

1 An insect-inspired asymmetric hinge in a double-layer membrane

2
3 Hamed Rajabi^{1,2}, Sepehr H Eraghi¹, Ali Khareshi^{1,2}, Arman Toofani¹, Cheryl Hunt³, Robin J
4 Wootton³

5
6 ¹ Mechanical Intelligence (MI) Research Group, BioEngineering Research Centre, School of
7 Engineering, London South Bank University, London, UK

8 ² Division of Mechanical Engineering and Design, School of Engineering, London South
9 Bank University, London, UK

10 ³ Department of Biosciences, University of Exeter, Exeter, UK

11 12 13 **Abstract**

14 Insect wings are deformable aerofoils, in which deformations are mostly achieved by
15 complicated interactions between their structural components. Due to the complexity of
16 the wing design and technical challenges associated with testing the delicate wings, we
17 know little about the properties of their components and how they determine wing
18 response to flight forces. Here we report a novel, previously undescribed structure from
19 the hind wing membrane of the beetle *Pachnoda marginata*. The structure, a transverse
20 section of the claval flexion line, consists of two distinguishable layers: a bell-shaped upper
21 layer and a straight lower layer. Our computational simulations showed that this is an
22 effective one-way hinge, which is stiff in tension and upward bending but flexible in
23 compression and downward bending. By systematically varying its design parameters in a
24 computational model, we showed that the properties of the double-layer membrane
25 hinge can be tuned over a wide range. This enabled us to develop a broad design space,
26 which we later used for model selection. We used selected models in three distinct
27 applications, which proved that the double-layer hinge represents a simple, yet effective
28 design strategy for controlling the mechanical response of structures using a single
29 material and with no extra mass. The insect-inspired one-way hinge is particularly useful
30 for developing structures with asymmetric behaviour, exhibiting different responses to
31 the same load in two opposite directions. This multidisciplinary study not only advances
32 our understanding of the biomechanics of complicated insect wings, but also informs the
33 design of easily tuneable engineering hinges.

34
35 **Keywords:** Wing; flight; flexion line; compliant joint; shape morphing; adaptive system;
36 mechanical intelligence.

37 **Significant statement**

38 Insect wings present striking examples of automatic shape morphing in both nature and
39 technology, the mechanisms of which are not fully understood. Here we present a new
40 discovery from wings of a flying beetle that can shed light on wing shape changes in flight:
41 an unusual bell-shaped structure, which is compliant in one direction and almost 10 times
42 stiffer in the opposite direction. Our results show that the structure is an effective one-
43 way hinge that achieves functionality using a single material with no extra mass. The use
44 of the insect-inspired hinge in applications, including easily assemblable modular designs,
45 adaptive airless tires, and metamaterials with zero Poisson's ratio, suggests that the
46 structure can have biomimetic applications over a considerable size range.

47 **1. Introduction**

48 The wings of insects are remarkable examples of complex microengineering. Unlike those
49 of birds, bats and the extinct pterosaurs, insect wings lack internal muscles. Hence the
50 aerodynamically essential cyclical changes in shape and orientation that they undergo in
51 flapping flight are semi-automatic. These changes result from elastic interactions between
52 the structure of the wings and the aerodynamic and inertial forces they receive and are
53 modulated remotely by muscular action at the wing base [1-5].

54

55 In simplest terms, typical wings consist of membrane supported by a shallow three-
56 dimensional framework of tubular veins. However, both the detailed structural geometry
57 and material properties vary around the wing in ways which are often highly non-linear, so
58 that deformations in flight – bending, torsion, alteration in section, reversible buckling –
59 can be caused by local lines or areas of asymmetric flexibility, patches and pads of
60 elastomeric cuticle [2,6-13]; and also by internal mechanisms, such as planar levers [14-16].
61 Further, the hind wings of beetles (Coleoptera), earwigs (Dermaptera) and a few
62 cockroaches (Blattodea) fold up under the protective forewings when at rest. The folding
63 and unfolding, often highly complex processes, again involve a combination of internal
64 planar levers, cuticle elasticity and simple basal muscular action [17,18]. Such mechanisms
65 are usually extremely simple, but sometimes have unexpected - even counterintuitive
66 effects. Butterflies and dragonflies, for example, use the asymmetric twisting response of
67 thin cambered cantilevered plates when loaded behind the torsional axis to allow passive
68 supination for the upstroke, but minimal passive pronation in the downstroke [4,19,20].

69

70 In this paper, inspired by a detail in an insect wing, we describe and analyse what may be
71 another such simple, unexpected mechanism. We believe that the mechanism can have
72 potential applications in the design of novel structures and metamaterials; and we give
73 some examples of these.

