

1 **How lizards fly: A novel type of wing in animals**

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11 ABSTRACT

12

13 Flying lizards of the genus *Draco* are famous for their gliding ability, using an aerofoil formed by
14 winglike patagial membranes and supported by elongated thoracic ribs. It has remained unknown,
15 however, how the lizards manoeuvre during flight. Here, I show that the patagium is deliberately
16 grasped and controlled by the forelimbs while airborne. This type of composite wing is unique
17 inasmuch as the lift-generating and the controlling units are formed independently by different parts
18 of the body and are connected to each other only for the duration of the flight. The major advantage
19 for the lizards is that the forelimbs keep their entire movement range and functionality for climbing
20 and running when they are not used as the controlling unit of the wing. These findings not only shed
21 a new light on the flight of *Draco* lizards but also have implications for the interpretation of gliding
22 performance in fossil species.

23 KEYWORDS: *Draco*, flying lizard, gliding flight, patagium

24

25 INTRODUCTION

26 A number of vertebrates as well as invertebrates are known to perform gliding flights (Dudley *et al.*,
27 2007; Socha *et al.*, 2015; Lingham-Soliar, 2015). Flying Lizards of the agamid genus *Draco* are the most
28 specialized and best-studied gliding reptiles (McGuire, 2003; McGuire & Dudley, 2005, 2011; Socha *et al.*
29 *et al.*, 2015). Their patagium is supported by five to seven greatly elongated thoracic ribs and spread by
30 specialized iliocostalis and intercostal muscles (Colbert, 1967; Russell & Dijkstra, 2001; McGuire,
31 2003; Dudley *et al.*, 2007; McGuire & Dudley, 2011; Lingham-Soliar, 2015). It is commonly assumed
32 that flying lizards use the unfurled patagium to glide but hold the forelimbs free in front of the body
33 while airborne. This assumption was manifested about 300 years ago, when the first preserved
34 specimens were brought to Europe and reports on Flying Lizards were accompanied with drawings
35 showing artistic interpretations of “gliding” lizards holding their forelimbs in front of the body (e.g.

36 Seba, 1734; Marsden, 1811; Günther, 1872; Maindron, 1890). The patagium-associated musculature
37 has been suspected to control the direction of the glide path (Colbert, 1967; Russell & Dijkstra, 2001;
38 Dudley *et al.*, 2007; McGuire & Dudley, 2011; Lingham-Soliar, 2015), but it has remained unclear how
39 the lizards are able to manoeuvre in the air (McGuire & Dudley 2011).

40 Anatomical properties of the patagium as well as behavioural observations challenge the assumption
41 that the associated muscles alone can perform the sophisticated movements required for
42 manoeuvring. (1) Only two muscles insert the first elongated ribs (Colbert, 1967) and therefore allow
43 movements in only a limited number of different directions, mainly spreading (forward) and furling
44 (backward) the patagium. (2) The patagium-spreading muscles stem from musculature originally used
45 for breathing (Colbert, 1967; John, 1970). In the original state, the intercostal muscles of both sides
46 contract simultaneously in order to expand and contract the thorax (e.g. Ratnovsky *et al.*, 2008). If
47 the muscles of only one side contracted, the thorax would be rotated. One-sided contractions of
48 intercostal muscles could so far be demonstrated only in anaesthetized dogs and in humans in
49 response to passive rotations of the thorax (Decramer *et al.*, 1986; Whitelaw *et al.*, 1992), and
50 therefore it seems unlikely that *Draco* lizards are able to deliberately execute one-sided contractions
51 of these muscles. (3) The patagium is spread not only to form an aerofoil but also for display in
52 intraspecific communication, and photographs and observations of display in different species of
53 *Draco* indicate that both sides of the patagium are always moved simultaneously (Hairstone, 1957;
54 John, 1967; Mori & Hikida, 1993; McGuire & Dudley, 2011; J. M. Dehling, unpubl. data). If *Draco*
55 lizards were able to perform sophisticated one-sided movements required for glide-path control with
56 their patagium-associated muscles alone, they would probably show them during display as well, but
57 all they display are simultaneous spreading and furling of the patagium on both sides. Therefore, it
58 appears unlikely that *Draco* lizards are able to manoeuvre in the air using the specialized muscles of
59 the trunk alone.

