Jumping and the aerial behavior of aquatic mayfly larvae (*Myobaetis ellenae*, Baetidae)☆

Stephen P. Yanoviak [a, c, *], Robert Dudley [b, c]

[a] *Department of Biology, University of Louisville, 139 Life Sciences Building, Louisville, KY 40292, USA*
[b] *Department of Integrative Biology, University of California, Berkeley, CA 94720, USA*
[c] *Smithsonian Tropical Research Institute, Balboa, Panama*

ARTICLE INFO

ABSTRACT

Mayfly larvae generally are aquatic, but some madicolous taxa (i.e., living in thin water films) crawl over rocks within streams and waterfalls. When startled, these larvae can break the water film, jump, and enter an aerial phase of locomotion. Because mayfly larvae have been suggested as potential exemplars for the origin of insect wings as tracheal gills, and furthermore represent the most basal extant lineage of pterygotes, we analyzed jumping behavior and free-fall trajectories for one such species of mayfly (*Myobaetis ellenae*, Baetidae) in Costa Rica. Jumping was commonplace in this taxon, but was undirected and was characterized by body spinning at high angular velocities. No aerodynamic role for the tracheal gills was evident. By contrast, jumping by a sympatric species of bristletail (*Meinertellus* sp., Archaeognatha) consistently resulted in head-first and stable body postures during aerial translation. Although capable of intermittently jumping into the air, the mayfly larvae could neither control nor target their aerial behavior. By contrast, a stable body posture during jumps in adult bristletails, together with the demonstrated capacity for directed aerial descent in arboreal representatives of this order, support ancestrally terrestrial origins for insect flight within the behavioral context of either jumping or falling from heights.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

Current understanding of the origins of winged flight in insects is limited due to a lack of fossil intermediates. Various hypotheses have suggested that insect wings evolved either in a terrestrial ancestor for which wings served to effect controlled aerial behavior in falls and when gliding, or in aquatic ancestors for which winglike structures were initially used in underwater flapping (reviewed by Dudley, 2000; Grimaldi and Engel, 2005). Hexapods are a monophyletic group derived from a lineage of terrestrialized crustaceans (Grimaldi, 2010); all extant apterygotes are terrestrial with the exception of some secondarily derived aquatic collembolans (D'Haese, 2002). Developmental studies also suggest that the insect wing derives from a complex integration of lateral thoracic outgrowths and possibly limb exites, but does not incorporate gills *per se* (Clark-Hachtel et al., 2013; Engel et al., 2013; Ohde et al., 2013; Prokop et al., 2017). Moreover, an insect fossil from the Late Devonian (Garrouste et al., 2012) exhibits no obvious morphological adaptations for aquatic life, a finding also consistent with ancestral terrestriality in pterygotes. Absent relevant paleontological information, we can alternatively look to extant taxa and behaviors to try to infer the feasibility of different scenarios for flight origins.

Recent studies have suggested that, for both volant vertebrates and pterygote insects, controlled aerial behaviors may have preceded the origin of wings proper (Dudley et al., 2007; Dudley and Yanoviak, 2011). For example, many wingless arboreal arthropods can control their trajectories whilst falling via the steep form of gliding termed directed aerial descent (Yanoviak et al., 2005, 2009; Dudley and Yanoviak, 2011). Similarly, a dorsoventral aerial righting reflex characterizes certain squamate taxa as well as some larval hemimetabolous insects (Jusufi et al., 2011), and jumping via a startle reflex is widespread in terrestrial animals (Eaton, 1984). The origin of wings is not, therefore, necessarily congruent with the origin of flight if we construe the latter phenomenon to indicate a broader spectrum of controlled aerial behaviors, including jumping

from heights (Dudley and Yanoviak, 2011). Suggestively, a recently proposed fossil sister group to the pterygote insects (Order Carbotriplurida) shows no obvious adaptations for aquatic life, and moreover exhibits pronounced lateral lobes consistent with controlled gliding and maneuvering (Staniczek et al., 2014).