74

75 **1.1. An asymmetric hinge in a double-layer membrane?**

76 The wing membrane of adult insects is a double-layer structure. It is formed at the final
77 moult by the juxtaposition, expansion and toughening of the cuticle of the dorsal and
78 ventral sides of the juvenile wing pads, with the elimination of the intervening
79 haemolymph and cellular material. The membrane is continuous with the veins:
80 haemolymph-filled tubes of variable cross-section with thickened walls that provide
81 support for the wing [21,22].

82

83 **Fig. 1A** is a transmission electron micrograph of a detail of the membrane of a hind wing of
84 the scarabaeid beetle *Pachnoda marginata* (Drury 1773); a section of the claval flexion line,
85 about which the wing profile changes cyclically in flight [1,23] (see **Fig. S1** for magnified
86 images and the position of the structure within the wing). The section is of a tube and is
87 approximately triangular, with the ventral membrane forming a nearly straight lower side,

88 but the dorsal membrane forming an arch with a curved apex. The section has some
89 similarity to those of the wing veins, but is far smaller, and differs from them in that the
90 sides of the structure are structurally identical with the adjacent membrane, whereas wing
91 veins normally have some parts of their walls thickened and stiffened by sclerotization.
92 We believe it instead to be an asymmetric, linear hinge of a kind which seems not
93 previously to have been analysed. 3D printed physical models show that such a structure
94 distorts readily when bent downwards but is resistant to upward bending (**Fig. 1B, Movie**
95 **S1**).

96

97 We have investigated and characterised the biomechanics of the structure using a
98 combination of multidisciplinary approaches, including microscopy techniques,
99 parametric modelling, computational simulations, 3D printing and mechanical testing. We
100 have studied the effects of the structural and material properties; and have examined
101 some possible biomimetic applications.

102

103 **2. Results**

104 The micrograph of the unusual double-layer structure is presented in **Fig. 1A**. The upper
105 and lower layers separate for a linear distance of 20 μm , with one – the ‘upper’ for
106 reference – forming a bell-shaped curve of 36 μm length, while the lower component is
107 nearly straight. Each layer is approximately 1.37 μm thick. The upper layer shows creases
108 at the vertex and one curved side. The creases, which may be the result of the sectioning,
109 suggest that the walls are flexible and could crease during wing deformation.

110

111 To understand the potential biomechanical advantages of the double-layer membrane
112 over the typical single-layer membrane, we performed a computational study. We
113 developed two models with the same volume: a double-layer membrane model based on
114 the microscopic observations described earlier, and a single-layer membrane model, in
115 which the two layers are merged. We subjected the models to an equal force in bending,
116 both upward and downward, and in axial loading, both compression and tension (**Fig. 2**).
117 We used the simulation data to compare the displacements of the models in each loading.
118 We noticed that both the double-layer and single-layer models showed an asymmetric
119 response to loads in two opposite directions (i.e., downward bending vs. upward bending
120 and compression vs. tension) (**Fig. 2A**; see **Fig. S2** for the stresses developed within the
121 models). Asymmetry was defined as the ratio of the displacement in downward bending
122 to the displacement in upward bending and as the ratio of the displacement in
123 compression to the displacement in tension. The strongest asymmetric response of both
124 models was observed in axial loading, with displacements in compression being larger
125 than those in tension. The asymmetric response was noticeably stronger in the double-
126 layer membrane model; this model showed an asymmetry of 9.3 in axial loading and 2.2 in
127 bending, in contrast to 2.1 times and 1.5 times asymmetry recorded for the single-layer
128 model for the same comparisons, respectively.

129

130 Applying a load to the double-layer membrane model from below (i.e., upward bending)
131 put the lower, nearly straight layer into tension. There was minimal distortion of the
132 curved upper layer, so that the structure acted as a rigid tube. Loading from above (i.e.,
133 downward bending), however, caused the lower layer to bend into the lumen of the tube,
134 pulling the sides together (**Fig. 2B**). Under tension, the double-layer membrane model
135 underwent minor stretching with no noticeable shape change. In contrast, the
136 deformations were notably larger in compression under the same force. This was caused
137 by the collapse of both the upper and the lower layers under compression (**Fig. 2B**). The
138 slight curvature of the lower layer gave a predisposition to downward buckling when the
139 double-layer membrane was loaded in compression.

140

141 To characterise the influence of the structure and material of the double-layer structure
142 on its asymmetric behaviour, we performed a set of computational simulations. We varied
143 the design parameters of our double-layer membrane model and developed 28 new
144 models with distinct structural/material properties (**Fig. 2C**). The design parameters varied
145 among the models are shown in the right-hand side panel in **Fig. 2C**. The left-hand side
146 panel presents the compression/tension asymmetry vs. the downward/upward
147 asymmetry for each model set. Here, for example, when the height of the upper layer was
148 increased (triangle symbol), the downward/upward asymmetry decreased from 2.5 to 1.6,
149 whereas the compression/tension asymmetry increased from 4.5 to 11.

