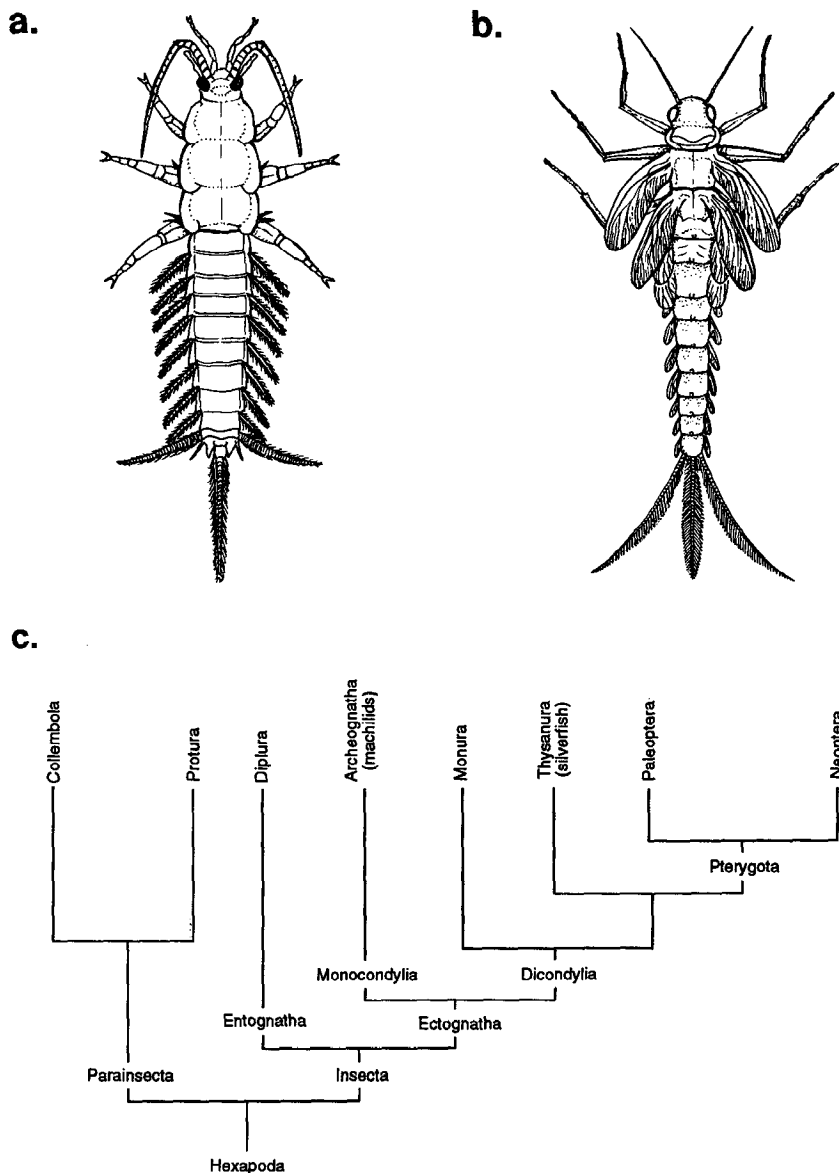


Figure 1 Relevant insect fossils and hexapod phylogeny. (a) Paleozoic (Upper Carboniferous) silverfish (*Thysanura*). Note presence of thoracic side lobes and abdominal leglets. Redrawn from Figure 15 in Ref. 38. (b) Typical Paleozoic (Lower Permian) mayfly (Protoereismatidae: Ephemeroptera), older nymph. Note presence of both thoracic and abdominal protowings. Redrawn from Figure 28 in Ref. 36. (c) Basic phylogeny of major hexapod and insect groups, based on Kukalova-Peck (38). Note the sister group relationship between *Thysanura* and Pterygota. This phylogeny differs in some respects from those by Hennig (25) and Kristensen (35), for example in the position of Diplura.

involved in the generation of flight motor activity occur in the first three abdominal ganglia in some insects (as well as in thoracic ganglia) (13, 62). The existence of apparently homologous interneurons in abdominal segments clearly supports the idea of articulated, moveable winglets that are serially homologous on both abdominal and thoracic segments. These neurophysiological studies also suggest that the organization of the central nervous system in insects (and perhaps other hexapods) is quite conservative evolutionarily (13, 15–17). For example, abdominal giant interneurons in primitively wingless (e.g. Thysanura) and pterygote (e.g. Orthoptera) insect orders represent cellular homologues that are derived from the same set of neuroblasts in the embryonic central nervous system (see below) (15).

Fossil and Phylogenetic Evidence

Pterygote insect fossils first appear at the end of the Lower Carboniferous (Namurian), some 325 mya (6, 7, 79–81). By this time both paleopterous and neopterous lines had undergone substantial radiations (6, 7, 79); the evolution of pterygotes clearly occurred considerably earlier.

Unfortunately, the fossil record for hexapods before the Upper Carboniferous is almost entirely lacking. Early Devonian localities (375–395 mya) have revealed several hexapod fossils: apparent Collembola (springtails) from the Rhynie Chert in Scotland (76) and apparent Archaeognatha (bristletails) in Quebec (43). These fossils are all quite small in size. Their occurrence during this period suggests that entognathous and ectognathous hexapods likely diverged during the Silurian (Figure 1c). There are no well-established insect fossils between the early Devonian and the Namurian, a crucial period of nearly 75 million years. Many authors suggest that the divergence of pterygotes from other (primitively wingless) insect groups occurred during the Devonian (7, 79, 81), whereas Kukalova-Peck (39) argues that this divergence occurred earlier during the Silurian. However, direct evidence is lacking.

Phylogenetic relationships among the major hexapod groups are still in flux, but several main features seem generally established (Figure 1c) (see also 26, 36, 38). First, the divergence of collembolans and proturans from other groups occurred early in the history of hexapods (the precise branching position of diplurans is in some doubt). Second, the ectognaths form a monophyletic group consisting of the Archeognatha, extinct Monura, Thysanura, and Pterygota. Third, the Thysanura (silverfish) are the sister group of the Pterygota, sharing an immediate common ancestor. Thus, the morphology and habits of the Archeognatha and Thysanura are of special interest in understanding the evolution of pterygotes. Unfortunately, the earliest fossil Thysanura do not appear until the Upper Carboniferous (7, 39).

All of the nonpterygote hexapods are primarily or entirely terrestrial throughout their lives. Present-day representatives typically reside in or under

soil, leaf litter, logs, bark, and similar habitats. The lack of wings for flying as well as the terrestrial habits of these groups likely contribute to the lack of fossils during the Devonian and Lower Carboniferous (as most of the early fossil materials are wing fragments) (65). The paleopterous orders with extant representatives [Ephemeroptera (mayflies) and Odonata (dragonflies)] have aquatic juvenile stages. However, for several extinct paleopterous orders from the upper Carboniferous and Permian, including the Diaphanopteroidea, Megasecoptera, and Paleodictyoptera, the juveniles are commonly regarded as terrestrial (5, 7, 8). The phylogenetic relationships among recent and extinct orders within the Paleoptera is not clearly resolved, though the Ephemeroptera are widely believed to possess many primitive features relevant to the origins of the pterygotes.

