

Plecopteran Surface-Skimming and Insect Flight Evolution

The origin of insect flight has been fertile ground for hypotheses (1). A recent addition to this debate is the hypothesis of James H. Marden and Melissa G. Kramer that skimming on the water surface in stoneflies represents an intermediate stage in insect flight evolution (2). This hypothesis is based on three components: (i) observed skimming behavior in *Taeniopteryx burksi* (Plecoptera: Taeniopterygidae); (ii) experiments showing improved skimming performance with increases in size of wings and power of the flight motor; and (iii) phylogeny suggesting this is ancestral for Plecoptera and all pterygote (winged) insects.

Observed skimming behavior, and experimental results supporting improved skimming performance with size and power increase, are not sufficient reasons to accept skimming as a precursor to flight. As with any evolutionary scheme, a character, morphological (3) or behavioral (4), must be assigned polarity on the basis of ancestor-descendant relationships to have value for phylogenetic inference.

Marden and Kramer suggest that Plecoptera represents a basal insect order. They state that the extant insect orders Ephemeroptera and Plecoptera are anatomically and phylogenetically closest to pre-flight fossil insects and that stoneflies are generally archaic in their morphology. However, phylogenetic studies supporting this opinion are not presented. Major works on the insect orders refute this hypothesis (5–8).

Plecoptera represent a potentially basal group in Neoptera, either together with other "orthopteroid" orders (6, 8) or with close affinities to Embioptera or Dermaptera (5–7). Even if Paleoptera represents an evolutionary grade paraphyletic to Neoptera, there is a clear distinction between Paleopteran and all Neopteran orders based on wing and genitalic morphology (5, 6). Phylogenetic and fossil evidence support an origin of flight in a common ancestor of Neoptera + Paleoptera, not in a common ancestor of Plecoptera versus other Pterygota. Falcate wing hairs, cited by Marden and Kramer as homologous in Plecoptera and Ephemeroptera, represent convergence on hydrofuge-hair surfaces analogous to those found in Trichoptera and Diptera (9). Ephemeropteran "skimming," referred to by Marden and Kramer, whether subimago behavior when escaping accidental water contact or "skimming" of some adults during mating flight (10), cannot be interpreted as homologous to skimming in *T. burksi* on the basis of established methods for determining homologies (4).

Marden and Kramer also use phylogenetic relationships within Plecoptera to support the plesiotypic nature of skimming, citing Nelson (11), Brodsky (12), and Zwick (12) for evidence of a basal position for the superfamily Nemouroidea, which contains *Taeniopteryx*, in Plecoptera. Nelson (11) places Nemouroidea as sister to the Systellognatha (including Perlodea) and

derived relative to Gripopterygoidea and Eusthenioidea. The position of Nemouroidea is clearly not basal in this analysis. Nelson (11) discusses the works of Brodsky (12) and Zwick (12) and considers them "closely congruent" with his own. I reanalyzed Nelson's matrix, eliminating uninformative autapomorphies and recoding non-independent characters. My consensus tree places Nemouroidea as a relatively derived superfamily (Fig 1A). Thus, Marden and Kramer's hypothesis "that this lineage has never contained more than marginal fliers . . ." must be rejected, or we must accept multiple origins of flight within insects, several times within Plecoptera alone (Fig. 1, A and B). The alternative, a reappropriation of the existing flight apparatus, would require only a single additional step.

Phylogenetic evidence does not support the hypothesis that the flight apparatus in Plecoptera is plesiomorphic. Marden and Kramer's hypothesis is not based on sound phylogenetic analyses and has resulted in a misconstrued evolutionary scenario. Skimming behavior in stoneflies is an evolutionary terminal of its own and not an ancestral state. Surface skimming can be added to the list of feasible scenarios put forward (1), but without the support of phylogeny it remains speculative.

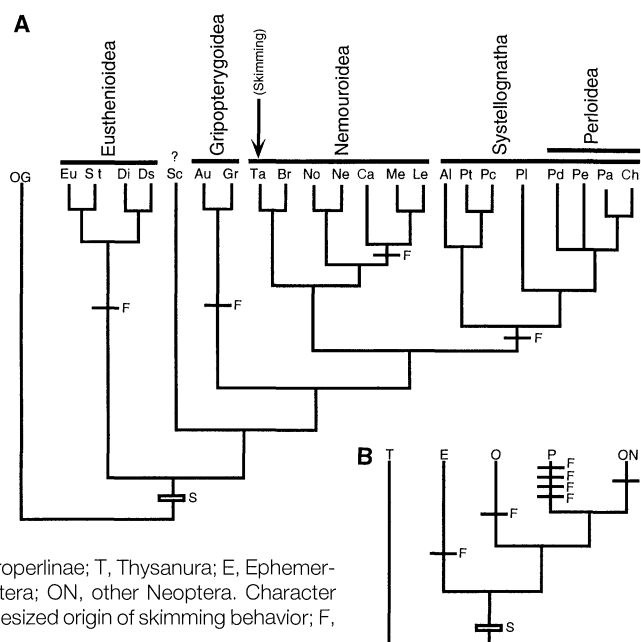
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13. Sets of characters recoded from Nelson (11); Non-independent characters (1, 16), (19, –24), (25, 26), (83, 88), (82, 53); Uninformative characters eliminated (10–12, 29–37, 50, 51, 55, 61–65, 69–71, 73–78, 89–95, 100, 102–108, 111–113); Data analyzed with the use of HENNIG86 computer program (14). Two most parsimonious trees were found using ie* and the successive weighting routine. Polarization of characters follows Nelson's assessments (11). Tree statistics are ri = 81, ci = 59, and I = 109.