60 Here, I report on the results of a study I carried out on the aerial behaviour of Dussumier's Flying
61 Lizard (*Draco dussumieri*) in order to investigate if the patagium is controlled in a different way.

62 Observations and documentations of the gliding flight in the habitat are supplemented with
63 examinations of morphological characteristics in preserved specimens of *D. dussumieri* and 17 other
64 species of the genus *Draco*. My findings demonstrate that the patagium is actually controlled by the
65 forelimbs and thus reveal a hitherto unknown type of wing in animals.

66

67 MATERIAL AND METHODS

68 *Behavioural observations.* I observed gliding flights of *Draco dussumieri* in an abandoned areca nut
69 (*Areca catechu*) plantation near the town of Agumbe, southwestern India (13.517628°N,
70 75.088542°E, WGS 84), during the late morning and early afternoon (10–12 h, 13–14.30 h) on seven
71 non-consecutive days in March 2015. The observations were made in a non-experimental approach
72 on the natural behaviour in the habitat, where the lizards performed gliding flights from one tree to
73 another. No animal was captured, handled, or manipulated in any other way during the study. A total
74 of approximately 200 gliding flights performed by at least seven different individuals were observed,
75 partly using Minox 10x50 binoculars. I documented about 50 glides photographically, focusing mainly
76 on the initial phases of the gliding flight. Sequential short-exposure photographs were taken at a rate
77 of 5.5 frames per second with a Nikon D600 full-frame digital single-lens reflex camera equipped with
78 a Nikon AF-S 200–400 mm telephoto zoom lens (manually focused).

79 *Morphological examination.* In order to corroborate observations of morphological adaptations to the
80 gliding flight in *Draco* lizards, I examined voucher specimens of 18 species of *Draco* and 21 species of
81 12 representative genera of other arboreal Asian agamid lizards deposited in the herpetological
82 collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany (online
83 supporting information, Table S1). I took measurements (to the nearest 0.1 mm) with a digital calliper
84 of snout-vent length (SVL, from tip of snout to vent), arm length (AL, from the forelimb insertion to
85 the distal end of the antebrachium, measured with the arm extended perpendicularly to the median
86 body plane), and length of the leading edge of the patagium (LL, from the insertion of the first

87 elongated rib to the point where the leading edge starts to bend posteriorly; given as a percentage of
88 the corresponding arm length, rounded to the nearest 1 %). I checked the ability to deviate the wrist
89 ulnarly and radially in all specimens. The results of the examination are given in the online supporting
90 information, Table S1.

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92 RESULTS

93 Sequential photographs of gliding *Draco* lizards revealed that the patagial musculature is not the
94 major element controlling the glide path. The explanation of how *Draco* lizards achieve
95 manoeuvrability while airborne is surprising: Instead of being held free in front of the body, as
96 previously assumed, the powerful and highly movable forelimbs are attached to the leading edge of
97 the patagium for the duration of the flight and control the aerofoil (Fig. 1).

98 The movements and actions of the forelimbs and the patagium followed a certain pattern in all
99 observed and documented gliding flights. Initially, a lizard launched itself from the tree with a jump
100 and descended head first. After takeoff, it reoriented its body dorsoventrally, the extended forelimbs
101 reached behind the back, and the trunk muscles started to spread the anterior patagium-supporting
102 ribs (Fig. 1C). When the hands got hold of the outer margins of the leading edge of the patagium,
103 they pulled it forward, and the patagium was unfurled to its full extent (Fig. 1C). The flight path then
104 soon became more horizontal. The forelimbs remained attached to the patagium for the duration of
105 the gliding flight (Fig. 1A, B), enabling changes of direction through unilateral movements of the
106 aerofoil. Shortly before reaching the landing point, the leading edge of the patagium was raised
107 above the body plane and the hind limbs were lowered, causing a change of the angle of attack and
108 an upturn of the glide path. Immediately before landing, the forelimbs released the patagium and
109 were flexed forward to diminish the impact and take hold of the surface. During the landing process,
110 the patagium was furled against the sides of the body.

