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 Taeniopygus burksi (Plecoptera: Taeniopygidae); (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 the concept of 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 Paleoptera and all Neopteran orders based on wing and genital 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 hydrophuge-hair surfaces analogous to those found in Trichoptera and Diptera (9). Ephemeropteron “skimming,” referred to by Marden and Kramer, whether subimaginal 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 superfamly Nemuroidea, which contains Taeniopygus, in Plecoptera. Nelson (11) places Nemuroidea as sister to the Systellognathidae (including Perloidea) and derived relative to Grippopterygoidea and Eustemioidea. The position of Nemuroidea 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 excluding non-independent characters. My consensus tree places Nemuroidea as a relatively derived superfamly (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. 1A and B). The alternative, a reappraisal 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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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 selected orders of Insecta. OG, outgroup; Eu, Eustheniineae; S, Sternalopelineae; D, Diaphninoidea; Ds, Diaphniniopsida; AU, Austroperleidae; Gr, Grisopterygidae; Sc, Sco- purinae; Ta, Taeniopyginae; Br, Brachyptera; No, Notonemuridae; Ne, Nemuridae; Ca, Capniidae; Me, Megalacucininae; Le, Leuctrinae; Pct, Pteronarcicellus; Pl, Pteronarcy; Al, Allenarocy; Pl, Peltoperleidae; Pd, Perlidae; Pa, Paraperleidae; 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.

REFERENCES AND NOTES
13. Sets of characters recoded from Nelson (11): Non-independent characters (1, 16), (19, -24), (25, 26), (53, 68), (82, 53); Uninformative characters eliminated (10–12, 20–37, 50, 51, 55, 61–65, 67–71, 73–78, 89–95, 100, 102–108, 111–113); Data analyzed with the use of HENNY86 computer program (14). Two most parsimonious trees were found using and the successive weighting routine. Polarization of characters follows Nelson’s assessments (11). Tree statistics are r = 81, cl = 59, and I = 109.