As for whether the immature stages of protopterygotes were aquatic or terrestrial (5, 37–39, 68), several points are relevant. First, because thysanurans, archeognathans, and other primitively wingless hexapods are terrestrial as immatures, one might assume that the common ancestor of thysanurans and pterygotes was also terrestrial in all stages. Second, fossils demonstrate the presence of thoracic side lobes (paranota) in Paleozoic archeognathans and thysanurans, and of abdominal side lobes in Paleozoic diplurans (39) (Figure 1). Kukalova-Peck has interpreted these thoracic lobes as “composed of two elements, the epicoxa and the protowing, which are [secondarily] fused together into a lobe adjacent to the tergum....Protowings originated from the first exite (exopodite) on the epicoxa” (39, p. 2335). This interpretation of side lobes implies that articulated protowings (or lobe-like structures homologous to such protowings) predate the common ancestor of Thysanura and Pterygota. The initial functions of such structures in nonpterygote hexapods remain obscure. Third, the presence of many homologous features of the aquatic immature stages in several of the more primitive Paleoptera suggests that the earliest pterygotes may have had aquatic immatures (37, 38, 68). The fact that the juveniles of many primitive groups within insect orders are aquatic or semiaquatic also seems to support this suggestion (37).

Speculations on Protopterygotes

What are the characteristics of the stem-group for pterygotes before the full development of wings and flight? As evident from the above discussion and stated by Wootton & Ellington (82), “There is no insect *Archaeopteryx*.” The detailed fossils of *Archaeopteryx*, *Sinornis* (another early bird), and contemporary theropod dinosaurs have provided the morphological bases for speculation and modeling of the evolution of flight in birds; the complete lack of such transitional insect fossils between the early Devonian and the Upper Carboniferous poses considerable problems for analogous studies of evolution of insect wings and flight.

One phylogenetic approach to the problem is to identify the features of the common ancestor of Pterygota and Thysanura in terms of shared ancestral traits. Unfortunately, this approach provides little unambiguous information about the size or shape of protowings, body size, or habits in such a common ancestor. As discussed above, the current evidence appears to support a pleural origin of articulated wings on both abdominal and thoracic segments. Drawing on the available fossil and comparative evidence, Kukalova-Peck (38, 39) and others (81, 82) have suggested that the protopteryogote had well-developed, moveable winglets on both thoracic and abdominal segments and was aquatic in its nymphal stages (Figure 1*b*). In this scenario, the initial evolution of the protowings occurs in aquatic nymphs, by analogy with the nymphal appendages or structures of Ephemeroptera and Odonata. The abdominal and thoracic winglets were then subsequently utilized for some function in the terrestrial environment, presumably in the adult stage.

On the other hand, a pleural origin for wings does not necessarily imply that the initial evolution of protowings occurred in aquatic nymphs with both abdominal and thoracic winglets. As noted above, the terrestrial habits of the relevant primitively wingless hexapods and insects supports the possibility of terrestrial habits for the common ancestor of Thysanura and Pterygota. The existence of thysanuran thoracic lobes (Figure 1*a*), interpreted by Kukalova-Peck (39) as involving secondarily fused protowings, is key here: it implies that the evolution of articulated protowings predates the divergence of Thysanura from Pterygota in presumably terrestrial animals, with no evidence that abdominal epicoxal exites were wing-like in form at this stage.

In contrast to earlier suggestions (77), some workers have recently proposed that protopterygotes were relatively larger than present-day insects (81). This suggestion is apparently based on the observation that some pterygotes, thysanurans, and diplurans from the Upper Carboniferous and Permian were very large, but the inference seems rather weak. First of all, the few early Devonian fossils are small in size and represent a time after the divergence of ectognaths from other hexapods; thus large size in both Pterygota and Diplura is not a shared ancestral trait. Second, among the Carboniferous and Permian fossils, the sizes range throughout many pterygote orders; hence, large size is not clearly ancestral for the pterygotes. Finally, phyletic increases in body size within lineages frequently occur in many animal groups (66), making it difficult to establish size as a shared ancestral trait. Kukalova-Peck (39, and personal communication) has suggested that the earliest pterygotes were larger than the size of aerial plankton (77, 78) because the proposed basic plan for the pterygote wing includes main wing veins that branch no less than three times. She argues that if

the basic wing was very small, one or more branches would be absent, as they are in very small extant insects.

Present-day pterygotes use active flapping flight, rather than gliding or soaring, as the major means of aerial locomotion. When did true flapping flight first arise during the evolution of wings and flight? Comparative studies indicate that different pterygote orders and suborders possess quite different adaptations for flapping flight (42). This suggests that specific adaptations for flapping evolved after the evolution of wings and initial flight in pterygotes (42). For this reason, we do not consider flapping flight in detail in this review.

In summary, the divergence of pterygotes from other hexapods likely occurred during the Devonian or perhaps the Silurian. The balance of evidence suggests that protowings are derived from epicoxal structures occurring on both thoracic and abdominal segments, and that such protowings were articulated initially. In addition, articulated lobe-like structures homologous to protowings may predate the divergence of Thysanura and Pterygota. The initial evolution of protowings in protopterygotes may have occurred in either terrestrial or aquatic environments, or in both simultaneously (Figure 1). The body size of ancestral pterygotes may or may not have been large by present standards.

SELECTIVE FACTORS IN THE EVOLUTION OF WINGS

Evaluating Functional Hypotheses

To understand the evolution of complex structures such as insect wings, we need to identify their possible adaptive value during the transition from wingless to winged forms. Not only must we consider the possible functions that such protowings may have served, we also need to consider how the performance (and presumably, the fitness) of the insect might have been enhanced by (a) the presence of protowings, (b) increases in protowing size, and (c) the effect of moveability on protowing function.

The lack of hard evidence regarding the morphology of transitional forms during the evolution of wings has not prevented the proliferation of imaginative (often fanciful) hypotheses about selective factors in the evolution of wings. This proliferation in part results from the uncertainties regarding body size, protowing morphology, and the habits of protopterygotes as described above. Given these uncertainties, our discussion of possible functions of protowings focuses on two issues. First, does performance of some proposed function increase continuously as wing size increases? Only in this case would selection for increased functional performance lead to

directional evolutionary increases in wing size. The answer to this question may depend on the function in question, but also on body size, habit, environmental conditions, and other factors (as discussed below). Unfortunately, few studies have directly examined how functional performance changes with wing size. Second, in most cases, the competing hypotheses do not represent mutually exclusive alternatives. Thus, evidence supporting one hypothesis does not constitute evidence against another. At best, we can exclude some functions as implausible in certain cases.

