The surface-skimming hypothesis for the evolution of insect flight

James H. MARDEN

Abstract. The surface-skimming hypothesis for the evolution of insect flight poses that insects first used wings and aerodynamic locomotion to move in two dimensions across water surfaces. Here I present an overview of recent advances in our understanding of surface-skimming locomotion, and how these findings relate to phylogenetic origins of insects and developmental and anatomic origins of insect wings. Behavioral surveys show taxonomically widespread use of skimming by Plecoptera and more taxonomically restricted use of skimming by Ephemeroptera. Because these two orders arose near the root of the early split of pterygote insects into the Paleoptera and Neoptera, traits that appear in both groups are strong candidates for traits possessed by the first winged insects. Comparisons across plecopteran species show that skimming speed increases as contact with the water surface decreases, thereby providing a mechanical pathway over which directional selection may have acted to improve aerodynamic capability in early skimmers. Evolution along this route may have occurred within species in response to factors such as scramble competition and sexual selection. Phylogenetic analyses suggest that the common ancestor of modern Plecoptera was capable of both skimming and flying; such dual ability is widespread among extant stoneflies, including the most basal families. Both the mechanics and the semi-aquatic setting of skimming fit well with the growing understanding that insects and crustaceans are sister clades and that insect wings evolved from gills.

Key words: Plecoptera, Ephemeroptera, gradual evolution, complexity.

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I. INTRODUCTION

The evolutionary origin of insect flight is a popular topic for study and debate by biologists and paleontologists (e.g. KUKALOVÀ-PECK 1978; ELLINGTON 1991; KINGSOLVER & KOEHL 1994; DUDLEY 2000). Because there are no known fossils of the earliest stages of winged insects, information must be drawn from fossils that post-date the major radiation of pterygote insects during the Carboniferous (WOOTTON & KUKALOVÀ-PECK 2000), from physical models of insects (e.g. KINGSOLVER & KOEHL 1985; WOOTTON & ELLINGTON 1991), or from living insects. All of these approaches are indirect and leave much room for alternative interpretations and lively discussion.

In 1994, observations and experiments based on extant stoneflies (Plecoptera) produced the novel hypothesis that insect flight originated on the surface of water (Marden & Kramer 1994). The surface-skimming hypothesis posed that flying insects evolved from semi-aquatic ancestors that used rudimentary flapping wings to achieve weight-supported, two dimensional locomotion. Because the body weight of skimmers is supported by water, any small improvement in thrust generation can be advantageous and selected. Thus, a fundamental strength of the surface-skimming hypothesis is that it provides a mechanical solution for the puzzle of how a small, weak flight motor and wing primordia could be gradually elaborated prior to the evolution of true flight.

The original presentation of the skimming hypothesis also contained a glaring weakness in that it contained no phylogenetic analysis to show that skimming is an ancestral condition rather than a taxonomically isolated loss of flight (Will 1995). Subsequent research efforts in my laboratory have focused on performing phylogenetic analyses aimed at testing the hypothesis that skimming is an ancestral trait in Plecoptera.

Here I present a short overview of developments that have occurred since the initial exposition and early discussion of the surface-skimming hypothesis. These include i) a greatly elaborated understanding of the diversity of skimming behaviors within Plecoptera, and to a more limited extent, within Ephemeroptera, ii) phylogenetic analyses of skimming within Plecoptera, and iii) advances in our general understanding of the phylogenetic position of insects within Arthropoda and the anatomical origin of insect wings.

II. THE DIVERSITY OF SKIMMING BEHAVIORS WITHIN PLECOPTERA AND EPHEMEROPTERA

The following skimming behaviors have been described to date in Plecoptera and Ephemeroptera. More detailed descriptions can be found in the original reports (Marden & Kramer 1994, 1995; Kramer & Marden 1997; Ruffieux et al. 1998; Marden et al. 2000; Thomas et al. 2000). Video segments of all of these behaviors are available at
www.bio.psu.edu/People/Faculty/Marden/PNASFig2.html and
www.famu.org/mayfly/sartori/movies.html

Swimming and swimming-skimming

Stonefly nymphs swim by performing rhythmic lateral undulations of their body axis. *Taeniopteryx burksi* Ricker and Ross 1968 nymphs (Fig. 1A) 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 (s.d. = 0.1; N=3).