150

151 The results showed the strong influence of the design parameters on the behaviour of the
152 model. The width of the bell-shaped curve, here referred to as 'upper layer width', and the
153 thickness of the upper layer had the strongest influence on the downward/upward
154 asymmetry of the models (i.e., displacement in downward bending in comparison to
155 upward bending). Changing the width of the upper layer by ~3.5 times resulted in ~4 times
156 increase in the downward/upward asymmetry. Likewise, increasing the thickness of the
157 upper layer by 3 times led to ~3 times increase in the downward/upward asymmetry. On
158 the other hand, the strongest control over the compression/tension asymmetry of the
159 models (i.e., displacement in compression to that in tension) was achieved through
160 simultaneous manipulation of the thickness of both the upper and lower layers. Increasing
161 the thickness of the two layers by 3 times reduced the compression/tension asymmetry by
162 ~5 times.

163

164 We also tested the performance of the double-layer hinge in application. The first
165 application was a modular structure, in which double-layer membrane models were used
166 as compliant one-way hinges. Considering that the hinges had to be bent in downward
167 bending but resist upward bending, we could choose among many models in the upper
168 half-plane of the graph shown in **Fig. 2C**. However, we decided to use a model with an
169 increased lower layer height, as we wanted to rely only on the structural strategies and

170 minimise the use of material in our 3D printed parts. We fabricated the selected model
171 using 3D printing, and characterised its performance under loading (**Fig. 3Ai, Aii, Movie**
172 **S2**). The model appeared to be particularly suitable for this application, enabling us to
173 easily assemble any number of modules, fold them on each other and further form a
174 variety of geometric shapes (**Fig. 3Aiii-ix**). This was facilitated by the flexibility of the
175 hinges when bent downwards, enabling them to remain in a deformed state with minimal
176 forces. **Fig. 3B,C** and **Movie S3** show the disassembly and assembly processes of the
177 modular cube in **Fig. 3Aix**.

178

179 In the second application, we implemented a double-layer hinge model in an airless tire
180 (**Fig. 3D, E**). We used a hinge with an increased lower layer height in comparison to the
181 reference model. This was because the deformations of the inner compliant hinges are
182 caused by both axial forces and bending moments, depending on the direction of contact.
183 Hence, we required hinges that could offer a compromise between load bearing and
184 deformability in compression and downward bending but a reasonable resistance to
185 upward bending. The hinges were radially oriented within an airless tire, which was
186 fabricated using 3D printing and then tested in compression, both along the direction of
187 the hinges and between them (**Fig. 3D, Movie S4**). We also tested the tire in application;
188 In contact with an obstacle, the tire underwent limited deformation and adapted to the
189 obstacle (**Fig. 3E**), a process that can increase the stability and controllability of vehicles.

190

191 We also used a double-layer hinge model to develop a metamaterial with zero Poisson's
192 ratio. We developed metamaterials that consisted of unit cells in form of squares and used
193 double-layer membrane models with increased lower layer height at the edges of each
194 square. This enabled us to develop a metamaterial that can collapse under compression
195 with no or only minor transverse deformation (**Fig. 3F, Movie S5**). As seen in **Fig. 3F**, the
196 metamaterial exhibited two distinct stiffness regimes: a low stiffness regime up to 15 mm
197 displacement, during which the hinges collapsed under compression, and a high stiffness
198 regime just after that, during which the adjacent hinges interlocked. When the pressure
199 was removed, the material returned to its initial state with no apparent plastic
200 deformation.

201

202 **3. Discussion**

203 One-way hinges and asymmetric bending and twisting are widespread in insect wings
204 [1,2,12,19,24-27]. They operate in flight, allowing the wings to deform automatically and
205 asymmetrically between the upstroke and the downstroke; and also in controlling the
206 precise, complex patterns of folding and unfolding in the hind wings of beetles
207 (Coleoptera) and of earwigs (Dermaptera) [17,18,28,29]. The mechanisms often involve
208 specific areas of elasticity within the wing cuticle, sometimes including lines or patches of
209 the protein elastomer resilin [6,30-34] but other examples depend on reversible thin plate
210 buckling in which the shape and height as well as the elastic properties of the wing section

211 are of major importance [1,8,15,19]. The double-layer membrane structure described here
212 can fit into the latter category. Our real-scale computational simulations and up-scaled
213 physical modelling confirmed the original hypothesis that the double-layer membrane can
214 act as a one-way hinge, stiff in tension and upward bending but unstable in compression
215 and downward bending. The structure is unique in its simplicity; the double-layer
216 membrane can achieve functionality using a single material and requiring almost no extra
217 mass.

