

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

2

3 J. Maximilian Dehling<sup>1,\*</sup>

4

5 <sup>1</sup> IfIN, Department of Biology, Zoology Group, University of Koblenz-Landau, Universitätsstraße 1, D-  
6 56070 Koblenz, Germany.

7

8 \* Corresponding author: E-mail: [dehling@uni-koblenz.de](mailto:dehling@uni-koblenz.de)

9

10

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.

91

## 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.

#### 184 ACKNOWLEDGEMENTS

185 I am grateful to R. Rao, D. Bhaire, A. Giri and colleagues at the Agumbe Rainforest Research Station  
186 for their help during my stay. W. Böhme (ZFMK) kindly provided access to material under his care.



187

188 REFERENCES

189 Colbert E. H. (1966) A gliding reptile from the Triassic of New Jersey. *American Museum Novitates*  
190 2246: 1–23.

191 Colbert E. H. (1967) Adaptations for gliding in the lizard *Draco*. *American Museum Novitates* 2283: 1–  
192 20.

193 Colbert E. H. (1970) The Triassic gliding reptile *Icarosaurus*. *Bulletin of the American Museum of*  
194 *Natural History* 143: 85–142.

195 Decramer M., Kelly S. & de Troyer A. (1986) Respiratory and postural changes in intercostal muscle  
196 length in supine dogs. *Journal of Applied Physiology* 60: 1686–1691.

197 Dudley R., Byrnes G., Yanoviak S. P., Borrell B., Brown R. M. & McGuire J.A. (2007) Gliding and the  
198 functional origins of flight: biomechanical novelty or necessity? *Annual Review of Ecology,*  
199 *Evolution, and Systematics* 38: 179–201.

200 Emerson S. B. & Koehl M. A. R. (1990) The interaction of behavioral and morphological change in the  
201 evolution of a novel locomotor type: “Flying” frogs. *Evolution* 44: 1931–1946.

202 Fraser N. C., Olsen P. E., Dooley A. C. & Ryan T. R. (2007) A new gliding tetrapod (Diapsida:  
203 ?Archosauromorpha) from the upper Triassic (Carnian) of Virginia. *Journal of Vertebrate*  
204 *Paleontology* 27: 261–265.

205 Frey E., Sues H. D. & Munk W. (1997) Gliding Mechanism in the Late Permian reptile *Coelurosauravus*.  
206 *Science* 275: 1450–1452.

207 Günther A. C. L. G. (1872) On the reptiles and amphibians of Borneo. *Proceedings of the Zoological*  
208 *Society of London* 1872: 586–600.

209 Hairstone N. G. (1957) Observations on the behavior of *Draco volans* in the Philippines. *Copeia* 1957:  
210 262–265.

211 John K. O. (1967) Observations on the mating behaviour and copulation in *Draco dussumieri* Dum. &  
212 Bib. (Reptilia: Sauria). *Journal of the Bombay Natural History Society* 64: 112–115.

- 213 John K. O. (1970) On the 'patagial musculature' of the South Indian flying lizard *Draco dussumieri*,  
214 Dum & Bib. *British Journal of Herpetology* 4: 161–168.
- 215 Lee C. (2015) On the wings of dragons. Online article published 14 January 2015, available at  
216 <http://www.wildborneo.com.my/blog/> (last accessed 8 November 2016).
- 217 Li P. P., Gao K. Q., Hou L. H. & Xu X. (2007) A gliding lizard from the early Cretaceous of China.  
218 *Proceedings of the National Academy of Sciences U.S.A.* 104: 5507–5509.
- 219 Lingham-Soliar T. (2015) *The vertebrate integument, volume 2: Structure, design and function*. Berlin  
220 & Heidelberg: Springer.
- 221 Maindron M. M. (1890) Dragons, fabled and real. *Popular Science Monthly* 36: 808–813.
- 222 Marsden W. (1811) *The history of Sumatra, containing an account of the government, laws, customs*  
223 *and manners of the native inhabitants. Third edition*. London: The author, J. M'Creery, Black-Court  
224 and Longman, Hurst, Rees, Orme, and Brown, Paternoster-Row.
- 225 McGuire J. A. (2003) Allometric prediction of locomotor performance: An example from Southeast  
226 Asian flying lizards. *The American Naturalist* 161: 337–349.
- 227 McGuire J. A. & Dudley R. (2005) The cost of living large: Comparative gliding performance in flying  
228 lizards (Agamidae: *Draco*). *The American Naturalist* 166: 93–106.
- 229 McGuire J. A. & Dudley R. (2011) The biology of gliding in flying lizards (genus *Draco*) and their fossil  
230 and extant analogs. *Integrative and Comparative Biology* 51: 983–990.
- 231 Mori A. & Hikida T. (1993) Natural history observations of the flying lizard, *Draco volans sumatranus*  
232 (Agamidae, Squamata) from Sarawak, Malaysia. *Raffles Bulletin of Zoology* 41: 83–94.
- 233 Norberg U. M. (1990) *Vertebrate flight*. Berlin: Springer.
- 234 Ratnovsky A., Elad D. & Halpern P. (2008) Mechanics of respiratory muscles. *Respiratory Physiology &*  
235 *Neurobiology* 163: 82–89.
- 236 Robinson P. L. (1962) Gliding lizards of the Upper Keuper of Great Britain. *Proceedings of the*  
237 *Geological Society of London* 1601: 137–146.
- 238 Russell A. P. & Dijkstra L. D. (2001) Patagial morphology of *Draco volans* (Reptilia: Agamidae) and the  
239 origin of glissant locomotion in flying dragons. *Journal of Zoology* 253: 457–471.

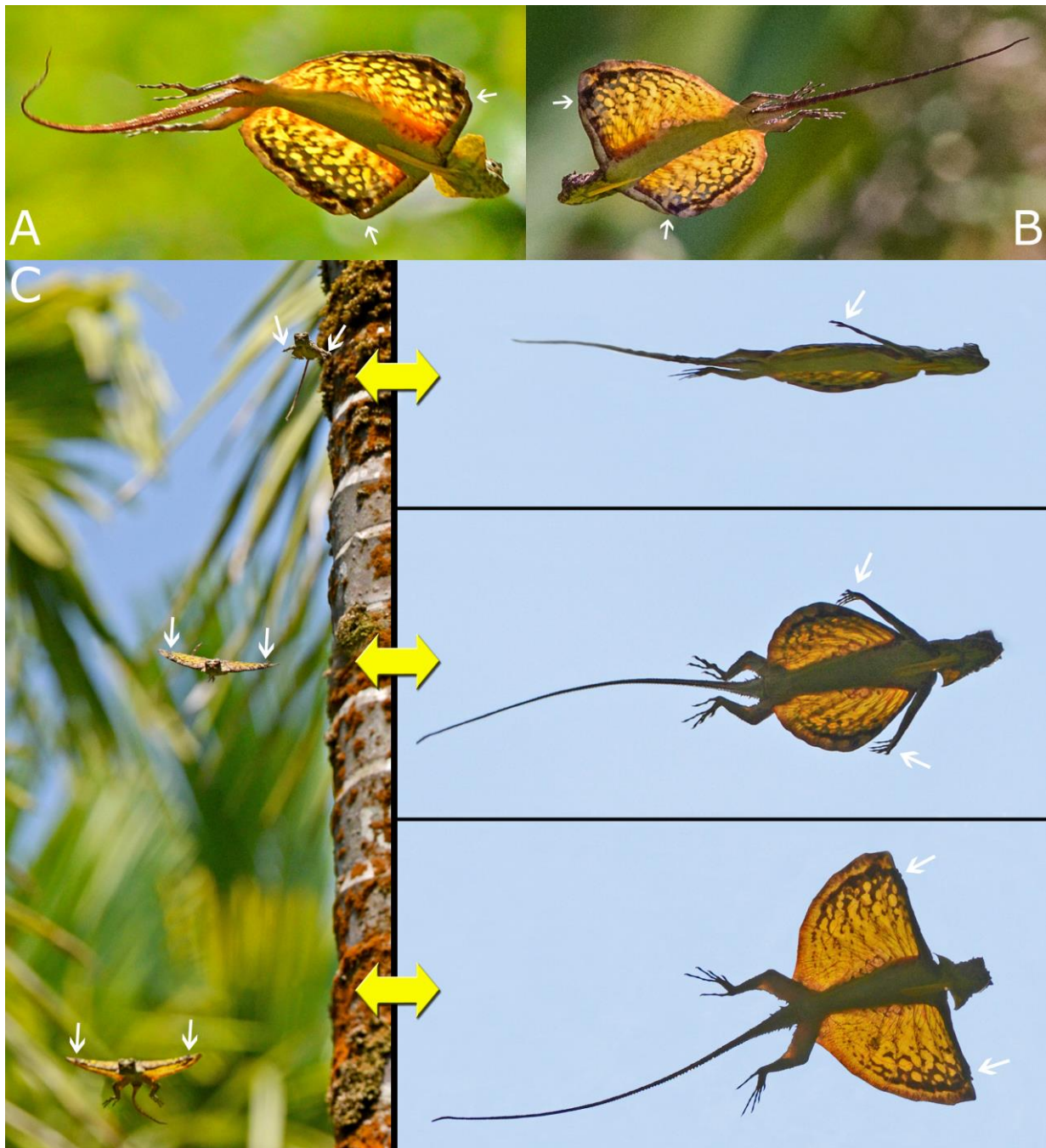
- 240 Seba A. (1734) *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus*  
241 *artificiosissimis expressio, per universam physices historiam. Cui, in hoc rerum genere, nullum par*  
242 *exstitit. Ex toto terrarum orbe collegit, digessit, descripsit, et depingendum curavit. Tomus I.*  
243 Amstelaedami: J. Wetstenium, & Gul. Smith, & Janssonio-Waesbergios.
- 244 Socha J. J., Jafari F., Munk Y. & Byrnes G. (2015) How animals glide: from trajectory to morphology.  
245 *Canadian Journal of Zoology* 93: 901–924.
- 246 Stein K., Palmer C., Gill P. G. & Benton M. J. (2008) The aerodynamics of the British late Triassic  
247 Kuehneosauridae. *Palaeontology* 51: 967–981.
- 248 Vanhooydonck B., Meulepas G., Herrel A., Boistel R., Tafforeau P., Fernandez V. & Aerts P. (2009)  
249 Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis*  
250 *guentheri*. *Journal of Experimental Biology* 212: 2475–2482.
- 251 Whitelaw W. A., Ford G. T., Rimmer K. P. & de Troyer A. (1992) Intercostal muscles are used during  
252 rotation of the thorax in humans. *Journal of Applied Physiology* 72: 1940–1944.
- 253 Yanoviak S. P., Dudley R. & Kaspari M. (2005) Directed aerial descent in canopy ants. *Nature* 433:624–  
254 626.
- 255 Young B. A., Lee C. E. & Daley K. M. (2002) On a flap and a foot: Aerial locomotion in the “Flying”  
256 Gecko, *Ptychozoon kuhli*. *Journal of Herpetology* 36: 412–418.