Adult *Tasmoperla thalia* Newman 1839 (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. 1B). The long axis of the abdomen oscillates laterally at a frequency of 7 Hz through an arc of approximately +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 hindlegs extend posteriorly alongside the abdomen. Thus, there is extensive contact between the ventral body surface and the water, so that
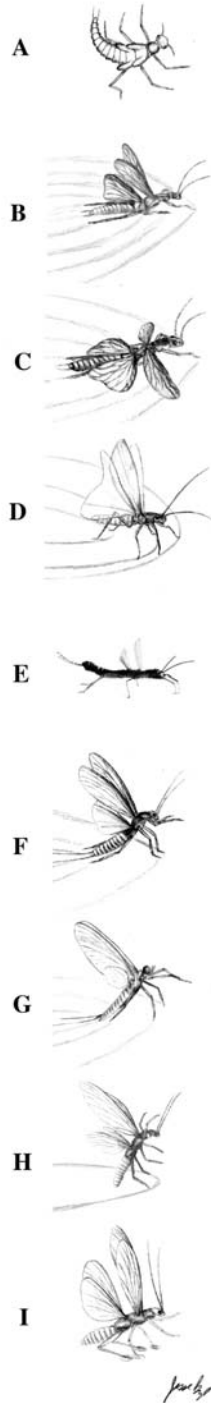
Fig. 1. Drawings made from individual frames of video recordings of different forms of aquatic and semi-aquatic locomotion used by stoneflies and mayflies. All except swimming (a) depict movement on the surface of water. Samples of video recordings are available at http://www.bio.psu.edu/People/Faculty/Marden/PNASFig2.html.

swimming motions may contribute, albeit weakly, to thrust and maneuverability. Certain insects use a non-oscillatory lateral flexure of the abdomen as a steering mechanism (DUDLEY 2000; GROD-NITSKY 1999), but there are apparently no other insects in which the abdomen oscillates laterally during wing flapping.

Even at warm temperatures (20-25°C) *T. thalia* does not attempt to fly. Wing flapping in this species has been observed only as an immediate and stereotypical response to contact with water. A related species, *Acruroperla atra* SAMAL 1921, uses a similar form of skimming (MARDEN et al. 2000) and does attempt to fly when tossed into the air, but none of the individuals tested were able to maintain altitude. Thus, it appears that neither of these species is capable of flying.

Rowing

Adults of *Diamphipnopsis samali* ILLIES 1960 (Diamphipnoidae) stoneflies accomplish surface-skimming locomotion by using a combination of drag and lift-based mechanisms. The forewings are elevated to only about 45-60° above the horizontal at the dorsal apex of the wing-stroke. At the bottom of the downstroke, the forewings make broad and prolonged contact with the water (Fig. 1C). During the interval between the end of the downstroke and the start of the upstroke, the distal 25-50% of the ventral forewing surface lies flat upon the water while the wing is moved posteriorly before the initiation of the upstroke. Rearward movement of the forewing while it is in contact with the water constitutes a drag-based, rowing stroke that propels the insect forward. The forewing kinematics feature a long duty cycle for the rowing portion of the stroke, with time on the water exceeding time in the air by a factor of nearly two. The hindwing kinematics indicate a more typical lift-based function, with a 90° stroke amplitude and relatively little contact with the water. Both the forward velocity during rowing (mean = 23 cm/s) and the wingbeat frequency (17 Hz) are among the slowest recorded from any surface skimming stoneflies (Fig. 2; range = 15-63 cm/s and 20-45 Hz in 16 species from 6 families; MARDEN et al. 2000).

D. samali are marginal fliers, capable of gradually gaining altitude but unable to maneuver to avoid stationary objects; they appear to fatigue after only a few seconds of flying.

Six-leg skimming

Stoneflies 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, this form of locomotion is called six-leg skimming.

At cool air temperatures (-18°C), stoneflies in the families Chloroperlidae and Perlodidae use intermittent forms of six-leg skimming. 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 below). Thus, these species use a limited form of six-leg skimming as a conditional strategy to remain mobile at cool air temperatures.