218

219 The asymmetric response of the double-layer membrane is a geometric nonlinearity effect,
220 which results from changes in the geometric configuration of the structure under loading.
221 The reason for the stronger asymmetric response of the double-layer membrane in
222 comparison with the single-layer membrane is that such configuration changes increase
223 the resistance of the double-layer membrane to displacements in one direction but
224 decrease the resistance to displacements in the opposite direction. This effect is
225 noticeably smaller in the single-layer membrane. Considering that the geometric
226 nonlinearity occurs under large deformations, it is likely that both the double- and single-
227 layer membrane structures show symmetric behaviour for small deformations.

228

229 Our computational analyses showed that the structural and material properties, here
230 referred to as 'design parameters', have a strong influence on the mechanical behaviour,
231 particularly on the asymmetry, of the double-layer membrane hinge. This means that the
232 design parameters can be used to tune the properties of the structure in a wide range. This
233 characteristic enabled us to develop a broad design space, which later facilitated the
234 process of model selection. Furthermore, the design parameters influenced the
235 asymmetric response of the models to different extents. For example, the width of the
236 upper membrane appeared to impact the down/up asymmetry more than any other design
237 parameter. The design parameters also exhibited different impacts on the asymmetric
238 response of the double-layer membrane in two orthogonal directions tested here, i.e.,
239 down/up vs. compression/tension. Our findings, therefore, suggest that to obtain desired
240 properties in an application the design parameters should be carefully chosen, as any
241 design parameter allows tuning the properties within a certain range and in a specific
242 direction.

243

244 An interesting observation is the formation of an interlocking effect in some double-layer
245 membranes. This effect results from the physical contact between the upper and lower
246 layers and can be seen mostly in models with small upper layer heights. When the
247 interlocking takes place, the hinge cannot be closed and thereby its stiffness increases
248 (**Fig. S3**). This effect can be used, for example, to develop bioinspired compliant hinges
249 with a 'closing limit'. There are also a few other mechanisms for interlocking in insect
250 wings, including joint-associated spikes [14,31,35] and nodus [12,34,36], which are situated
251 on the wing and therefore can be more easily examined. These mechanisms prevent

252 detrimental deformations in certain wing areas and by that play a key role in insect flight
253 efficiency. The discovery of the double-layer membrane hinge suggests that there might
254 be other, yet undiscovered mechanisms hidden in the wing design.

255

256 Double-layered membranes are not uncommon in nature. The phospholipid bilayers that
257 surround all living cells are a particularly active area of study. Synthetic lipid bilayers have
258 proved to be a useful tool in investigating their properties on the nanometre scale, and Lu
259 et al. [37] have used these to model membranes whose layers have different properties.
260 Double membranes also have technological applications. For example, Zuo et al. [38] have
261 combined layers with different properties and dimensions to develop dual-membrane
262 hollow fibres for vacuum membrane distillation in desalination processes.

263

264 Our manufactured models showed the effectiveness of the discovered double-layer hinge
265 in applications. Generally, the double-layer membrane can be used where a structure
266 should undergo large deformations only in a certain direction and/or when it should exhibit
267 different, but tuneable stiffness levels in opposite directions. The deformability in
268 combination with high tunability make the double-layer hinge particularly interesting for
269 designing adaptive structures, such as the airless tire developed here. The structure is also
270 particularly suitable for providing asymmetric deformations, where properties in two
271 opposite directions drastically differ. This is a desirable property for development of shape
272 morphing systems that should resist loads in a certain direction but need to be compliant
273 in a different direction. In metamaterials, as shown here, the double-layer membrane can
274 give rise to potentially unique properties, for example by locally varying the stiffness of
275 the material.

276

277 Two directions for future research are particularly worth following. First, studies should
278 test the scalability of the double-layer membrane hinge. Scalability is a reasonable concern
279 when translating small-scale biological strategies into engineering applications. Recent
280 studies have tested and verified the scalability of some of the wing-derived strategies. A
281 few examples include the development of durable kites, stiffness-varying splints, insect-
282 inspired wings for medium-sized flapping-wing drones, aeroplane wing models and
283 origami arms that resist collisions by undergoing reversible buckling, extensible robotic
284 arms, confined-space crawling robots, and unlockable revolute joints [27,39-46]. Based on
285 our results, the double-layer membrane can work at different scales but its effectiveness
286 will clearly depend on overall size, relative wall thickness and section shape, and on the
287 properties of the material. It is necessary to understand whether and how the relationship
288 between the geometry and functionality of the double-layer membrane would change by
289 changing the scale. It is possible that for larger objects the problem of strength may arise
290 while using stronger materials can be limited by required large deformations. Second,
291 future research should focus on identifying other factors that might influence the
292 behaviour of the double-layer membrane. For example, in real insect wings, there might

293 be a hydraulic dimension involved. If this is the case, any fluid in the double-layer
294 membrane would strongly influence the operation of the system particularly in downward
295 bending during which the internal volume would be reduced. Future works will shed more
296 light on both the functionality and biomimetic applications of the double-layer membrane
297 hinge and its presence in other insect wings.