Such behaviors tend not to be found, however, among the diverse fauna of aquatic and semiaquatic arthropods. Presumably because of physical constraints imposed by surface tension on such small-bodied animals, rapid transitions across the air/water interface are rare. However, larvae of the mayfly *Mayobaetis ellenae* (Ephemeroptera: Baetidae) voluntarily jump from wet surfaces when disturbed, a behavior otherwise not documented in this order. These mid-elevation, Neotropical insects are madicolous, inhabiting millimeter-thick water films over rock faces in seeps and waterfall spray zones (Waltz and McCafferty, 1985; Lugo-Ortiz and McCafferty, 1996). The larvae also intermittently crawl from rock surfaces into surrounding bryophyte mats, where they presumably forage in a wet but effectively terrestrial environment (Fig. 1). Given the fairly basal placement of Baetidae within the Ephemeroptera (Sun et al., 2006), along with the potential evolutionary relevance of movable tracheal gills in this group, we hypothesized that examination of jumping in *M. ellenae* could clarify the origins of aerial behavior in pterygotes. Specifically, if wings evolved from gills in mayfly precursors or similarly basal (and putatively aquatic) hexapods, then *M. ellenae* might be expected to exhibit stable body postures and possibly directed trajectories when airborne. Contrariwise, if pterygotes are ancestrally terrestrial, then today's aquatic larvae of the basal winged lineages (i.e., the Ephemeroptera and Odonata) are secondarily derived (see Grimaldi and Engel, 2005), and would be expected to have no capacity for targeting or aerial control.

Here, we examine jumping (also termed here to be takeoffs) and subsequent aerial behavior in larval mayflies to assess their capacity for gliding and directional control during a fall. Specifically, we quantify trajectories and landing patterns of *M. ellenae* larvae following their jumps from variably oriented flat surfaces, and also compare their initiation of jumps to that of a fully terrestrial adult archaeognathan, which serves as a representative apterygote that is ancestrally terrestrial. Our goals were to: 1) characterize jumping takeoffs in *M. ellenae*, 2) determine if jumping *M. ellenae* larvae exhibit targeting once airborne, and 3) compare this jumping behavior with that in a syntopic but fully terrestrial bristletail species capable of controlled jumps and gliding.

2. Material and methods

In March 2008 and December 2010, we collected *M. ellenae* larvae from rock faces above the water line and from waterfalls in the rivers Alondra and Guacimal near the University of Georgia Research St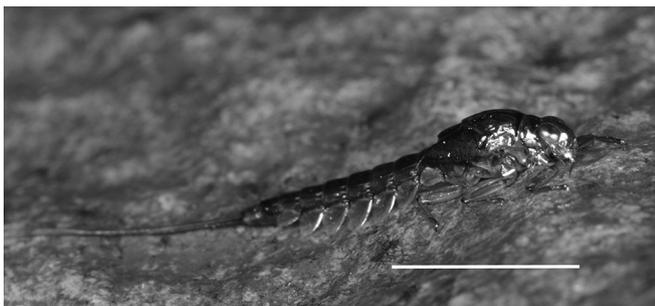ation (UGACR) in the village of San Luis, near Monteverde in Costa Rica (10.282°N, 84.799°W). Larvae were patchily distributed within streams and in boulder fields at the base of waterfalls, and were most common on larger boulders and along steeper inclines. Larvae tended to jump in response to approaching objects, and also in response to water flow induced along rock faces as we moved upstream against the current. All sizes of larvae were present and co-occurred. Subimagos were occasionally observed, and possessed flight-capable wings. Observations of lab-housed larvae suggested that the jumping tendency ceased at least 12 h prior to eclosion as a subimago.

Following collection in the field, larvae were maintained individually in plastic Petri dishes in the UGACR laboratory. The bottom of each dish was lined with a disc of filter paper saturated with tap water. Larvae kept under these conditions and covered with only a thin layer of water survived for >24 h. Larvae that were either completely immersed or that were trapped within water droplets with no underlying filter paper tended to die within 2 h. The filter paper was changed and the Petri dishes were cleaned every 6—10 h.