Wingbeat kinematics during six-leg skimming are much the same as described above for *T. thalia*, except that elevation of the body above the water allows a greater stroke amplitude. The wingstroke of six-leg skimmers extends approximately 20° below the horizontal, thus extending the total stroke amplitude to 110°. Wingbeat frequency of six-leg skimmers reaches frequencies as high as 45Hz in *Strophopteryx fasciata* BURMEISTER 1839 (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 (LEHMANN & DICKINSON 1997). Larger aerodynamic forces and reduced contact with the water result in higher skimming velocities (mean = 32 cm/s; N= 7 species from 6 families; s.d. = 2.9; Fig. 2).

Flight ability of six-leg skimmers varies widely. At the low end of the scale is the capniid *Paracapnia angulata* HANSON 1961, 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 release point. Other six-leg skimmers are marginally flight capable. At warm air temperatures, approximately 50% of individuals of *T. burksi* and *S. fasciata* stoneflies can maintain or gradually gain altitude, whereas the remainder cannot remain airborne (MARDEN & 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.

Sailing

An additional capniid species, *Allocapnia vivipara* CLAASSEN 1924, 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. 1E; MARDEN & KRAMER 1995).

Four-leg skimming

The family Gripopterygidae is the most diverse plecopteran family in the southern hemisphere. Gripopterygids skim by raising their forelegs above the water surface (Fig. 1F), which creates a more head-up body angle and a greater wingstroke amplitude than that of six-leg skimmers (MARDEN et al. 2000). Stroke amplitude of the forewings is nearly 180°, whereas the hindwings are constrained by the water surface to a stroke amplitude of approximately 110-120°. Wingbeat frequency ranges widely among four-leg skimmers, from a low of 23 Hz in *Illiesoperla* MCLELLAN, 1971 to a high of 42 Hz in *Leptoperla* NEWMAN 1839. Velocity of four-leg skimmers averages 44 cm/s (s.d. = 16.6; Fig. 2).

In the field at cool air temperatures (12-18°C), gripopterygids are incapable of flying, but reflexively (i.e. immediately upon contact with the water) utilize surface skimming when dislodged from

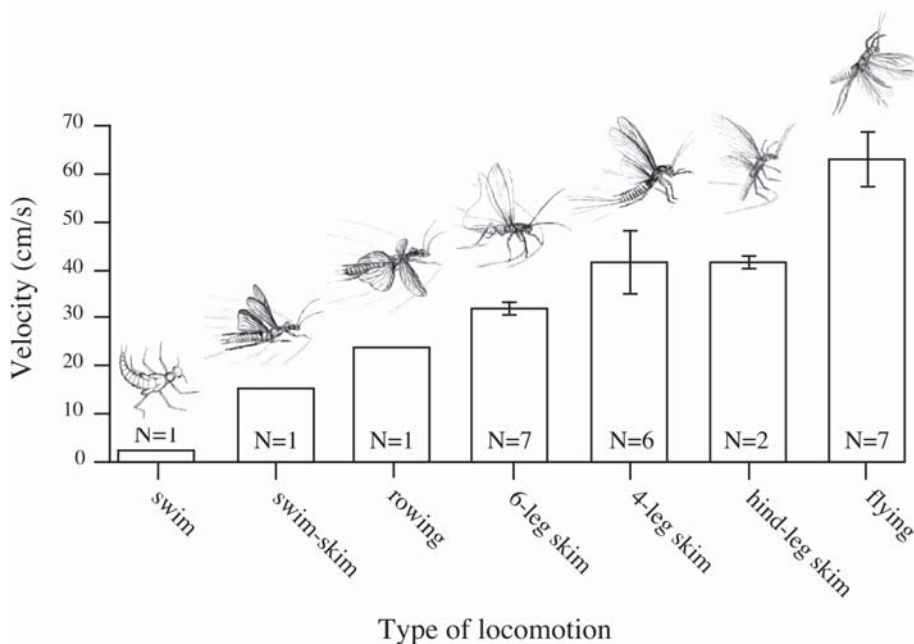Fig. 2. Mean velocity of stoneflies using different forms of aquatic, semi-aquatic, and aerial locomotion. Sample sizes refer to the number of species; error bars represent the standard error of the grand mean (i.e. variability among means derived from multiple species). Note the trend of increasing velocity as contact with water decreases. Body size had no significant effect on skimming speed.

midstream rocks. They readily reach shore even on fast-moving, cold water. At warmer air temperatures (18-23°C) gripopterygids are marginal fliers, barely able to maintain altitude. However, on a warm, sunny day (23°C), I have observed thousands of *Dinotoperla* spp. ascending into the air above the Delatite River (Victoria, Australia). Air driven upward by thermal convection 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.

