

## AERODYNAMICS, THERMOREGULATION, AND THE EVOLUTION OF INSECT WINGS: DIFFERENTIAL SCALING AND EVOLUTIONARY CHANGE

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**Summary.**— We examine several aerodynamic and thermoregulatory hypotheses about possible adaptive factors in the evolution of wings from small winglets in insects. Using physical models of Paleozoic insects in a wind tunnel, we explore the potential effects of wings for increasing gliding distance, increasing dispersal distance during parachuting, improving attitude control or stability, and elevating body temperatures during thermoregulation. The effects of body size and shape, wing length, number, and venation, and meteorological conditions are considered. Hypotheses consistent with both fixed and moveable wing articulations are examined.

Short wings have no significant effects on any of the aerodynamic characteristics, relative to wingless models, while large wings do have significant effects. In contrast, short wings have large thermoregulatory effects relative to wingless models, but further increases in wing length do not significantly affect thermoregulatory performance. At any body size, there is a wing length below which there are significant thermoregulatory effects of increasing wing length, and above which there are significant aerodynamic effects of increasing wing length. The relative wing length at which this transition occurs decreases with increasing body size.

These results suggest that there could be no effective selection for increasing wing length in wingless or short-winged insects in relation to increased aerodynamic capacity. Our results are consistent with the hypothesis that insect wings initially served a thermoregulatory function and were used for aerodynamic functions only at larger wing lengths and/or body sizes. Thus, we propose that thermoregulation was the primary adaptive factor in the early evolution of wings that preadapted them for the subsequent evolution of flight. Our results illustrate an evolutionary mechanism in which a purely isometric change in body size may produce a qualitative change in the function of a given structure. We propose a hypothesis in which the transition from thermoregulatory to aerodynamic function for wings involved only isometric changes in body size and argue that changes in body form were not a prerequisite for this major evolutionary change in function.

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The first winged insects arose apparently during the early to late Devonian, some 350–400 million years ago (Wootton, 1976). The evolution of wings capable of sustained, flapping flight was perhaps the most important evolutionary event in the enormous diversification of insects during the Carboniferous, so it is of some interest to understand possible adaptive factors associated with the evolution of wings.

Hypotheses on the structural origins of insect wings continue to focus on the lateral thoracic lobes, found in many

nymphal and adult insects from the Carboniferous and Permian (Wootton, 1981). The orthodox paranotal lobe hypothesis suggests that wings arose from rigid lateral extensions of the terga. Recently, evidence and support has gathered for a pleural origin of wings, in which wings derived from pre-existing mobile structures (Wigglesworth, 1976; Kukulova-Peck, 1978; Robertson et al., 1982). While there is disagreement as to whether the winglets of primitive Paleozoic nymphs were articulated (Wootton, 1981; Kukulova-Peck, 1983), the embryological evidence for a pleural origin appears strong, and this hypothesis avoids the difficulties, inherent in the paranotal hypothesis, in the development of a complex articulation *de novo*.

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To understand the evolution of a complex structure like the insect wing, we need to identify its possible adaptive value during the transition from wingless to winged insects, before the development of flapping flight. A variety of hypotheses have been suggested, involving aerodynamics (Hinton, 1963; Wigglesworth, 1976), courtship display (Alexander and Brown, 1963), gill ventilation and aquatic locomotion (Kukalova-Peck, 1978) and temperature regulation (Douglas, 1981), but almost no tests of these hypotheses have been made. Flower (1964) used engineering formulae for short, blunt cylinders to suggest the size range within which selection for aerodynamic characteristics could have operated but did not consider the effects of wings. Douglas (1981) presented results of an experiment with butterflies to support his thermoregulatory hypothesis.

The potential functional importance of the nature of the articulation in insect winglets is highlighted by recent work on the evolution of preflight in vertebrates (Cagle et al., 1983). This study suggests that the control of body motion during leaping (or falling) is crucial to the evolution of flight and proposes a mechanism by which lift forces contribute to attitude control. It is well-known that, because of differences in physical scaling, the aerodynamics of insect flight differ importantly from those in vertebrates (Ellington, 1984), and the results of Cagle et al. should be applied to insect flight with caution. Nevertheless, because of continuing disagreement as to the nature of the articulation of winglets, it seems prudent to consider hypotheses for both fixed and moveable winglets.

The purpose of this study is to evaluate several aerodynamic and thermoregulatory hypotheses about the evolution of wings. Our approach is to construct a series of physical models of Paleozoic insects, and to measure aerodynamic and heat transfer characteristics of these models as functions of body size and shape, and the number, size, and physical characteristics of wings. Our results il-

lustrate how the differences by which aerodynamics and heat transfer scale with body and wing size have important consequences for the evolution of insect wings. Such differential scaling yields an evolutionary mechanism by which a purely isometric change in body size can lead to a major evolutionary change in function.

## HYPOTHESES

### *Aerodynamics*

Several popular hypotheses for adaptive factors in the early evolution of wings involve aerodynamics (Hinton, 1963; Wigglesworth, 1963). One can identify three distinct roles for wings in relation to aerodynamics: gliding, parachuting or ballooning, and attitude stability or control. Note that the gliding and parachuting hypotheses may apply to either fixed or moveable wings, while the attitude stability hypothesis assumes moveable wings.

*Gliding.*—In this view, wings initially functioned as aerofoils for steady-state gliding. This capacity for gliding could allow insects to leap from vegetation and glide as a means of movement or predator escape (Hinton, 1963). For steady-state gliding (Fig. 1A), the horizontal distance ( $G$ ) that a glider travels before landing is proportional to the ratio of lift ( $L$ ) to drag ( $D$ ):

$$G \propto L/D. \quad (1)$$

Thus, glide distance is maximum at the angle of attack that maximizes lift/drag.

*Parachuting.*—In this view, wings initially functioned to slow the rate of descent of a falling insect by increasing drag on the insect. By decreasing the descent rate, the insect could be passively dispersed by the wind for long distances, as occurs in many present-day insects (Johnson, 1969). For parachuting, the time aloft ( $P$ ) is:

$$P \propto [D/m]^{0.5} \quad (2)$$

where  $m$  is the mass of the insect. The maximum drag force  $D_m$  generally occurs at an angle of attack ( $a$ ) of 90°; thus the

maximum time aloft  $P$  can be evaluated by determining  $D_m$  at  $a = 90^\circ$ .

*Attitude Stability.*—In this view, wings initially functioned as lateral stabilizers, which could help a falling insect to land right-side-up (Flower, 1964; Hinton, 1963). The strength of this potential stabilization can be evaluated by measuring the moment ( $M$ ) about the body axis produced by the wings (Fig. 1B). To estimate the maximum  $M$  that could be produced by winglets, we consider moments on models with the body axis perpendicular to wind direction ( $a = 90^\circ$ ) with the wings on the left side extending laterally from the body (i.e., normal to the wind) and the wings on the right side extending dorsally from the body (i.e., parallel to the wind). In addition, we consider the effects of legs as stabilizers by measuring  $M$  for wingless models with the legs on the left side extending laterally from the body and the legs on the right side extending ventrally from the body.