2.1. Takeoff performance

Jumping takeoffs were recorded for *M. ellenae* larvae in the UGACR research lab using a high-speed digital video camera (TroubleShooter TS1000CS, Fastec Imaging) operated at 1000 frames/s (Fig. 2). Artificial illumination was provided by a halogen lamp mounted on a flexible tripod (Fig. 2). Wet body mass, mean length of the two caudal cerci, and the distance between the anterior tip of the head and the base of the median filament (i.e., the effective body length) were measured immediately before recordings. Air temperature was 28 °C during experiments. All jumps were initiated from a rigid stage fitted with a scale bar (1 mm increments) and a plumb line for vertical reference. Individual larvae
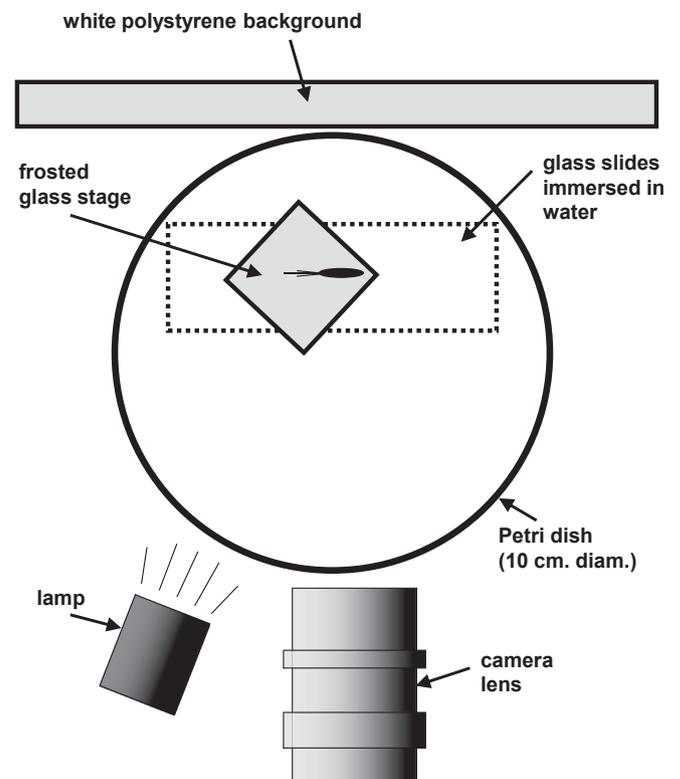

Fig. 1. Larva of *Mayobaetis ellenae* on rock surface in natural habitat in Costa Rica (scale bar = 5 mm), with tracheal gills extending laterally from abdominal segments.

Fig. 2. Vertical schematic view of the jumping takeoff recording theater. In each case, the specimen (either a bristletail or mayfly larva, indicated by the dark ellipse) was positioned orthogonal to the camera axis.

were placed on the stage such that their longitudinal body axis was perpendicular to the optical axis of the camera; this posture ensured that, following takeoff, both body trajectory and mid-air rotation of the body were nominally confined to the two-dimensional plane of the camera image (Fig. 2). Inclination of the jump surface was adjusted to three experimental angles (0°, 45°, and 90°), and jumps from 5 to 8 individuals were recorded at each of these angles, with 3–7 jumps recorded per individual. Caudal appendages (i.e., both cerci and the median filament) were also ablated using fine forceps from five mayfly larvae that were subsequently filmed as they jumped from a horizontal surface, and from five larvae filmed jumping from the vertical surface. Filming of jumps from the horizontally and vertically oriented stages, respectively, was then repeated to yield 1–6 recordings per ablated individual. Between recordings, all mayflies were placed within a Petri dish (4 cm diameter) containing water-saturated filter paper which served to extend the gills of the mayfly via surface tension, but not to fully suspend the body in water.