Mayfly (Ephemeroptera) subimagos from a number of families in the northeastern U.S. use 4-leg skimming at cool air temperatures (<13°C; posture similar to Fig. 1G). Their forewings achieve a 180° stroke amplitude, and there is no restriction on the stroke amplitude of the hindwings, which in mayflies are much smaller than the forewings. Mayfly skimming features a slight pitching motion of the body during the wingstroke cycle, causing the hindlegs 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 wingstroke.

Four-leg skimming by mayflies has also been observed in sub-tropical Madagascar. Three species in the genus *Cheirogenesia* DEMOULIN, 1952 have lost the ability to fly, yet move about on the water surface using 4-leg skimming (RUFFIEUX et al. 1998; M. SARTORI pers. comm.). Male imagines 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.

A mayfly mating system that involves a mixture of flying and skimming has also been found in *Palingenia* BURMEISTER, 1839 mayflies in Hungary. Extraordinary video collected by M. SARTORI (www.famu.org/mayfly/sartori/movies.html) shows huge swarms of males skimming to locate and mate on the water surface with emerging female subimagos. This mating system appears to involve a high degree of scramble competition among males, in which case their skimming speed is likely to have a strong effect on their mating success.

Hind-leg skimming

Stoneflies in the family Leuctridae (*Leuctra hippopus* KEMPNY 1899 and *L. sibleyi* CLAASSEN 1923) use a form of skimming (KRAMER & MARDEN 1997) that has not been observed in any other taxa. At air temperatures that are too cool to fly (<13°C), *Leuctra* STEPHENS 1835 stoneflies use a stereotypical series of motions that raise their body into a nearly vertical posture. The hindlegs are flexed anteriorly to bring the tarsi forward to a position under the middle of the thorax. Subsequent extension of the hindlegs, 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. 1H). This is not an entirely stable body position, as there is sometimes excessive forward pitch that is controlled by temporarily placing the tarsi of the middle legs down on the water. During most wingbeat cycles *Leuctra* has only its two hind tarsi and the tip of its abdomen in contact with the water. By minimizing body contact with water and by producing vertical force, hindleg skimmers minimize drag on the water surface. Average velocity of *Leuctra* was 42 cm/s (s.d. = 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 fliers, whereas at cool air temperatures we have observed large numbers of *L. sibleyi* using hindleg 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 hindlegs to jump from water into the air, thereby initiating aerial flight (Fig. 1 I). 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 hindlegs, thus bringing the tarsi forward to a position under the middle of the thorax. Rapid extension of the hindlegs, 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. Mean horizontal velocity of flying stoneflies exceeded that of all forms of surface skimming (Fig. 2; mean = 63 cm/s, s.d. = 15; N= 7 species).

II. THE 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 & 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 outgroup labeled "OG" in WILL's figure 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 (i.e. a recently derived trait).

Our reanalysis of NELSON's morphological character data (MARDEN et al. 2000) yielded twelve equally parsimonious trees with 153 steps (for each tree RC=0.61, RI=0.83). A strict consensus of these trees is shown in Fig. 3. 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. 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 *Pteronarcys* NEWMAN, 1838, or *Pteronarcella* BANKS, 1900, nor have we examined any peltoperlids. Scopurids are wingless and therefore not amenable to analyses of winged locomotion.

In order to further examine the phylogenetic distribution of skimming in Plecoptera using a rooted tree, we have also constructed a molecular phylogeny. For this, we used nucleotide sequence data from the small subunit rRNA (18S) gene obtained from 34 stonefly species representing all families of Plecoptera (THOMAS et al. 2000). Sequences were aligned using Clustal W, which resulted in an alignment comprising 1,696 sites, of which 331 were variable (133 non-parsimony informative and 198 parsimony informative) and 787 were constant. Sequences from a diverse set of Hemiptera, Orthoptera, Dermaptera, Phasmida, Embiidina, Grylloblattodea, and Blattodea were used as outgroups. A tree constructed using neighbor joining indicated that the family Nemouridae is the basal plecopteran clade (Fig. 4). In addition to a strongly supported basal position for Nemouridae, our phylogeny showed strong support for Taeniopterygidae as the next most basal clade. This topology is a significant departure from previous phylogenies constructed using morphological data (NELSON 1984; WILL 1995), which place the Nemouridae and the rest of the superfamily Nemouroidea, including Taeniopterygidae, among the more derived groups of Plecoptera.

