

Gliding hexapods and the origins of insect aerial behaviour

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Directed aerial descent (i.e. gliding and manoeuvring) may be an important stage in the evolution of winged flight. Although hypothesized to occur in ancestrally wingless insects, such behaviour is unexplored in extant basal hexapods, but has recently been described in arboreal ants. Here we show that tropical arboreal bristletails (Archaeognatha) direct their horizontal trajectories to tree trunks in approximately 90 per cent of falls. Experimental manipulation of the median caudal filament significantly reduced both success rate (per cent of individuals landing on a tree trunk) and performance (glide index) versus controls. The existence of aerial control in the ancestrally wingless bristletails, and its habitat association with an arboreal lifestyle, are consistent with the hypothesis of a terrestrial origin for winged flight in insects.

Keywords: aerial gliding; Archaeognatha; evolution; flight; tropics

1. INTRODUCTION

The question of the origin of wings in insects is unresolved, in part due to the lack of fossil intermediates (Dudley 2000; Grimaldi & Engel 2005). Two prevailing hypotheses are: (i) insect wings evolved terrestrially, as extensions of the thoracic pleura of primitive hexapods gliding from tall vegetation, and (ii) insect wings evolved in an aquatic setting, derived from gills or gill plates of primitively aquatic forms (reviewed in Dudley *et al.* 2007). Directed aerial descent (DAD) in the absence of wings has recently been described in worker ants (Yanoviak *et al.* 2005); however, as a derived lineage within the pterygotes, ants cannot phylogenetically illustrate the origins of flight in insects. By contrast, controlled aerial behaviour in the apterygote hexapods—the exclusively terrestrial (Grimaldi & Engel 2005) sister taxa to the winged insects—probably preceded the acquisition of true (i.e. flapping) flight (Hasenfuss 2002, 2008). Moreover, bristletails possess elongate caudal

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filaments that, via dorsoventral and lateral abdominal flexion, could serve as rudders to control pitch and yaw, respectively (Hasenfuss 2008).

Tree crowns present unstable and potentially hazardous substrates for wingless arthropods. In extant forests, numerous taxa (e.g. spiders, ants, insectivorous birds) dislodge or prey upon wingless invertebrates, and bristletails will readily jump from tree surfaces in response to an approaching disturbance (e.g. Murphy 1973; S. P. Yanoviak 2005, personal observation). Fossil evidence indicates that Devonian vegetation exceeded 5 m in height (Dilcher *et al.* 2004) and probably presented similar opportunities for gravitationally assisted descent to ancestral hexapods (Dudley *et al.* 2007).

Here we show that arboreal jumping bristletails (Archaeognatha: Apterygota) are capable of gliding and controlled manoeuvres when falling from trees. We test the hypotheses that caudal appendages and/or antennae affect aerodynamic control in bristletails, and that aerial performance is a function of body size. We predicted that experimental manipulation of appendage length would reduce the frequency of successful trunk landings and glide performance. We further expected that glide performance would decline with increasing body size, as observed in ants (Yanoviak *et al.* 2005).

2. MATERIAL AND METHODS

(a) Study sites

Fieldwork was conducted in March and May 2005, and in January of 2006 and 2007 at the Amazon Conservatory for Tropical Studies (ACTS) canopy walkway 67 km northeast of Iquitos, Peru (3.25° S, 72.91° W). Secondary field sites included Barro Colorado Island (BCI), Panama (09.15° N, 79.85° W; May 2003) and the Shell hydrocarbon extraction facility in Gamba, Gabon (02.73° S, 10.01° E; April 2005). Characteristics of the study sites are summarized elsewhere (Yanoviak *et al.* 2007).

(b) Drop tests

We quantified the directed descent behaviour of jumping bristletails (Archaeognatha) and silverfish (*Thysanura s.s.*) by dropping individuals from the lower crown branches (more than 15 m) of their resident trees in Panama and Gabon (Yanoviak *et al.* 2007), or from the ACTS canopy walkway in Peru (Yanoviak & Dudley 2006). The focal taxa differed by region (table 1). Following similar methods used for ants, each animal was lightly dusted with orange fluorescent powder and placed in a plastic vial coated internally with Fluon. The vial was held 1–2 m horizontally from the trunk and lightly agitated until the animal exited (see video in the electronic supplementary material). Each animal was used only once, and all drops were made under windless conditions. None of the tested silverfish demonstrated aerial control; remaining methods and results pertain exclusively to bristletails.