111 During the gliding flight, the fully extended patagium was strongly cambered, and the lizards actively
112 arched their backs when airborne and thereby increased the camber of the aerofoil (Fig. 2). The
113 attached forelimbs formed a straight, thick leading edge of the aerofoil compared to the thin trailing
114 edge (Figs. 1, 2). When pulling the patagium forward and holding on to it, the wrist was deviated
115 ulnarly about 90° to the extended arm (Figs. 1, 3).

116

117 DISCUSSION

118 My findings demonstrate that, contrary to previous assumptions, the forelimbs of *Draco* lizards are
119 not held free next to the body during flight but constitute an essential part of the wing. This wing is
120 unparalleled in the animal kingdom, as it represents the only case in which the lift-generating and the
121 controlling units are formed independently by different parts of the body and must be connected to
122 each other at the beginning of the gliding flight (Figs. 1–3). Apart from few groups of gliding or
123 parachuting animals that use only their flattened bodies and unmodified, outstretched limbs to
124 generate lift and drag forces (Yanoviak, Dudley & Kaspari, 2005; Vanhooydonck *et al.*, 2009; Socha *et*
125 *al.*, 2015), all other groups of flying and gliding animals have developed enlarged aerodynamic
126 surfaces, i.e. wings and patagia, that are permanently attached to the skeletal and muscular elements
127 that control them (Norberg, 1990; Lingham-Soliar, 2015; Socha *et al.*, 2015). The enlarged
128 aerodynamic surfaces of vertebrates are usually attached to modified limbs or fins (Fig. 3). In
129 contrast to the hindlimbs, which possess moderate modifications, such as a lateral compression and a
130 row of enlarged scales at the trailing edge of the thigh (Russell & Dijkstra, 2001; McGuire & Dudley,
131 2011), the forelimbs of *Draco* lizards lack modifications that would increase the surface. Such
132 modifications could be expected if the forelimbs were held free next to the body and used to
133 generate greater drag and lift forces, like in parachuting geckos and frogs (Emerson & Koehl, 1990;
134 Young, Lee & Daley, 2002; Fig. 3). The major advantage of the composite wing of *Draco* is that the
135 forelimbs keep their entire movement range and full functionality for agile climbing and running

136 when they are not used as the controlling unit of the wing. Although this study reports the control of
137 the patagium through the forelimbs only in *D. dussumieri*, the behaviour can be recognised in
138 previously published photographs of gliding specimens of other *Draco* species (McGuire & Dudley,
139 2005; Socha *et al.*, 2015; Lee, 2015). Given the conserved patagial and forelimb morphology across all
140 species of *Draco* (McGuire & Dudley, 2011; online supporting information, Table S1), the patagium is
141 very likely controlled in the same way by all species of the genus.

142 The patagium of *Draco* differs functionally from the patagia of the parachuting geckos *Ptychozoon*
143 and *Hemidactylus* (Fig. 3F), as the latter are unsupported by ribs, not controlled by muscles, and
144 unfold passively as they catch air during descent (Russell & Dijkstra, 2001). Functionally, the patagium
145 of *Draco* closely resembles the plagiopatagia of gliding squirrels and colugos, which extend between
146 the arms and legs and are controlled by limb movements (Socha *et al.*, 2015; Fig. 3G). The patagium
147 of *Draco* lizards, however, is not spread as a result of the limbs assuming a posture while airborne,
148 but has to be deliberately grasped and extended.