One can use several approaches to evaluate these functional hypotheses. For instance, all of the hypotheses involve analogies to current functions of wings. A limitation of this approach is that the morphologies of extant insects differ in important respects from those of plausible early pterygotes (described above). Mathematical models may also be used to develop predictions about the relationship of functional performance to size, shape, and environmental factors. These models are presently limited to quite simple geometries; they may be most valuable for gaining mechanistic insight and for making qualitative, rather than quantitative, predictions. For example, the lift generated by short rectangular winglets on a cylindrical body, a situation of obvious relevance, cannot be readily predicted from aerodynamic theory (18). In a third approach, measurements on physical models may be used to evaluate geometries and motions somewhat more realistic than the simple mathematical models can define. However, the design of a physical model (e.g. its dimensions and motions, and the physical characteristics of the materials from which it is built) also implies certain assumptions about important processes (31, 82).

The hypotheses about the initial functions of winglets in protopterygotes that have been proposed can be usefully grouped into four main categories: (a) courtship display (winglets used in mate attraction); (b) aquatic respiration (protowings served as gas exchange surfaces and/or produced ventilation currents that increased gas exchange rates); (c) thermoregulation (winglets functioned as radiation-absorbing solar panels that increased body temperature); and (d) aerodynamics (protowings were used in steady-state gliding or parachuting, in controlling orientation while airborne, and/or in predator escape via jumping or flinging). We briefly consider each of these hypotheses and the available evidence to address it. We also briefly consider possible functional disadvantages of protowings, in particular with respect to aerodynamics and hydrodynamics.

Courtship Display

Alexander & Brown (3) proposed that thoracic wings first evolved as structures for courtship display in male insects. Many current pterygotes do use their wings in courtship displays, and in some cases such displays do

not involve flight activities. One attractive feature of this hypothesis is that directional sexual selection for increased display structures has been documented in many animal groups, and in the absence of opposing natural selection, sexual selection can lead to rapid evolutionary changes in these structures (44). Presumably, evolutionary increases in wing size in females occurred as a result of genetic correlations between male and female wing size (44). West-Eberhard (74) recently based arguments in favor of this hypothesis on the proposed roles of sexual selection in rapid morphological evolution and diversification.

Studies of secondarily flightless insects are particularly useful in addressing this question. In many flightless male ensiferan Orthoptera (crickets and longhorn grasshoppers), the hindwings are reduced or absent, but the insects have retained their forewings as stridulatory elytra to produce sounds to attract females (69). Males of at least one cricket species cannot stridulate but still use the elytra in visual signaling during courtship (69). These and similar observations indicate that the display and flight functions of wings need not be closely coupled evolutionarily.

The courtship display hypothesis is plausible for almost any scenario in which wings initially evolved in a terrestrial environment. On the other hand, the lack of well-defined constraints on possible female choice for display structures makes rejection of the hypothesis difficult.

Aquatic Ventilation and Respiration

Edmunds & Traver (14), Wigglesworth (77, 78), and others have suggested that wings initially evolved on both thoracic and abdominal segments of aquatic nymphs as structures used in ventilation and/or gas exchange. The juveniles of many primitive groups within insect orders are aquatic or semiaquatic (37). For example, the nymphs of present-day Ephemeroptera, which is generally considered the most primitive pterygote order (37–39), are aquatic and possess tracheal gills in which a network of tracheoles is covered by a very thin cuticle, thus allowing gas exchange. Many Ephemeroptera possess gill plates that act as paddles to provide ventilation (water movement) over the tracheal exchange surfaces. In some of these insects considerable gas exchange occurs through the gill plates themselves, whereas in others the gill plates serve almost entirely for ventilation (10). As noted above, these gill plates on the abdominal segments have been considered by many authors as serial homologues to thoracic wings.

Physiological studies with *Ephemera simulans* show that increasing the frequency of gill-plate beating can raise rates of oxygen uptake, allowing effective gas exchange in water with a lower oxygen content (20). The importance of gill-plate beating in oxygen exchange should decrease as external flow rates increase. By analogy with heat transfer, the effectiveness

of stationary (nonflapping) gill plates as exchange surfaces should increase continuously with increasing plate length (29) only while protowings are relatively short (see thermoregulation section, below). Thus, if winglets indeed initially evolved in an aquatic setting, then aquatic respiration and ventilation is an obvious hypothesis for the initial function of such structures. The effectiveness of winglets as exchange surfaces and as paddles providing ventilation should be experimentally tested as functions of winglet size, body size, and flapping speed.

Thermoregulation

Whalley (75) and Douglas (12) have suggested that wings initially functioned as thermoregulatory structures to increase body temperature by absorbing radiation, thus allowing more vigorous or longer periods of locomotory activity. The importance of thermoregulation both for flight and terrestrial locomotion has been widely documented, and the use of wings in basking occurs in many groups of insects (25).

How do changes in wing and body size affect the contribution of wings to body temperature? Douglas (12) experimentally manipulated butterflies

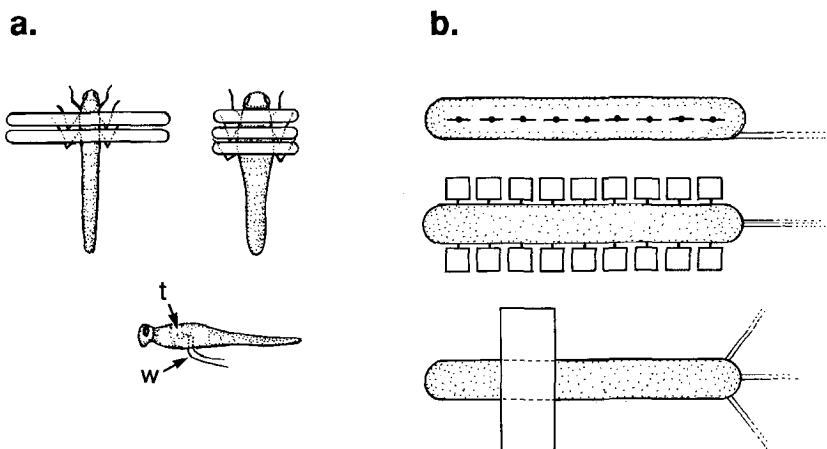


Figure 2 Physical models of protopterygotes. (a) Examples of our models (30), which had slim cylindrical bodies (*top left*) or wide flattened bodies (*top right, bottom*) that were 2 cm, 6 cm, or 10 cm in length. Winglets of various lengths were attached dorsally or laterally to two, three, or no thoracic segments for aerodynamic experiments, as well as to various numbers of abdominal segments for thermoregulatory experiments. Models were made of epoxy and had density and thermal conductivity similar to those of present-day insects, and a thermocouple (t) was embedded within the mesothorax with its wires (w) exiting ventrally. (b) Balsa models of Wootton & Ellington (78) shown with their anterior ends to the left in lateral (*top*) and dorsal views (*middle and bottom*). Models were 8 or 16 cm long, bore nine pairs of lateral winglets or one pair of dorsally mounted winglets, and could have caudal filaments (redrawn from 78).

