Surface-Skimming Stoneflies and Mayflies: The Taxonomic and Mechanical Diversity of Two-Dimensional Aerodynamic Locomotion[*]

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ABSTRACT

The best supported hypothesis for the evolutionary origin of insect wings is that they evolved from articulated, leg-derived respiratory structures of aquatic ancestors. However, there are no fossils of the immediate ancestors of winged insects, and it is difficult to imagine how a functional transition from gills to wings could have occurred. Recent studies of surface-skimming locomotion in stoneflies and mayflies offer a plausible solution by showing how rudimentary wings and muscle power can be used to accomplish two-dimensional aerodynamic locomotion on the surface of water. Here we extend that line of research by examining the phylogenetic distribution and mechanistic diversity of surface skimming in stoneflies, along with a limited examination of mayflies. These investigations reveal both a broad taxonomic occurrence and a fine gradation of mechanically distinct forms. Distinct forms of wing-flapping surface skimming include (1) stoneflies that flap their wings weakly while maintaining their body in contact with the water and undulating their abdomen laterally in a swimming-like motion, (2) stoneflies that skim while elevating their body above the water and maintaining all six legs on the surface, (3) stoneflies and mayflies that skim with only four legs on the water surface, (4) stoneflies that skim with only their two hind legs on the surface, and (5) stoneflies that, beginning with a series of leg motions nearly identical to hind-leg skimmers, use their hind legs to jump from the water into the air to initiate flapping flight. Comparisons across these forms of skimming show that wing-beat amplitude, horizontal velocity, and the verticality of aerodynamic force production increase as the body orientation becomes more upright and contact with the water is minimized. These behaviors illustrate a mechanical pathway by which flying insects could have evolved from swimming ancestors via a series of finely graded intermediate stages. The phylogenetic distribution of skimming and flight in stoneflies does not indicate any clear directionality toward either greater or lesser aerodynamic abilities; however, the broad and apparently basal phylogenetic distribution of skimming taxa supports the hypothesis that the common ancestor of stoneflies was a surface skimmer. This may also be true for the common ancestor of stoneflies and mayflies, that is, the first winged insects. We combine these data with fossil evidence to form a synthetic model for the evolution of flying insects from surface skimmers.

Introduction

Flight in animals may have originated in species that jumped from elevated perches (the trees-down model; Bock 1986) or, alternatively, from animals that first used a rudimentary form of aerodynamic locomotion while moving across the ground (the ground-up model; Ostrom 1979). Ground-up hypotheses have traditionally been viewed as implausible and weakly supported (Rayner 1991); however, new data and analyses have given ground-up hypotheses renewed vigor and interest (Padian and Chiappe 1998; Shipman 1998; Burgers and Chiappe 1999).

Recent fossil discoveries have greatly strengthened the evidence that birds evolved from small running dinosaurs, whose ability to perch on tree limbs evolved after, rather than before, the ability to fly (Padian and Chiappe 1998; Sereno 1999). There is also new evidence for ground-up origins of insect flight. Studies of modern insects (Marden and Kramer 1994, 1995; Kramer and Marden 1997; Ruffieux et al. 1998) have revealed nonflying forms of aerodynamic locomotion, called surface skimming, which could have been used before the evolution of aerial flight by ancestral semiaquatic insects possessing rudimentary wings and thoracic muscles. Surface skimming consists of planar movement across a water surface, wherein propulsion is supplied by aerodynamic thrust, while continuous

contact with the water removes the need for total aerodynamic weight support. All components of a surface-skimming flight motor (wings, wing articulations, muscles, and neuromotor patterns) could have simultaneously undergone gradual selection for improved aerodynamic performance before the evolution of true flight. By providing a scenario that allows for incremental improvement and elaboration, this model offers a solution to the riddle of how flight could arise through non-flying intermediate stages. A particularly exciting possibility is that surface skimming in modern stoneflies may be a retained ancestral trait, which if correct, indicates that we have a unique opportunity to examine living forms that embody the evolutionary transition between nonflying and flying animals.

The surface-skimming hypothesis for insect flight origins has been both lauded (Samways 1996; Thomas 1996; Thomas and Norberg 1996) and denounced (Will 1995). Will used a phylogenetic approach to address the suggestion that surface skimming might be a retained ancestral trait in modern stoneflies. However, at the time of Will's critique, the presence or absence of skimming behavior was known for only two taxa, one of which was ignored in Will's analysis. Thus, Will's phylogenetic analysis lacked even a rudimentary sample of the distribution of character states among the taxa in question and therefore is not likely to be informative.

A specific goal of this study is to test the hypothesis presented by Will (1995) that surface skimming is an apomorphic (i.e., recently derived) trait used by a restricted subset of stonefly (Plecoptera) taxa and that surface skimming in stoneflies bears little or no resemblance to locomotor behaviors used by mayflies (Ephemeroptera). Similarities between stoneflies and mayflies are particularly interesting because these two groups have retained many primitive morphological traits (Matsuda 1970; Brodsky 1994), and each may occupy a basal position (Boudreaux 1979; Hennig 1981) in the radiation of the two main clades of insects, the Paleoptera and the Neoptera (Kristensen 1991). Traits shared by these two taxa are good candidates for traits possessed by the common ancestor of all flying insects.

Material and Methods

Streams in central Pennsylvania were checked frequently for adult stoneflies during all seasons of the year between 1994 and 1999. In order to include stonefly taxa that are restricted to the southern hemisphere, streams and rivers in southern Australia (Victoria and Tasmania) were sampled during a 3-w period of October 1998. Mayfly subimagos were also collected during the spring and summer of 1998 from central Pennsylvania.

Upon capture, stoneflies and mayflies were kept in an insulated cooler at approximately 10°–15°C. Within 24 h, they were dropped onto the surface of a shallow tank of water (40 × 50 × 3–4 cm) and filmed from the side at 500 frames/s with a high-speed video recording system (Redlake HR 1000).

Drawings of surface-skimming postures were made from print-outs of single frames from the high-speed video sequences. Velocities were measured from the subset of records in which the insect's movement was nearly parallel to the film plane.

Surface-skimming ability is strongly dependent on both the physical integrity of the insect and characteristics of the water. Stoneflies and mayflies were handled as little as possible to prevent damage to their delicate wings and legs. Our preferred method was to capture insects in the field by inducing them to walk into clean, dry collection vials from which they were shaken onto the surface of our test tank (i.e., no direct handling). Tap water was used for all experiments. We avoided any contact between our fingers and the water in the test tank since even trace amounts of oils from human skin disrupt surface tension and impair or eliminate skimming.

Many of our video recordings were made at locations away from the laboratory where we had no control over ambient temperature. In order to compare velocity measurements from trials performed at different temperatures, we adjusted all skimming velocities to an estimated value at 20°C by using the slope of a regression of skimming velocity on temperature (0.8 cm/s/°C) that was derived from extensive experiments with *Taeniopteryx burksi* at temperatures from 2° to 23°C (Marden and Kramer 1994).