149 The wing of *Draco* is characterized by distinct adaptive morphological features. According to
150 aerodynamic theory, the camber of the aerofoil and the presence of a thick leading edge compared to
151 the thin trailing edge create greater lift forces than flat wings could achieve (Norberg, 1990; Lingham-
152 Soliar, 2015). The pronounced adduction of the wrist during the handling of the patagium enables the
153 fingers to exert maximum forward traction on enlarged scale rows along the first two pairs of ribs on
154 the dorsal surface of the patagium (Russell & Dijkstra, 2001). *Draco* species are able to deviate the
155 wrist ulnarly, but not markedly radially, whereas other arboreal agamid lizards can neither adduct nor
156 abduct their wrists (online supporting information, Table S1). Therefore, the adduction ability is
157 obviously not related to climbing activities but appears to be a specific adaptation to grasp the
158 patagium. As *Draco* lizards show a conserved morphology of the patagium in all species (McGuire &
159 Dudley 2011) and the extended forelimb constantly reaches close to the lateral margin of the leading
160 edge (online supporting information, Table S1), the need for control of the patagium through the

161 forelimbs is probably an important constraint that prevents further rib elongation and increase in
162 wing area.

163 The fact that a patagium can be controlled by largely unmodified limbs needs to be taken into
164 consideration when interpreting finds of possible fossil gliders. A number of fossil lineages, including
165 the Late Permian *Coelurosauravus*, the Late Triassic *Kuehneosaurus*, *Kuehneosuchus* and *Icarosaurus*,
166 the Late Triassic *Mecistotrachelos*, and the Early Cretaceous *Xianglong*, possess elongated ribs or
167 bony rib-like structures that are hypothesized to have supported a patagial membrane and thus
168 resemble the glide-associated morphological modifications of the modern *Draco* lizards (Robinson,
169 1962; Colbert, 1970; Frey, Sues & Munk, 1997; Fraser *et al.*, 2007; Li *et al.*, 2007; Stein *et al.*, 2008).
170 These fossil taxa are assumed to have glided through the air with the hands held free next to the
171 body and to have changed direction by unilateral adjustments of the aerofoil through contractions of
172 the trunk musculature (Colbert, 1970; Frey *et al.*, 1997; Stein *et al.*, 2008; McGuire & Dudley, 2011).
173 Since *Draco* lizards use the forelimb to control the patagium, it is reasonable to presume that the
174 fossil gliders regulated their glide path in a similar way. Skeletal properties of the fossil gliders allow
175 this interpretation. The forelimb is shorter than the first elongated rib in these species and would
176 have constituted a straight, thickened leading edge when extended and attached to the patagium. To
177 hold on to the dorsal surface of the patagium, adduction of the wrist is advantageous, a condition
178 which is apparent in the holotypes of *Icarosaurus siefkeri* and *Mecistotrachelos apeoros* and in a well-
179 preserved specimen of *Coelurosauravus jaekeli* (Colbert, 1966; Frey *et al.*, 1997; Fraser *et al.*, 2007).
180 Hence, it seems plausible that these early reptile gliders likewise controlled the patagium with their
181 forelimbs. This would imply that the manner how the modern *Draco* lizards form and control an
182 aerofoil while simultaneously retaining full movability of the forelimb was developed convergently in
183 the past by several non-related reptile lineages.

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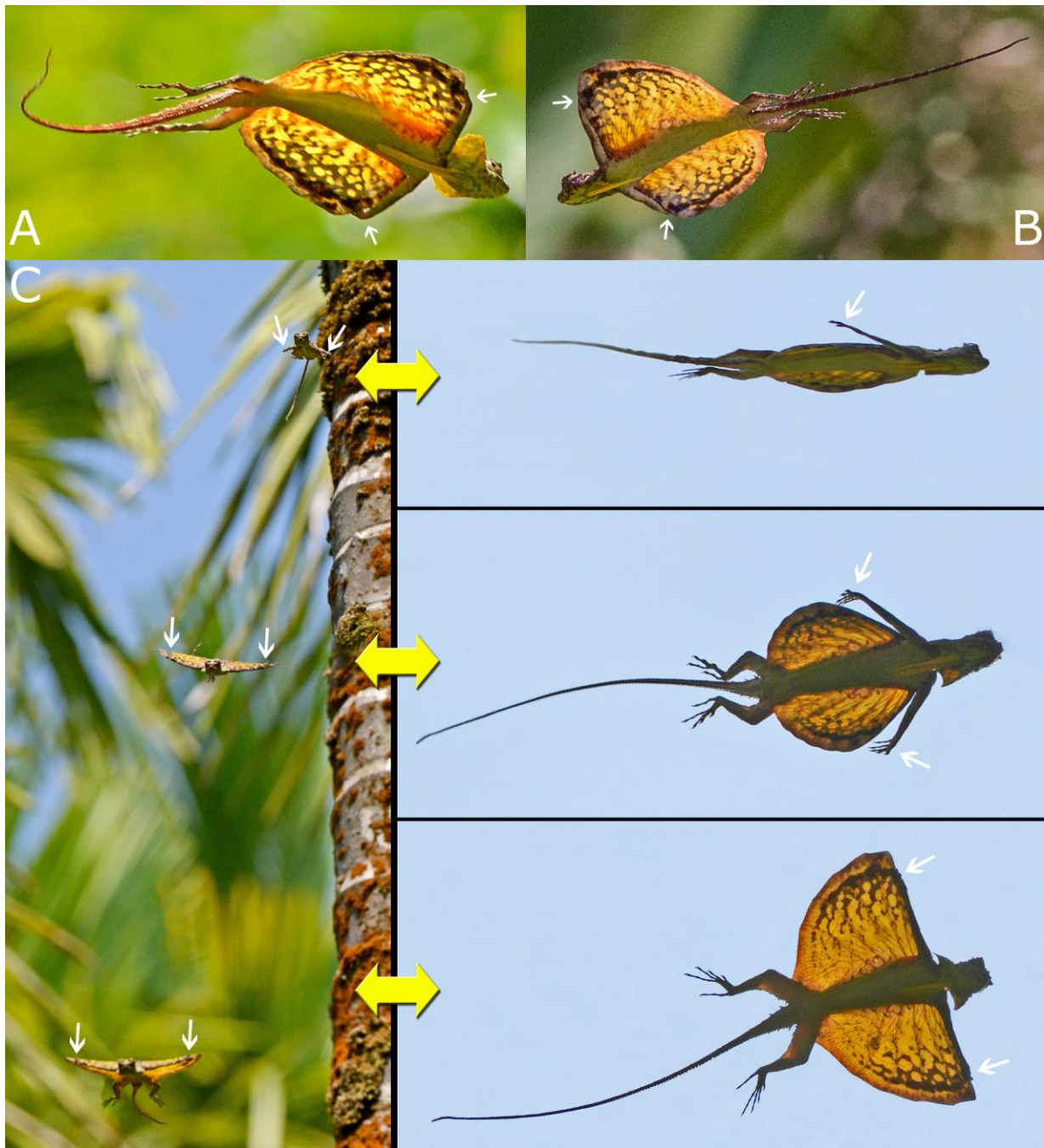
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258

259 SUPPORTING INFORMATION

- 260 Table S1. Results of the morphological examination of voucher specimens of arboreal agamid lizards.
261 For details and abbreviations see Materials and Methods. Symbols indicate the ability to deviate the
262 wrist more than 80° (*) or less than 20° (–).



263

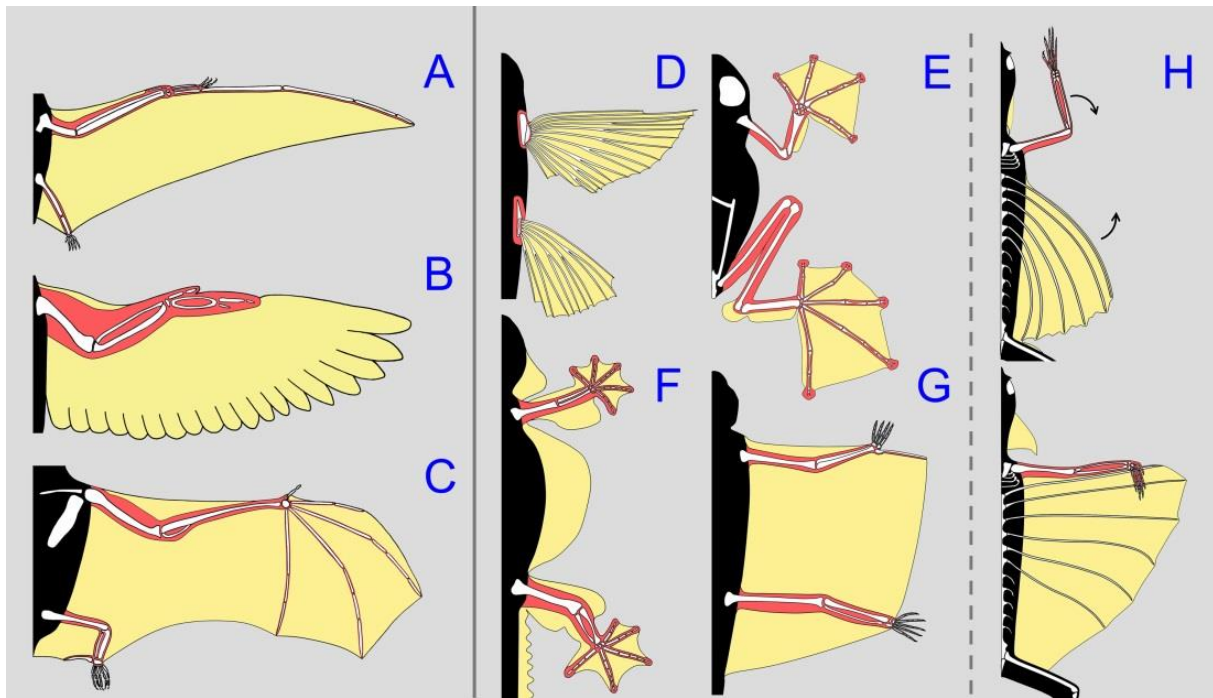
264 **Figure 1.** Gliding specimens of *Draco dussumieri*. A, B, in mid-flight; note the attachment of the arms
265 to the leading edge of the patagium and the marked adduction of the wrists. C, formation of the
266 composite wing during the initial phases of the gliding flight of *Draco dussumieri* seen from the front
267 (left) and from below (right; corresponding photos of the same phases). The lizard jumps from the
268 tree, reorients the body dorsoventrally and starts to spread the anterior ribs; the extended arms
269 reach behind the back (top). The anterior ribs are further spread by the trunk musculature; the hands
270 grasp the leading edge of the patagium and pull it forward (middle). The patagium is fully extended
271 and controlled by the forelimbs; the glide path becomes more horizontal (bottom). White arrows
272 indicate the positions of the hands.



273

274 **Figure 2.** *Draco dussumieri* during takeoff jump (top) and during gliding flight (bottom). Note the
275 cambered shape of the patagium and the arching of the back when the patagium is extended
276 (bottom), in comparison to the straight back during takeoff with furled patagium (top).

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278

279 **Figure 3.** Wings and patagia of vertebrate groups with flapping (A–C) and gliding flight (D–H). Colours
280 mark the major aerodynamic surfaces (yellow) and the skeletal and muscular structures that control
281 them (red). A, pterosaur (*Rhamphorhynchus*, extinct); B, bird (*Columba*); C, bat (*Phyllostomus*); D,
282 flying fish (*Hirundichthys*); E, flying frog (*Rhacophorus*); F, parachuting gecko (*Ptychozoon*); G, flying
283 squirrel (*Petaurista*); H, flying lizard (*Draco*). In *Draco* lizards, the controlling unit is connected to the
284 lift-generating surfaces only for the duration of the flight.