298

299 **Video S6** summarises our study in a short video.

300

301 **4. Conclusion**

302 In this paper, we presented a new discovery – a double-layer membrane structure in the
303 wings of *Pachnoda* beetles. Despite its remarkable simplicity, we cannot find that it has
304 previously been described. We showed that the structure works as a one-way hinge, the
305 functionality of which may rely on reversible buckling of thin sheets and plates that insects
306 use very effectively.

307

308 This study is important for two distinct reasons. First, the results advance our
309 understanding of the biomechanics of insect wings. The previously undescribed structure
310 potentially contributes to automatic shape changes of insect wings in flight, although the
311 extent of the contribution still needs further evaluation. Second, the biological one-way
312 hinge described here offers biomimetic inspiration for the design and development of
313 engineering structures that exhibit asymmetric responses to equal forces applied in
314 different directions. This is particularly interesting because the double-layer membrane
315 offers a simple, inexpensive way of making a one-way hinge without increasing the mass.

316

317 **5. Methods**

318 **5.1. Microscopic analysis of the wing membrane.**

319 The detail illustrated in Fig. 1a was discovered in the course of an unpublished investigation
320 into the microstructure and ultrastructure of the hindwing of the beetle *Pachnoda*
321 *marginata*. Elements of the wing were fixed in 3% glutaraldehyde in sodium cacodylate
322 buffer, embedded in Spurr's resin (Sigma-Aldrich), sectioned with a diamond knife, and
323 examined and photographed with a JEOL 100S transmission electron microscope.

324

325 **5.2. Investigation of the structure-material-mechanics of the double-layer hinge**

326 We used computational modelling to investigate the mechanical behaviour of the double-
327 layer membrane structure in its original scale. A computational approach was chosen, as it
328 enabled us to systematically alter the structural and material properties of the double-
329 layer membrane and test their influence on its response to applied loads. The models were
330 developed using the state-of-the-art parametric modelling tool Grasshopper 3D (Rhino).
331 First, we developed a model inspired by the double-layer hinge shown in **Fig. 1**. Next, to
332 assess the advantage of the double-layer membrane over the typical single-layer
333 membrane structure, we developed a second model in which we shifted the upper and

334 lower layers towards the midline of the double-layer membrane model and merged them
335 together. Both the 'double-layer membrane model' and the 'single-layer membrane
336 model' had the same volume. We have added both the models as the supplementary
337 materials.

338

339 We then systematically changed the design parameters of the double-layer model,
340 including the height, thickness and width of the upper layer, the height and thickness of
341 the lower layer, and the thickness of the upper and lower layers at the same time. We also
342 changed the material properties of the upper and lower layers. This enabled us to develop
343 28 extra models, which we used to establish a link between the design and performance
344 of the double-layer membrane structure. See supplementary materials for the individual
345 models (**Dataset S1**) and the full parametric model (**Dataset S2**).

346

347 After modelling, we then exported the models to the commercial finite element software
348 package ABAQUS (Simulia) for the analysis. We assigned the same properties to the
349 models, except for the models that were designed to test the effect of the material
350 properties. Assigning the same properties to the models enabled us to obtain results that
351 were only influenced by the geometry of the models. For our models, we used the same
352 material properties as those reported for the wing membrane of the desert locust [47,48].
353 These included an elastic modulus of 1.86 GPa, a density of 1200 kg/m³, and a Poisson's
354 ratio of 0.3. The models were assumed to be homogeneous and isotropic. The same
355 approach was applied to the models with altered material properties. The only difference
356 was that in these models we once reduced the elastic modulus of the upper layer and then
357 that of the lower layer each in two steps from 1.86 GPa to 0.93 GPa and then to 0.47 GPa.

358

359 We meshed the models using the general purpose eight-node brick elements with reduced
360 integration (C3D8R) with second-order accuracy. A reduced integration scheme was used
361 to reduce the computational runtime. Using the hourglass control, and distortion control
362 prevented detrimental mesh distortions. We then subjected the models to four loading
363 scenarios: tension, compression, upward bending and downward bending. In all scenarios,
364 the displacements and rotations of the models were fixed at the uppermost point of their
365 axis of symmetry. The models were subjected to an equal force (2.4 mN) at their free ends.
366 We then measured the displacements of the models and recorded their deformation
367 patterns. We used the results to investigate the mechanical behaviour of the models under
368 each loading scenario and compare among them.