A phylogenetic tree for Plecoptera was constructed using PAUP[*] 4.0b2 (Swofford 1999) with all 113 characters (67 are parsimony informative) coded by Nelson (1984). All characters were coded as unordered (i.e., nonpolar), thus forming an unrooted tree since Nelson did not sample any out-group taxa. There were no missing data or multistate taxa. Reliability of the tree and homoplasy were examined by calculating the rescaled-consistency (RC) and retention (RI) indices, based on a heuristic search (settings = stepwise addition for the starting tree; random addition sequence with 100 replicates; tree bisection-reconnection swapping algorithm). These indices can range from 0 to 1, with higher values indicating a more strongly supported tree.

Results

We made high-speed video recordings of surface locomotion for 22 species of stoneflies from 10 families (Table 1). Species in eight families (Austroperlidae, Gripopterygidae, Taeniopterygidae, Capniidae, Leuctridae, Nemouridae, Perlodidae, Chloroperlidae) utilized some form of wing-propelled surface skimming to move horizontally across the water surface. Of the remaining two families, one (Perlidae) contains species that use only runninglike motions of the legs to propel themselves along the surface of water. Another family (Notonemouridae) is represented in our sample by a single species that we have not observed to skim; this species instead initiates flight by jumping from the water into the air using a powerful thrust of its hind legs. As we show below, the hind-leg motions involved in in-

Table 1: Summary of stoneflies sampled, their family affiliation, body length, type of skimming, and a qualitative judgement of their flight ability

Family and Species	Body Length (mm)	Skimming Mode	Flight Ability [a]
Austroperlidae:			
Acruroperla atra	12.9	Swim skim	No
Tasmoperla thalia	17.2	Swim skim	No
Capniidae:			
Paracapnia angulata	6.1	Six-leg skim	No
Allocapnia vivipara	5.3	Sail	No
Chloroperlidae:			
Swelta onkos	6.8	Six-leg skim; jump	Agile
Gripopterygidae:			
Cardioperla diversa	8.0	Four-leg skim	Marginal
Dinotoperla cristinae	8.6	Four-leg skim	Marginal
Leptoperla sp.	11.4	Four-leg skim	Marginal
Leptoperla beroe	11.7	Four-leg skim	Marginal
Rickoperla rugosa	5.1	Four-leg skim	Marginal
Illiesoperla mayi	8.6	Four-leg skim	Marginal
Leuctridae:			
Leuctra hippopus	6.5	Hind-leg skim	Agile
Leuctra sibleyi	5.0	Hind-leg skim	Agile
Nemouridae:			
Ostrocerca albidipennis	4.7	Six-leg skim	Agile
Paranemoura perfecta	4.7	Six-leg skim	Marginal
Amphinemoura nigritta	5.1	Six-leg skim	Agile
Notonemouridae:			
Notonemoura lynchi	7.9	Jump	Agile
Perlidae:			
Paragnetina media	16.4	No	Marginal
Perlodidae:			
Isoperla sp.	7.8	Six-leg skim; jump	Agile
Isoperla sp.	12.0	Six-leg skim; jump	Agile
Taeniopterygidae:			
Strophopteryx fasciata	6.5	Six-leg skim	Marginal
Taeniopteryx burksi	7.9	Six-leg skim	Marginal

[a] No = flightless; marginal = poor maneuverability and not all individuals capable of gaining altitude at room temperature; and agile = can gain altitude and avoid stationary objects while flying.
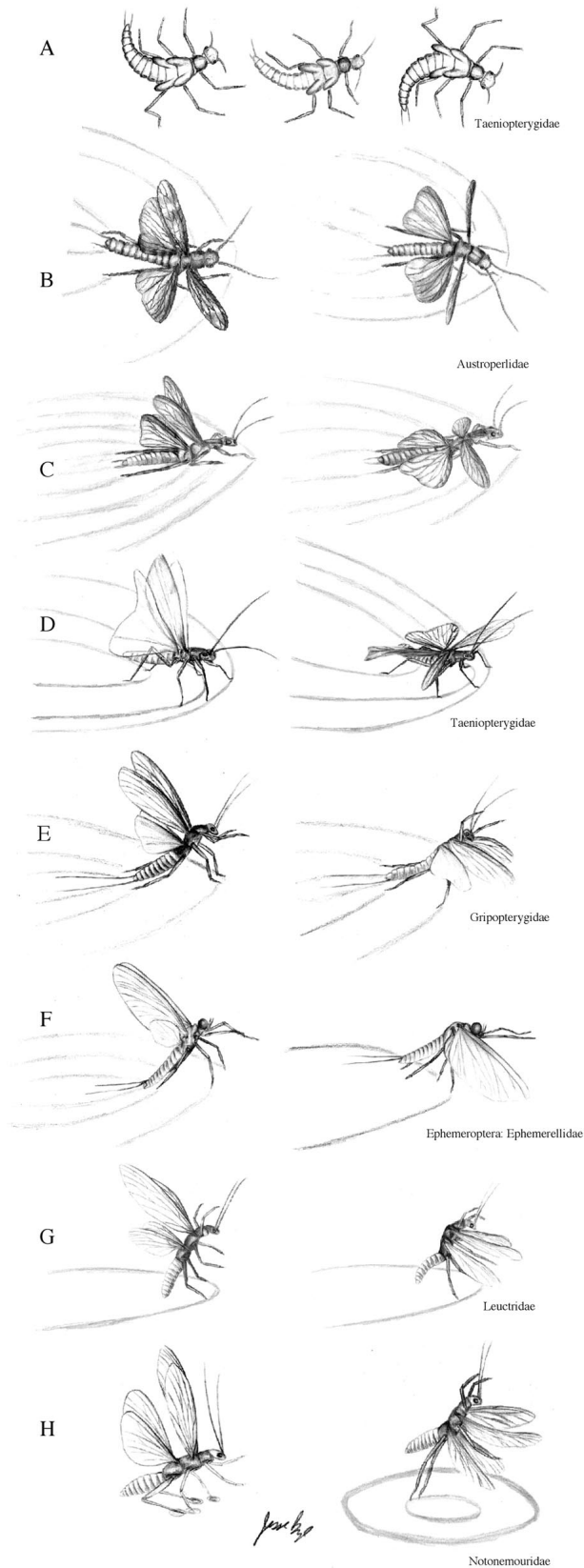
itiating these jumps are identical to hind-leg motions involved in one form of surface skimming.

A striking feature of the diversity of surface-skimming locomotion in stoneflies is the fine gradation of mechanically distinct forms. Each of these forms of surface locomotion are described below in rank order of decreasing contact with water (note that this ordering is based on mechanical rather than phylogenetic criteria). Readers are encouraged to access a Web-based version of Figure 1 that contains hyperlinks to platform-independent QuickTime movies of each of these types of locomotion (http://www.bio.psu.edu/People/Faculty/Marden/PBZFig1.html).