For each successfully filmed jump, we quantified the time required for takeoff as the interval between the first frame of apparent body motion initiating the jump, and the final frame at which no contact between either body or caudal segments and the takeoff substrate was evident. NIH ImageJ was used to analyze video sequences of all takeoffs, measuring the position of the anterior tip of the head and posterior point of the thorax at the junction with the abdomen. These two points were used to derive the longitudinal body axis orientation as a function of post-takeoff time, as well as a midpoint between the points to approximate body position, with which to calculate average angular and translational velocities following takeoff. For comparative purposes, we also recorded jumping takeoffs from six adult bristletails (*Meintertellus* sp., Meinertellidae) collected from understory tree trunks near UGACR. Individual bristletails were placed on a frosted glass stage (2 × 2 cm) supported horizontally within a water-filled Petri dish (Fig. 2). Filming methods were otherwise identical to those used for mayfly larvae.

2.2. Jump trajectories and landing orientations

We recorded the aerial trajectories and landing positions of *M. ellenae* larvae following their voluntary jumps initiated above the floor of an experimental theater. The theater consisted of two muslin cloth walls, each 3 m high and 0.7 m wide. The walls were joined orthogonally along one long edge and were suspended above a 0.7 × 0.7 m cardstock floor. The floor was delineated with radii at 5° intervals centered on a geometric origin directly beneath the initiation point of jumping. Mayflies were placed individually on a small piece of wet filter paper secured to the muslin wall 2.5 m above the floor. A fine paintbrush was used to coax the larva into a head-up vertical orientation on the filter paper. About half of the larvae positioned in this manner then voluntarily jumped from the paper within 15 s of placement. Jumps were induced in the more reluctant larvae by lightly touching their antennae with the tip of the paintbrush. Larvae in their final instar (as indicated by their size and the presence of large, dark wing pads) were unwilling to jump even when repeatedly prodded.

Body trajectories following jumps from the vertical stage were also filmed using the aforementioned high speed video camera (operated at 500 frames/s) oriented orthogonally to the background sheet of the filming theater. Only those jumps for which the trajectory was nominally parallel to the background plane, as assessed visually both at the time of filming and from the depth of field of the resulting video, were used in subsequent analysis. We used NIH ImageJ to determine anterior and posterior body coordinates in consecutive frames of recorded video sequences;

displacement of the midpoint of these two points was used to derive vertical acceleration through time using Euler's method, with a rejection filter for local estimates deviating by more than 50% of the mean value for any given sequence.

We also evaluated the landing point of each larva on the cardstock floor immediately following its jump (Fig. 3), measuring the distance of the body centroid from the horizontally projected point of takeoff (d), the angular position of body center (θ) relative to the horizontal projection of the takeoff point, and the angular orientation of the longitudinal body axis relative to the line segment connecting body and origin (φ). We hypothesized that mayflies exhibiting aerial control would land in a non-random pattern with respect to the takeoff point. Specifically, we predicted that most larvae would land facing the origin (i.e., $\varphi = 0$). This prediction was based on the observation that larvae consistently swam across open water and crawled up the nearest rock face following jumps initiated in the field, suggesting avoidance of potential predation by fish, and some capacity for visually-based orientation during or subsequent to a fall (e.g., Yanoviak et al., 2005). We further predicted that landings would be randomly dispersed about the origin (i.e., $|\theta - 90°| \neq 0$), and that the horizontal distance between the landing point and the origin (d) would not vary with body size.