(c) Ablation experiments

We manipulated the median caudal filament (MF), lateral cerci (LC) and antennae of bristletails in Peru to determine the effects of these appendages on gliding success and aerial performance. Experimental animals were collected from trees along the ACTS canopy walkway shortly after sunset and held overnight in an ambient laboratory. The following morning, each animal was weighed to the nearest 2 mg on a portable electronic balance and anaesthetized by cooling prior to appendage manipulation. Appendages were ablated by pinching with fine forceps. Animals in the control treatment were similarly sedated and handled. Body length (from the maxillary palp insertions to the MF insertion) and the lengths of the MF, LC and antennae were measured for a subset of the experimental animals. Individuals were assigned to treatment groups haphazardly. We included juveniles in tests to maximize the size range and sample sizes. Adults were not separated by gender.

We quantified gliding success rate as the proportion of individuals in a treatment that landed on a nearby trunk before reaching the ground. The frequency of trunk landing success in each ablation treatment was compared with the control frequency with a log-likelihood goodness-of-fit test (*G*-test; Sokal & Rohlf 1995).

Table 1. Taxa tested for directed aerial descent behaviour. (A, arboreal; U, understorey; DAD, evidence for directed aerial descent behaviour.)

Taxon	habitat	location	<i>n</i>	DAD
Archaeognatha, Meinertellidae, <i>Meinertellus</i> sp.	A, trunk	Peru	159	yes
Archaeognatha, Meinertellidae, nr. <i>Neomachilellus</i> sp.	A, trunk	Panama	5	yes
Archaeognatha, Machilidae, <i>Janetschekilis</i> sp.	A, trunk	Gabon	5	yes
Archaeognatha, Meinertellidae, indeterminate	U, leaf litter	Peru	2	no
Archaeognatha, Meinertellidae, indeterminate	U, low vegetation	Panama	5	no
Thysanura s.s., Lepismatidae, indeterminate	A, under bark	Gabon	7	no
Thysanura s.s., Lepismatidae, indeterminate	U, leaf litter	Peru	5	no

We quantified glide performance as the horizontal distance travelled per unit vertical distance fallen (i.e. glide index). Vertical distances were measured with a string marked at 1 m intervals and suspended adjacent to the tree trunk (Yanoviak *et al.* 2005). We estimated glide indices to the nearest 0.5 m, based on the point where the bristletail either passed or struck the string.

To assess the effects of appendage ablation on glide performance, average glide indices were compared among treatments using ANOVA and *post hoc* Tukey tests. We used linear regression to examine relationships between body size and glide performance of animals in each ablation treatment and overall. We additionally tested for allometric relationships between appendage length and body length by comparing the slopes of length versus mass plots using ANOVA followed by independent contrasts (SAS Institute 2002). Normality was determined with Kolmogorov–Smirnov tests, and data were log transformed before analysis when necessary.

Representative specimens from each site were preserved in 95 per cent ethanol. Vouchers were deposited at the National Museum of Natural History (Washington, DC), the Universidad de Córdoba (Spain) and the Museo de Historia Natural Javier Prado (Peru).

3. RESULTS

Arboreal bristletails at all study sites demonstrated DAD behaviour, whereas understorey bristletails and all silverfish did not (table 1). After release, arboreal bristletails consistently exhibited an initial period of freefall and dorsoventral righting followed by a steep controlled glide, generally to the nearest tree trunk, with an overall successful landing rate of near 90 per cent (figure 1; see video in the electronic supplementary material). Unlike some gliding ants (Yanoviak *et al.* 2005), arboreal bristletails flew head-first while targeting the trunk. The average ratio of horizontal to vertical distance travelled during descent (i.e. the glide index) was 0.4, corresponding to an average glide angle, from drop point to landing, of 68°. The glides of most bristletails were strongly curvilinear. However, approximately 25 per cent of all individuals glided directly to the nearest tree trunk from the moment of release, and several of the associated glide indices exceeded 0.5.

Experimental ablation of the MF significantly reduced the percentage of bristletails successfully landing on a tree trunk ($G > 8.7$, d.f. = 1, $p < 0.005$ in all tests) and their glide indices ($F_{5,112} = 9.35$, $p < 0.0001$) relative to controls (figure 1). By contrast, removal of either lateral filament failed to affect glide success rates and the glide index.