Swimming and Swimming Skimming

Stonefly nymphs swim by performing rhythmic lateral undulations of their body axis. *Taeniopteryx burksi* nymphs (Fig. 1*A*) are fairly representative of swimming by all types of stonefly nymphs. At a water temperature of 5°C, they undulate their body axis at a frequency of 2–3 Hz, accomplishing a net forward velocity of 2.4 cm/s (SD = 0.1; $N = 3$).

Adult *Tasmoperla thalia* (Austroperlidae) stoneflies use a form of surface skimming that combines wing flapping with body undulations similar to the motion used by stonefly nymphs during swimming (Fig. 1*B*, 1*C*). The long axis of the

A

Taeniopterygidae

B

Austroperlidae

C

D

Taeniopterygidae

E

Gripopterygidae

F

Ephemeroptera: Ephemerellidae

G

Leuctridae

H

Notonemouridae

abdomen oscillates laterally at a frequency of 7 Hz through an arc of approximately $\pm 15°$ in relation to the long axis of the head and thorax (air temperature = 23°C). The phase of this oscillation appears to be independent of wing motions.

The middle (mesothoracic) and hind legs of *T. thalia* do not hold the abdomen above the water. The mesothoracic legs are flexed under the thorax, and the hind legs extend posteriorly alongside the abdomen (Fig. 1*C*). Thus, there is extensive contact between the ventral body surface and the water so that swimming motions may contribute to thrust and maneuverability. It should be noted, however, that swimming motions probably degrade aerodynamic performance since the leading edges of the wings are oriented at angles other than perpendicular to the oncoming airflow at certain points of the wing-stroke cycle (Fig. 1*B*). Certain insects use a nonoscillatory lateral flexure of the abdomen as a steering mechanism (Grodnitsky 1999; Dudley 2000), but we know of no other insects in which the abdomen oscillates laterally during wing flapping.

Tasmoperla thalia flaps its wings at a frequency of 20 Hz through a stroke amplitude of approximately 90°. The wings clap together and are peeled apart (Weis-Fogh 1973; Ellington 1984) at the start of the downstroke. The forewings slightly lead the hind wings throughout the stroke cycle. This kinematic pattern, called "anteromotoric in-phase functional four-wingedness," is thought to be the ancestral condition for flying insects (Grodnitsky 1999). Pronation of the forewings at the start of the downstroke and suppination at the start of the upstroke (Fig. 1*B*, *right panel*) creates the kinematic asymmetry between the downstroke and upstroke that is necessary for producing a net force. Video records show that the tip of the forewing bends forward during the initial portion of the upstroke, which indicates an aerodynamic force acting on the wing in a direction that is parallel to the longitudinal body axis, that is, thrust. Skimming velocity of *T. thalia* averaged 15.6 cm/s, which is considerably faster than the swimming velocity of stonefly nymphs but slower than all other types of surface skimming (Fig. 2).

Another austroperlid stonefly, *Acruroperla atra* (not depicted in Fig. 1), skims without body undulations but with a similar body position and extensive contact between the ventral abdomen and the water. This species raises its thorax above the water by extending the mesothoracic legs anteriorly. However, the entire tibia of these legs remains on the water surface, and the extensive water contact creates a large amount of drag. Thus, like *T. thalia*, this species is a comparatively slow skimmer (mean velocity = 22.4 cm/s; air temperature = 20°C).

Figure 1. Drawings made from individual frames of video recordings of different forms of aquatic and semiaquatic locomotion used by stoneflies and mayflies. All except swimming (series *A*) depict movement on the surface of water. Samples of video recordings are available at http://www.bio.psu.edu/People/Faculty/Marden/PBZFig1.html.
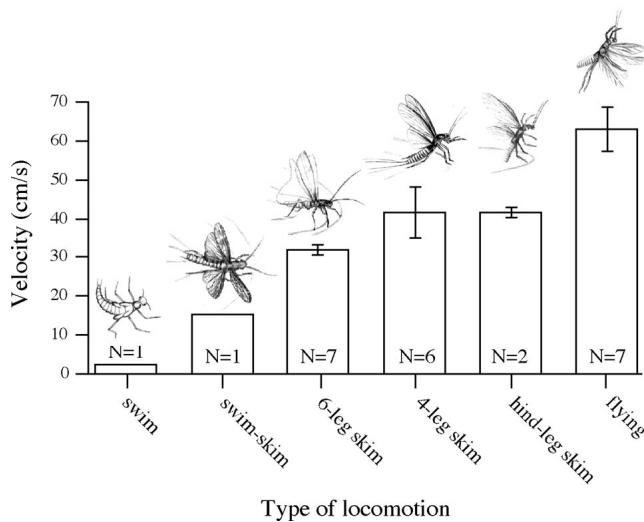
Figure 2. Mean velocity of stoneflies using different forms of aquatic, semiaquatic, and aerial locomotion. Sample sizes refer to the number of species; error bars represent the standard error of the grand mean (i.e., variability among means derived from multiple species). Note the trend of increasing velocity as contact with water decreases. Body size had no significant effect on skimming speed.

Even at warm temperatures (20°–25°C), we were unable to elicit flight attempts from any *T. thalia* individuals ($N = 3$). Wing flapping in this species was observed only as an immediate and stereotypical response to contact with water. *A. atra* did attempt to fly when tossed into the air, but none of the six individuals tested were able to maintain altitude. Thus, it appears that these species are not capable of flying.

Six-Leg Skimming

Species ($N = 6$) that we have examined in the families Taeniopterygidae, Nemouridae, and Capniidae use their legs to elevate their entire body above the water while they continuously flap their wings during surface skimming (Fig. 1D). Because these taxa maintain the tarsi of all six legs in continuous contact with the water surface, we have termed this form of locomotion "six-leg skimming." An additional capniid species that we have examined, *Allocapnia vivipara*, shows no ability to flap its wings but also accomplishes six-leg skimming by raising its wings in response to wind, thereby sailing across the water surface (Fig. 3; Marden and Kramer 1995).

At cool air temperatures (<15°–18°C), stoneflies in the families Chloroperlidae and Perlodidae use intermittent forms of six-leg skimming ($N = 3$ species; we have also observed this behavior in four additional chloroperlids that we have not identified). These stoneflies periodically beat their wings through 3–5 cycles and then coast. At warmer air temperatures, they jump from the water to initiate flight (see "Jumping from Water"). Thus, these species use a limited form of six-leg skimming as a conditional strategy to remain mobile at cool air temperatures.

Wing-beat kinematics during six-leg skimming are much the same as described above ("Swimming and Swimming Skimming") for *T. thalia*, except that elevation of the body above the water allows a greater stroke amplitude. The wing stroke of six-leg skimmers extends approximately 20° below the horizontal, which extends the total stroke amplitude to 110°. Wing-beat frequency of six-leg skimmers reaches frequencies as high as 45 Hz in *Strophoteryx fasciata* (Taeniopterygidae) at warm air temperature (22°C). The combination of greater stroke amplitude and frequency yields a much greater angular velocity of the wings, which increases aerodynamic force production (Lehman and Dickinson 1997). Larger aerodynamic forces and reduced contact with the water result in higher skimming velocities (mean = 32 cm/s; $N = 7$ species from six families; SD = 2.9; Fig. 2).