369

370 **5.3. Using the double-layer hinge in applications**

371 To test the performance of the double-layer hinge models in application, we used them in
372 three distinct designs. First, we used a set of similar double-layer membrane models as
373 compliant joints in a modular design, where they were used to connect a series of stiff flat
374 plates together at their edges. In this application, the models were used as one-way hinges

375 by which we could fold the flat plates on each other and further form a variety of
376 geometric shapes. Second, we combined the double-layer hinge models in an airless tire.
377 The models were situated along the radius of the tire. The double-layer membranes were
378 intended to enable the tire to deform and adapt to uneven surfaces. In the third
379 application, we employed a combination of the double-layer membrane models to develop
380 a two-dimensional metamaterial. The metamaterial consisted of square-shaped unit cells,
381 where each edge of the squares is formed by a double-layer hinge model. The
382 metamaterial was intended to collapse under compression in one direction without being
383 deformed in the perpendicular direction, i.e., behaving as a zero Poisson's ratio material.
384

385 The models for the applications were developed using Rhino and manufactured by 3D
386 printing. We used 3D printing, because it is a cost- and time-efficient prototyping method
387 that allows manufacturing of complicated models as those developed here. We used a
388 Raise3D E2 3D printer, as this is a high-precision 3D printer that is compatible with the
389 thermoplastic polyurethane (TPU) used for manufacturing of the models. The TPU (Sunlu
390 filament, 1.75 mm dia.) was selected as the building material, because of its high elasticity
391 and toughness, which enabled us to develop deformable parts.
392

393 Prior to 3D printing, the stl./obj. files of the models (available as supplementary materials,
394 **Dataset S3**) were exported to the 3D slicing software IdeaMaker (Raise3D), where they
395 were prepared for manufacturing. Here the models were rescaled and reoriented.
396 Considering the geometry of the models and their relatively thin walls, no support or infill
397 was added. After slicing the models, the gcodes were extracted and prints were done at a
398 layer height of 0.2 mm, nozzle temperature of 200 °C, bed temperature of 60 °C, and print
399 speed of 40 mm/s. No postprocessing was performed on the 3D printed parts.
400

401 To characterise the mechanical performance of the manufactured parts, we tested them
402 under loading. Mechanical tests were performed using a universal testing machine (1ST,
403 Tinius Olsen) equipped with a 500N loadcell. Specifically, we tested the hinge used in the
404 modular designs in three-point bending (**Movie S2**), and both the airless tire and the
405 metamaterial in compression between two flat plates (**Movies S4, S5**). The hinge and the
406 tire were subjected to 10 mm and 20 mm displacements, respectively. The displacement
407 on the metamaterial was continued until the maximum capacity of the loadcell was
408 reached. We tested at least three specimens of each part. All experiments were performed
409 at an increasing displacement of 1 mm/sec. The data from the experiments, including force,
410 displacement, and time, were continuously recorded using the software Horizon (Tinius
411 Olsen) and are available as supplementary material (**Dataset S4**). We also recorded the
412 tests using a digital camera (SONY RX100vi).
413

414 **Data availability**

415 The authors declare that the data supporting the findings of this study are available

416 within the paper and its supplementary information files. Supplementary materials are
417 additionally available via the following link: <https://figshare.com/s/bb7ba43b371cfb7aaf63>
418

419 **Acknowledgements**

420 The authors would like to thank Mr Shayan Ramzanpour for his support with
421 computational analysis. We are grateful to our three anonymous reviewers for their
422 insightful suggestions and invaluable comments.

423

424 **Funding**

425 This project was partially supported by the LSBU Mechanical Engineering and Design's
426 (MED's) Seed Funding to AK.

427

428 **Competing interests**

429 The authors declare no competing interests.

430

431 **Author contributions**

432 Conceptualisation: RJW; research design: HR, RJW; investigation-microscopy: CH;
433 investigation-computational modelling: SHE; investigation-manufacturing and testing: AK,
434 HR; methodology: RJW, HR, AT, SHE, AK, CH; product/application ideation and design:
435 SHE, AT, AK, HR; project administration: RJW, HR; resources: RJW, HR; supervision: RJW,
436 HR; visualization: AT, HR; writing-original draft preparation: RJW, HR; writing-review &
437 editing: RJW, SHE, AT, AK, CH.

