Gliding hexapods and the origins of insect aerial behaviour

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Direct 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 primative 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 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 further expected that glide performance would decline with increasing body size, as observed in ants (Yanoviak et al. 2005).
Table 1. Taxa tested for directed aerial descent behaviour. (A, arboreal; U, understorey; DAD, evidence for directed aerial descent behaviour.)

<table>
<thead>
<tr>
<th>Taxon habitat</th>
<th>location</th>
<th>n</th>
<th>DAD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archaeognatha, Meinertellidae, Meinertellus sp.</td>
<td>Peru</td>
<td>159</td>
<td>yes</td>
</tr>
<tr>
<td>Archaeognatha, Meinertellidae, nr. Neomachilleus sp.</td>
<td>Panama</td>
<td>5</td>
<td>yes</td>
</tr>
<tr>
<td>Archaeognatha, Machilidae, Janatscheckii sp.</td>
<td>Gabon</td>
<td>5</td>
<td>yes</td>
</tr>
<tr>
<td>Archaeognatha, Meinertellidae, indeterminate</td>
<td>Peru</td>
<td>2</td>
<td>no</td>
</tr>
<tr>
<td>Archaeognatha, Meinertellidae, indeterminate</td>
<td>Panama</td>
<td>5</td>
<td>no</td>
</tr>
<tr>
<td>Thysanura s.s., Lepismatidae, indeterminate</td>
<td>Gabon</td>
<td>7</td>
<td>no</td>
</tr>
<tr>
<td>Thysanura s.s., Lepismatidae, indeterminate</td>
<td>Peru</td>
<td>5</td>
<td>no</td>
</tr>
</tbody>
</table>

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 Cordoba (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 headfirst 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 (F5,112=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=3.86M0.30 (R2=0.90, n=107). Average mass did not differ among treatments in the ablation experiment (F5,153=0.68, p=0.64). There was no relationship between M and glide index both within treatments and overall (p>0.5, R2<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 (F1,37=4.40, R2=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; F=2.76, d.f.=1, p=0.008).

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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 reorienting 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 ablative 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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