#### Thermoregulation

Douglas (1981) suggested that wings initially functioned as thermoregulatory structures to increase body temperatures by absorbing radiation, thus allowing more vigorous or longer periods of locomotory activity, as occurs in many present-day insects (see Heinrich, 1981, for a recent review). Consider an insect at a steady-state body temperature  $T_b$  at which heat flux ( $Q$ ) inputs and outputs balance:

$$Q_{in} = Q_{out} \quad (3a)$$

$$\beta AS = H(T_b - T_a) \quad (3b)$$

$$(T_b - T_a) = \beta AS/H \quad (3c)$$

where  $\beta$  is the absorptivity of the insect,  $A$  is an effective surface area for radiation absorption,  $S$  is the radiation flux density,  $H$  is the total heat transfer coefficient, and  $T_a$  is air temperature (see Gates, 1980, for a discussion of energy balance models). The transfer coefficient  $H$  is a function of wind speed, insect size and shape, and the effective radiative temperature of the environment. As (3c) il-

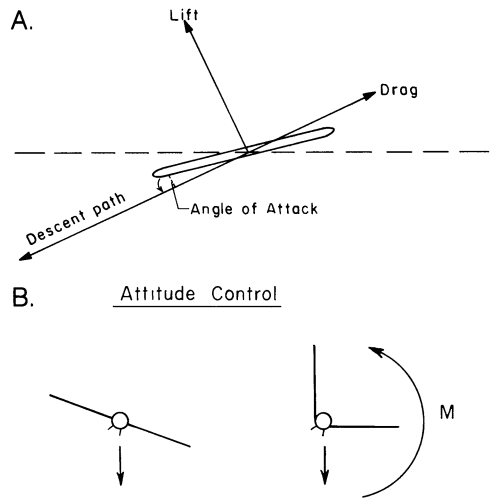


FIG. 1. A) Diagram of gliding wing, illustrating the definitions of lift ( $L$ ), drag ( $D$ ), and angle of attack ( $a$ ). B) Diagram illustrating the use of wings for attitude control, showing the moment  $M$  produced by wing positioning during a vertical descent.

lustrates, there are two possible effects of wings on the body temperature excess over air temperature ( $T_b - T_a$ ): 1) wings may change the effective area  $A$  or absorptivity for radiation absorption, and/or 2) wings may change the heat loss coefficient  $H$ .

The conductivity of heat in the wings of present-day insects is quite small, with a thermal conductivity on the order of that of paper (Douglas, 1978; Kingsolver and Moffat, 1982). The fossil record suggests that the wings of early insects were thicker and more heavily venated, and that they contained more hemolymph than do wings of present-day insects (Kukalova-Peck, 1978). These factors would increase the conductance of heat through the wings, with potentially important implications for thermoregulation. We shall consider the effects of conductivity of wings in the design of our models and experiments.

#### MATERIALS AND METHODS

##### *The Models*

Models were made of insects with two different body shapes, representing both

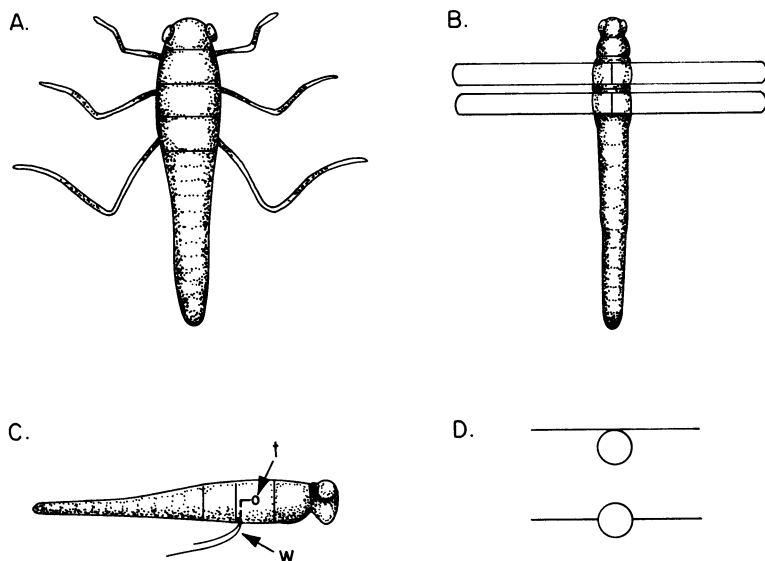


FIG. 2. Models of Paleozoic insects. A) Dorsal view of the wide, flattened body shape, with legs attached. B) Dorsal view of the slim, cylindrical body shape, with wings mounted dorsally. C) Side view of the wide, flattened body. The positions of the thermocouple (t) within the mesothorax and of the thermocouple wires (w) are indicated. D) Cross-sections of the mesothorax of a slim, cylindrical body with wings mounted dorsally (top diagram) and laterally (bottom diagram).

flying and non-flying forms; these were based on published reconstructions of Paleozoic insect fossils. The shapes were chosen to represent a range of possible forms, rather than particular ancestral forms with winglets, since the fossil record is clearly inadequate to identify such ancestral forms. One shape used was a wide-body form (Fig. 2A, C) similar to the bodies of such insects as an adult Paleodictyopteran from the upper Carboniferous (Kukalova-Peck, 1978 fig. 23) or a young nymphal Protorthopteran from the lower Permian (Kukalova-Peck, 1978 fig. 35). The other shape used was a slim, cylindrical form (Fig. 2B) similar to the bodies of animals such as an adult Megasecopteran from the upper Carboniferous (Kukalova-Peck, 1978 fig. 32) or an old nymphal Prottereismatid from the lower Permian (Kukalova-Peck, 1978 fig. 28). The models were made of an epoxy (Uniset A-312; Amicon Corp.) that was chosen because its density and thermal conductivity are similar to those of pres-

ent-day insects (Kingsolver and Moffat, 1982). Three body lengths ( $B$ ) were considered for each body shape: 2, 6, and 10 cm. Legs were constructed from either wire (aerodynamic experiments) or balsa wood (thermoregulatory experiments) (Fig. 2A). Unless otherwise stated, all results reported are for models with three pairs of thoracic legs.

For the aerodynamic experiments, wings were constructed with copper wire enclosing thin, plastic membranes (Forma-Film; Joli Plastic Co.). Flat wings were used, differing in wing length ( $W$ ) (distance from wing tip to the point of articulation on the body) and mounting position (lateral or dorsal) (Fig. 2D). The width of each wing was approximately 95% of the length of the corresponding thoracic segment.

For the thermoregulatory experiments, a copper-constantan thermocouple wire was implanted in the second thoracic segment of each model (Fig. 2A, C). Two materials of very different thermal con-

ductivity were used in the wings: construction paper and aluminum foil (thickness = 0.2–0.4 mm).

### *The Experiments*

All experiments were conducted in an open circuit, open jet wind tunnel with a 30-cm working section. Two wire mesh screens were used in the tunnel to suppress turbulence generated by the fan. Wind velocity was measured with a constant temperature hot-wire anemometer (Thermonetics Co.).

*Aerodynamics.*—All measurements of aerodynamic force used resistance-type strain gages (Micromasurements, Inc.) mounted on shimstock steel beams. Gage output was inserted into a bridge circuit and amplified (Gould Bridge Amplifier), passively filtered to eliminate high frequency noise, and monitored with a digital voltmeter.

Lift and drag were measured separately with gage and beam devices, with the models mounted on hollow aluminum rods 6–8 cm in length. Measurements were made for angles of attack from  $-10^\circ$ – $45^\circ$  at  $5^\circ$  intervals, for four to six different wing lengths at several wind speeds. The wind speeds chosen were within the range of sinking speeds estimated for present-day insects during gliding (Vogel, 1981). Preliminary results indicated that mounting position of the wings (dorsal or lateral) did not significantly affect lift or drag; thus all aerodynamic results reported here are for dorsally mounted wings. We present results in terms of a dimensionless wind speed, the Reynolds number:  $Re = Vx/\nu$ , where  $V$  is wind speed,  $\nu$  is the kinematic viscosity of air, and the characteristic dimension  $x$  of the model is the maximum width of the thorax.