Flight ability of six-leg skimmers varies widely. At the low end of the scale is the capniid *Paracapnia angulata*, which attempts flapping flight when dropped or thrown into the air but even at warm air temperatures (25°C) can only spiral downward to a spot on the ground almost directly below the point from which it was dropped. The capniid that accomplishes six-leg skimming by sailing rather than flapping (*A. vivipara*; Fig. 3) is also flightless, although it does extend its wings and glide when tossed into the air (Marden and Kramer 1995). Other six-leg skimmers are marginally flight capable. At warm air temperatures, approximately 50% of individuals of *Taeniopteryx* and *Strophopteryx* stoneflies can maintain or gradually gain altitude, whereas the remainder cannot remain airborne (Marden and Kramer 1994). Certain nemourids, chloroperlids, and perlodids are agile fliers; they are capable of steeply angled takeoffs and can turn to evade fixed and slowly moving objects.

Four-Leg Skimming

We have examined the skimming behavior of six species (*Cardioperla diversa*, *Dinotoperla cristinae*, *Leptoperla beroe*, *Leptoperla* sp., *Illiesoperla mayi*, and *Ricoperla rugosa*) of stoneflies in the family Gripopterygidae, the most diverse plecopteran family in the southern hemisphere. Gripopterygids raise their forelegs above the water surface (Fig. 1E), which creates a more upright body angle and a greater wing-stroke amplitude. Stroke amplitude of the forewings is nearly 180°, whereas the hind wings are constrained by the water surface to a stroke amplitude of approximately 110°–120°. Wing-beat frequency ranges widely among four-leg skimmers, from a low of 23 Hz in *Illiesoperla* to a high of 42 Hz in *Leptoperla*.

The more upright posture of four-leg skimmers creates a wing-stroke angle that orients the net aerodynamic force more vertically. Development of a significant vertical force during four-leg skimming is readily apparent in one of our films, which shows a skimming gripopterygid stonefly becoming airborne

Figure 3. Photograph of a short-winged *Allocapnia vivipara* male. This species does not flap its wings but raises them in response to wind, thereby accomplishing sailing (Marden and Kramer 1995).

for a few wing-stroke cycles before it stalls and returns to the water surface (http://www.bio.psu.edu/People/Faculty/Marden/movies/FourLeg.mov). Presumably, there is partial aerodynamic weight support during normal four-leg skimming, which should have the beneficial effect of reducing indentation of the water surface and consequently the size of the bow wave pushed by the legs, that is, less drag. Velocity of four-leg skimmers averaged 44 cm/s (SD = 16.6; Fig. 2).

Our video records of skimming gripopterygids were obtained at air temperatures of 20°C. In the field at cooler air temperatures (12°–18°C), gripopterygids were incapable of flying but reflexively (i.e., immediately on contact with the water) utilized surface skimming when dislodged from midstream rocks. They readily reached shore even on fast-moving cold water. At warmer air temperatures (18°–23°C), gripopterygids were marginal fliers, barely able to maintain altitude. However, on a warm sunny day (23°C), we observed thousands of *Dinotoperla* spp. ascending into the air above the Delatite River (Victoria, Australia). They were air-driven upward by thermal convection that carried the marginally flight-capable stoneflies above the tops of the trees and apparently far from the river. This observation demonstrates that flight and dispersal ability need not be tightly coupled, since air currents can greatly augment the mobility of insects that are just barely able to remain airborne.

A number of mayfly subimagoes (Ephemeroptera) also use four-leg skimming at cool air temperatures (<13°C; Fig. 1*F*). Their forewings achieve a 180° stroke amplitude, and there is no restriction on the stroke amplitude of the hind wings, which in mayflies are much smaller than the forewings. Mayfly skimming features a slight pitching motion of the body during the wing-stroke cycle, which causes the hind legs and the tip of the abdomen to rise off the water during the latter half of the downstroke. Only the tarsi of the middle legs remain in contact with the water throughout the entire wing stroke.

It is interesting to note that both gripopterygid stoneflies and mayflies have long abdominal cerci that trail behind the body on the water surface. The consistent association between four-leg skimming and long cerci suggests a functional connection.

One possibility is that cerci counteract a tendency to pitch backward. Another possibility is that cerci widely distribute downward forces generated by the tip of the abdomen, thereby reducing surface deformation and drag.

Hind-Leg Skimming

Stoneflies in the family Leuctridae (*Leuctra hippopus* and *Leuctra sibleyi*) use a form of skimming (Kramer and Marden 1997) that we have not observed in any other taxa. At air temperatures that are too cool to fly (<13°C), *Leuctra* stoneflies use a stereotypical series of motions that raise their body into a nearly vertical posture. The hind legs are flexed anteriorly to bring the tarsi forward to a position under the middle of the thorax (Fig. 4, *upper series*). Subsequent extension of the hind legs, accompanied by the first downstroke of the wings, raises the body into a nearly vertical posture. This posture is maintained during continued wing flapping, in which both the fore- and hind wings achieve a stroke amplitude that approaches the maximal 180° (Fig. 1*G*). This is not an entirely stable body position because there is sometimes excessive forward pitch that is controlled by temporarily placing the tarsi of the middle legs down on the water. During most wing-beat cycles, *Leuctra* has only its two hind tarsi and the tip of its abdomen in contact with the water. As noted above for other types of skimming, video records of *Leuctra* show that the forewings bend during the wing stroke, thus indicating a net aerodynamic force acting on the wing in a direction that is parallel to the longitudinal body axis. This is a vertically oriented net force when the body is oriented in a head-up posture. By minimizing body contact with water and by producing vertical force, hind-leg skimmers minimize drag on the water surface. Average velocity of *Leuctra* was 42 cm/s (SD = 1.9), which is not significantly different from the mean velocity of four-leg skimmers (44 cm/s) but is significantly higher than all other forms of skimming (Fig. 2).

Adult *Leuctra* stoneflies are active during spring (late April and early May in Pennsylvania) when the weather is highly variable. At warm air temperatures, *Leuctra* are relatively strong

Figure 4. Sequence of movements and body positions (progressing from left to right) during the initiation of hind-leg skimming (Fig. 1*G*) by stoneflies in the family Leuctridae (*upper series*) and takeoff from the water (Fig. 1*H*) by stoneflies in the family Notonemouridae (*lower series*). Note the similarity in the way the hind limbs are used and positioned during these two forms of locomotion.

fliers, whereas at cool air temperatures, we have observed large numbers of *L. sibleyi* using hind-leg skimming to move about on the surface of a stream. Thus, it appears that *Leuctra* stoneflies use surface skimming to remain mobile over a broad range of ambient temperatures.