3. Results

3.1. Takeoff behavior and trajectories

A total of 101 takeoffs was filmed using the high speed camera from eighteen individual mayfly larvae ranging in body mass from 1 to 32 mg. Both body length and caudal filament length of the larvae scaled isometrically (Fig. 4). Mayflies with ablated caudal filaments were very reluctant to jump, whereas non-ablated individuals jumped voluntarily within a few seconds of placement on the stage. Dorsal flexion of the body often was initiated or facilitated by the legs in a "push up" maneuver, breaking the surface tension of the adhering water layer. Following pronounced dorsal and backwards bending, intact mayfly larvae always launched themselves rapidly from the substrate via straightening of their longitudinal body axis while the caudal appendages maintained ground contact, thus propelling the body into the air (Supplementary Video 1). This process initiated rapid spinning about a transverse body axis which continued throughout the trajectory (Fig. 5), along with cyclical dorosoventral flexion of the abdomen.
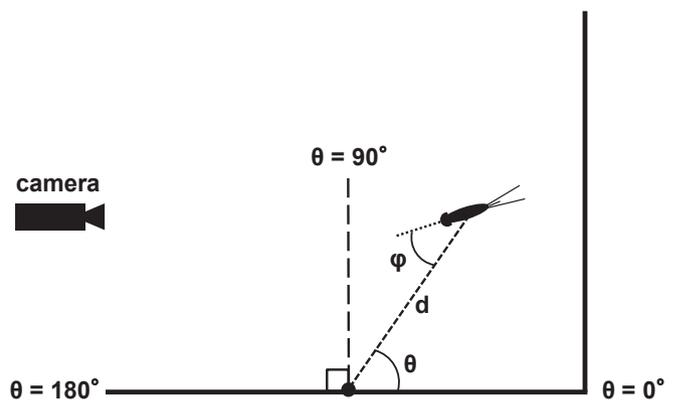

Fig. 3. Vertical view of the drop-test filming theater. Measurements taken manually for each landed mayfly included distance of the body center from the horizontally projected takeoff point (d), the angular orientation of the body center relative to this point (θ), and the angular orientation of the longitudinal axis of the mayfly relative to the line segment connecting the body center and the origin (φ). See text for details of camera position and selection of jump trajectories for use in analysis.
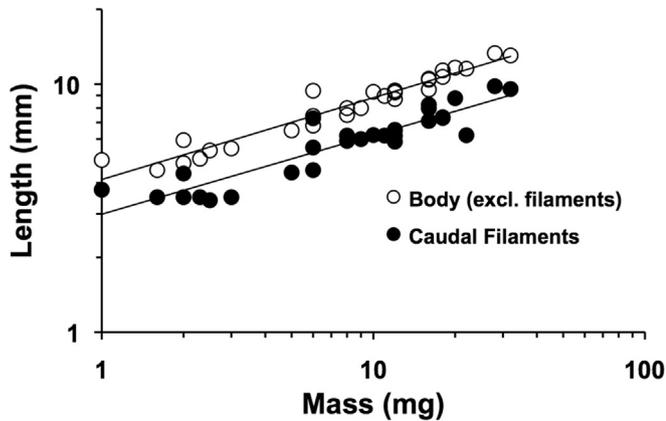
Fig. 4. Log–log plots of body length versus body mass (log *length* = 0.62 + 0.33 log *mass*; R^2 = 0.94, P < 0.0001) and caudal filament length vs. body mass (log *length* = 0.48 + 0.32 log *mass*; R^2 = 0.84, P < 0.0001) for *Mayobaetis ellenae* larvae.

By contrast, mayflies lacking caudal filaments exhibited greater variability and instability during takeoff, albeit using the same general pattern of dorsoventral flexion and subsequent body straightening to generate ground reaction forces with the abdomen and associated body spinning (Supplementary Video 2). In all cases of both intact and ablated larvae, the relatively small tracheal gills (Fig. 1) remained adhered to the body throughout the takeoff, and served no obvious aerodynamic function during subsequent spinning.

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.asd.2017.06.005

Jumping takeoffs by intact mayflies were fast, lasting only about 34 ms (mean: 33.6 ms, range 22–49 ms). Angular velocities of the longitudinal body axis during the first cycle of aerial rotation were also high, averaging about 12,000° s^{-1} (range 4900–21200° s^{-1};

N = 17 individuals, 1–4 trials per individual). Takeoff duration was independent of substrate orientation (one-way ANOVA, $F_{2,63}$ = 1.71, P = 0.12). Jump durations for ablated individuals declined significantly, by 12% on average, relative to the non-ablated condition (paired t-test, P < 0.001), presumably reflecting the absence of caudal filament contact and associated contributions to takeoff duration. Initial takeoff velocities following loss of contact with substrate averaged 1.25 m s^{-1} (SD ± 0.27 m s^{-1}) over the first 35 ms of fully aerial displacement. For post-takeoff trajectories, jumps from a total of 23 individual mayfly larvae were used to estimate accelerations over longer vertical distances (mean = 100.3 cm, range = 54–217 cm). The mean vertical accelerations for these trajectories, as averaged among individuals, was 9.5 m s^{-2} (SD ± 1.2 m s^{-2}), with the 95% confidence interval (9.0–10.0 m s^{-2}) including the value for gravitational acceleration.