to show that shortening a butterfly's wings has little effect on body temperature. Using a series of physical models of fossil insects in a wind tunnel (Figure 2a), we (31) showed that body temperature increases rapidly over air temperature as wing length increases from 0 to about 1 cm. For thoracic wing lengths above about 1 cm, further increases have little additional effect on temperature excess. This qualitative result was independent of body size (2–10 cm body length) and wind speed (1.0–2.5 m/s). For wingless models, the addition of short wings has a relatively greater effect on temperature excess at smaller body sizes; and the relative wing length at which increases in length no longer improve thermoregulatory performance is larger for small insects than for larger ones. These results are primarily a consequence of the poor conductance of heat along the wing relative to the rate of convective heat loss from the wing surface (73).

These experimental findings suggest that selection for increased body temperature could favor protopterygotes with short winglets over those with none and could act to increase thoracic wing size in insects with short wings. This scenario could work at any body size, although the effects of short wings are relatively greater for smaller body sizes. However, the addition of short wings to the abdominal segments of the models had little effect on thoracic temperature (and hence on the temperature of the main locomotory muscles of insects) (31).

The thermoregulatory hypothesis is consistent with either a fixed wings or a moveable wings scenario. Indeed, many present-day insects, such as butterflies and dragonflies, use wing positioning as a means of behavioral thermoregulation (9). The hypothesis also implies that the intimate relationship between thermoregulation and flight found in recent insects (4) dates from the origins of flight in insects.

Of course the thermoregulatory hypothesis requires that at least some of the early evolution of wings occurred in a terrestrial context. One possibility that has not received attention is simultaneous selection for wing evolution in aquatic nymphs and the terrestrial adults, involving different selective factors.

Aerodynamics

The variety of aerodynamic functions that have been postulated for pro-towings can be grouped into three main categories: parachuting, gliding, and attitude control. Gliding and parachuting (Figure 3) may serve several nonexclusive biological roles, including energetically inexpensive horizontal travel (57); relatively fast, energetically inexpensive vertical descent from e.g. vegetation (52, 53, 67); pursuit of aerial prey (61, 64); escape from predators (15); or protection from injury during vertical descent (18, 21, 64). Attitude (orientation) control may enhance gliding or parachuting

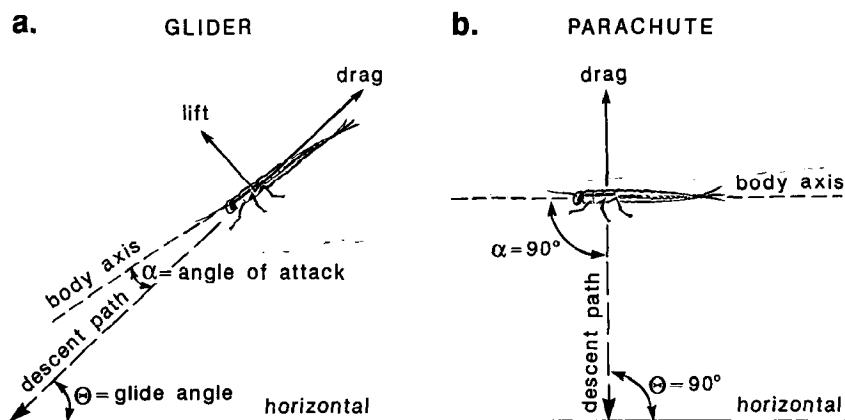


Figure 3 Diagram of a side view of a gliding (a) and a parachuting (b) protopterygote, illustrating the definitions of drag, lift, angle of attack (α), and glide angle (Θ).

performance (21, 82), enable a falling organism to land right-side-up so that it can run from predators (27), and enable an organism to steer as it falls (19).

Only a few quantitative studies have evaluated hypotheses about the aerodynamics of protopterygotes, using either of two basic approaches: (a) mathematical models of falling cylinders (18, 21) or (b) physical models of cylinders bearing thoracic and abdominal winglets (82) or of fossil insects with and without thoracic winglets of various sizes (31) (Figure 2). In evaluating the results of these studies one should remember that they consider various body sizes and air speeds, body morphologies and appendages (including the form and presence or absence of legs, thoracic winglets, and adominal winglets), and performance criteria, as well as use different methods of measurement and/or analysis (32). Here we aim to identify how the various results thus obtained may be related to these differing approaches and assumptions.

The first step in analyzing the aerodynamics of falling or jumping insects is to assess the relative importance of inertial and viscous forces in determining the air velocity and force distributions around an animal. The Reynolds number (Re) represents the relative importance of inertial to viscous forces for a particular flow situation; $Re = dU/\nu$, where d is some linear dimension of the object (in our case, thorax width), U is the velocity of the fluid relative to the object, and ν is the kinematic viscosity of the fluid. Note that a doubling in size or a doubling in velocity will have the same

effect on Re , and hence on velocity and flow patterns around a falling insect.

In order to assess the Re at which protopterygotes fell through the air, we must make some reasonable assumptions about both their size and falling velocity. As discussed above, the current fossil and comparative evidence is inadequate for determining the size(s) of the ancestral insects on which wings evolved, so exploring a range of possible sizes is most appropriate. Falling speeds are also not clearly resolved, although we can define a reasonable range. In our modeling study (31), we assumed that they fell at speeds similar to the sinking speeds estimated for present-day insects of similar size during gliding. In contrast, Ellington (18) argued that such speeds were too low because protopterygotes did not have fully developed wings to slow their descents; he instead assumed that the insects fell at rates similar to those of cylinders of similar size and weight. Although protopterygotes did not have fully developed wings, they did have legs, cerci, and other protrusions from their bodies that would have substantially increased their drag and hence slowed their rate of descent (71) (drag, D , is the component of the aerodynamic force on the insect that acts in the direction opposite to its motion through the air; see Figure 3). Therefore, the descent velocities for these animals probably fell somewhere between the two assumed speeds—the Re values used by Ellington are probably too high (i.e. his results actually refer to bigger insects than he proposed), whereas our Re numbers are probably too low (i.e. the results actually refer to smaller insects than we proposed). This issue could be resolved with better estimates of the airspeeds of more realistic models of protopterygotes (with legs, cerci, caudal filaments, antennae, and protowings of various sizes) during free-fall. Despite these uncertainties, some likely bounds may be identified: for body lengths of 1–10 cm, Res of 10^2 to 10^4 (where d is body diameter) are appropriate for insects falling in air.