Surface skimming behavior is distributed widely across this molecular phylogeny, including the basal nemourids and taeniopterygids (Fig. 4). Flight capability is also widely distributed, as most
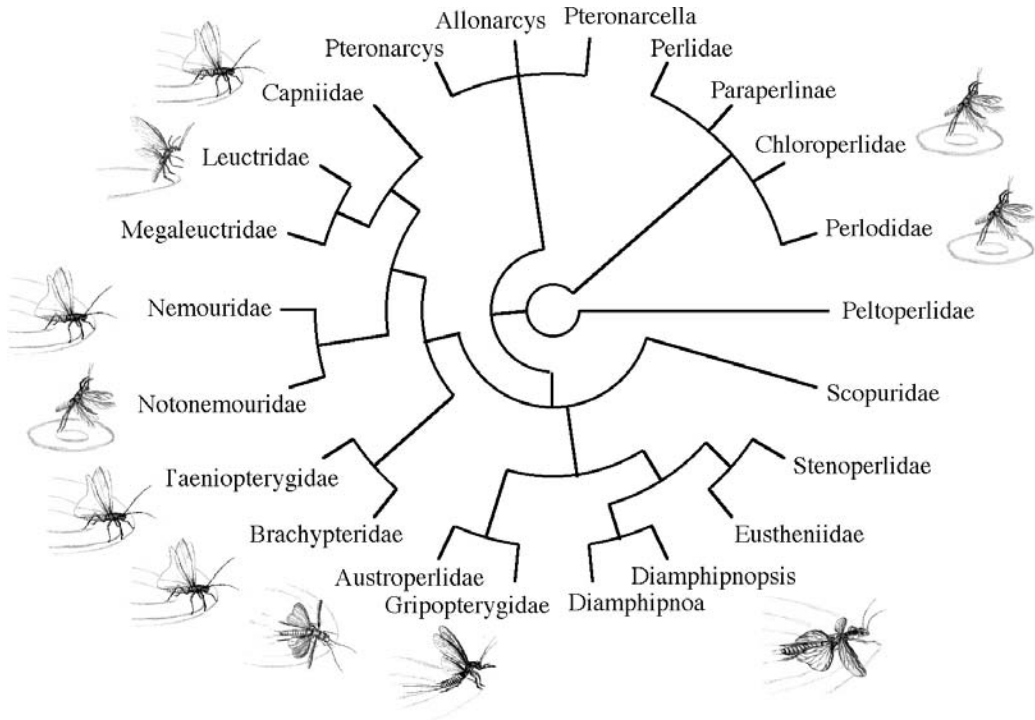
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Fig. 3. Maximum parsimony tree (unrooted; RC=0.61, RI=0.83) constructed using 67 parsimony informative morphological characters from data in Nelson (1984). Surface-skimming behavior is mapped onto the tree by using graphical icons from Fig. 1. Except 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.

stoneflies that use skimming, including all of the nemourids that have been examined, can also fly, albeit quite weakly in comparison to the vast majority of other insects. Thus, the ancestral condition for Plecoptera was most likely a combination of relatively weak flight and surface skimming. 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 weakly in three dimensions.

III. THE ORIGIN OF INSECTS AND THEIR WINGS

Recent phylogenetic analyses based on molecular (Friedrich & Tautz 1995; Regier & Schultz 1997; Aguinaldo & Lake 1998; Winnepenninckx et al. 1998; Boore et al. 1998; Garcia-Machado et al. 1999; Hwang et al. 2001), morphological (Strausfeld 1998; Strausfeld et al. 1998), and combined data sets (Giribet et al. 2001) 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 & Cohen 1997; but see Williams 1999 for a note of caution in interpreting this apparent homology). Other support for the wings-from-gills hypothesis comes from the observation

Skimming behaviors

Six-leg skimming

Sailing

Hind-leg skimming

Jumping takeoff from water

Rowing

Four-leg skimming

Swim-skim

98 *Acruroperla*
Tasmanoperla | Austroperlidae

75 *Leptoperla*
Zelandoperla
Newmanoperla | Gripopterygidae

Diamphipnopsis | Diamphipnoidae
Cosmoperla

Stenoperla | Eustheniidae
Scopura | Scopuridae

80 *Mesoperlina*
Megarcys
86 *Isoperla* | Perlodidae

96 93 *Beloneuria*
Claassenia
94 *Hesperaperla* | Perlidae
Siphonoperla | Chloroperlidae