257

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

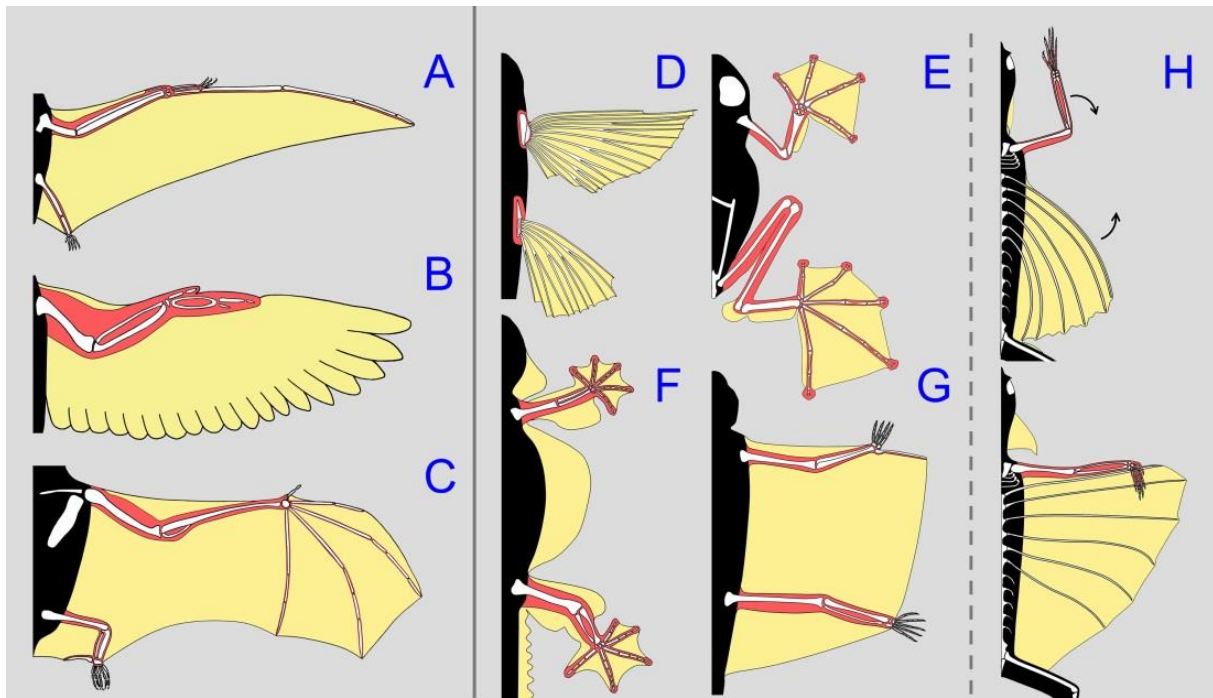
264 **Figure 1.** Gliding specimens of *Draco dussumieri*. A, B, in mid-flight; note the attachment of the arms  
265 to the leading edge of the patagium and the marked adduction of the wrists. C, formation of the  
266 composite wing during the initial phases of the gliding flight of *Draco dussumieri* 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).

277



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.