Jumping takeoffs were filmed for six individual bristletails (mean body length excluding caudal filaments = 9.66 mm; range = 8.83–10.42 mm), with a median of 7.5 jumps per individual (range = 5–9 jumps). In contrast to takeoff behavior in mayfly larvae, jumping in bristletails typically involved a pronounced ventral bending of both head and abdomen against the substrate, subsequent straightening along the longitudinal axis, and no mid-air rotation (Supplementary Video 3). Takeoffs were typically much quicker than those obtained for mayfly larvae, averaging 10.9 ms in duration (range = 7–13 ms). Jumps also tended to be much more stereotypical, both within and among individuals, when compared to the variability seen among mayfly larvae.

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.asd.2017.06.005

3.2. Landing orientations

Takeoff jumps in the experimental theater to evaluate orientations were obtained from 61 individual mayfly larvae. The frequency of landings in which landed larvae were facing toward the origin (56%) was comparable to the landing frequency for those facing away from the origin (44%; binomial test, P = 0.44). The average (±1 SD) radial deviation of landing points from the origin (i.e., |θ-90°|) was 6.7° ± 37.5°. This value was normally distributed (Shapiro–Wilk test, W = 0.97, P = 0.08) and did not differ from zero (t = 1.4, df = 60, P = 0.17). Likewise, the frequency of landings within three angular ranges of deviation from the origin (i.e., 0–30°, 31–60°, and >60° did not differ significantly from frequencies predicted under the normal distribution (G-test with Williams correction, G = 0.77, df = 2, P = 0.68). The horizontal distance between the landing point and the origin (*d*) showed no correlation with either radial angle (θ: $F_{1,59}$ = 3.17, R^2 = 0.05, P = 0.08) or body mass ($F_{1,59}$ = 0.49, R^2 < 0.01, P = 0.49).

4. Discussion

Jumping larvae of *M. ellenae* demonstrated rapid takeoffs, spinning trajectories, and no capacity for mid-air directional control on the physical scale of this investigation. Dorsal flexion of the abdomen was used to initiate the jump, followed by repeated abdominal oscillations during the aerial phase. Together with body rotations at high angular velocities and the absence of targeted orientations in landing, these results in aggregate indicate an undirected escape response. Body kinematics for takeoffs in air are similar to those described for other mayfly species initiating rapid-start maneuvers from substrates in water (Brackenbury, 2004), and even in terrestrial jumping by fish (Gibb et al., 2011). The propensity of *M. ellenae* larvae to forage on inclined or even vertical rock faces within streams and waterfalls (S.Y. and R.D., pers. obs.)
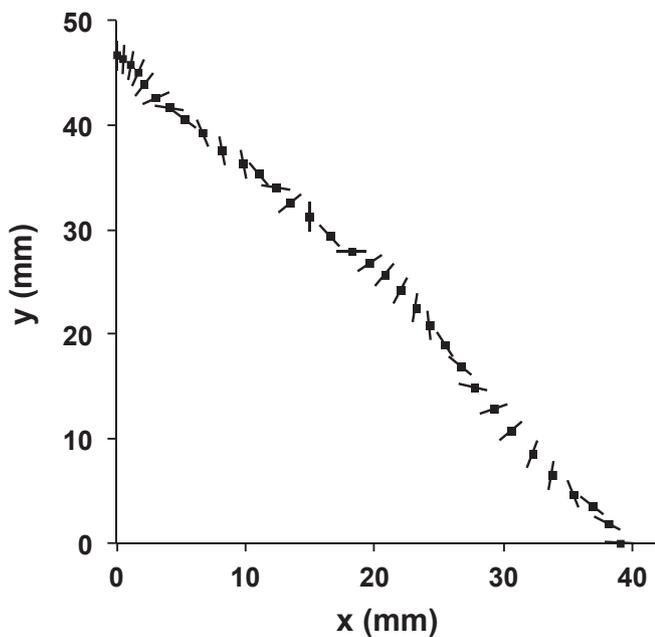