89 100 *Sierraperla*
Talloperla | Peltoperlidae

78 *Pteronarcys*
Pteronarcella | Pteronarcidae

78 *Notonemoura* | Notonemouridae
Austrocerca

72 100 *Leuctra niga*
Leuctra hippopus | Leuctridae

99 *Paracapnia*
Allocapnia | Capniidae

87 *Megaleuctra*

100 *Taeniopteryx burksi*
94 *Taeniopteryx nebulosa* | Taeniopterygidae
Brachycera

76 *Protonemoura*
72 *Malenka*
Amphinemura | Nemouridae
100 *Nemurella*

100 *Ostrocerca*

Gromphadorhina (Blattodea)

Forficula (Dermaptera)

100 *Agathemera* (Phasmatodea)
81 *Phyllium* (Phasmatodea)
Oligotoma (Embioptera)
Grylloblatta (Grylloblattodea) outgroups

Oedipoda (Orthoptera)
Paratettix (Orthoptera)

89 *Spissistilus* (Hemiptera)
Okanagana (Hemiptera)
Philaenus (Hemiptera)
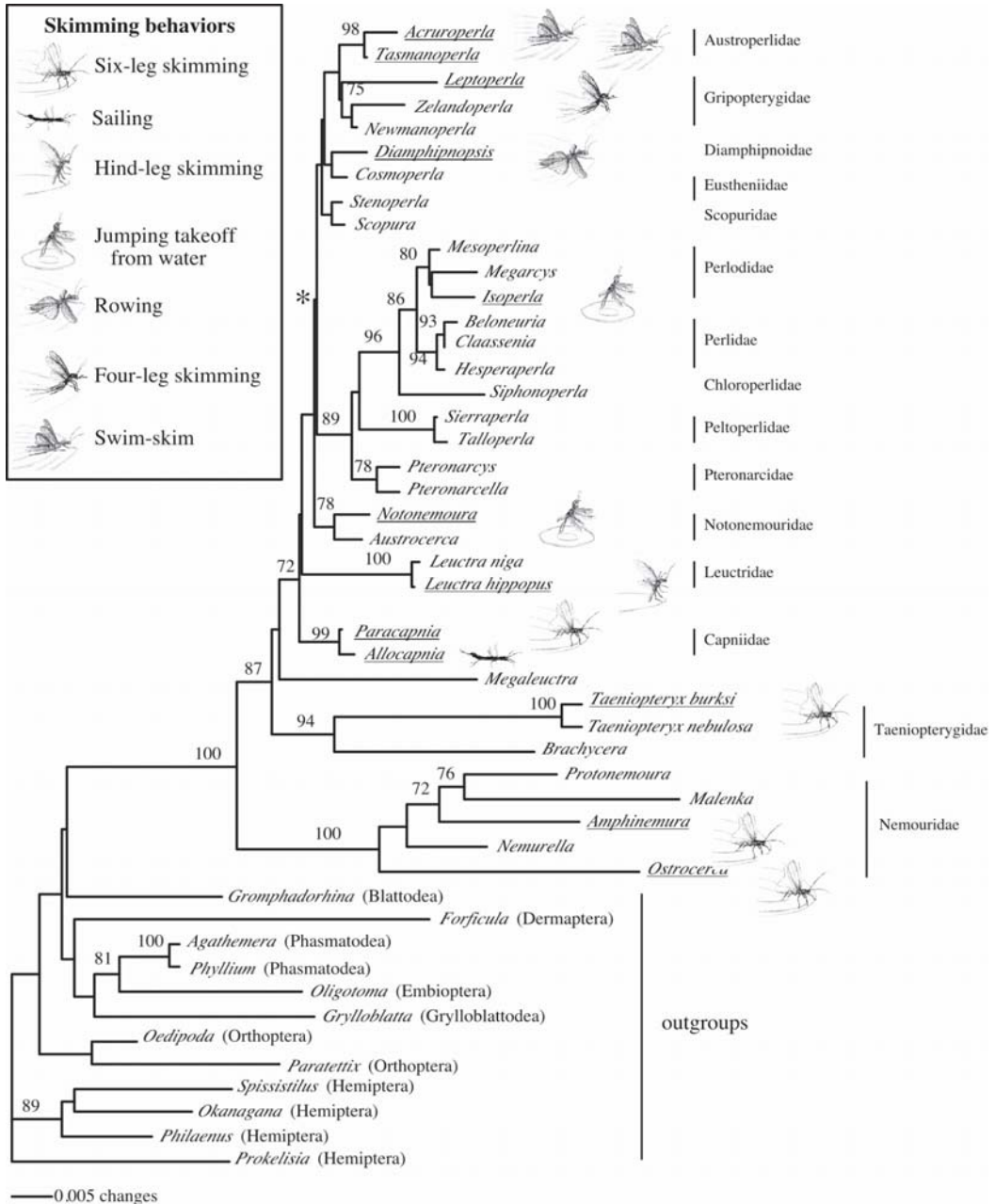*Prokelisia* (Hemiptera)