Moment measurements were made with the model fixed vertically on a vertical aluminum rod (1 mm diameter) mounted with pivot pin bearings (Fig. 1B). A shimstock steel beam with strain gage was mounted perpendicular to the rod, with the far end of the beam fixed to a vertical post.

*Thermoregulation.*—The principal output parameter considered was the steady-state body temperature above air temperature ( $T_b - T_a$ ). The heat transfer coefficient  $H$  (see Eq. 3) was also evaluated using transient cooling experiments (Kingsolver and Moffat, 1982), but the results for  $H$  are used only in passing (see Discussion).

Models were mounted from below on a wooden toothpick, placed in the wind tunnel ( $\alpha = 10^\circ$ ), and radiated from above with a photoflood lamp (500 W, 3200K; Kodak Co.). Both body and wings were painted flat black (Solar absorptivity = 95%) to eliminate effects of differential absorptivity. Air temperature was measured with a radiation-shielded thermocouple; air ( $T_a$ ) and body ( $T_b$ ) temperature signals were electronically referenced (Omega-CJ), amplified (Omega Omni-amp, Omega Engineering Inc.), and recorded on a two-channel chart recorder (Gould Equipment Corp.).

Steady-state body temperature was monitored at specified radiation, wind speed, and air temperature conditions for each model as a function of wing length and wing thermal conductivity. The radiation source was then turned off, and the transient cooling response of the model, from which the heat transfer coefficient  $H$  may be estimated (see Kingsolver and Moffat, 1982, for details), was measured.

### *Data Presentation*

To examine the effects of wing length on aerodynamic and heat transfer characteristics, we wish to present results in a form that is standardized relative to wingless models. Thus, we define the relative temperature excess  $RTE$  as the body temperature excess over air temperature for a model with wings of length  $W = x$ , relative to the temperature excess for the corresponding wingless model ( $W = 0$ ):

$$RTE(x) = \frac{(T_b - T_a)|_{w=x}}{(T_b - T_a)|_{w=0}}. \quad (4a)$$

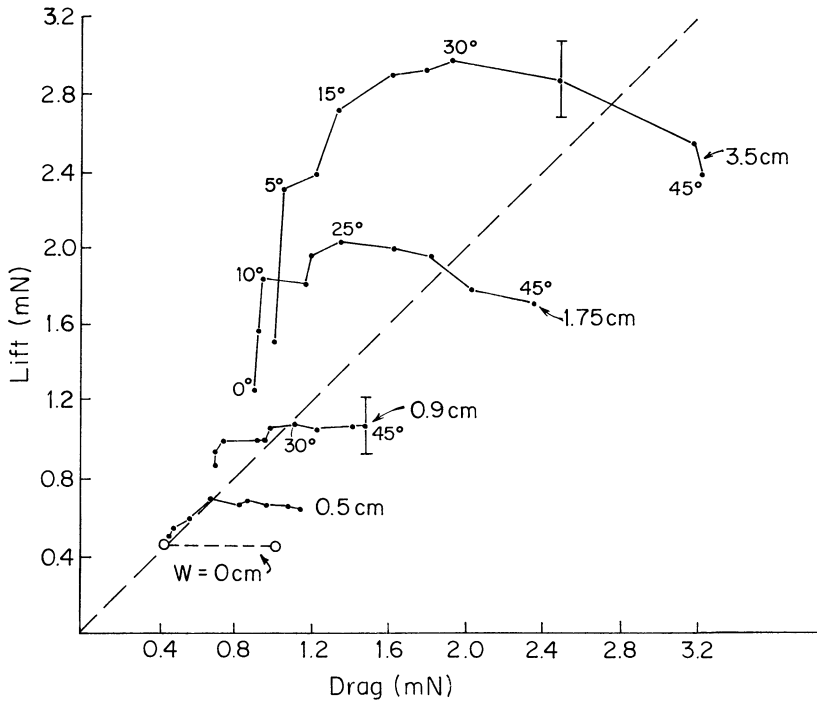


FIG. 3. Polar diagram of lift (in mN) as function of drag (in mN) for a model of cylindrical body shape and 6 cm body length at a wind velocity of 2.5 m/sec. Each solid line represents results for a particular wing length  $W$  (in cm); points along each line represent different angles of attack. In all figures, vertical bars indicate 95% uncertainty intervals.

Thus, for example, an *RTE* of 1.5 indicates that wings increase the body temperature excess by 50% relative to a wingless model. To compare geometrically similar models at different sizes, we also often wish to consider results in terms of a relative wing length  $RWL = W/B$ , where  $B$  is body length.

Similar measures are used for the aerodynamic variables. Thus, relative maximum drag is defined as the maximum drag for a model with wings of length  $x$ , relative to the maximum drag for the corresponding wingless model:

$$\frac{D_m|_{w=x}}{D_m|_{w=0}} \quad (4b)$$

The relative maximum lift-to-drag ratio is similarly defined. Because the moments  $M$  produced by wingless models

are near zero, we report absolute rather than relative values of  $M$ .

The 95% uncertainty intervals are given for all output results. Uncertainty analysis takes into account how uncertainty in measured outputs (e.g., millivolts, cm) translates into uncertainty in the desired calculated outputs (e.g., *RTE*, lift/drag). See Kingsolver and Moffat (1982) for a discussion and application to physiological data. In reporting results, we define a significant difference as one which falls outside the 95% uncertainty intervals.

## RESULTS

### Aerodynamics

Figure 3 shows the polar diagram for one model, body length  $B = 6.0$  cm, at a wind velocity of  $v = 2.5$  m/sec ( $Re =$