Fig. 5. Body trajectory (points) and orientation of the longitudinal thoracic axis (line segments) following takeoff of a *M. ellenae* larva (12 mg) from a vertical substrate; time interval between points is 2 ms.

would make such jumping especially effective in escape. Potential predators of larvae in these terrestrial habitats include a diversity of insectivorous birds and various amphibians.

No functional role was identified for the tracheal gills during any phase of either the takeoff or subsequent aerial translation in these mayfly larvae. The gills are relatively small and flexible (Fig. 1), and would in any event be aerodynamically insignificant given the rapid spinning of the body and the simultaneous and repeated flexion of the abdomen. Although the caudal filaments are used to initiate takeoff (Supplemental Video 1), they similarly serve no obvious aerodynamic role once airborne.

By contrast, some arboreal bristletails are capable of controlled head-first glides, aerial maneuvers, and targeted landings on tree trunks when falling (Yanoviak et al., 2009). Ablation experiments have demonstrated an important role for the caudal filaments in the steering and success of such maneuvers. The bristletail species studied here also exhibited a stable body posture with no spinning following takeoff, as reported in two species of shore bristletail (Evans, 1975). The Archaeognatha are ancestrally terrestrial and routinely jump to escape from predators; these and other controlled aerial behaviors (including righting reflexes, targeting, and landing responses) likely preceded phylogenetically the origin of the pterygote wing (Yanoviak et al., 2009). Given the wide range of aerial maneuvers exhibited by archaeognathans and by wingless larvae of diverse hemimetabolous pterygotes, the presence of wings *per se* should not be viewed as solely diagnostic of the presence of aerial behavior and flight, broadly construed (see Dudley et al., 2007).

The absence of aerial control in jumping mayfly larvae is most parsimoniously interpreted as the consequence of a secondarily derived aquatic lifestyle for the larval Palaeoptera. Other than superficial similarities of tracheal gills to pterygote wings, there are no obvious traits or behaviors that link larval mayflies or any other aquatic insect group to the origins of insect flight (Grimaldi and Engel, 2005). Furthermore, the use of wings by some adult pterygotes to drift, row, or skim on water (e.g., Marden and Thomas, 2003) is a derived trait given their multiple independent origins within both the Paleoptera and the Neoptera (Will, 1995; Samways, 1996; Ruffieux et al., 1998; Dudley, 2000; Grimaldi and Engel, 2005). Water-related behaviors among hexapods, including the mayfly larvae studied here, are accordingly non-informative relative to the origins of insect flight.

Acknowledgments

References

Brackenbury, J., 2004. Kinematics and hydrodynamics of swimming in the mayfly larva. J. Exper. Biol. 207, 913–922.

Clark-Hachtel, C.M., Linz, D.M., Tomoyasu, Y., 2013. Insights into insect wing origin provided by functional analysis of vestigial in the red flour beetle, *Tribolium castaneum*. Proc. Natl. Acad. Sci. U. S. A. 110, 16951–16956.

D'Haese, C.A., 2002. Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. Proc. R. Soc. Lond. B 269, 1143–1151.

Dudley, R., 2000. The Biomechanics of Insect Flight: Form, Function, Evolution. Princeton Univ. Press, Princeton, New Jersey.

Dudley, R., Yanoviak, S.P., 2011. Animal aloft: the origins of aerial behavior and flight. Integ. Comp. Biol. 51, 926–936.

Dudley, R., Byrnes, G., Yanoviak, S.P., Borrell, B., Brown, R., McGuire, J., 2007. Gliding and the functional origins of flight: biomechanical novelty or necessity? Annu. Rev. Ecol. Evol. Syst. 38, 179–201.