—0.005 changes

Fig. 4. A phylogeny of the Plecoptera, constructed using a Neighbor-Joining (NJ) analysis with sequence data from the 18S gene. Taxa below *Ostrocerca* are outgroups. Numbers on branches indicate bootstrap support (1000 replicates; only values over 70% are shown). Trees recovered using optimality criteria (based on heuristic searches for minimum length, maximum parsimony, and minimum evolution trees) did not differ from the NJ tree for any parts of the tree for which bootstrap values are reported. Underlined taxa are those included in our phylogenetic analysis that are known to be surface skimmers; taxa not underlined have not been sampled (except *Scopura* which is wingless and therefore incapable of any form of winged locomotion). Icons to the right of each underlined taxon show the type of skimming used by that species. A version of this figure containing links to video recordings of skimming behaviors is available at http://www.bio.psu.edu/People/Faculty/Marden/PNASFig2.html

that *Drosophila* carrying mutant forms of the ultrabithorax and abdominal-a homeotic genes develop wing primordia on the first 7 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, whose thoracic equivalents were the evolutionary and mechanical precursors to wings (KUKALOVÀ-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.

Traditionally, a fundamental difficulty for the wings-from-gills hypothesis was 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, i.e. early stages in the evolution of surface skimmers. Indeed, such fossils from the upper Carboniferous and lower Permian are abundant and taxonomically diverse, including examples from the stem groups that led to modern Ephemeroptera, Hemiptera, and Plecoptera, along with the extinct order Megasecoptera (KUKALOVÀ-PECK 1991). Although it cannot be determined that the abdominal structures of these fossils did in fact serve as gills (TOMS 1984), or even if these insects were associated with the water surface, the surface skimming hypothesis offers 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 coexisted, 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 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.

IV. CONCLUSION

The surface skimming hypothesis for the origin of insect flight has gained considerable support in the time since its origination in 1994. The original strength of the hypothesis was that it provided a mechanical solution for the puzzle of how a small, weak flight motor and wing primordia could be gradually elaborated prior to the evolution of true flight. The body weight of skimmers is supported by water, and therefore any small improvement in thrust generation can be advantageous and selected. Behavioral studies have revealed that skimming is widespread among Plecoptera (MARDEN et al. 2000) and occurs at least sporadically in Ephemeroptera (RUFFIEUX et al. 1998) and Odonata (SAMWAYS 1994). Phylogenetic analyses have indicated that skimming is plesiomorphic (ancestral) within Plecoptera (THOMAS et al. 2000). Scramble competition and sexual selection for locomotor performance, as seen in modern Ephemeroptera in which males search for and compete for access to females on the water surface (RUFFIEUX et al. 1998), may have been the driving force for the evolutionary transition between initial, rudimentary forms of skimming and the eventual acquisition of true flight capability (MARDEN et al. 2000). Comparisons among species illustrate that

skimming velocity increases as the amount of contact with the water surface decreases (Fig. 2); this relationship provides empirical support for the argument that factors such as scramble competition for mates could have caused steady directional selection for increasing aerodynamic ability within species. The skimming hypothesis also fits well with the new understanding that insects and crustaceans are sister clades and that insect wings evolved from gills, presumably in a semi-aquatic setting. In summary, the surface skimming hypothesis has emerged as a plausible and well supported explanation for the origin of insect flight.

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