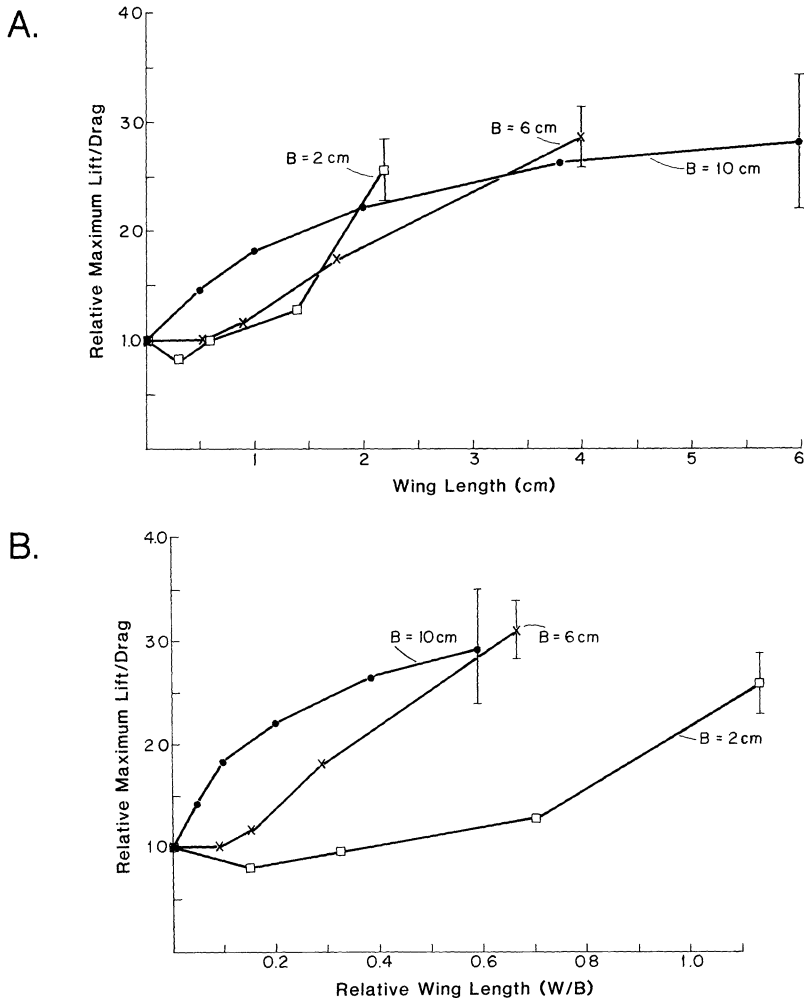


FIG. 4. Relative maximum lift/drag as a function of A) wing length (in cm) and B) relative wing length (wing length/body length) for several different body lengths.  $B$  = Body length: 2 cm (□); 6 cm (X); 10 cm (●). Wind velocity is 2.5 m/sec.

2600). The polar diagram gives lift and drag as a function of angle of attack  $\alpha$  for the model for a number of wing lengths  $W$ . For long wing lengths, lift increases rapidly with  $\alpha$  for values between  $0^\circ$  and  $15^\circ$ , while drag increases slightly; at large  $\alpha$ , lift remains constant or drops slightly, while drag increases rapidly. As wing length decreases, lift decreases and becomes independent of  $\alpha$ . These results are consistent with values reported for insect wings and other aerofoils in this  $Re$  range (see e.g., Vogel, 1981).

From such polar diagrams, we can identify the angle of attack yielding the maximum lift/drag ( $L/D$ ) for a particular model as a function of wing length. Recall that  $L/D$  is directly related to gliding distance. We report maximum  $L/D$  for models with wings in terms of a relative maximum  $L/D$ , which has been standardized relative to the maximum  $L/D$  for a wingless model (see Data Presentation). There is no significant effect of increasing wing length on relative maximum  $L/D$  for wing lengths less than 1.0—

1.5 cm (Fig. 4A), except perhaps at the largest body size. For lengths greater than 1.0 cm, relative maximum  $L/D$  increases significantly with wing length. These results are independent of body shape, wind velocity, the presence or position of legs, and the mounting position of the wings on the thoracic segments.

To consider geometrically similar models of different size, we can replot these data in terms of wing length relative to body length ( $W/B$ ). Such plots (Fig. 4B) reveal that the  $W/B$  above which there is a significant effect of wing length on relative maximum  $L/D$  decreases with body length ( $B$ ). Thus for the  $B = 2.0$  cm model, wing length must exceed 70% of body length before there is any effect on  $L/D$ ; for the 6.0 cm model the corresponding relative wing length is 10%.

While the relation of relative  $L/D$  to wing length is similar at different body lengths, the absolute maximum  $L/D$  is about 4–5 times larger for the 2 and 6 cm body lengths than for the 10 cm length. (This is the reason for the large uncertainty intervals for the 10 cm curves in Figs. 4A and 4B.) Flow visualization experiments suggest that, for the large models, 1) the point of initial separation of flow from the upper surfaces occurs earlier and 2) the downwash angle (the angle through which flow is diverted from free stream as it passes over the upper surface) is much smaller. These two factors reduce the maintenance of a bound vortex around the wing, thus reducing lift production for the large models.

The relationship of relative maximum drag (at an angle of attack of  $90^\circ$ ) to wing length is given in Figure 5A. Recall that the maximum drag ( $D_m$ ) is directly related to the time aloft during parachuting. For wing lengths less than 1.0–2.0 cm, there is no significant effect of increasing wing length on relative  $D_m$ . For wing lengths above about 1.0–2.0 cm, relative  $D_m$  increases significantly with wing length. These qualitative results are independent of body size and shape, wind velocity, and the presence of legs. Again considering geometrically similar models

(Fig. 5B), the relative wing length ( $RWL$ ) above which there is a significant effect of increasing  $RWL$  on relative  $D_m$  is about 0.2 for all body sizes.

The maximum moment  $M$  produced by the wings shows a similar relationship to wing length (Fig. 6A, solid lines). There is no significant effect of wing length on  $M$  for wing lengths less than 1.0–2.0 cm, regardless of body size. For wing lengths greater than 1.0–2.0 cm the maximum moment increases significantly with increasing wing length for all body sizes. Note that increases in leg length alone can be quite effective in producing a moment (Fig. 6A, dashed line). If we consider geometrically similar models (Fig. 6B), the relative wing length  $RWL$  above which there is a significant effect of increasing  $RWL$  on  $M$  decreases with body size.  $RWL$  must exceed 50–90% for effects on  $M$  to be observed for the 2 cm model, but only 20% for the 10 cm model.

Finally, we consider the aerodynamic effects of adding prothoracic lobes: i.e., the effects of three pairs of short ( $W = 0.9$  cm) thoracic wings rather than two (Fig. 7). There is no significant effect of adding prothoracic lobes on lift, drag or  $L/D$  at any angle of attack. This result is independent of body size and shape and of wind speed.

In summary, we emphasize the following aerodynamic results:

1. Relative maximum lift/drag (i.e., gliding distance), relative maximum drag (i.e., time aloft), and maximum moment (i.e., attitude control) do not change significantly for wing lengths less than about 1 cm, regardless of body size and shape. One possible exception is for relative maximum  $L/D$  for the 10 cm model, for which wings less than 1 cm long may have important effects. Relative  $L/D$ ,  $D_m$ , and  $M$  do increase significantly for wing lengths greater than 1.0 cm.
2. The relative wing length  $RWL$  above which relative  $L/D$  and  $M$  increase with  $RWL$  decreases with body size.