Jumping from Water

Stoneflies in the families Notonemouridae, Chloroperlidae, and Perlodidae use their hind legs to jump from water into the air, thereby initiating aerial flight (Fig. 1*H*). The series of leg motions used to perform this jump are strikingly similar to those used by *Leuctra* stoneflies to initiate hind-leg skimming. Jumpers flex their hind legs, thus bringing the tarsi forward to a position under the middle of the thorax (Fig. 4, *lower series*). Rapid extension of the hind legs accompanied by the first downstroke of the wings launches the insect into the air. Flight is then maintained by continued wing flapping while the body remains oriented at an angle similar to that at takeoff (Fig. 4, *lower series, far right panel*). Mean horizontal velocity of flying stoneflies exceeded that of all forms of surface skimming (Fig. 2; mean = 63 cm/s, SD = 15; *N* = 7 species).

Phylogenetic Distribution of Skimming in Plecoptera

Will (1995) began to examine the question of how surface skimming and flying are distributed phylogenetically among stoneflies with the aim of evaluating our hypothesis (Marden

and Kramer 1994, 1995) that surface skimming is a plesiomorphic (i.e., basal) trait. Will used morphological character data from Nelson (1984) to construct a phylogenetic tree of Plecoptera families. This tree was presented as if it were a rooted phylogeny; however, Nelson's data set contains no analysis of taxa other than Plecoptera. Thus, the out group labeled *OG* in Will's figure (1995, Fig. 1) does not exist, and the rooting of the tree remains uncertain. Nevertheless, it is possible to use Nelson's data to construct an unrooted phylogeny and thereby test Will's hypothesis that surface skimming occurs only in an isolated place on the tree, which would indicate that it is most likely an apomorphy.

Our phylogenetic analysis of Nelson's morphological character data yielded 12 equally parsimonious trees with 153 steps (for each tree, RC = 0.61 and RI = 0.83). A strict consensus of these trees is shown in Figure 5, *upper panel*. Onto this tree, we have mapped the occurrence of particular types of surface skimming. Skimming is universal among taxa belonging to the superfamily Nemouroidea and is present in all of the taxa examined to date within the clade that contains the superfamilies Eusthenioidea and Gripopterygoidea (Fig. 5, *lower panel*). A very limited form of skimming (intermittent rather than continuous flapping) is used by certain taxa in the superfamily Perloidea, although stoneflies in this group are much more inclined to jump from the water and fly than they are to skim. The only taxon sampled to date that shows no use of winged locomotion on the water surface (the Perlidae) is in this clade. We have not yet examined any species in the clade containing
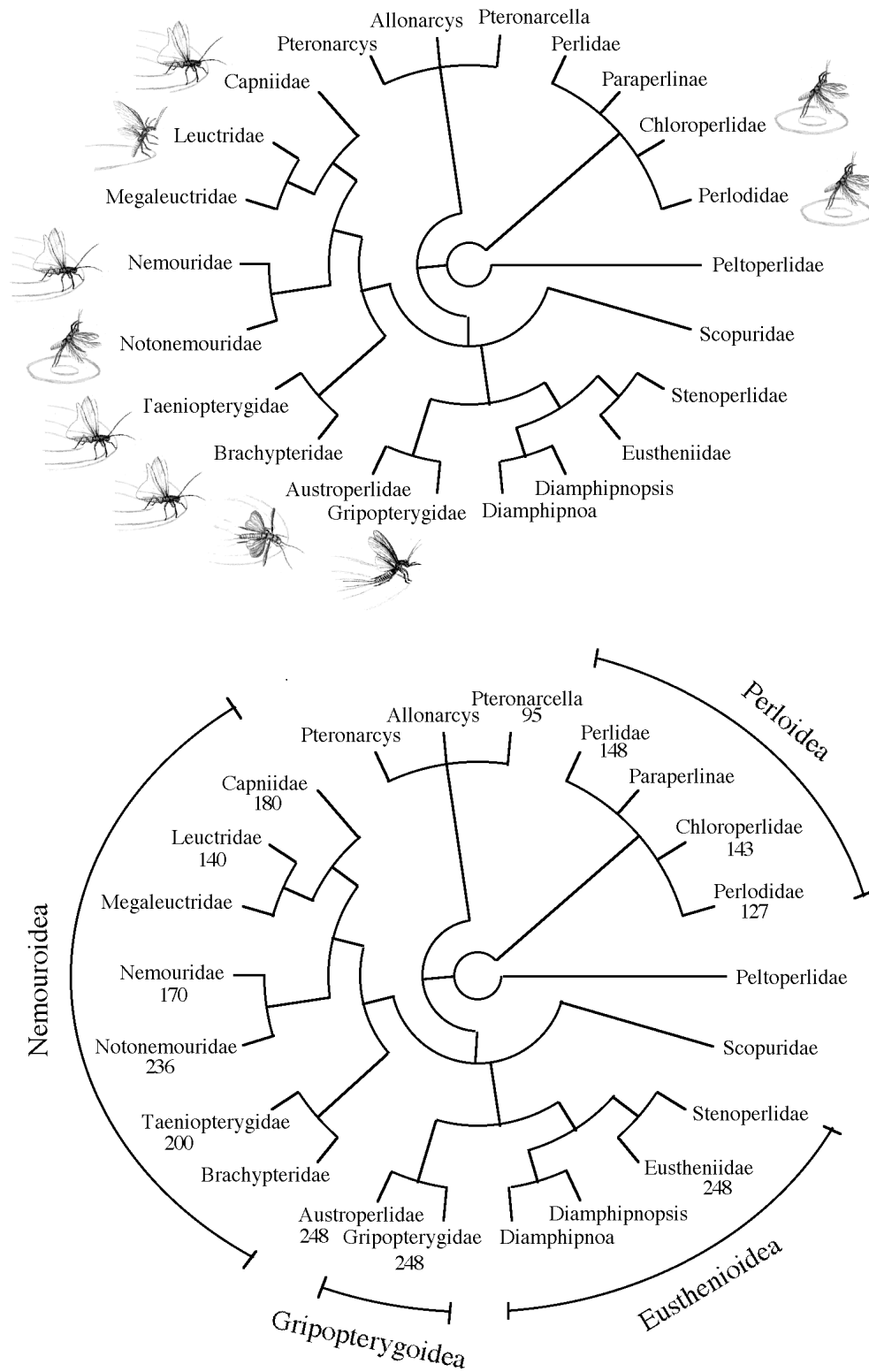
Figure 5. Maximum parsimony tree (unrooted; rescaled-consistency index [RC] = 0.61, and retention index [RI] = 0.83) constructed using 67 parsimony-informative morphological characters from data in Nelson (1984). Surface-skimming behavior is mapped onto the tree in the upper panel by using graphic icons from Figure 1. Except for Perlidae, which display no use of winged locomotion on the water surface, and Scopuridae, which are wingless, taxa without icons have not yet been tested for surface locomotion behavior. The lower panel shows numbers that indicate the date (millions of years ago) of the first fossil record for each family (Labandeira 1994). Note that there are older fossils (ca. 260 million years ago) of what appear to be taeniopterygids and eustheniids (Illies 1965), so these dates are conservative.