These Reynolds numbers represent a range in which the nature of fluid flow changes in ways that have interesting consequences for analyses of insect wings. First, small surface irregularities (including edges and bristles) on smooth surfaces (including simple cylinders) may affect the transition to turbulent flow and thus alter aerodynamic forces. As a result, predictions based on insects as variations on smooth cylinders may not always be an appropriate quantitative guide. Second, bodies such as cylinders (72) and insect models (31) shed alternating vortices in their wakes (this type of wake is called a von Karman trail). As a result, the instantaneous forces measured on such a body fluctuate as vortices are shed, limiting the quantitative precision of mean force measurements.

In fact, biomechanical measurements of mean aerodynamic forces or

coefficients in this *Re* range frequently have confidence limits of at least 10%, and often considerably larger (72). In evaluations of the product or ratio of measured forces (e.g. the ratio of lift to drag), or of the relative effects of changes in a physical model (e.g. the effects of winglets relative to wingless models), the uncertainty in the estimates is inflated (see 31, 33 for a discussion of uncertainty analysis). For example, of the two experimental studies on aerodynamic effects of insect winglets, one (31) had 95% uncertainty intervals of 10–50% on the relative effects of winglets in most cases; the other (82) presented only the results of “good” glides, ignoring issues of bias, variability, and uncertainty altogether. Such uncertainties limit our ability to detect small effects, yet an important question is whether small winglets affect aerodynamic performance. Here we must remember that confidence or uncertainty intervals allow us to potentially reject relevant null hypotheses (e.g. that winglets have no effect) and also provide information on the degree of support for the null hypothesis. Second, the entire approach is based on the notion that performance is directly related to fitness, yet the quantitative relationship between performance and fitness (and hence the strength of selection) undoubtedly varies among functions and among performance criteria. Finally, because we are considering multiple, nonexclusive hypotheses in many instances, a more productive discussion would focus on the relative magnitude of effects on variation in size and morphology rather than the presence or absence of such effects.

PARACHUTING Protowings may initially have functioned to slow a falling insect's rate of descent by increasing drag (Figure 3*b*). By thus increasing its time aloft, the insect could have been passively dispersed by the wind for long distances, as occurs with many present-day insects and plant seeds (51, 77, 78). Time aloft for a parachuting organism is proportional to $(D/m)^{1/2}$, where *D* is drag and *m* is body mass (51). Another consequence of lowered air speed would have been a reduction in the force with which a falling insect hit the ground, which might have been an advantage for insects large enough to be damaged by the impact at the end of a fall (18, 21). The damage to a landing insect depends on the kinetic energy (*K*) per unit of body mass of the animal as it hits the ground, which equals $U^2/2$, where *U* is the animal's velocity (18). Because the terminal velocity of a parachuting insect is proportional to $D^{-1/2}$ (18), *K*/*m* is inversely proportional to drag.

We (31) measured drag on protopterygote models in a wind tunnel at right angles to the airflow direction (e.g. the orientation at which drag is highest for horizontally oriented insects falling straight down; Figure 3*b*). The results, for *Re* values of order 10^2 and 10^3 and independent of body shape or the presence of legs, showed that short (less than about 20% of

body length) thoracic winglets had no significant effect on drag, whereas drag increased significantly with increases in length for longer winglets. Hence, selection for parachuting performance could have increased proto-wing length for protowings longer than about 20% of body length.

Other investigators have addressed the issue of damage to protopterygotes upon landing by calculating the velocities with which cylinders of various sizes hit the ground (18, 21). By choosing a plausible critical velocity at which unacceptable injury occurs, they predicted the body size above which a falling insect with no appendages would be damaged (5–6 cm for cylinders). Flower (21) calculated that cylinders with legs would achieve lower terminal velocities, and reasoned (with no supporting calculations) that rudimentary wings would have little effect on terminal velocity when compared with the effects of reducing body size or increasing leg length. In contrast, Ellington (18) suggested that the sharp edges of small winglets could increase drag by altering airflow patterns around a cylinder in the *Re* range of protopterygotes, citing Hoerner's (28) drag data for squares and triangles. However, given that insects are hardly smooth round cylinders, one might expect that the effect of sharp winglet edges on flow patterns would be less than that predicted for smooth cylinders (see above). Ellington also reasoned that, once winglets were present, the relative risk upon landing should decrease linearly as winglet planform area increased. This conclusion is not supported by the data discussed above (31), i.e. that winglets had to be about 20% of body length before they had a significant effect on drag. Ellington (18) has argued, based on his calculations of the total planform area of our models' winglets, that this empirical result is unlikely, but measurements on our original models and wings indicate that his calculations overestimated the total planform area by a factor of two. An answer to the question of whether small winglets could have substantially affected the risk of damage to landing insects requires both additional drag data and quantification of the damage to insects of morphologies similar to protopterygotes as a function of the kinetic energy of their landings.

GLIDING Gliders travel horizontally as they fall (Figure 3a). Protowings initially may have functioned as aerofoils that improved the gliding performance of protopterygotes. Gliding allows insects to leap from vegetation to escape predators or to travel across the habitat (22, 23, 27, 59).

One standard measure of gliding performance is the horizontal distance traveled for a given loss in height as the glider descends through the air, which for steady-state gliding is proportional to the ratio of lift to drag (56), where lift (*L*) is the component of the aerodynamic force on the glider that acts at right angles to the drag (Figure 3a). The angle of attack (α) is the angle between the the glider and its descent path. The lift and drag on

a body can vary as a function of α , and the horizontal distance traveled is greatest at the angle of attack that maximizes L/D .

Theoretical results for steady-state gliding by cylinders without protowings (18, 21) indicated that L/D increased as body size increased. Flower (21) also calculated that the horizontal travel of small cylinders in a slow wind (1 m/s) was greater if they parachuted than if they glided, because small cylinders have low L/D values and parachutes fall more slowly than gliders. Both he and Ellington concluded that if the selective advantage of protowings was an improved L/D , then protowings arose on large insects.

We (31) found that the maximum L/D of models of small protopterygotes (body length = 2 cm; $Re = 450$ using thorax width, d , as the characteristic dimension) was not significantly increased by thoracic winglets until winglet length exceeded 60–70% of body length, whereas the performance of larger models (6 cm body length, $Re = 1300$) was significantly improved by shorter winglets (30% of body length). With longer wings, increases in wing length led to improved horizontal travel. For the largest models considered (10 cm body length, $Re = 2170$), even very short wings apparently increased gliding performance. These results suggest that for the smaller models with no or short winglets, increases in wing length have no significant effect on L/D ; but as body size (and Reynolds number) increases, shorter winglets could improve L/D substantially.

Once again Ellington's estimates of the total planform area of winglets led him to question the above results for our smallest model (18)—those suggesting that rather long winglets are required for substantial improvements in L/D . As before his calculations overestimated wing planform area by more than a factor of two. However, Ellington's suggestion that cambered rather than flat winglets in these studies would have improved the L/D performance is probably correct: some schemes suggest that protowings were initially nearly symmetric anteroposteriorly and strongly fluted (38, 39), but the degree of camber in primitive insect wings is unknown. The relative performance consequences of changes in wing shape vs wing size for short protowings remains unexplored.