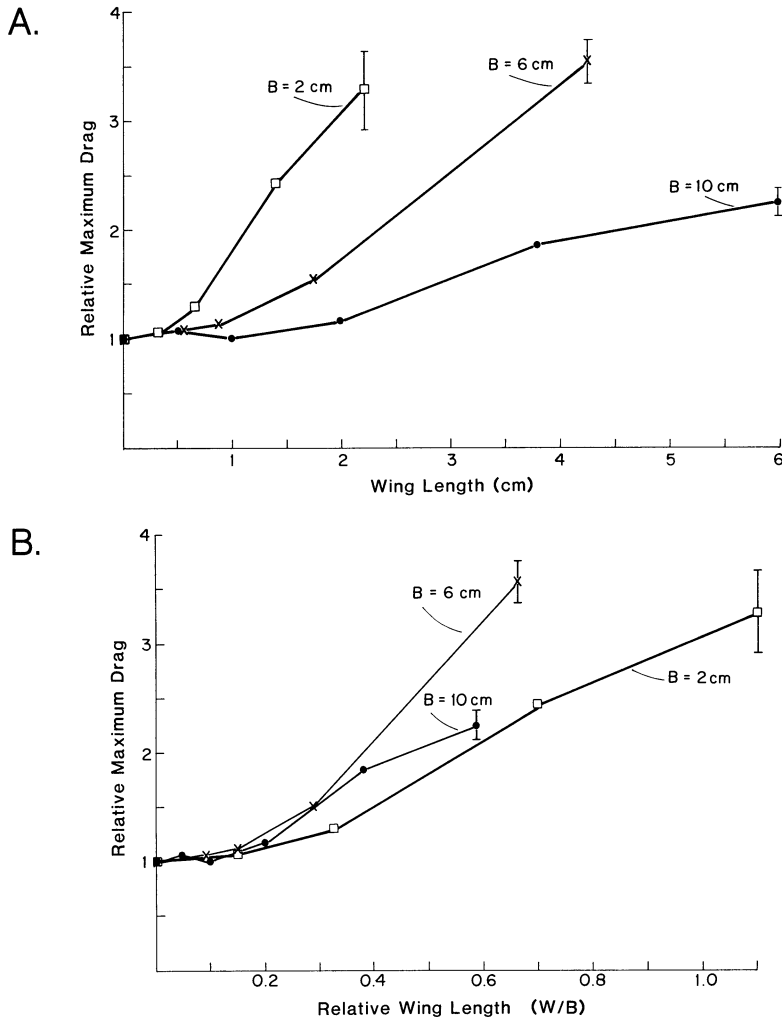


FIG. 5. Relative maximum drag (in mN) during ballooning ( $\alpha = 90^\circ$ ) as a function of A) wing length (in cm) and B) relative wing length ( $W/B$ ) for several different body lengths.  $B$  = Body length: 2 cm ( $\square$ ); 6 cm (X); 10 cm ( $\bullet$ ). Wind velocity is 2.5 m/sec.

The relative wing length above which relative  $D_m$  increases with  $RWL$  is independent of body size.

3. Short prothoracic lobes have no significant effects on lift, drag, or lift/drag.

#### *Thermoregulation and Combined Effects*

The effects of wings on thoracic temperature are revealed by comparing the body temperature excess of a model with

wings to the excess for the same model without wings (i.e., relative temperature excess,  $RTE$ , as defined in Materials and Methods).

Figure 8 shows the relative temperature excess  $RTE$  as a function of wing length for several body lengths and wind velocities. At all body sizes,  $RTE$  increases rapidly for wing lengths from 0 to about 0.5–1.0 cm; for lengths greater than 1.0 cm, there is no significant effect

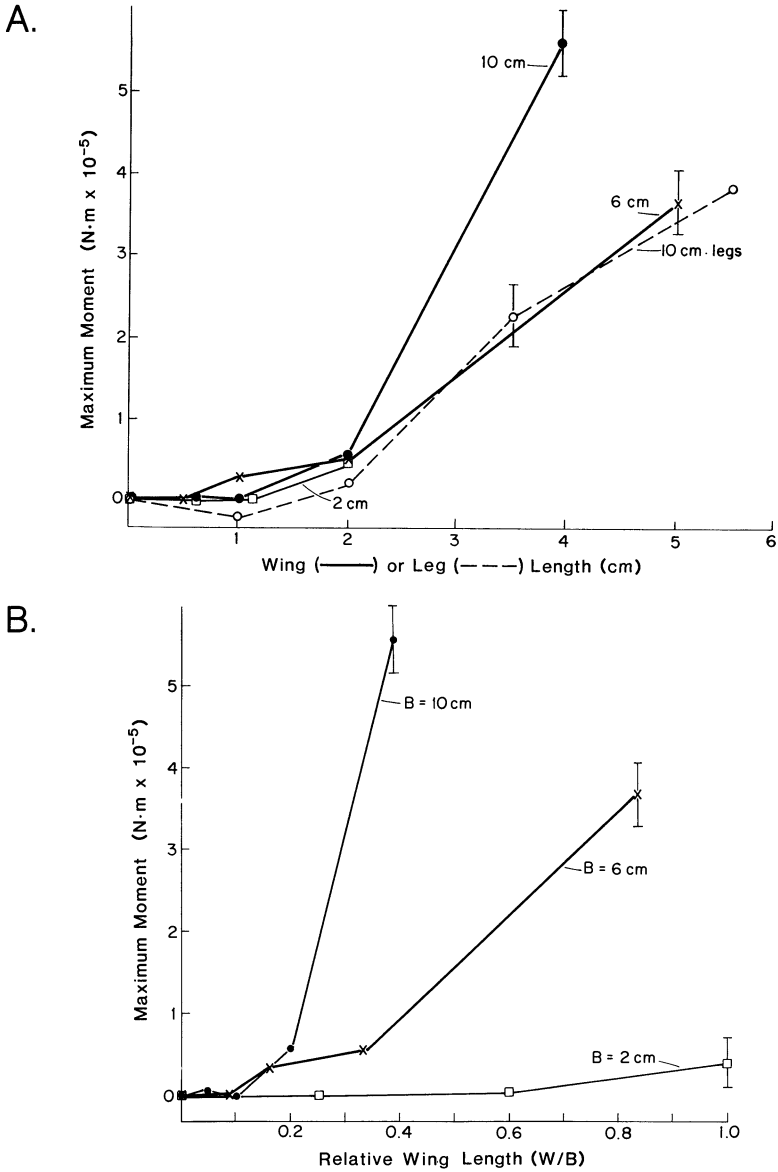


FIG. 6. Maximum moment (in  $Nm \times 10^{-5}$ ) for attitude stability as a function of A) wing (solid lines) or leg (dashed line) length (in cm) and B) relative wing length ( $W/B$ ) for several different body lengths.  $B$  = Body length: 2 cm (□); 6 cm (X); 10 cm (●). Wind velocity is 2.5 m/sec. Dashed line (in 6A) indicates results for a wingless model for various leg lengths.

of wing length on *RTE*. Wind velocity does not affect *RTE*. The maximum effect of wings on *RTE* decreases significantly with body size. These results are independent of air temperature, radia-

tion intensity, body shape, and the presence of legs.

The relative temperature excess is also independent of the thermal conductivity of the wings (Fig. 9A). Again note the

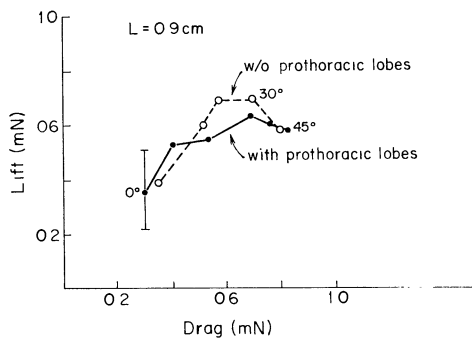


FIG. 7. Lift (in mN) as a function of drag (in mN) for models of body length  $B = 6$  cm with (solid line) and without (dashed line) prothoracic lobes. Wing length ( $L$ ) is 0.9 cm on each winged segment; wind velocity is 2.5 m/sec. Points along each line represent different angles of attack.

strong effects of body size: the presence of wings increases the maximum temperature excess by about 80% for small ( $B = 2.0$  cm) models, but by only 20–25% for large (10.0 cm) models.

If we consider geometrically similar models by using relative wing lengths,  $RWL$  (Fig. 9B), we see that the  $RWL$  above which there is no significant change in  $RTE$  decreases with body size. Thus, the maximum  $RTE$  is achieved by a  $RWL$

of about 0.35–0.40 for the small model, but at a  $RWL$  of only 0.05 for the large model.

Finally, we can consider the effects on  $RTE$  of adding a pair of short (1.0 cm) wings to the prothoracic segment (Fig. 10). Except for the large body size, the addition of prothoracic lobes significantly increases  $RTE$ . The addition of wings on abdominal segments has no significant effect on  $RTE$ .

Figure 11 summarizes both the aerodynamic and heat transfer consequences of wings: Relative temperature excess  $RTE$  and maximum lift/drag  $L/D$  are plotted as functions of relative wing length  $RWL$ . At any body size, there is a relative wing length above which there is no additional thermal effect, and below which there is no significant aerodynamic effect. The relative wing length at which this transition from thermal to aerodynamic effects occurs decreases with body size. For the 2.0 cm model the transition occurs at a wing length of 40–60% of body length; for the 10.0 cm model, it occurs at about 10%.

In summary, we emphasize the following thermal and combined results:

1. The relative temperature excess  $RTE$

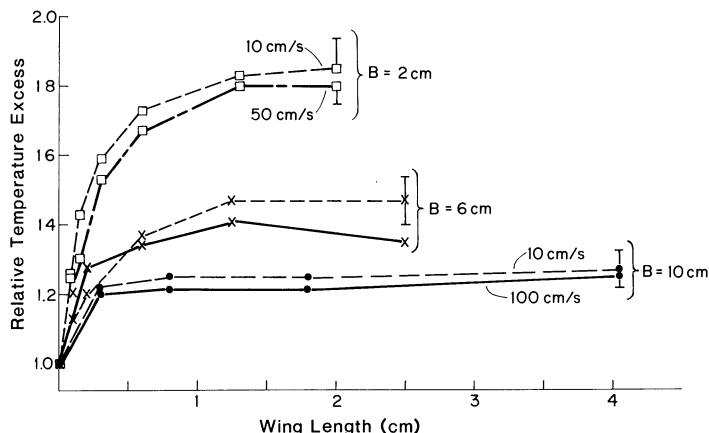


FIG. 8. Relative body temperature excess (see Data Presentation) as a function of wing length (in cm) for several body lengths  $B$  and wind velocities.  $B =$  Body length: 2 cm ( $\square$ ); 6 cm ( $\times$ ); 10 cm ( $\bullet$ ). Wind velocity: 10 cm/sec (---); 50 cm/sec (- - -); 100 cm/sec (—).

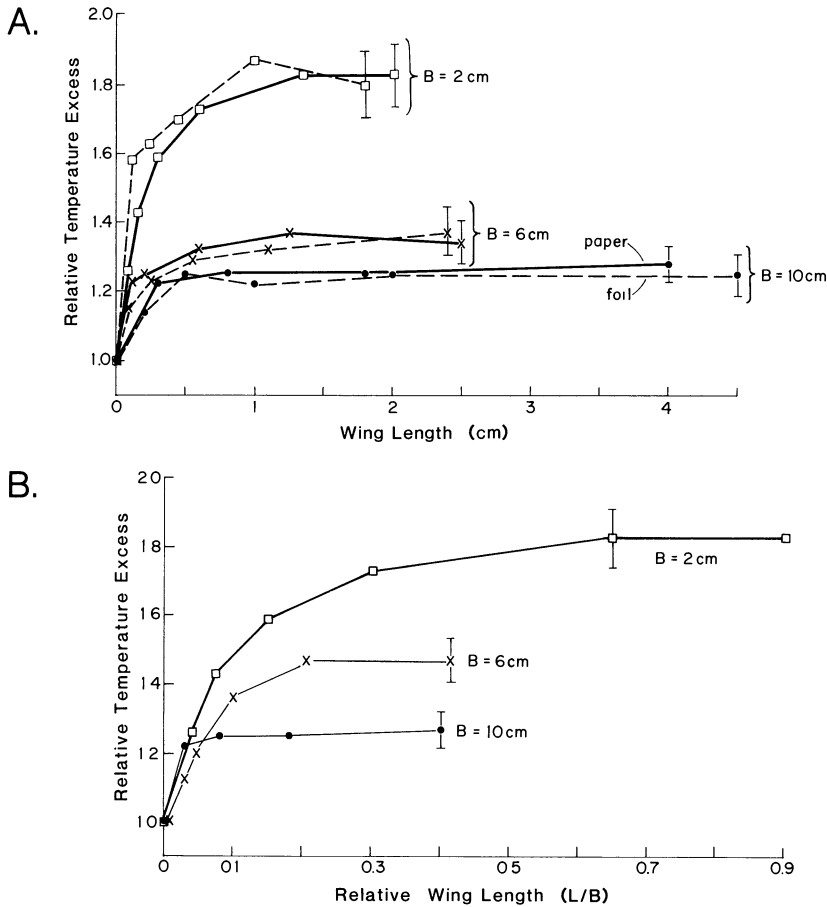


FIG. 9. Relative temperature excess as a function of A) wing length (in cm) and B) relative wing length ( $W/B$ ) for several different body lengths and wing thermal conductivities. Wind velocity is 50 cm/sec.  $B$  = Body length: 2 cm ( $\square$ ); 6 cm ( $\times$ ); 10 cm ( $\bullet$ ). Wing thermal conductivity: paper (low conductivity), solid lines; foil (high conductivity), dashed lines.

- is independent of wind speed, body shape, and the thermal conductivity of the wings. The maximum RTE decreases significantly with body size.
- Relative temperature excess RTE increases rapidly for wing lengths from 0 to about 1 cm, regardless of body size and shape. RTE does not change significantly for wing lengths greater than about 1 cm.
- The relative wing length above which there is no significant change in RTE decreases with body size.
- The addition of prothoracic wings or lobes significantly increases RTE for the smaller body sizes.
- At any body size, there is a relative wing length below which there are significant thermal effects, and above which there are significant aerodynamic effects due to increasing wing length. The relative wing length at which this transition occurs decreases with body size.

#### DISCUSSION

##### *The Evolution of Insect Wings*

The early fossil record for insects is very incomplete. There are no fossils representing transitional stages between wingless and flying insects (Kukalova-

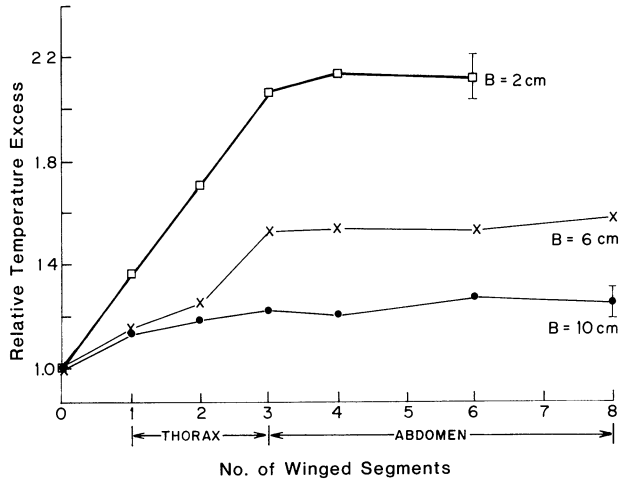


FIG. 10. Relative temperature excess as a function of the number of winged segments for several body lengths. Wind velocity is 50 cm/sec. The order for thoracic segments 1, 2, and 3 is mesothorax, metathorax, and prothorax, respectively. Symbols as in Figure 9.

Peck, 1978). Based on morphological and systematic evidence, it is generally believed that winged insects arose from ancestors of about 2–4 cm body length during the early to late Devonian (Wootton, 1976; Wigglesworth, 1976). Given these uncertainties, any understanding of selective factors operating during this crucial period in insect evolution must be speculative. At best, we can eliminate certain hypotheses as untenable and document other hypotheses as at least plausible.

Our results indicate that, of the three aerodynamic hypotheses that have been proposed for selection for insect wings, there are no significant aerodynamic differences between wingless and short-winged insects. One possible exception is for relative maximum lift/drag (i.e., glide distance) for the 10 cm model, for which wings less than 1 cm long may have important effects. For insects in the size range from which winged insects probably arose, wing lengths more than 30–60% of body length are required before there are any significant aerodynamic effects of wings. Thus, gradual selection for increased wing length in wingless insects could not occur on the basis of aerody-

amic performance. In addition, the presence of prothoracic lobes would have no effects on aerodynamic capacity.

These results follow from the nature of fluid flow at the tips of aerofoils (Lighthill, 1977). Fluid vortices are generated and shed at the tips of the wings; the energy lost to these vortices prevents the effective generation of lift (or in the case of  $\alpha = 90^\circ$ , effective generation of pressure drag). It is only when wings are of sufficient length that the energy lost in tip vortices becomes small relative to the energy gained in lift. The size dependence of this phenomenon, such that smaller models are less effective aerodynamically than are geometrically similar larger models, relates to the greater importance of friction drag at lower  $Re$  (e.g., Vogel, 1981).

We emphasize that these aerodynamic results hold for hypotheses consistent with both fixed (gliding, parachuting) and moveable (attitude stability) winglet articulations. Our results provide a contrast to those of a recent analysis of the evolution of preflight in vertebrates (Capple et al., 1983). These workers conclude that small increments of lift generated by the limbs could dramatically improve at-

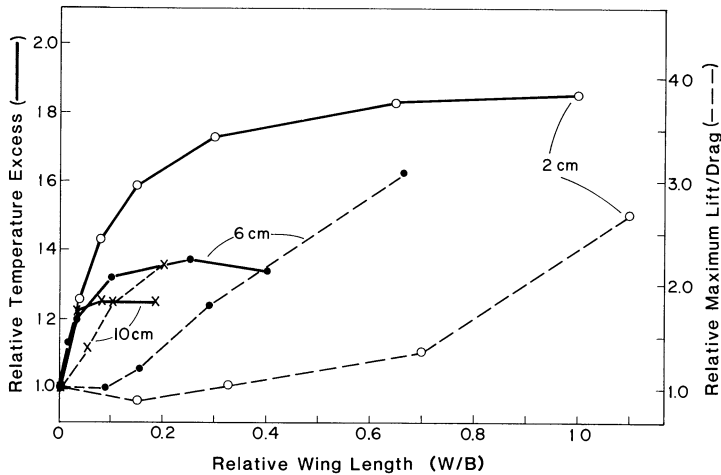


FIG. 11. Relative temperature excess (left ordinate, solid lines) and maximum lift/drag ratio (right ordinate, dashed lines) as a function of relative wing length (wing length/body length) for several body lengths. Data from Figures 4B and 9B.  $B$  = Body length: 2 cm (O); 6 cm (●); 10 cm (X).

titude (roll) stability. Their result assumes that the lift force is applied on a limb extended three body radii to one side of the body. This is an appropriate assumption for vertebrates, but clearly does not apply to insect winglets. In fact, our results (Fig. 6A) suggest that increases in leg length alone could be nearly as effective in improving attitude stability as are increases in wing length. Thus, the "leap control" hypothesis for vertebrates is not valid for insects.

Our aerodynamic results can also address the question of aquatic locomotion in a limited way. This question is of interest because a number of workers have proposed that wings evolved in an aquatic setting and were perhaps involved in aquatic locomotion (Kukalova-Peck, 1978). Using Reynolds number scaling, the results on the effects of wing length apply to aquatic locomotion for models in the size range considered for velocities of movement of 10–20 cm/sec, a low to moderate swim speed. Our results thus suggest that, at least for fixed wings, short wings would not have been effective in aquatic locomotion or attitude control. Further experiments would be needed to see whether flapping would alter this pre-

dition. We note that our results do not address the gill ventilation hypothesis on the evolution of wings (Kukalova-Peck, 1978).

On the other hand, as suggested by Douglas (1981), short wings can have large thermoregulatory effects, particularly at the small body sizes probably typical of the early insects. For these small sizes, increasing wing length significantly increases temperature excess for wing lengths up to 20–40% of body length. These effects are largely independent of details of body and wing shape, radiation and wind conditions, and the conductance of heat through the wings. Our transient analyses indicate that, for wings of low thermal conductivity (as in present-day insects), the wings act to increase the effective surface area for radiation absorption, rather than to decrease the heat transfer coefficient. For wings of high thermal conductivity, wings both greatly increase the effective surface area and increase the heat transfer coefficient.

Recent studies of butterfly thermoregulation have clarified the physical basis for the use of wings as radiation-absorbing devices (Wasserthal, 1975; Douglas, 1978). To affect body temperature, heat

absorbed by the wings from radiation must be conducted along the wings to the body before being lost to convection from the wing. This balance between conduction and convection determines the distance along the wing beyond which absorbed radiation cannot be effectively conducted to the body. For this reason, changes in wing length have little effect on body temperature for wing lengths greater than about 1 cm. We note that, for insects that bask on substrate surfaces, increases in wing lengths may contribute to thermoregulation even at long wing lengths, since such insects may trap hot surface air under their wings (Tracy et al., 1979).

The possible adaptive advantages of increasing body temperature in early winged insects depend in part on climatic conditions in the Devonian period during which pterygotes probably first appeared. The later early Devonian was characterized by a high climatic gradient, with a cool high latitude region and warm and seasonally dry regions at middle and low latitudes. The late Devonian had a lower climatic gradient with less latitudinal variation (Boucot and Gray, 1983). Unfortunately, the spatial and temporal scales at which Devonian climate is known are far greater than those relevant to evolution within an insect population or species. We point out that many present-day insects from all latitudes exhibit adaptations for elevating body temperatures (Casey, 1981).

Our results are consistent with the hypothesis that the initial evolution of wings from ancestors with small winglets was related to selection for increased thermoregulatory capacity, which would be particularly effective at the small body sizes of the earliest insects. After this initial period, effective selection for increased aerodynamic capacity could occur. For small insects, this could only occur for wing lengths greater than about 50–60% of body length; for larger insects this could occur at relatively smaller wing lengths. Thus, we propose that thermo-

regulation was the primary adaptive factor in the early evolution of wings, pre-adapting them for the subsequent evolution of flight.

Two consequences of this hypothesis are particularly relevant to the evolution of flapping flight. First, the effectiveness of wings as structures for regulating body temperature is greatly enhanced if the wings can be moved. Many present-day insects, such as butterflies and dragonflies, use wing positioning as an important means of thermoregulation (Casey, 1981). Thus, moveable articulations would have considerable adaptive value for thermoregulation, an essential prerequisite for the evolution of flapping flight. Second, this scenario suggests that, during the period in which flight evolved, insects already possessed some thermoregulatory capacity. Thermoregulation and flight are intimately associated in present-day insects: a high and narrow range of body temperatures is necessary for vigorous flight in many insects (Heinrich, 1981). We suggest that this association began at the origins of flight.

Finally, these results provide new insight into the thermoregulatory role of wings in present-day insects. Previous work established that the basal regions of wings in many insects are important in thermoregulation (Watt, 1968; Wasserthal, 1975). Our study indicates that the thermal effects of wings are strongly size dependent and that the relative length of the wings contributing to heat transfer is also size dependent. This information is essential to understanding the allometry of thermoregulatory mechanisms in insects and in interpreting the thermal significance of wing pigmentation patterns. In this regard, it is useful to note that many Paleozoic Paleodictyoptera had complex wing pigmentation patterns, including basal wing pigmentation (see Carpenter, 1969).

#### *Scaling and the Evolution of Function*

The basis for our results lies in the different ways in which mechanics and heat

transfer scale with wing length. One consequence of this differential scaling is that a given structure may serve different functions at different stages in its evolution. On this basis, we have suggested that wings represent a preadaptation with respect to flight. For the present case, there are two distinct aspects to the evolution of flight through preadaptation. First, what was the primary adaptive factor favoring increasing wing length before the development of flight? We have argued that this primary adaptation may have involved thermoregulation. Second, how did the transition from thermoregulatory to aerodynamic function occur? In the previous section, we suggested that this transition could have occurred as a result of further small changes in wing length, once wings had achieved lengths of 1 cm or so. We now propose an alternative hypothesis for this transition, involving not changes in wing length but changes in body size.

We have shown that there is a switch in functional capacity from thermoregulation to aerodynamics with increasing wing length at all body sizes. However, the relative wing length, or geometry, at which this switch occurs depends on body size. This means that geometrically identical (i.e., isomorphic) forms may serve different functions at different body sizes. Consider, for example, an insect with wings 50% as long as the body. In a small insect, these wings could function effectively for thermoregulation, but not for aerodynamics; in a large insect, these same wings could serve quite effectively as aerodynamic structures. Thus, a purely isometric change in body size during evolution may yield a change in function of a given structure.

Most interest in scaling phenomena in evolution has focused on the allometric changes with size required to maintain a given function. Accordingly, much recent emphasis has been placed on the developmental mechanisms and selective pressures by which geometrically dissimilar structures could be generated, with the associated maintenance of the func-

tion of these different structures (e.g., Alberch et al., 1979). We wish to emphasize the converse phenomenon as a potentially important mechanism in evolution: that isometric changes in body size may produce qualitative shifts in the function of a given structure, with the associated changes in selective pressure.

The potential for isometric growth in overall body form in insects is well developed. Dyar's rule and Przibam's rule for insect development, which state that cuticular structures increase in linear dimensions by a constant ratio at each moult (see Wigglesworth, 1965) imply isometric growth. More detailed studies suggest that these rules strictly hold only for a minority of cuticular structures: examples both of different ratios for different structures and of a changing ratio for a single structure during development have been documented (Brown and Davies, 1972; Davies, 1966). Nevertheless, at a gross level, growth that is approximately isometric appears commonly in insects.

These considerations suggest an alternative scenario for the transition from a thermoregulatory to an aerodynamic function for insect wings. Elongation of the wings first evolved in small insects as a result of selection for thermoregulatory capacity, followed by an isometric increase—either gradual or abrupt—in body size, after which wings could function as aerodynamic structures. Thus, we argue that changes in body form were not a prerequisite for this major evolutionary change in function.

Note that this scenario would not work for increasing glide distance for large insects. At large body lengths (6–10 cm), increasing body size may decrease glide distance, because of changes in the nature of the fluid flow affecting lift production, even though the relative effect of wings increases with body size. These effects make the very large Protodonates with extremely long wings in the Carboniferous particularly interesting.

Finally, our results 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 thermoregulation and aerodynamics, depending on body size and wing length. It is in exploring the functional consequences of such structural changes that engineering analyses can play a useful role.

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#### LITERATURE CITED

- ALBERCH, P., S. J. GOULD, G. OSTER, AND D. WAKE. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.
- ALEXANDER, R. D., AND W. L. BROWN. 1963. Mating behavior and the origin of insect wings. *Occas. Papers Mus. Zool. Univ. Michigan* 628:1-19.
- BOUCOT, A. J., AND J. GRAY. 1983. A Paleozoic Pangaea. *Science* 222:571-581.
- BROWN, V., AND R. G. DAVIES. 1972. Allometric growth in two species of *Ectobius* (Dictyoptera: Blattidae). *J. Zool. Lond.* 166:97-132.
- CAPLE, G., R. P. BALDA, AND W. R. WILLIS. 1983. The physics of leaping animals and the evolution of preflight. *Amer. Natur.* 121:455-476.
- CARPENTER, F. M. 1969. Adaptations among Paleozoic insects. *Proc. N. Amer. Paleontol. Conv.* 1969:1236-1251.
- CASEY, T. 1981. Behavioral mechanisms of thermoregulation, pp. 79-114. *In* B. Heinrich (ed.), *Insect Thermoregulation*. Academic Press, N.Y.
- DAVIES, R. G. 1966. The postembryonic development of *Hemimerus vicinus* (Dermaptera: Hemimeridae). *Proc. R. Ent. Soc. Lond. A* 41:67-77.
- DOUGLAS, M. M. 1978. The behavioral and biophysical strategies of thermoregulation in temperate butterflies. Ph.D. Diss., Univ. of Kansas, Lawrence.
- . 1981. Thermoregulatory significance of thoracic lobes in the evolution of insect wings. *Science* 211:84-86.
- ELLINGTON, C. P. 1984. The aerodynamics of hovering insect flight. *Phil. Trans. R. Soc. Lond. B* 305:1-181.
- FLOWER, J. W. 1964. On the origin of flight in insects. *J. Insect Physiol.* 10:81-88.
- GATES, D. M. 1980. *Biophysical Ecology*. Springer-Verlag, Berlin.
- HEINRICH, B. 1981. *Insect Thermoregulation*. Academic Press, N.Y.
- HINTON, H. E. 1963. The origin of flight in insects. *Proc. R. Entomol. Soc. Lond.* 28:24-26.
- JOHNSON, C. G. 1969. Migration and Dispersal of Insects by Flight. Methuen, London, U.K.
- KINGSOLVER, J. G., AND R. J. MOFFAT. 1982. Thermoregulation and the determinants of heat transfer in *Colias* butterflies. *Oecologia* 53:27-33.
- KUKALOVA-PECK, J. 1978. Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil record. *J. Morphol.* 156:53-126.
- . 1983. Origin of the insect wing and wing articulation from the arthropodan leg. *Can. J. Zool.* 61:1618-1668.
- LIGHTHILL, J. 1977. Introduction to the scaling of aerial locomotion, pp. 350-384. *In* T. Wu (ed.), *Scaling and Locomotion*. Academic Press, N.Y.
- ROBERTSON, R. M., K. G. PEARSON, AND H. REICHERT. 1982. Flight interneurons in the locust and the origin of insect wings. *Science* 217:177-179.
- TRACY, C. R., B. J. TRACY, AND D. S. DOBKIN. 1979. The role of posturing in behavioral thermoregulation by black dragons (*Hagenius brevistylus* Selys; Odonata). *Physiol. Zool.* 52:565-571.
- VOGEL, S. 1981. *Life in Moving Fluids*. Willard Grant, London.
- WASSERTHAL, L. T. 1975. The role of butterfly wings in regulation of body temperatures. *J. Insect Physiol.* 22:1921-1930.
- WATT, W. B. 1968. Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution* 22:437-458.
- WIGGLESWORTH, V. 1963. The origin of flight in insects. *Proc. R. Entomol. Soc. Lond.* 28:23-32.
- . 1965. *The Principles of Insect Physiology*. Methuen, London, U.K.
- . 1976. The evolution of insect flight. *Symp. Roy. Entomol. Soc. Lond.* 7:255-269.
- WOOTTON, R. J. 1976. The fossil record and insect flight. *Symp. R. Entomol. Soc. Lond.* 7:235-254.
- . 1981. Palaeozoic insects. *Ann. Rev. Entomol.* 26:319-344.

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