Bristletail mass (M) and body length (BL) followed the power function $BL = 3.86M^{0.30}$ ($R^2 = 0.90$, $n = 107$). Average mass did not differ among treatments in the ablation experiment ($F_{5,153} = 0.68$, $p = 0.64$). There was no relationship between M and glide index both within treatments

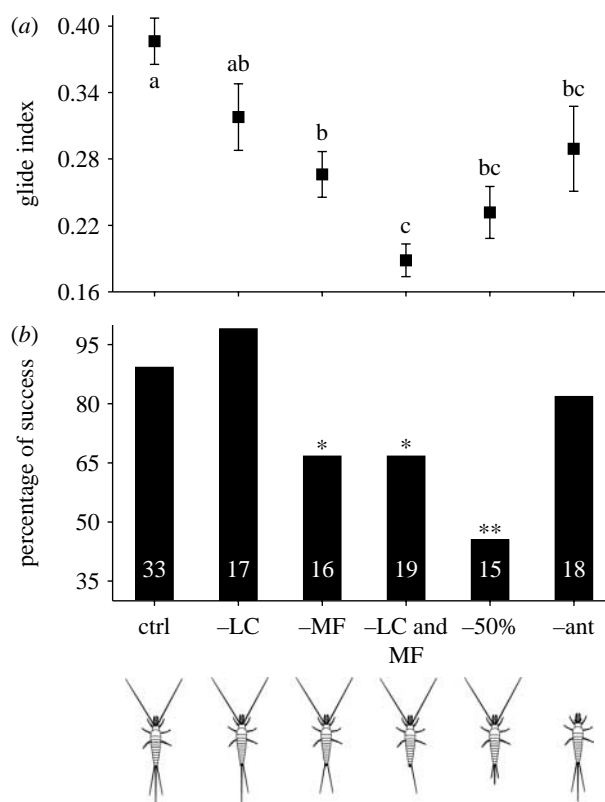


Figure 1. Average (± 1 s.e.) (a) glide performance and (b) gliding success in neotropical arboreal bristletails (*Meinertellus* sp.) dropped from 22 m in the Peruvian forest canopy. ctrl, control; -LC, one lateral cercus ablated; -MF, median filament ablated; -LC and MF, one lateral cercus and median filament ablated; -50%, half of the total length of both LC and the median filament ablated; -ant, both antennae ablated. Similar letters in (a) indicate means that do not differ. Values superimposed on the bars in (b) are the number of successful glides, corresponding to sample sizes for the means in (a). Goodness-of-fit tests of gliding success compared treatment frequencies with the control frequency (89.2%). * $p < 0.005$; ** $p < 0.001$.

and overall ($p > 0.5$, $R^2 < 0.1$ for all regressions), in part due to trajectory variability and targeting decisions. By contrast, glide performance increased linearly with the area of the caudal appendages ($F_{1,37} = 4.40$, $R^2 = 0.11$, $p = 0.04$).

Independent contrasts showed that MF length increases isometrically with BL as mass increases ($F = 1.20$, d.f. = 1, $p = 0.27$). When the various appendage lengths were plotted against BL, only the antennae showed a significant departure from unity (i.e. antennae were relatively longer in larger individuals; $t = 2.76$, d.f. = 1, $p = 0.008$).

4. DISCUSSION

Here we provide the first, to our knowledge, quantitative assessment of gliding flight in an extant apterygote insect, confirming theoretical predictions of DAD in basal hexapods (Hasenfuss 2002, 2008). An aerial righting reflex reorients falling bristletails from a vertical tumble to a stable dorsoventral and headfirst posture characterized by non-trivial lift:drag ratios (i.e. trajectory-averaged descent angles of 68°) and targeted manoeuvres towards a nearby tree trunk. Aerial control is presumably mediated visually as in gliding ants (Yanoviak & Dudley 2006). Results of ablation experiments (figure 1) suggest that dorsoventral and lateral ruddering of the abdominal filaments, with their substantial moment arm relative to the body centre of mass, are used to steer continuously and to effect targeting. In aggregate, these results demonstrate that the sensory and biomechanical capacities to orient during free fall and to effect controlled gliding phylogenetically precede the origin of wings.