Pteronarcys, Allonarcys, or Pteronarcella, nor have we examined any peltoperlids. Scopurids are wingless and therefore not amenable to analyses of winged locomotion.

Discussion

The Diversity of Surface Skimming in Stoneflies

> The stoneflies are the most primitive members of the contemporary winged Polyneoptera. They have retained a lot of primitive structural features, such as thysanuran-like nymphs, the meso- and metathorax movable relative to each other, the absence of a distal medial plate in the axillary apparatus, an equal stroke amplitude by fore- and hind wings, the same yawing flight as in mayflies, and so on. All this makes stoneflies especially interesting. (Brodsky 1994, p. 116)

As suggested by Brodsky (1994), the behavior and mechanics of stoneflies are potentially highly relevant for understanding the origins of insect flight. Despite this potential, little effort has been made to examine how this widespread group of insects accomplishes winged locomotion. Our recent studies (Marden and Kramer 1994, 1995; Kramer and Marden 1997) and the data presented here show that stoneflies utilize a wide variety of mechanically distinct forms of surface skimming. These data can now be used to address two distinct questions: (1) Is there a likely mechanical pathway for the gradual evolution of flying from skimming, and (2) What is the evolutionary status (ancestral or derived) of the skimming behavior of modern stoneflies?

The answer to the first of these questions is that there is a very clear stepwise pathway that could have been used to achieve the transition from aquatic to aerial locomotion (Fig. 1). At the base of this hypothetical pathway is skimming using a horizontal body posture, a mixture of swimming and flying motions, and extensive contact between the body and the water surface (Fig. 1B, 1C). A key innovation from this stage would have been using the legs to elevate the body above the water, thereby reducing drag (Fig. 1D). A next step would be to raise the forelegs off the water surface and elevate the anterior portion of the body, thereby further reducing drag on the water, enhancing wing stroke amplitude, and orienting the net aerodynamic force more vertically (Fig. 1E, 1F). Raising the middle legs off the water allows further enhancement of wing-stroke amplitude and drag reduction (Fig. 1G). Finally, elaboration of the leg motions used to elevate the body into a head-up skimming posture may have been used to propel the insect into the air, thereby accomplishing true powered flight (Figs. 1H, 4). We have shown previously (Marden and Kramer 1994) that stoneflies can accomplish skimming with experimentally reduced wing size and muscle power output and that certain extant stoneflies possess and utilize rudimentary wings and wing motions for surface skimming (Fig. 3; Marden and Kra-

mer 1995). Together, these data constitute the only empirical demonstration of a pathway by which flapping flight could have evolved through a series of intermediate stages. It is worth noting that certain reptiles (Glasheen and Mcmahon 1996) and birds (Livezy and Humphrey 1985) are also active on the surface of water. Thus, general features of the pathway that we have proposed for the evolution of insect flight may also be a reasonable mechanical model for the evolution of avian flight. Alternatively, the water surface may only be a particularly advantageous setting for insect flight evolution since larger animals can reach higher running speeds and are less impeded by the irregular surfaces of terrestrial habitats. Ground-up evolution of flight in vertebrates may have occurred through a roughly analogous series of stages by terrestrial vertebrates running over solid surfaces (this is essentially what has been proposed in Burgers and Chiappe [1999]).

To address the second question regarding the evolutionary history of aerodynamic performance in modern stoneflies, we have mapped surface-skimming behavior onto a phylogenetic tree for Plecoptera (Fig. 5). This figure shows that skimming is much more widespread among stonefly taxa than has previously been assumed. Rather than being an apomorphy (Will 1995), skimming is ubiquitous among the Gripopterygoidea and Nemouroidea superfamilies. Families within these two clades are among the oldest Plecoptera, with fossil records dating back as far as 248 million years (Fig. 5, *lower panel*; Labandeira 1994). Families within the Eusthenioidea (Fig. 5, *lower panel*) are equally old, but unfortunately, we did not find any adults to examine for skimming behavior during our 3 w of fieldwork in Victoria and Tasmania (note, however, that as we were preparing the final draft of this paper, we found a eusthenioid stonefly in Chile, *Diamphipnopsis samali*, that uses its wings to row along the water surface; this behavior will be described in a subsequent publication). The Eusthenioidea have traditionally been assumed to be the basal lineage of stoneflies (Illies 1965); however, our tree suggests that the Gripopterygoidea and Eusthenioidea are a monophyletic group that contains, in the case of austroperlids, flightless stoneflies that combine skimming with swimming (Fig. 1B, 1C). In general, the widespread occurrence of skimming among the oldest families of Plecoptera supports the hypothesis that skimming is a retained ancestral trait. We present elsewhere a rooted molecular phylogeny of Plecoptera based on 18S rRNA sequence data (Thomas et al., in press) that indicates a well-supported basal position of the superfamily Nemouroidea in which all of the species that we have sampled ($N = 6$ species) are six-leg skimmers. This does not imply that the first stoneflies were flightless, since most of the stonefly species that we have examined, including Nemourids and Taeniopterygids, are capable of flying in addition to surface skimming (Table 1). Thus, the ancestral condition for Plecoptera was most likely a combination of skimming and flying. In general, the order Plecoptera is a group of insects that are dual-mode aerodynamic locomotors; they

use their wings to move in two dimensions across water surfaces, and most species are able to fly in three dimensions (albeit quite weakly compared to most types of insects).

Surface Skimming in Mayflies

Ephemeroptera are widely believed to possess many primitive features relevant to the origins of the pterygotes. (Kingsolver and Koehl 1994, p. 429)

Certain mayflies (Ephemeroptera) use four-leg skimming in a manner that is mechanically similar to gripopterygid stoneflies (Fig. 1E, 1F). However, they do so only in the subimago stage and only when they are too cold to fly (i.e., air temperatures below about 13°C). At warmer temperatures, they are strong fliers, departing immediately from the water surface and showing no conspicuous use of four-leg skimming in the field. This is appropriate behavior for insects that are active in seasons and habitats where surface-feeding fish are abundant and highly active and eagerly consume mayflies that linger on the surface. Most of the stoneflies that we have studied make either occasional or frequent use of surface skimming in the field, but they emerge earlier in the spring than do most mayflies, when the water is cold and fish are not yet feeding on the surface. The hypothesis that skimming behavior is related primarily to predation, and only secondarily to temperature, is supported by the finding that a mayfly species in tropical Madagascar has lost the ability to fly yet moves about on the water surface using four-leg skimming (Ruffieux et al. 1998; M. Sartori, personal communication). Male imagoes skim to search for females, and the females do not progress beyond the subimago stage. Notably, this species exists in a river system that lacks surface feeding fish, which suggests that in the absence of modern forms of predation, the locomotor and mating behavior of modern aquatic insects, even at warm temperatures, can readily collapse from three-dimensional to two-dimensional and still remain mechanically and ecologically viable.