438

439 **References**

- 440 [1] R. J. Wootton, Support and deformability in insect wings. *J. Zool.* **193**, 447-468 (1981).
441 [2] R. J. Wootton, Functional morphology of insect wings. *Annu. Rev. Entomol.* **37**, 113-140
442 (1992).
443 [3] A. K. Brodsky, The evolution of insect flight. (Oxford University Press, 1994).
444 [4] R. J. Wootton, D. J. Newman, In: Dragonflies & Damselflies: Model Organisms for
445 Ecological and Evolutionary Research, A. Córdoba-Aguilar Ed., (Oxford University
446 Press, 2008), pp. 261–274.
447 [5] H. Rajabi, H., S. N. Gorb, How do dragonfly wings work? A brief guide to functional roles
448 of wing structural components. *Int. J. Odonatol.* **23**, 23-30 (2020).
449 [6] S. N. Gorb, Serial elastic elements in the damselfly wing: mobile vein joints contain
450 resilin. *Naturwissenschaften* **86**, 552-555 (1999).
451 [7] R. J. Wootton, Wings. In: Encyclopedia of insects, V. H. Resh, R. T. Cardé Eds. (Academic
452 Press, 2009), pp. 1055-1061.
453 [8] R. J. Wootton, The geometry and mechanics of insect wing deformations in flight: a
454 modelling approach. *Insects* **11**, 446 (2020).
455 [9] E. Appel, S. N. Gorb, Comparative functional morphology of vein joints in Odonata.
456 (Schweizerbart Science Publishers, 2014).

- 457 [10] S. Fauziyah, C. Alam, R. C. H. Soesilohadi, B. Retnoaji, P. Alam, Morphological and
458 mechanical characterisation of the hindwing nodus from the Libellulidae family of
459 dragonfly (Indonesia). *Arthropod Struct. Dev.* **43**, 415-422 (2014).
- 460 [11] H. Rajabi, N. Ghoroubi, A. Darvizeh, E. Appel, S. N. Gorb, Effects of multiple vein
461 microjoints on the mechanical behaviour of dragonfly wings: numerical modelling. *R.*
462 *Soc. Open Sci.* **3**, 150610 (2016).
- 463 [12] H. Rajabi, N. Ghoroubi, K. Stamm, E. Appel, S. N. Gorb, Dragonfly wing nodus: a one-
464 way hinge contributing to the asymmetric wing deformation. *Acta Biomater.* **60**, 330-
465 338 (2017).
- 466 [13] K. Yazawa, K. Numata, Y. Norma-Rashid, Morphological and mechanical properties of
467 flexible resilin joints on damselfly wings (*Rhinocypha* spp.). *PLoS ONE* **13**, e0193147
468 (2018).
- 469 [14] D. J. Newman, The functional wing morphology of some Odonata (Doctoral
470 dissertation, University of Exeter, Exeter (1982).
- 471 [15] A. R. Ennos, A comparative study of the flight mechanism of Diptera. *J. Exp. Biol.* **127**,
472 355-372 (1987).
- 473 [16] A. R. Ennos, The importance of torsion in the design of insect wings. *J. Exp. Biol.* **140**,
474 137-160 (1988).
- 475 [17] F. Haas, R. J. Wootton, Two basic mechanisms in insect wing folding. *Proc. Royal Soc.*
476 *B* **263**, 1651-1658 (1996).
- 477 [18] F. Haas, S. N. Gorb, R. J. Wootton, Elastic joints in dermapteran hind wings: materials
478 and wing folding. *Arthropod Struct. Dev.* **29**, 137-146 (2000).
- 479 [19] R. J. Wootton, Leading edge section and asymmetric twisting in the wings of flying
480 butterflies (Insecta, Papilionoidea). *J. Exp. Biol.* **180**, 105-119 (1993).
- 481 [20] A. R. Ennos, Mechanical behaviour in torsion of insect wings, blades of grass, and
482 other cambered structures. *Proc. Royal Soc. B* **259**, 15-18 (1995).
- 483 [21] G. Pass, Beyond aerodynamics: The critical roles of the circulatory and tracheal
484 systems in maintaining insect wing functionality. *Arthropod Struct. Dev.*, **47**, 391-407
485 (2018).
- 486 [22] M. K., Salcedo, J. J. Socha, Circulation in insect wings. *Integr. Comp. Biol.* **60**, 1208-1220
487 (2020).
- 488 [23] R. J. Wootton, Function, homology and terminology in insect wings. *Syst. Entomol.* **4**,
489 81-93 (1979).
- 490 [24] R. J. Wootton, A. R. Ennos, The implications of function on the origin and homologies
491 of the dipterous wing. *Syst. Entomol.* **14**, 507-520 (1989).
- 492 [25] S. A. Combes, T. L. Daniel, Flexural stiffness in insect wings I. Scaling and the influence
493 of wing venation. *J. Exp. Biol.* **206**, 2979-2987 (2003).
- 494 [26] A. Toofani, S. H. Eraghi, M. Khorsandi, A. Khaheshi, A. Darvizeh, S. N. Gorb, H. Rajabi,
495 Biomechanical strategies underlying the durability of a wing-to-wing coupling
496 mechanism. *Acta Biomater.* **110**, 188-195 (2020).