Winged insects probably evolved within the late Palaeozoic context of rapidly diversifying terrestrial ecosystems and abundant opportunities for aerial displacement (Shear & Kukalová-Peck 1990; Grimaldi & Engel 2005). The earliest archaeognathan fossils date to the Mid-Devonian (Grimaldi & Engel 2005) at a time when forest canopies already exceeded 5 m in height (Dilcher *et al.* 2004). These canopies bore terminal reproductive structures (sporangia) that provided nutritional rewards for herbivorous hexapods. Given the diversity of insectivorous predators in the late Palaeozoic (Shear & Kukalová-Peck 1990), jumping escapes from plants would also have selected for enhanced aerial performance. Neurobiological studies support the ancestral presence of wind-based sensorimotor pathways underlying escape jumps in apterygotes (Edwards 1997).

The morphological precursors to pterygote wings remain enigmatic (Grimaldi & Engel 2005; Hasenfuss 2008). Our results suggest that small but ancestrally mobile winglets, originating from either thoracic or leg segments, could have served in control during gliding and targeting manoeuvres (see also Wootton & Ellington 1991; Kingsolver & Koehl 1994). Such an unsteady aerodynamic role would not necessarily exclude additional functions (e.g. thermoregulation) postulated for early wings. More generally, DAD in arboreal bristletails lends support to the terrestrial hypothesis for the origin of pterygotes, and suggests that a diversity of aerial behaviours preceded the appearance of wings in the history of insects.

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- Dilcher, D. L., Lott, T. A., Wang, X. & Wang, Q. 2004 A history of tree canopies. In *Forest canopies*, 2nd edn (eds M. D. Lowman & H. B. Rinker), pp. 118–137. New York, NY: Elsevier.
- Dudley, R. 2000 *The biomechanics of insect flight: form, function, evolution*. Princeton, NJ: Princeton University Press.
- 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. (doi:10.1146/annurev.ecolsys.37.091305.110014)
- Edwards, J. S. 1997 The evolution of insect flight: implications for the evolution of the nervous system. *Brain Behav. Evol.* **50**, 8–12. (doi:10.1159/000113317)
- Grimaldi, D. A. & Engel, M. S. 2005 *Evolution of the insects*. New York, NY: Cambridge University Press.
- Hasenfuss, I. 2002 A possible evolutionary pathway to insect flight starting from lepismatid organization. *J. Zool. Syst. Evol. Res.* **40**, 65–81. (doi:10.1046/j.1439-0469.2002.00180.x)
- Hasenfuss, I. 2008 The evolutionary pathway to insect flight: a tentative reconstruction. *Arthropod Syst. Phylogeny* **66**, 19–35.
- Kingsolver, J. G. & Koehl, M. A. R. 1994 Selective factors in the evolution of insect wings. *Annu. Rev. Entomol.* **39**, 425–451. (doi:10.1146/annurev.en.39.010194.002233)
- Murphy, D. H. 1973 Animals in the forest ecosystem. In *Animal life and nature in Singapore* (ed. S. H. Chuang), pp. 53–73. Singapore: University of Singapore Press.
- SAS Institute 2002 *SAS/STAT user's guide*, v. 9. Cary, NC: SAS Institute.
- Shear, W. A. & Kukalová-Peck, J. 1990 The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Can. J. Zool.* **68**, 1807–1834. (doi:10.1139/z90-262)
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*, 3rd edn. New York, NY: W.H. Freeman & Co.
- Wootton, R. J. & Ellington, C. P. 1991 Biomechanics and the origin of insect flight. In *Biomechanics in evolution* (eds J. M. V. Rayner & R. J. Wootton), pp. 99–112. Cambridge, UK: Cambridge University Press.
- Yanoviak, S. P. & Dudley, R. 2006 The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera: Formicidae). *J. Exp. Biol.* **209**, 1777–1783. (doi:10.1242/jeb.02170)
- Yanoviak, S. P., Dudley, R. & Kaspari, M. 2005 Directed aerial descent in canopy ants. *Nature* **433**, 624–626. (doi:10.1038/nature03254)
- Yanoviak, S. P., Fisher, B. L. & Alonso, A. 2007 Arboreal ant diversity (Hymenoptera: Formicidae) in a central African forest. *Afr. J. Ecol.* **46**, 60–66. (doi:10.1111/j.1365-2028.2007.00810.x)