Surface skimming in mayflies has two other potentially important evolutionary implications. First, because mayflies and stoneflies represent relatively basal lineages in each of the two major branches of winged insects (the Paleoptera and Neoptera; Kristensen 1991), traits shared by these two groups, such as skimming and wet-resistant hydrofuge hairs on the wings (Marden and Kramer 1994), may have been retained from the initial radiation of winged insects. Second, because the forelegs of four-leg skimmers are held above the water (Fig. 1E, 1F), they are free to be used for functions other than support and locomotion. If ancestral mayflies carried out their mating activities using four-leg skimming, the forelegs of males might have become elongated and specialized for grasping females before mayflies evolved the ability to fly. The mating system of modern mayflies, which involves both elongated male forelegs and female oviposition on the water surface, may simply be a three-dimensional extension of an ancestral mating system that was carried out using four-leg skimming on the surface of water (Fig. 6). Stoneflies and dragonflies (Odonata) also oviposit on water and share with mayflies a simple egg chorion that cannot withstand desiccation (Hinton 1981). These features may be the result of convergent evolution, but it is also possible that they are shared ancestral traits. If so, then scramble competition for access to females and evasion of surface-feeding predators may have selected for progressively faster forms of surface skimming (Fig. 2) and ultimately the adoption of aerial mating systems that minimized contact with the water surface.

Evolutionary Origins of Insects and Their Wings

Proto-wings probably functioned initially as respiratory organs in amphibious or aquatic conditions (as do the flattened exites of other arthropods). (Kukalova-Peck 1991, p. 144)

Recent phylogenetic analyses based on both molecular (Friedrich and Tautz 1995; Regier and Schultz 1997; Aguinaldo and
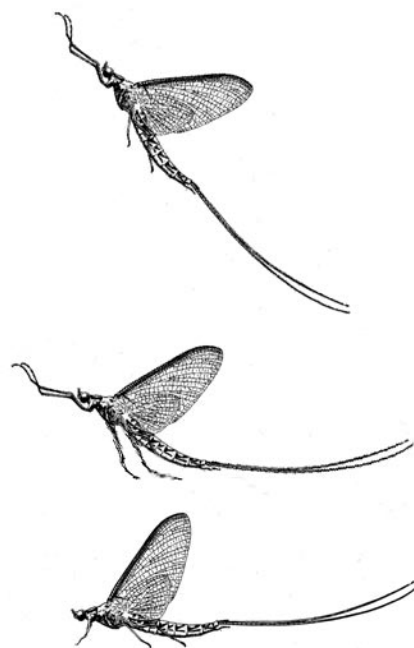

Figure 6. Drawings showing a hypothetical progression (in bottom-to-top order) for locomotion and foreleg size in male mayflies. The bottom image (hypothetical) shows six-leg skimming with normal-sized forelegs; the middle image shows four-leg skimming with elongated forelegs used for grasping females encountered on water (as occurs in the species described in Ruffieux et al. [1998]); and the top image shows a modern species with elongated forelegs used for grasping females during aerial flight.

Lake 1998; Boore et al. 1998; Winnepenninckx et al. 1998; Garcia-Machado et al. 1999) and morphological (Strausfeld 1998; Strausfeld et al. 1998) characters support the hypothesis that insects are a sister clade of the Crustacea. Recent data also indicate a homology between crustacean gills and insect wings based on the demonstration that two of the genes involved in morphogenesis of a particular dorsal exite of the brine shrimp gill are involved in a similar stage of development in *Drosophila* wings (Averof and Cohen 1997; but see Jockusch and Nagy [1997] and Williams [1999] for notes of caution in interpreting this apparent homology). Other support for the wings-from-gills hypothesis comes from the observation that *Drosophila* carrying mutant forms of the *ultrabithorax* and *abdominal-a* homeotic genes develop wing primordia on the first seven abdominal segments (Carroll et al. 1995), in the same location that both fossil mayflies and modern mayfly nymphs have gill plates. These gill plates have long been argued to be serial homologs of wings, the thoracic equivalents of which were the evolutionary and mechanical precursors to wings (Kukalova-Peck 1978, 1983, 1987, 1991). Thus, it appears that modern homeotic regulation represses the initiation of wing/gill development on all but the meso- and metathorax of extant pterygotes (Carroll et al. 1995). The wings-from-gills model is also supported by the finding that wings carry sensilla and chemoreceptors that are present on arthropod appendages (i.e., the leg exites that became gills) but not on the thoracic body wall (Dickinson et al. 1997). Together with fossil data, these studies represent a growing body of evidence that insects and their wings evolved from a crustacean-like ancestor and its moveable leg-derived gills.

A fundamental difficulty for the wings-from-gills hypothesis has been the implausibility of gills being maintained during the terrestrial and presumably arboreal stage that preceded flying insects. This argument is based largely on the assumption that terrestriality is the primitive condition for insects, dating back at least as far as a terrestrial Hexapoda-Myriapoda stem group (Pritchard et al. 1993), but this interpretation has been rendered obsolete by the present understanding that myriapods and hexapods are not closely related and that hexapods are the sister clade of crustaceans. A crustacean-like root for insects makes it much more plausible that apterygote insects lost gills (perhaps independently, since apterygotes do not appear to be a monophyletic group) as they invaded land, thereby diverging from a gill-bearing stem that ultimately gave rise to pterygote insects (Toms 1984). A prediction that emerges from this model is that the fossil record should contain insects that possess both wings and gills, that is, early stages in the evolution of surface skimmers. Indeed, such fossils from the upper Carboniferous and lower Permian are abundant and taxonomically diverse (Fig. 7), including examples from the stem groups that led to modern Ephemeroptera, Hemiptera, and Plecoptera along with the extinct order Megasecoptera (Fig. 7). Although it cannot be determined that the abdominal structures of these fossils
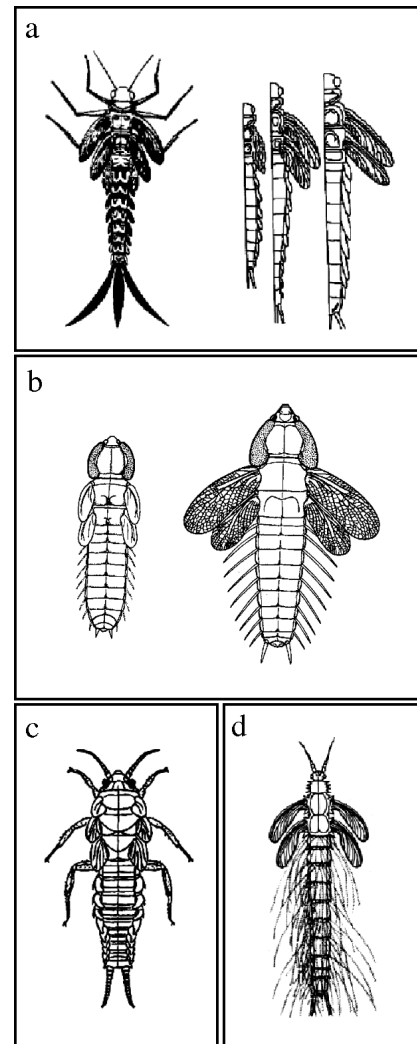

Figure 7. Fossil insects with rudimentary wings and abdominal structures that may have functioned as gills during activity on the water surface. The top two panels (*a, b*) show variations in wing and body size that are thought to represent ontogenetic stages (i.e., instars) within species. These fossils are representatives of the stem groups that gave rise to the modern orders Ephemeroptera (*a*), Hemiptera (*b*), and Plecoptera (*c*). Panel *d* belongs to the order Megasecoptera, part of the extinct superorder Paleodictyoptera. Drawings are reproduced from Kukalova-Peck (1978, 1991).

did in fact serve as gills, or even if these insects were associated with the water surface, this is the first attempt to offer a synthetic explanation for the common co-occurrence in fossils of rudimentary wings and abdominal structures that look like gills. Surface skimming provides a behavioral and environmental context in which gills and rudimentary wings could have co-existed during a time when tracheae were perhaps gradually invaginating and becoming elaborated, ultimately replacing an ancestral blood-based system of gas exchange. Such a scenario

also refutes the hypothesis that tracheae-bearing modern insects are necessarily secondarily aquatic (Pritchard et al. 1993; Grodnitsky 1999), since tracheal respiration may have originated on the water surface in a gill-bearing lineage.

A Synthetic Model for the Evolution of Flying Insects from Aquatic Ancestors

> Most of the literature [about insect flight origins] hasn't reached the first base of applying functional shift in the first place, not to mention the later stations of substituting direct evidence for verbal speculation. Most reconstructions are still trying to explain the incipient stages of insect wings as somehow involved in airborne performance from the start—not for flapping flight, of course, but still for some aspect of motion aloft rather than, as Darwin's principle would suggest, for some quite different function. (Gould 1985, p. 21)

We have met the challenge laid out by Gould's (1985) critique by demonstrating how real insects can use rudimentary flight motor function for something other than motion aloft. However, a robust model for the evolution of insect flight from surface skimming must consider ecological factors in order to understand how natural selection could have favored surface activity by formerly aquatic insects and how surface skimming could give way to flying. Rather than emphasize any single factor, we prefer to argue that many environmental factors could have acted in concert. One potentially important abiotic factor is the much greater availability of oxygen in air than in water (Schmidt-Nielsen 1990), especially during the Carboniferous, when atmospheric oxygen may have been elevated (Graham et al. 1995; Dudley 1998) and organic decomposition in freshwater swamps is likely to have greatly depleted dissolved oxygen.

Another abiotic factor that is important in many aquatic habitats is current drag, which creates a net downstream transport of stream-dwelling insects during their lifetime. Downstream drift must be counteracted at some point in the life cycle by upstream dispersal (otherwise all populations end up in the ocean), which modern insects accomplish by flying upstream during the adult stage (Müller 1982). This need not be a group-selection argument, since upstream regions can be richer in oxygen and food, which would allow higher rates of egg and nymph survival. Before the evolution of flight, upstream dispersal was probably accomplished by slow movement along the bottom (where exposure to predators may have been high) or along the water surface (where current drag is greatly reduced and where predators may have initially been nonexistent). Current drag on the surface could have been reduced by using the legs to elevate the anterior portion of the body above the water (Fig. 1C) while thrust was generated by axial bending (Fig. 1B) and flapping of the abdominal gills. Elevation

of the anterior part of the body would reduce the ability of the thoracic gills to contribute to swimming but would have freed them to become specialized for other forms of locomotion. This may have occurred initially as rowing in a manner similar to what occurs in *Diamphipnopsis* stoneflies and in a small group of marine chironomid flies that apparently use their greatly modified wings to row along the ocean surface (Cheng and Hashimoto 1978; this particular case is undoubtedly a recent loss of normal Dipteran wing function but nonetheless demonstrates a mechanically feasible role for early protowings). Alternatively, small gill plates may have been useful primarily as sails (Fig. 3), as occurs in modern *Allocapnia vivipara* stoneflies that raise their wings in response to wind currents (Marden and Kramer 1995). Increasing the frequency of wing-raising and lowering motions would constitute crude flapping and some degree of independence from wind.

Biotic factors may also have been important contributors to the evolution of activity on the water surface. Terrestrial Carboniferous habitats featured great forests of wind-pollinated plants, whose pollen, seed pods, and leaves presumably collected in large quantities on the surface of freshwater swamps and lakes. Floating pollen and seeds accumulate along the downwind shore of bodies of water, where they would have been abundant, easily collected, and nutritious food sources for surface-dwelling insects. The hypothesis that surface-based pollen feeding may have been an important niche for early insects is consistent with the large percentage (50%) of Carboniferous fossil insects that possessed sucking or semisucking mouthparts. For example, haustellate paledictyopteroids are thought to have imbibed mostly "spores" or "juices" (Kukalova-Peck 1991). Scramble competition for floating foods as well as access to mates and avoidance of predators that evolved to exploit surface-active insects would eventually have favored faster and more mobile surface skimmers, that is, a progression through the mechanical stages and velocities shown in Figures 1 and 2. As blood-based gas exchange and skimming gave way to tracheal-based gas exchange and three-dimensional flight, insects that fed on pollen, seeds, and leaves on the water surface may have evolved into arboreal plant feeders, thus triggering the rapid and extensive coevolution of plants and their insect pollinators, seed predators, and herbivores.

This is a grandiose evolutionary scenario derived from a fairly limited set of data. Many other scenarios have been proposed previously (e.g., Kingsolver and Koehl 1985; Kukalova-Peck 1991; Brodsky 1994; Leech and Cady 1994; Dudley 2000), and it has been estimated that there have been perhaps 10^6 words published in the scientific literature on the subject of insect wing and flight origins based on only about 10^2 or 10^3 data points (Kingsolver and Koehl 1994). Thus, our presentation of yet another scenario might be perceived as having limited utility. However, our model has certain unique features that can potentially make important contributions to both the current understanding and the way future workers approach the problem. One of these is an em-

phasis on understanding the range of variation in locomotor behavior and mechanics of relatively basal insects, a feature that has been largely absent from previous models of flight evolution. A second important contribution is that our model does not assume that the evolution of winged locomotion in insects necessarily involved a terrestrial stage. A strict equation of wings and terrestriality, which is characteristic of all previous models, is perhaps best exemplified by the following train of thought from the broad-minded review presented by Kingsolver and Koehl (1994). They carefully developed the argument that "the current evidence appears to support the pleural origin of articulated wings on both the abdominal and thoracic segments," that "initial evolution of the protowings occurs in aquatic nymphs," and that "the abdominal and thoracic winglets were then subsequently utilized for some function in the terrestrial environment" (Kingsolver and Koehl 1994, p. 430). As this thought process demonstrates, even scenarios based on the wings-from-gills model have been wedded to the assumption that wings are useful only in a terrestrial environment. In contrast, our model suggests that winged locomotion may have progressed to a flight-capable stage before pterygotes ever became terrestrial or airborne. By presenting a synthetic model that challenges conventional thinking, we aim to stimulate new and possibly fertile perspectives.

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