- 497 [27] S. H. Eraghi, A. Toofani, A. Khareshi, M. Khorsandi, A. Darvizeh, S. N. Gorb, H. Rajabi,
498 Wing coupling in bees and wasps: From the underlying science to bioinspired
499 engineering. *Adv. Sci.* **8**, 2004383 (2021).
- 500 [28] F. Haas, R. G. Beutel, Wing folding and the functional morphology of the wing base in
501 Coleoptera. *Zoology* **104**, 123-141 (2001).
- 502 [29] K. Saito, S. Nomura, S. Yamamoto, R. Niiyama, Y. Okabe, Investigation of hindwing
503 folding in ladybird beetles by artificial elytron transplantation and microcomputed
504 tomography. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 5624-5628 (2017).
- 505 [30] F. Haas, S. N. Gorb, R. Blickhan, The function of resilin in beetle wings. *Proc. Royal Soc.*
506 *B* **267**, 1375-1381 (2000).
- 507 [31] S. Donoughe, J. D. Crall, R. A. Merz, S. A. Combes, Resilin in dragonfly and damselfly
508 wings and its implications for wing flexibility. *J. Morphol.* **272**, 1409-1421 (2011).
- 509 [32] A. M. Mountcastle, S. A. Combes, Biomechanical strategies for mitigating collision
510 damage in insect wings: structural design versus embedded elastic materials. *J. Exp.*
511 *Biol.* **217**, 1108-1115 (2014).
- 512 [33] H. Rajabi, A. Shafiei, A. Darvizeh, S. N. Gorb, Resilin microjoints: a smart design strategy
513 to avoid failure in dragonfly wings. *Sci. Rep.* **6**, 1-5 (2016).
- 514 [34] H. Rajabi, K. Stamm, E. Appel, S. N. Gorb, Micro-morphological adaptations of the wing
515 nodus to flight behaviour in four dragonfly species from the family Libellulidae
516 (Odonata: Anisoptera). *Arthropod Struct. Dev.* **47**, 442-448 (2018).
- 517 [35] H. Rajabi, N. Ghoroubi, A. Darvizeh, J. H. Dirks, E. Appel, S. N. Gorb, A comparative
518 study of the effects of vein-joints on the mechanical behaviour of insect wings: I.
519 Single joints. *Bioinspir. Biomim.*, **10**, 056003 (2015).
- 520 [36] Y. H. Chen, M. Skote, Y. Zhao, W. M. Huang, Dragonfly (*Sympetrum flaveolum*) flight:
521 kinematic measurement and modelling, *J. Fluids Struct.* **40**, 115–126 (2013).
- 522 [37] L. Lu, W. J. Doak, J. W. Schertzer, P. R. Chiarot, Membrane mechanical properties of
523 synthetic asymmetric phospholipid vesicles. *Soft Matter* **12**, 7521-7528 (2016).
- 524 [38] J. Zuo, T. S. Chung, G. S. O'Brien, W. Kosar, Hydrophobic/hydrophilic PVDF/Ultem®
525 dual-layer hollow fiber membranes with enhanced mechanical properties for vacuum
526 membrane distillation. *J. Membr. Sci.* **523**, 103-110 (2017).
- 527 [39] K. Jayaram, R. J. Full, Cockroaches traverse crevices, crawl rapidly in confined spaces,
528 and inspire a soft, legged robot. *Proc. Natl. Acad. Sci. U.S.A.* **113**, E950-E957 (2016).
- 529 [40] S. Mintchev, J. Shintake, D. Floreano, Bioinspired dual-stiffness origami. *Sci. Robot.* **3**,
530 eaau0275 (2018).
- 531 [41] H. V. Phan, H. C. Park, Mechanisms of collision recovery in flying beetles and flapping-
532 wing robots. *Science* **370**, 1214-1219 (2020).
- 533 [42] S. Büsse, A. Koehnsen, H. Rajabi, S. N. Gorb, A controllable dual-catapult system
534 inspired by the biomechanics of the dragonfly larvae's predatory strike. *Sci. Robot.* **6**,
535 eabc8170 (2021).
- 536 [43] A. Khareshi, H. T. Tramsen, S. N. Gorb, H. Rajabi, Against the wind: A load-bearing, yet
537 durable, kite inspired by insect wings. *Mater. Des.* **198**, 109354 (2021).

- 538 [44] A. Khaheshi, S. N. Gorb, H. Rajabi, Spiky-joint: a bioinspired solution to combine
539 mobility and support. *Appl. Phys.* **127**, 1-7 (2021).
- 540 [45] A. Khaheshi, S. N. