1	Adaptive shifts underlie the divergence in wing morphology in bombycoid moths
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38 ABSTRACT

39 The evolution of flapping flight is linked to the prolific success of insects. Across Insecta, wing 40 morphology diversified, strongly impacting aerodynamic performance. In the presence of ecological opportunity, discrete adaptive shifts and early bursts are two processes hypothesized 41 to give rise to exceptional morphological diversification. Here, we use the sister-families 42 43 Sphingidae and Saturniidae to answer how the evolution of aerodynamically important traits is 44 linked to clade divergence and through what process(es) these traits evolve. Many agile 45 Sphingidae evolved hover-feeding behaviors, while adult Saturniidae lack functional mouth 46 parts and rely on a fixed energy budget as adults. We find that Sphingidae underwent an 47 adaptive shift in wing morphology coincident with life history and behavior divergence, evolving small high aspect-ratio wings advantageous for power reduction that can be moved at high 48 49 frequencies, beneficial for flight control. In contrast, Saturniidae, which do not feed as adults, 50 evolved large wings and morphology which surprisingly does not reduce aerodynamic power, 51 but could contribute to their erratic flight behavior, aiding in predator avoidance. We suggest that after the evolution of flapping flight, diversification of wing morphology can be potentiated 52

by adaptative shifts, shaping the diversity of wing morphology across insects.

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57 **INTRODUCTION**

58 The evolution of flight is thought to be a key innovation [1] foundational to the success of 59 insects, one of the most speciose clades of animals on Earth. In flying insects, flight is critical for 60 most aspects of life history including dispersal, migration, predator avoidance, feeding, and courtship behaviors. The flight morphology of flying insects, therefore, likely faces strong 61 62 selective forces to meet the functional demands of a species [2, 3]. Selection can act on flight 63 morphology to significantly impact flight performance [4]. Indeed, flying insects show an extraordinary diversity of wing and body sizes and shapes [2, 5, 6]. Revealing the phylogenetic 64 65 patterns of insect flight morphology and the processes driving its evolution is a prime 66 opportunity to examine how the evolution of aerodynamically important traits is linked to the 67 divergence of diverse clades.

68 Clade divergence and the subsequent diversification of lineages and morphology can occur through different evolutionary processes. In the presence of an ecological opportunity, 69 70 the tempo of trait evolution can accelerate and its mode can deviate from a random Brownian 71 Motion (BM) process, the null model of trait evolution. Early bursts [7-9] and discrete 72 adaptative shifts [10-12] are two alternative processes hypothesized to give rise to exceptional 73 morphological diversity. An early burst is associated with the adaptative radiation of a clade 74 where morphological disparity is established early and followed by a subsequent slowdown in 75 diversification rate [8, 9]. Adaptive shifts are when discrete shifts occur along a single branch 76 and are not followed by a slowdown in diversification rate [10-12]. Traits with known functional 77 consequences (e.g. wing morphology) are more likely to reflect the ecology of a species [13], and therefore are more likely to be associated with non-BM processes when ecologically 78

distinct clades evolve. Therefore, testing if insect wing and body morphology evolution deviates
from BM and shifts in tandem with life history and behavior will demonstrate the evolutionary
processes driving morphological diversification as clades diverge to occupy different biological
niches.

83 Wing size and shape, as well as body size have known aerodynamic consequences for 84 maneuverability, force production, and power requirements. Nearly any aspect of shape can 85 affect aerodynamics, but several metrics of wing morphology are common predictors of flight performance, notably wing loading (W_s) , aspect ratio (AR), and radius of the second moment of 86 area (\hat{r}_2) . A lower W_s , the ratio between body mass (m_t) and wing area (S), typically enhances 87 88 maneuverability, increasing the wing force production to body mass ratio, as seen in birds [14-89 16], bats [17-19], and moths and butterflies [20, 21]. Larger AR wings (long, slender) can reduce 90 the power requirements of flight [6, 19, 22], but can also reduce maneuverability [3, 21, 23]. High \hat{r}_2 wings will have more area concentrated distally, which increases force production 91 92 because more of the wing is moving more quickly. But high \hat{r}_2 can increase power 93 requirements and reduce maneuverability [24]. Finally, interspecific variation in wing and body 94 morphology will have direct consequences for wing beat frequency (n) [6, 25]. An increase in n 95 increases active force generation [26], but at the cost of increasing inertial power (P_{acc}), the 96 power required to oscillate the wing mass [27]. 97 The moth superfamily Bombycoidea provides an opportunity to test hypotheses related to the evolution of flight morphology within closely related, but divergent clades. Bombycoidea 98 99 is a globally distributed, diverse clade of more than 5,000 species [28]. The most diverse 100 families in the Bombycoidea are hawkmoths and wild silk moths (Sphingidae and Saturniidae,

101	respectively); sister families [29-31] of strikingly different life histories and flight behaviors.
102	Hawkmoths are active, fast flyers [32] known for their maneuverability and hover feeding
103	behavior [33, 34], where species can successfully track flower oscillations up to 14 Hz [33, 34].
104	However, hovering requires a high power output [35]. Wild silk moths (here forth "silkmoths")
105	display a flight behavior that is often described as bobbing or erratic, but fast and agile when
106	escaping from predators [32, 36-38]. Silkmoths lack functional mouth parts and must rely on
107	the strictly finite energy stores, gathered during the larval period, throughout their entire,
108	albeit short, reproductive adult life stage [38]. The divergence in life history and flight behavior
109	between hawkmoths and silkmoths represent different niches, and would be expected to have
110	correlated changes in flight morphology.
111	Here, we focus on the hawkmoths and silkmoths to test if each clade has evolved
112	distinct flight morphology and determine what evolutionary processes led to extant
113	morphological disparity. We hypothesize that hawkmoths evolved morphology favorable for
114	maneuverability in order to rapidly track flower movements during hover feeding, while
115	silkmoths evolved morphology favorable for power reduction in order to conserve limited
116	energy as adult stage silkmoths do not feed. We next examine the morphological disparity
117	through time (DTT) and compare different models of trait evolution to determine the processes
118	that led to the diversity of extant flight morphology. We hypothesize that the distinct
119	transitions in life history and flight behavior between hawkmoths and silkmoths were
120	accompanied by distinct adaptive shifts in flight morphology.

123 MATERIALS AND METHODS

124	We created a time-calibrated Bombycoidea phylogeny, sampling representatives of all families,
125	following published methods [31]. In total, the phylogenetic dataset of 606 loci included 57
126	species and one outgroup. The tree was inferred using a maximum likelihood approach and
127	time calibrated based on the dates of corresponding nodes in a recently published Lepidoptera
128	phylogeny that relied on 16 fossil calibrations with uniform priors and uncorrelated rates [30].
129	

130 Morphometrics

131 Body and wing morphology was digitized from museum images using StereoMorph 132 (V1.6.2) [39]. Male specimens were analyzed when available (53 of 57 species); males are 133 known to exhibit higher flight activity in comparison to females [5, 40]. Eight landmarks 134 characterized the body; Bézier curves outlined the right forewing and hindwing (Fig. S1). 135 Wing measurements for all species began by re-orienting each wing to a comparable 136 orientation consistent with known flight position. The forewing was rotated so its long axis was 137 perpendicular to the long axis of the body. In Sphingidae, the hindwing long axis was also 138 rotated perpendicular to the long axis of the body; the approximate orientation during flight. 139 The hindwing of Saturniidae and the "other bombycoid families" were kept in the same 140 orientation of dried museum specimens, which is the approximate orientation during flight and 141 provides a consistent and comparable orientation across species. A combined wing outline was 142 created from the non-overlapping portions of the rotated forewing and hindwing, resampled to 143 generate 75 evenly spaced points.