Eaton, R.C. (Ed.), 1984. Neural Mechanisms of Startle Behavior. Plenum, New York, 377 pp.

Engel, M.S., Davis, S.R., Prokop, J., 2013. Insect wings: the evolutionary development of nature's first fliers. In: Minelli, A., Boxhall, G., Fusco, G. (Eds.), Arthropod Biology and Evolution: Molecules, Development, Morphology. Springer-Verlag, Berlin, pp. 269–298.

Evans, M.E.G., 1975. The jump of *Petrobius* (Thysanura, Machilidae). J. Zool. 176, 49–65.

Garrouste, R., et al., 2012. A complete insect from the Late Devonian period. Nature 488, 82–85.

Gibb, A.C., Ashley-Ross, M.A., Pace, C.M., Long, J.H., 2011. Fish out of water: terrestrial jumping by fully aquatic fishes. J. Exp. Zool. 315, 649–653.

Grimaldi, D.A., 2010. 400 million years on six legs: on the origin and early evolution of Hexapoda. Arthropod Struct. Dev. 39, 191–203.

Grimaldi, D.A., Engel, M.S., 2005. Evolution of the Insects. Cambridge Univ. Press, Cambridge, UK.

Jusufi, A., Zeng, Y., Full, R.J., Dudley, R., 2011. Aerial righting reflexes in flightless animals. Integr. Comp. Biol. 51, 937–943.

Lugo-Ortiz, C.R., McCafferty, W.P., 1996. Phylogeny and classification of the *Baetodes* complex (Ephemeroptera: Baetidae), with description of a new genus. J. N. Am. Benthol. Soc. 15, 367–380.

Marden, J.H., Thomas, M.A., 2003. Rowing locomotion by a stonefly that possesses the ancestral pterygote condition of co-occurring wings and abdominal gills. Biol. J. Linn. Soc. 79, 341–349.

Ohde, T., Yaginuma, T., Niimi, T., 2013. Insect morphological diversification through the modification of wing serial homologs. Science 340, 495–498.

Prokop, J., Pecharová, M., Nel, A., Hörnschemeyer, T., Krzemińska, E., Krzemiński, W., Engel, M.S., 2017. Paleozoic nymphal wing pads support dual model of insect wing origins. Curr. Biol. 27, 263–269.

Ruffieux, L., Elouard, J.M., Sartori, M., 1998. Flightlessness in mayflies and its relevance to hypotheses on the origin of insect flight. Proc. Roy. Soc. Lond. B 265, 2135–2140.

Samways, M.J., 1996. Skimming and insect evolution. Trends Ecol. Evol. 11, 471.

Staniczek, A.H., Sroka, P., Bechly, G., 2014. Neither silverfish nor fowl: the enigmatic Carboniferous *Carbotriplura kukalovae* Kluge, 1966 (Insecta, Carbotriplurida) is the putative fossil sister group of winged insects (Insecta, Pterygota). Syst. Entomol. 39, 619–632.

Sun, L., Sabo, A., Meyer, M.D., Randolph, R.P., Jacobus, L.M., McCafferty, W.P., Ferris, V.R., 2006. Tests of current hypotheses of mayfly (Ephemeroptera) phylogeny using molecular (18s rDNA) data. Ann. Entomol. Soc. Am. 99, 241–252.

Waltz, R.D., McCafferty, W.P., 1985. *Moribaetis*: a new genus of tropical Baetidae (Ephemeroptera). Proc. Entomol. Soc. Wash. 87, 239–251.

Will, K.W., 1995. Plecopteran surface-skimming and insect flight evolution. Science 270, 1684–1685.

Yanoviak, S.P., Dudley, R., Kaspari, M., 2005. Directed aerial descent in canopy ants. Nature 433, 624–626.

Yanoviak, S.P., Kaspari, M., Dudley, R., 2009. Gliding hexapods and the origins of insect aerial behavior. Biol. Lett. 5, 510–512.