Wootton & Ellington (82) measured the glide angles (Θ , Figure 3) of cylindrical models bearing short winglets on both thoracic and abdominal segments (Figure 2b) that were dropped or thrown at Re values of 1000–7500 (based on body diameter). Their results show that, for models with both thoracic and abdominal winglets, winglets that are only 5% of body length can substantially improve gliding performance. Models with a single large thoracic winglet that was $\sim 20\%$ of body length also improved gliding performance relative to wingless cylinders. As discussed in detail by Ellington (18), these results are consistent with those for our two larger models (31) and suggest that, at least for Re values above 1000, the addition of

abdominal winglets will decrease the wing length at which short winglets can contribute to gliding performance by increasing the planiform area of the lifting surface.

Initiation of gliding during a fall Gliders cannot generate sufficient lift to glide below a minimum airspeed. The lower this minimum (U_{\min}), the sooner after takeoff an animal can begin to glide (2, 19). When Flower (21) incorporated this factor into his calculations of horizontal distance traveled by gliding cylinders, he concluded that an intermediate body length optimized performance (about 1 cm, depending on the height of the takeoff). This result contrasts with the prediction of steady-state calculations mentioned above (18, 21). Norberg (51) suggested that if an insect jumps at takeoff, it might reach U_{\min} without an initial steep fall.

The U_{\min} values calculated from our data (31) for winged and unwinged models revealed that, as with L/D , the relative wing length at which protowings substantially improve glide-initiation performance is greater for smaller insects than for larger ones (Figure 4a).

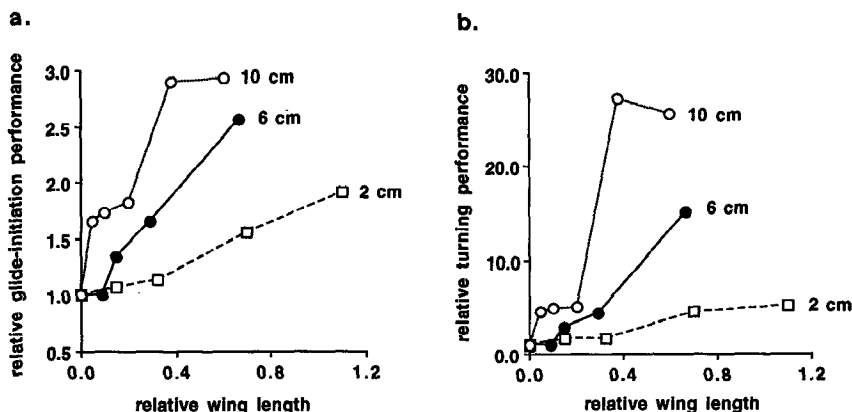


Figure 4 Aerodynamic performance of models of protopterygotes (Figure 2a, top left) with body lengths of 2 cm (dashed line), 6 cm (solid line), and 10 cm (dotted line), plotted as a function of relative wing length (wing length divided by body length). Calculations were done using the data (30) for the angles of attack at which the models had the highest ratio of lift to drag. For simplification, we assumed that thin protowings did not affect the mass of the animals. (a) The lower the minimum glide speed (U_{\min}) of an animal of a given mass, the shorter the distance it must fall before it builds up enough speed to begin gliding. Therefore, $1/U_{\min}$ is an index of glide-initiation performance; relative glide-initiation performance equals this index for models with protowings divided by the index for models without protowings. U_{\min} was calculated as described in Ref. 2. (b) The smaller the radius (r) of the turn that a gliding animal can execute at a given banking angle (F), the better its turning performance (Figure 5b). Therefore, we have used $1/r$ as an index of turning performance. Relative turning performance equals this index for a model with winglets divided by the index for a model without winglets. Turning radius was calculated as described in Ref. 51.

Glide speed Another important aspect of gliding performance is terminal velocity. Calculations of the velocities of falling cylinders show that gliders travel faster than parachuters, and hence that gliders incur damage at smaller body sizes than parachuters (18, 21). As with parachuting, the force of impact on landing can be reduced and the time aloft can be increased if glide speed is reduced. Wootton & Ellington's (82) studies at Re values of 1000–7500 showed that short thoracic and abdominal winglets can reduce glide speeds. Using our data (31) to calculate the time aloft and the K/m of landing at terminal velocity for model pterygotes gliding at their maximum L/D , we found that short thoracic protowings had no significant effect for the Re range considered (450–2100) and that the relative wing length at which winglets improved performance was greater for small models than for large ones. Interestingly, the glide speeds predicted from Wootton & Ellington's (82) studies exceed that presumed to cause damage upon landing (18). They suggested that damage on landing may also be avoided if a gliding animal can slow itself just before landing by stalling (e.g. by changing its angle of attack).

ATTITUDE CONTROL Protowings might have functioned to control the pitch, roll, or yaw orientation of airborne protopterygotes (Figure 5a). If winglets served as aerodynamic stabilizers, they could have helped a falling insect land right-side-up (27, 30), or they could have improved gliding performance by enabling an insect to maintain a stable angle of attack at which it had a good L/D (21, 82). Rather than being simple stabilizers, protowings could have been used as active control surfaces to permit falling insects to maneuver while airborne, to make corrections in their attitude in the face of perturbations (such as air turbulence), or to control their orientation when landing. These activities would necessitate a tradeoff between aerodynamic static stability (i.e. the tendency of a glider or parachuter to return to its equilibrium state after being perturbed) and maneuverability (i.e. the rapidity of the response of the organism's attitude, speed, or flight path to a control movement, such as changing the orientation of a winglet) (21, 47, 48, 63).

Wootton & Ellington (82) observed the static stability of cylinders bearing short winglets (Figure 2b). The models were stable in roll, but not in yaw unless they had at least one caudal filament. If the winglets were twisted (Figure 5d) to particular angles, the models bearing winglets on every segment were stable in pitch. Pitch was especially sensitive to the angle of the most posterior pair of winglets; their removal destroyed pitch stability unless posterolaterally directed filaments, analogous to cerci, were added to the models. Models with a single untwistable anterior pair of wings were only stable in pitch if their center was anterior to the model's center of mass. Although these experiments showed the importance of caudal filaments

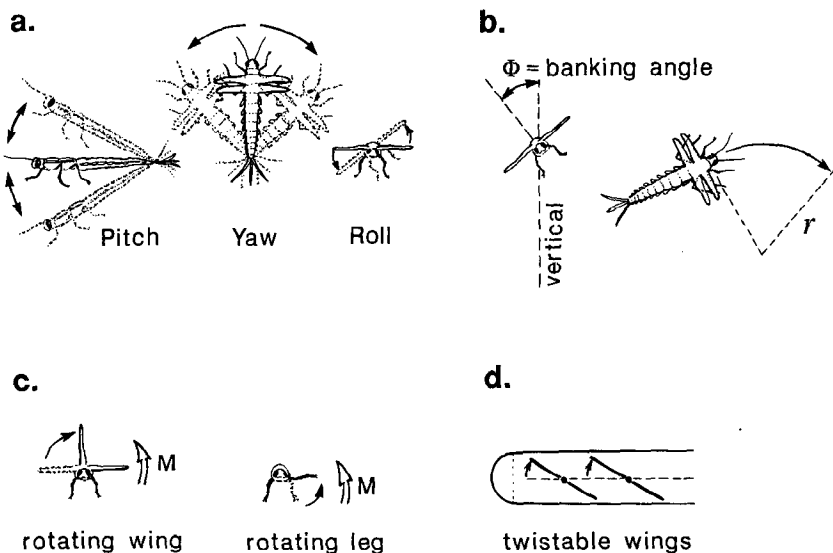


Figure 5 Attitude control. (a) An insect can reorient in pitch (body rotating in a vertical plane with its head moving up or down), in yaw (body rotating in a horizontal plane with its head swaying right or left), or roll (body rotating about its long axis). (b) If a glider rolls to a banking angle (Φ), it executes a turn of radius r . (c) Face-on views of an insect rotating the winglets on the right side of its body, and of a wingless insect rotating the legs on the left side of its body. As the insect falls, the drag is greater on the appendages extending laterally than on those extending dorso-ventrally, and a rolling moment (M) is exerted about the long axis of the animal. (d) Lateral view of the anterior end of a model of Wootton & Ellington (78), illustrating how the angle of attack of the winglets could be adjusted relative to that of the body.

and demonstrated that winglet orientation and placement on the body can affect stability, they did not compare winged with wingless models, nor did they assess the consequences of changing wing length.

In an exploration of the effects of repositioning thoracic protowings or legs on roll maneuvers (Figure 5c) (31), we found that that the relative wing length above which rolling moment could be significantly increased by an increase in wing length was greater for small models than for large ones. Also, legs alone produced rolling moments nearly as large as those exerted by protowings of similar length.

If a glider can adjust its roll, it can execute a banking turn (Figure 5b). We used lift and drag data (31) to calculate the radius (r) of the turn produced by a roll of a given banking angle (Φ) (55); the smaller the r (i.e. the tighter the turn), the better the turning performance of the model (19). For the smaller models, short thoracic protowings did not substantially affect turning performance, whereas longer ones did; for the larger models

even quite short thoracic protowings could substantially improve turning (Figure 4*b*).

Although our models (31) and those of Wootton & Ellington (82) explored different aspects of attitude control for pterygotes of different morphologies, both studies were based on the assumption that protowings were articulated and could be reoriented, and both suggest that protowings could under certain circumstances enhance aerodynamic performance.

JUMPING OR FLINGING Protowings may have enhanced the jumping performance of ground-dwelling insects in several ways. Although winglets might have improved the glide distance of a protopterygote following a running jump (39), a jumping or running insect would be unlikely to attain an airspeed fast enough to glide (18, 80, 82). Instead, winglets might have made jumping insects more stable (15), permitted them to steer while airborne, or slowed their fall back to the ground. In addition, rapid flinging by articulated protowings could perhaps generate sufficient acceleration for rapid escape from predators (15, 39).

Currently little biomechanical evidence is available to evaluate these ideas, but Edwards and colleagues (15–17) have argued compellingly for the potential importance of predator-evasion responses in the evolution of wings. In many primitively wingless insects and in pterygote orthopteroids, giant interneurons originating in the abdominal ganglia extend into the thorax and are involved in startle responses for predator evasion. Archaeognatha evade predators by rapidly flexing the abdomen with its long caudal filaments and abdominal cerci, producing substantial jumps. Edwards has reasoned that a similar rapid flexing of moveable protowings, perhaps on both thoracic and abdominal segments, could allow predator evasion in early protopterygotes as well. This hypothesis could also explain the apparent existence of articulated protowings (39) before the divergence of Thysanura and Pterygotes (see above). Because selection pressure on such predator-avoidance mechanisms can be strong (15), the adaptive value of such a system is clear, and the mechanical aspects of this hypothesis deserve quantitative exploration.

SUMMARY OF AERODYNAMIC PERFORMANCE Three general patterns emerge from these results on aerodynamic performance. First, at smaller body sizes and lower movement speeds, short thoracic protowings have little effect on aerodynamic performance. However, above some critical wing length, further increases in wing length alter performance and hence might be subject to natural selection. Second, for all the functions considered except parachuting, the relative wing length at which thoracic protowings improve aerodynamic performance decreased as body size increased. Thus at larger

sizes and higher movement speeds, even rather short protowings could improve performance. Third, the presence of both thoracic and abdominal winglets reduces the protowing length at which protowings can improve aerodynamic performance, at least for larger sizes and/or faster speeds.

Potential Costs of Protowings

So far we have reviewed potential benefits of protowings, but we need to consider their costs as well. One possible liability of winglets to propterygotes might have been an increased danger of being swept away (Figure 6*a*) (see 34, 35) or overturned (Figure 6*b*) (see 1) by wind or water currents. As illustrated in Figure 6*d*, the relative wing length at which

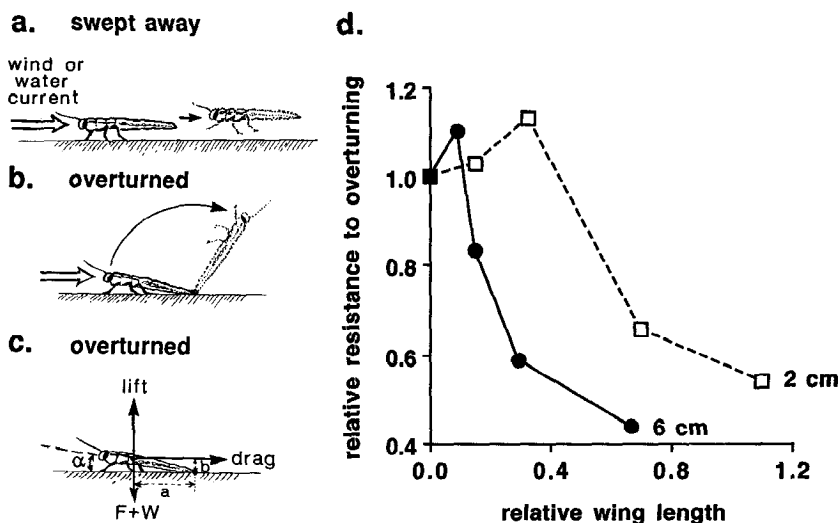


Figure 6 An insect can be swept away (*a*) or overturned (*b*) by wind or water currents. (*c*) Diagram of the forces on an insect facing into a wind or a water current moving from left to right: drag (D), lift (L), net weight of the insect (W = weight of the insect minus the weight of the fluid it displaces), and tenacity (F = force with which the insect adheres to the substratum). In this example all forces act at the center of mass of the insect. The posterior end of the animal touching the substratum forms the pivot about which the animal rotates if it is overturned. α is the animal's angle of attack to the oncoming flow. The moments tending to overturn the animal are aL and bD , whereas the moments tending to keep it in place are aW and aF . The critical wind or water velocity (U_{crit}) at which the animal overturns is the velocity at which $(aL + bD) = (aW + aF)$. (*d*) Relative resistance to overturning plotted as a function of relative wing length (wing length divided by body length) for models of propterygotes (Figure 2*a*, top left) with body lengths of 2 cm (solid line) or 6 cm (dashed line). The higher the U_{crit} , the more resistant an animal of a given W and F will be to overturning, and therefore the relative resistance to overturning is the U_{crit} of a model bearing protowings divided by the U_{crit} of that model when bearing no wings. U_{crit} was calculated using lift and drag data (30) for models at $\alpha = 10^\circ$ by assuming that protowings did not affect W or F or the location of the center of mass of the animal.

increases in length began to have a detrimental effect was greater for small models than for large ones (data from 31). We found a similar result when we calculated (as described in 11) the consequences of protowings as related to the danger of being swept away. Of course we cannot evaluate whether such increases in force or overturning moment posed a danger to protopterygotes without knowledge of their flow microhabitats or of how hard they held on to the substratum, but data about how the tenacity of various extant insects scales with body size might help us make some reasonable guesses. Another possible cost of winglets is that they might impede rapid terrestrial locomotion (51).

Functional Shift and the Importance of Body Size

Our attention thus far has focused on how evolutionary changes in protowing size and shape affect functional performance, thus generating selection on wing size in the evolutionary transition to flight. Because many aspects of performance scale with Reynolds number and thus body size, however, evolutionary changes in overall body size would influence this transition. For example, at a small body size, short thoracic protowings can improve thermoregulatory performance, but have little effect on aerodynamic performance (31). However, thoracic protowings of the same relative length on an insect of larger body size (that is, an isometric size increase) can have important aerodynamic effects. Therefore, if thoracic protowings first occurred on protopterygotes of small body size, simple isometric increases in overall size during evolution—by whatever mechanism—might have led to aerodynamic function (31). Thus, isometric size changes in the absence of shape changes can potentially generate important evolutionary shifts, a possibility that has received little attention from evolutionary biologists (24, 31).

Size and Re scaling also has other implications for functional shifts in the evolution of insect wings. Protopterygotes operated in a Re range in which slight changes in shape, as well as increases in size or speed, can lead to sudden transitions from laminar to turbulent flow. Drastic changes in performance can accompany such a flow transition (18, 72). Indeed, flow visualizations (31) reveal turbulent flow only around the largest models, and drag and lift coefficients are generally much lower around large models than smaller ones (31, 82). Such shifts between laminar and turbulent flow with changes in Re might have important consequences for animals making the transition from aquatic to terrestrial habitats (either during the ontogeny of an individual or the evolution of a lineage). Because Re is inversely proportional to the kinematic viscosity of the fluid, an animal of a given size and speed has a Re in air that is only 7% of its Re in water (i.e. when an organism becomes terrestrial, the transition has the same effect on the

flow and force patterns around it as shrinking to 7% of its length would have). The transition between laminar and turbulent flow provides another example of how a simple change in size or fluid medium can lead to a drastic shift in function.

Quantitative engineering analyses (18, 21, 31, 82) can identify the magnitude of the functional consequences of particular structural changes. These examples illustrate that one cannot predict a priori the functional consequences of small changes in a character. Changes in wing length may have large or insignificant effects on thermoregulatory, aerodynamic, and other functions, depending on body size, wing length, and wing number. Furthermore, these examples illustrate that simple changes in size can lead to novel functions without requiring the invention of novel structures. The available fossil evidence does not permit us to determine whether such functional shifts occurred in the evolution of insect wings, but in discussing the evolution of insect flight we should keep in mind that such shifts are rather likely for the Re range in which the earliest protopterygotes probably operated.

SUMMARY AND SYNTHESIS

Our consideration of selective factors in the evolution of insect wings emphasizes two main features. First, in many cases our answer to the question, "Which proposed selective factors in the initial and early evolution of wings are likely or plausible?" depends crucially on our assumptions about the habits, size, and morphology of ancestral pterygotes. For example, all of the aerodynamic hypotheses seem less important for smaller body sizes or for scenarios in which only thoracic wings are involved. Similarly, thermoregulation seems to have less value as a selective factor in the evolution of abdominal winglets. Although little direct evidence is available, the aquatic hypotheses will probably have comparable restrictions, because functional performance typically does not scale isometrically with changes in overall size (31). Given the uncertainties in the size of ancestral pterygotes, a systematic exploration of how variations in size, morphology, and environmental conditions affect functional performance for a variety of selective factors would profit researchers most.

Second, evidence in favor of one hypothesis does not constitute evidence against another. Indeed, multiple selective factors may well have been operating sequentially and/or simultaneously during the evolution of wings and flight. For example, for large body sizes, mate choice, thermoregulation, and aerodynamic factors may all have been important in the initial evolution of wings. Similarly, both aquatic respiration and ventilation in the aquatic nymphs and thermoregulation and/or aerodynamic performance in terrestrial

adults may have operated simultaneously at small or large body sizes. Various other combinations might be imagined.

So far, most authors have provided evidence to support particular hypotheses; given the nature of the problem, a more productive approach may be to focus on the range of possibilities. In this regard, the concepts of morphospace (60) and performance curves (30) may be helpful in directing our thinking: how does functional performance vary with size and shape (the morphospace) and with environmental conditions (the performance curve). In the multidimensional space representing functional performance, size and shape (e.g. body size, wing size, wing shape, wing number, body shape), and environmental conditions (e.g. terrestrial vs aquatic habits, flow velocity, thermal conditions), the change in performance with change in wing length at any given point affords a measure of the relative selection favoring changes in wing length. The development of such considerations for various selective factors may prove to be a useful way of unifying our thinking about the possible contributions of different selective factors toward selection for the evolution of insect wings.

Darwin's notion of functional shift with structural continuity is a compelling explanation for the evolution of complex adaptations. In applying this idea to the evolution of wings and flight in insects, we are challenged not by the lack of plausible hypotheses, but by their multiplicity. Much has been written on this subject (perhaps 10^6 words in the scientific literature in the past century), but the number of quantitative data evaluating functional hypotheses remains very small (perhaps 10^2 to 10^3 data points). In the absence of an insect *Archaeopteryx* (82), our understanding of selective factors in the evolution of insect wings will likely remain poor as long as the ratio of data points to words remains far below one.

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