144	Analysis of wing shape traits was conducted in Matlab (R2018b–9.5.0.944444). Wing
145	parameters (R , $ar{c}$, S , AR, \hat{r}_2 , and W_s) were calculated following Ellington [24]. n was estimated
146	from morphology [25].
147	
148	Phylogenetic comparisons
149	A phylogenetic principal components analysis (pPCA) [41] was conducted on forewing,
150	hindwing, and combined shapes. The dominant pPC axes for wing shape were determined using
151	the broken stick method implemented in the bsDimension function of the PCDimension R
152	package V 1.1.11 [42].
153	For each trait, we performed a disparity through time (DTT) analysis [8] (1000
154	simulations); a maximum likelihood estimation of the presence of shifts and their positions
155	using PhylogeneticEM [43]; and compared the fit of 10 different models of trait evolution using
156	mvMORPH [44]. These analyses were conducted in RStudio (V1.1.383) using R (V4.0.2).
157	Unabridged methods are supplementary material. See Table S1 for list of all variables and
158	derivation. Data is available on Dryad [45].
159	
160	RESULTS
161	Phylogeny
162	Phylogenetic relationships of the 57 species in this study show a monophyletic, well-supported
163	clade of the Sphingidae and Saturniidae as sister-lineages, with the Bombycidae as the sister to
164	those two (Fig. 1A; S2). Relationships are congruent with previous studies [29, 31, 46, 47].
165	

166 Hawkmoths and silkmoths each have diverse, but clustered wing shapes in morphospace. 167 We first used a phylogenetic principal components analysis to assess the variation in extant wing shape in a data-driven, evolutionary framework. For all three wing shapes (forewing, 168 169 hindwing, and combined), most of the variation is explained by the first two pPC axes (Fig. 1B-E; 170 Table S2); pPC three or four explained no more than 14% of the variation (Fig. S3A-D; Table S2). 171 Hindwing and combined wing morphospaces capture the evolution of hindwing tails in some 172 silkmoth species, but hawkmoths and silkmoths remain clustered (Fig. 1C-D). When tailed species (#1, 2, 3, 4, 20, 28) are removed (Fig. 1B), families remain clustered in combined-wing 173 shape space; variation along pPC1 generally corresponds to AR. 174 175 The wing shapes of hawkmoths and silkmoths are well separated in morphospace. We conducted a MANOVA on each wing shape; pPC1-4 scores were the response variables and 176 177 clade (hawkmoth; silkmoth; Other Bombycoid Families, abbreviated O.B.) was the factor. Each wing shape is significantly separated between clades (Forewing: F=14.91, $p < 10^{-13}$; hindwing: 178 F=10.84, $p<10^{10}$; combined wing: F=14.96, $p<10^{13}$). Separation persists when considering only 179 hawkmoths and silkmoths (Forewing: F=44.42, $p < 10^{-14}$; hindwing: F=10.84, $p < 10^{-10}$; combined 180 wing: F=101.17, $p<10^{-15}$), and for the combined wing when tailed silkmoths are removed from 181 the analysis (All families: F=16.19, $p<10^{-13}$; hawkmoths-vs-silkmoths: F=144.06, $p<10^{-15}$). 182



184 Figure 1. The evolution and trajectory of wing shape diversity.

185 (A) The phylogenetic relationships of bombycoids and outgroups (node labels in Fig. S2B).

186 O.B. refers to Other Bombycoid families (the name we give to all long-branched species that do

187 not belong to either the Saturniidae or Sphingidae clades). Clade color is consistent across

188 figures. Projections of shapes from (B) combined wing without tails, (C) forewing, (D) hindwing,

and (E) combined wing onto the first two pPCs demonstrates the separation between extant

190 hawkmoths and silkmoths (pPC 3 and 4 and species number key in Fig. S3). (F) Wing size and (G)

191 combined wing functional shape metrics also diverge between hawkmoths and silkmoths.

192

193 Wing area is greater in silkmoths than hawkmoths

194 In addition to shape, we determined if wing size is larger for a given body size between the two

195 clades. We conducted a linear regression between S and m_t (Fig. 1F), constraining the y-

intercept for each family to zero (Hawkmoths: r^2 =0.90, F=234.4, p<10⁻¹³; Silkmoths: r^2 =0.75,

197 F=66.8, $p < 10^{-7}$). An ANCOVA with family as a factor reveals significant differences in regression

198 slope (F=8.732, p=0.0005), indicating wing area is larger for a given body size in silkmoths than

199 hawkmoths. Next, before accounting for phylogeny, the relative wing area of each species

200 (S/m_t) is significantly different between hawkmoths and silkmoths (2-tailed t-test, $p < 10^{-9}$). A

201 comparison of absolute wing area between the clades reinforces these differences (Fig. 1F,G;

202 S4A,B).

203

204 Aerodynamic features of the wing and body also separate between clades

205 To complement the data-driven pPCA and relate variation in wing and body shape and size to

206 aerodynamic metrics, we next quantified several specific morphological variables:

207 nondimensional radius of second moment of area (\hat{r}_2) , aspect ratio (AR), wing loading (W_s) , and

208 the fraction of body length occupied by the abdomen (\hat{l}_{abd}) and thorax (\hat{l}_{tho}) . Before

accounting for phylogeny, combined wing AR, W_s , and \hat{r}_2 are all significantly greater in

210 hawkmoths than in silkmoths (Fig. 1G; Table S3). Finally, while variation in total body length $(l_{\rm h})$ 211 spans a similar range within each family, clade average \hat{l}_{abd} is significantly longer in hawkmoths than silkmoths and \hat{l}_{tho} is generally greater in silkmoths than in hawkmoths (Table S3). To 212 213 further ensure these multiple comparisons did not bias our statistics, we conduct a separate MANOVA of the wing (\hat{r}_2, AR, W_s) and body $(\hat{l}_{abd}, \hat{l}_{tbo})$ traits between hawkmoths and 214 215 silkmoths and, in both cases, find significant separation between the clades (wing: F=107.15, $p < 10^{-15}$; body: F=11.432, $p < 10^{-5}$). 216 217 218 Wing beat frequency diverges between hawkmoths and silkmoths. 219 Wing beat frequency (n) is also an important feature of flight that depends on wing and body 220 size. n, estimated from scaling relationships (Table S1; Deakin, 2010), is distinct from wing 221 shape, but not independent of wing and body size (total body mass, m_t , and the mass of the 222 wing pair, m_w , were estimated from museum specimens; see supplemental Fig. S6; Table S5). 223 Based on morphological differences, n is significantly greater in hawkmoths (n: mean±SD: 224 29.37±9.89 Hz) compared to silkmoths (*n*: mean±SD: 14.34±5.21Hz, *p*<0.0001; Table S3). 225 226 Relative subclade disparity through time (DTT) shows both an early and recent accumulation of 227 morphological diversity 228 A DTT analysis determines how morphological disparity accumulated over time. The relative 229 subclade disparity of each shape is similar through time. Early in evolutionary history, relative 230 subclade disparity is less than expected by BM for all three wings; the lowest values fall just 231 inside the 95% confidence interval of BM trait simulation at the point when hawkmoths and

silkmoths split (~66 MYA; Fig. 2A-C). From that time, subclade disparity remained relatively

233	static until sharply and significantly rising above BM expectations \sim 38 MYA (Fig. 2A-C),
234	indicating younger subclades evolved a greater proportion of modern disparity than expected
235	under BM. Removing tailed species from the analysis produces a similar result, but the rise in
236	relative subclade disparity above the BM expectation now occurs more recently (Fig. S4C). The
237	DTT of combined wing metrics ($W_s,n,S/m_t$) follow similar patterns (Fig. 2D-H), with the
238	exception of \hat{r}_2 (Fig. 2E). Notably, relative subclade disparity of AR significantly deviates below
239	the BM expectation coincident with the divergence of the two sister-clades (Fig. 2D). Again, at
240	approximately 38 MYA, the disparity of these wing traits begins to rise above the BM
241	expectation, but only S/m_t and W_s significantly rise above the expectation under a BM process
242	(Fig. 2F-G). A multivariate DTT of normalized functional wing metrics reveals a similar overall
243	trend (Fig. S5).
244	As relative subclade disparity shifts from consistently low values below the BM
245	expectation to high values above the BM expectation in recent evolutionary history,
245 246	expectation to high values above the BM expectation in recent evolutionary history, morphological disparity index (MDI) values for each trait are near zero and not statistically
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255

256 Figure 2. Disparity through time reveals that wing morphology diverged early between the 257 clades and additional variation accumulated within each clade in more recent time. 258 In each panel, the dashed line represents the median simulated subclade disparity under a 259 single rate BM process and includes the 95% confidence interval in grey. The observed relative 260 subclade disparity is presented as a solid black line. All traits other than show a similar trend in relative subclade disparity with low values deviating below the BM expectation in the early 261 evolutionary history of the clade and high values in recent time. The low values in the early 262 263 history of the clade indicate the disparity between clades was established early and the high 264 values in recent history indicate disparity within each clade was established in more recent 265 time. The brown vertical dashed line represents the time at which hawkmoths and silkmoths 266 split. 267

268 Adaptive shifts account for differences in the evolution of several traits of wing morphology. 269 Next, we tested whether an adaptive shift is responsible for the divergence in wing shape and 270 its associated traits between hawkmoths and silkmoths without *a priori* hypotheses of shift 271 location(s). We found support for an adaptive shift at the ancestral node of the hawkmoth 272 clade for combined wing shape, AR, and $W_{\rm s}$ (Fig. 3A-C). More recent adaptive shifts also 273 occurred for combined wing shape, W_s , \hat{r}_2 , S/m_t , and n (Fig. 3A-F). The recent adaptive shifts in 274 silkmoth combined wing shape are associated with the independent tail evolutions (Fig. 3A). 275 The recent adaptive shift for n occurs in the hawkmoth subfamily, Macroglossinae, known for 276 its particularly high n (Fig. 3F). Adaptive shifts did not occur at the ancestral node for either 277 sister family for combined wing \hat{r}_2 , S/m_t , or n. In the absence of an adaptive shift, a trait can 278 still have diverged between the sister-clades through other evolutionary processes. However, a 279 single adaptive shift is inferred at the ancestral hawkmoth node when all functional 280 (normalized) wing metrics are analyzed together, supporting the findings that hawkmoth wing 281 morphology undergoes an adaptive shift (Fig. S5). 282 283 Wing morphology does not evolve under a single-rate Brownian motion process 284 Next, we determined which model best fit the evolution of combined wing shape and its 285 associated morphological features. For all traits, the model representing the adaptive shifts 286 detected in the PhylogeneticEM analysis always fit best (Table S7). However, an adaptive shift was not detected in the previous analysis at the node for either sister family for \hat{r}_2 , S/m_t , or n, 287 288 and this study is focused on the sister-clade divergence; the absence of an adaptive shift is

289 likely due to the complex selective pressures on these traits that depend on both body and

290 wing morphology.



291

292 Figure 3. An adaptive shift is responsible for divergence in wing shape (A), aspect ratio (B), and 293

wing loading (C) between hawkmoths and silkmoths. Each branch color indicates a separate

294 regime (a set of branches evolving under a different set of model parameters). All branches 295 sharing the same color also share the same evolutionary mode. Shifts to new regimes are

296 indicated by dots. For univariate traits, red dots indicate shifts to a larger trait value optima and

- 297 blue dots indicate shifts to a smaller trait value. Black dots are used for shifts in multivariate
- 298 traits, but do not indicate a direction.

299

300 **DISCUSSION**

301	Flight morphology can have a strong influence on the aerodynamic performance of flying
302	animals. We find that early in the evolutionary history of the moth superfamily Bombycoidea,
303	wing shape and size were generally conserved until the ancestors of the hawkmoth and
304	silkmoth sister clades rapidly diverged (Fig. 3A-C), which is consistent with the early
305	establishment of morphological disparity between clades (Fig. 2).
306	The evolutionary split between these two families has been dated to have occurred
307	approximately 66 (confidence interval: 56.9 to 75.4) million years ago [30], suggesting that
308	these wing morphology trajectories may have been evolving since then. The initial divergence
309	in wing morphology between hawkmoths and silkmoths was followed by subsequent
310	diversification within each group, indicated by the rise in relative subclade disparity above a BM
311	expectation coinciding with the more recent speciation events occurring within each family (Fig.
312	2). However, despite recent diversification, wing morphology did not converge between the
313	two sister-families, indicated by the strong separation between the families in phylogenetic
314	morphospace (Fig. 1).

Even specific species that converged in life history did not fully converge to employ overlapping wing shapes. For example, while the majority of hawkmoths are known for their hovering nectaring behavior as adults, members of the hawkmoth subfamily, Smerinthinae (Node 67; Fig. 1A, S2B), have lost the ability to feed as adults [38], convergent with silkmoths. However, the combined wing morphology (shape, size, and most associated traits) of Smerinthinae species (Node 67 in Fig. S2B) remains divergent from silkmoths, implying that Smerinthinae wing morphology is constrained by its evolutionary history. Finally, while we

chose species to broadly cover the groups within bombycoids, sampling is far from complete.
Therefore, we remain conservative in our interpretation, focusing on the split between
hawkmoths and silkmoths for which we were able to accumulate broad sampling for our
analysis. In sum, these data provide phylogenetic evidence supporting our hypothesis that
distinct flight morphology evolved in each sister clade.

327

328 The evolutionary divergence of wing morphology has implications for flight performance.

329 Given that the hawkmoth and silkmoth clades diverged in wing morphology, we can 330 explore the consequences of these two morphologies for flight performance. While flight 331 performance depends on many other factors, most notably wing movement, shape and size do 332 have implications for aerodynamics. Contrary to our expectations, we did not observe 333 morphological changes that were consistent with extreme maneuverability in hawkmoths and 334 extreme power reduction in silkmoths. Hawkmoths, known to be maneuverable hover feeders, 335 have evolved small wings of high AR, W_s , and \hat{r}_2 ; all metrics typically associated with power 336 reduction, efficient force production, and lower degrees of maneuverability. In contrast, 337 silkmoths, a group that does not feed as adults and is known for its bobbing (erratic) flight 338 behavior, have evolved large wings of low AR, W_s , and \hat{r}_2 .

339

340 Hawkmoth wing morphology likely reduces power without sacrificing maneuverability

The high AR and \hat{r}_2 wings of hawkmoths might act to reduce power and increase force production efficiency while *not* sacrificing maneuverability in comparison to silkmoths that are employing wings of lower AR and \hat{r}_2 . All else being equal, high AR and \hat{r}_2 wings will reduce the

344	induced power (P_{ind}) requirements of flight [6, 19, 22] and increase force production efficiency
345	[5, 48, 49], respectively. However, both traits could come at the cost of reduced
346	maneuverability due to an increase in the moments of inertia of the wing pair [3, 5, 6, 21, 23].
347	For a wing of constant area, uniform thickness, and density, a larger AR and $\widehat{r_2}$ will necessarily
348	make the wing longer (increasing AR) while also concentrating more area distally along the
349	span of the wing (increasing $\widehat{r_2}$). Both scenarios correspond to an increase in wing moments of
350	inertia, suggesting silkmoths should be more maneuverable than hawkmoths [5, 24]. However,
351	wing size will also have a strong impact on wing moment of inertia, and silkmoths have evolved
352	larger wings (per body size) than hawkmoths (Fig. 1F-G; Table S3). Hawkmoths evolved high AR
353	by reducing mean chord length, $ar{c}$, rather than through an increase in wing span, R (Fig. 1B;
354	Table S4). Therefore, while selection for economical flight (increased AR) might often reduce
355	maneuverability, the evolution of small, high AR wings in the hawkmoth clade (achieved
356	through a reduction in $ar{c}$) could act to increase economy while not necessarily sacrificing
357	maneuverability.
358	The potential cost of small wing size is that proportionally smaller wings could reduce
359	wing stroke-averaged aerodynamic force production, if wing movement remains constant.
360	However, in flapping or revolving wings, when all other things are equal, the greater $\widehat{r_2}$ and n
361	(inferred through scaling relationships) of hawkmoths would increase their magnitude of
362	torque production relative to silkmoths. The velocity of a wing section increases with its
363	distance from the axis of rotation, and aerodynamic force production is proportional to velocity

squared. Therefore, shifting more area distally (increasing \hat{r}_2) and moving the wing at higher

speeds (increasing *n*) will increase aerodynamic force production [e.g. 26, 48, 49]. Additionally,

366 increasing n allows for more frequent modification of force vectors, which could enhance flight 367 control and maneuverability. Natural selection could thus act on wing shape, size, and 368 frequency (tradeoffs through scaling relationships) to modify the means of force production. 369 power, and flight control across species. 370 371 Lower wing loading (W_s) in silkmoths could contribute to maneuverability and erratic flight 372 It is possible that inter-clade differences in W_s contribute to inter-clade differences in 373 flight behavior between families. A lower W_s increases both maneuverability [14-21] and flight 374 path unpredictability [50]. Silkmoths, which evolved significantly lower W_s in comparison to 375 hawkmoths (Fig. 1G, Table S3), are well known for their erratic flight patterns [32, 38] where 376 vertical position is regularly changing throughout their flight bout. An erratic, or unpredictable 377 flight path, can enhance predator avoidance [15, 51], and therefore, survival and fitness. In hummingbird flight, positional predictability and W_s are positively correlated where 378 379 hummingbirds with lower wing loading are less predictable [50]. If the relationship between W_s and predictability is true in other systems, then the divergence in W_s between hawkmoths and 380 381 silkmoths is precisely the expectation based on the divergence in flight behavior between the 382 two clades. Therefore, it's likely that evolution of silkmoth wing morphology, particularly low 383 W_s , is directly tied to the production of erratic flight patterns and the ability to avoid predation. 384 385 Body shape evolution might aid predator avoidance in silkmoths 386 Next, we examined the implications of body size evolution for flight performance. In

387 comparison to hawkmoths, silkmoths have a shorter l_b and a longer thorax compared to the

388	abdomen, thereby decreasing I_{yy} and I_{zz} of the body and likely increasing maneuverability.
389	These patterns could allow silkmoths greater angular accelerations during pitch and yaw
390	maneuvers and might be complemented by a reduction in the distance between the center of
391	mass and wing hinge [52]. Indeed, species of neotropical butterflies equipped with a shorter
392	abdomen and larger thorax were more successful at evading predators than species with
393	shorter thoraces and longer abdomens [52]. Therefore, in addition to wing elaborations [32, 38,
394	46] and bobbing flight behavior [32, 36-38], our data suggest that the evolution of a large
395	thorax and short abdomen is an additional mechanism contributing to predator avoidance in
396	silkmoths.
397	
398	Adaptive shifts are responsible for the divergence in wing morphology between hawkmoths and
399	silkmoths
400	An adaptive shift Is found at the stem of hawkmoths for both wing shape, AR, and $W_{\!s}$ (Fig. 3A-
401	C), indicating that the shape and relative size of hawkmoth wings are evolving around an
402	adaptive peak. Although disparity was established early in the evolutionary history of the clade
403	(Fig. 2), rather than slow down in diversification rate, which would occur in an early burst [8, 9],
404	the initial divergence in life history and flight morphology gives rise to the accumulation of
405	additional disparity within each clade in recent time (Fig. 2). Indeed, the recent accumulation of
406	disparity within a subclade is associated with evolution around an adaptive peak [53], and the
407	absence of evidence for an early burst in the diversification of wing morphology is consistent
408	with major inter-continental radiations in other systems [7, 10, 11].

409 The discrete adaptive shift in hawkmoth wing morphology parallels the evolution of the 410 hover feeding behavior in hawkmoths and the loss of adult-stage feeding in silkmoths. The 411 adaptive shift in hawkmoth wing morphology to small, slender wings of high AR that can be 412 moved at high frequencies might be directly related to the evolution of hover feeding, which 413 requires enhanced flight control and high power output [35], as high AR wings are known to 414 reduce flight power requirements [6]. 415 An adaptive shift at the stem of hawkmoths was not found for all wing morphology 416 traits, suggesting a potential decoupling of the processes, and, therefore, selective pressures, 417 driving the evolution of overall wing shape, size, and specific features. It should not be expected that all features of wing morphology evolve under the same process. Wing metrics, like \hat{r}_2 , 418 419 which is related to force production efficiency [24], appear to be more conserved, and those 420 related to both wing and body size, like n and S/m_t , might be under particularly complex 421 selective pressures. 422 Differently, an adaptive shift was never found for any trait at the stem of the silkmoth clade, which could be expected given the less drastic separation in wing morphology traits 423 424 between silkmoths and the other bombycoid families (Fig. 2). In contrast, more recent adaptive 425 shifts were detected and associated with the evolution of hindwing tails in silkmoths (Fig. 3A)

427 through further sampling within these specific groups, it is exciting that they might be indicative

and high n in diurnal hawkmoths (Fig. 3F). While these recent shifts need to be supported

428 of recent shifts in flight morphology within these clades, providing a potential opportunity to

429 identify specialized species or subclades for future functional studies in live animals.

426

430	The overall combined wing morphology is derived from two functionally linked and
431	overlapping wing structures (forewing and hindwing) that can each potentially evolve
432	independently in size and shape, unlocking additional complexities unachievable by a single
433	wing alone. While forewing and hindwing morphology also diverge between groups, the
434	absolute values of these traits are different between the fore- and hindwing (Fig. S4). Different
435	components of the same functional system often evolve at different tempos and modes [54],
436	raising questions of whether or not certain aspects of wing morphology constitute evolutionary
437	modules. The integration of techniques from developmental and evolutionary biology will be
438	particularly fruitful when investigating the modularity of insect wing units.
439	
440	Conclusion
441	Silkmoths and hawkmoths evolved distinct flight morphology through an adaptive shift
442	in hawkmoth wing morphology, which occurred in parallel to the evolution of the hover feeding
443	behavior in hawkmoths. The sister-clade divergence of wing morphology metrics, which are
444	historically derived for fixed-winged aircrafts, is not totally consistent with initial expectations
445	of flight performance based on the life history of species in each clade. However, aerodynamic
446	performance emerges from the interaction of wing shape, size, and movement [6, 55], and it is
447	likely that hawkmoths achieve high levels of flight control through high n and other kinematic
448	adjustments. Our findings indicate that aerodynamically important morphological traits can
449	experience drastic shifts in parallel to the divergence in life history and flight behavior. While
450	the evolution of flapping flight in insects is thought to be a key innovation [1], diversification

- 451 can be further potentiated by more recent adaptive shifts, helping to shape the diversity of
- 452 wing morphology seen across extant aerial animals.
- 453

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