Fig. 1. Cladograms showing distribution of steps required to support the "skimming" hypothesis. (A) Consensus cladogram from two trees from recoded matrix. (B) Cladogram of derived orders of Insecta. OG, outgroup; Eu, Eustheniinae; St, Stenoperlinae; Di, Diamphipnoa; Ds, Diamphipnopsis; Au, Austroperlidae; Gr, Gripopterygidae; Sc, Scouridae; Ta, Taeniopterygidae; Br, Brachypterinae; No, Notonemouridae; Ne, Nemouridae; Ca, Capniidae; Me, Megaleuctrinae; Le, Leuctrinae; Pc, Pteronarcys; Al, Alionarcys; Pl, Peltoperlidae; Pd, Perlodidae; Pe, Perlidae; Pa, Paraperlinae; Ch, Chloroperlinae; T, Thysanura; E, Ephemeroptera; O, Odonata; P, Plecoptera; ON, other Neoptera. Character state transformations: S, hypothesized origin of skimming behavior; F, minimum origins of flight.



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15. Thanks to J. Liebherr, C. Gilbert, B. Peckarsky, C. Marshall, B. Danforth, and T. Schultz for encouragement and critical review.

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Response: Our study of surface skimming locomotion in stoneflies (1) has apparently run afoul with systematists because of a poorly worded sentence in our introduction. We stated (1, p. 427) that previous studies have not "utilized detailed examinations of . . . the extant insect orders (Ephemeroptera and Plecoptera) that are anatomically and phylogenetically closest to pre-flight fossil insects." The purpose of this sentence was to briefly reflect the current view that these two orders are both near the base of the as yet poorly resolved phylogeny of winged insects (2), and that they possess many morphologically primitive traits. The latter notion is not our "opinion," but rather comes from two authoritative 1994 reviews (3). We did not mean to imply that Ephemeroptera and Plecoptera are sister taxa, or that either of these orders are ancestral to any other flying insects, but we agree with Will's statement that it is the common ancestor of paleopterous orders (such as Ephemeroptera) and neopterous orders (such as Plecoptera) whose locomotor habits are of interest for resolving the mystery of insect flight evolution.

Because the common ancestor of mayflies and stoneflies first evolved wings, traits that are homologous in these two orders are of particular interest. Thus, our demonstration of morphologically similar water-resistant hairs on the wings of stoneflies and mayflies hints that their common ancestor may have used its wings in a semi-aquatic setting. The fact that other semi-aquatic insects also have these hairs has apparently led Will to the unfounded conclusion that this must reflect evolutionary convergence. We know of no data with which to resolve the issue of homology or convergence for wing hairs.

We described the Nemouridea super-

family (which contains our subject species) as "near the base of the Plecopteran lineage," which Will has misrepresented as a claim of "basal." The distinction is made insignificant by the fact that there is no strongly supported phylogeny for stoneflies. Basal position of the Eusthenioidea depends on questionable behavioral and morphological characters (4), which places the rooting of the tree in considerable doubt. Because nearly equally parsimonious cladograms yield fundamentally different phylogenies, Nelson concluded (5, p. 472) that "the present character data are not adequate for resolving phylogenetic relationships within Plecoptera." Even if a well-supported Plecopteran phylogeny existed, mapping flight ability onto it would be difficult. For all groups except those that we have recently studied, the literature contains only sparse and imprecise descriptions of flight ability. On the basis of the few descriptions available, the only stoneflies that might come close to being strong fliers are certain species in the Systellognatha and Perlodea, the most derived Plecopteran groups.

The earliest known Plecopteran fossils (6) (260 million years old) include the family Taeniopterygidae, whose wings show a less complex pattern of venation (the structural support elements that resist deformation during loading by aerodynamic forces) than modern *Taeniopteryx*; thus it appears that surface-skimming stoneflies are an ancient lineage whose wing evolution may have been progressive rather than digressive during the past quarter-of-a-billion years. Of the two species whose flight capacities we have examined (1, 7), one (*Allocapnia vivipara*) cannot fly except by very crude gliding, whereas certain individuals of the other species (*T. burksi*) can fly by wing-flapping when their muscle temperature is sufficiently warm. Thus, these insects blur the distinction between flying and nonflying and demonstrate that flight is but one extreme on a continuum of aerodynamically powered locomotion, whose evolutionary

origin may have been for horizontal movement across water, and whose ancestral state might be retained in lineages that never reached the end of the continuum. If indeed the original radiation of winged insects was among early surface skimmers, true flight would have evolved independently in various lineages, and perhaps even within modern stoneflies. Viewed in this light, the multiple origins of flight shown in figure 1B of the comment by Will is a pattern one would expect. A strict reliance on parsimony to guide our interpretation would blind us to a pattern of gradual transition along the various levels of a quantitative trait.

It remains uncertain whether surface skimming stoneflies represent a loss-of-flight or have retained a plesiomorphic condition. Our purpose in pointing out the latter possibility was to put forth a radically different interpretation from the "monophyletic origins of insect flight" scenario that had become a nearly unquestioned paradigm, and to thereby stimulate further functional and phylogenetic analyses that may resolve the issue.

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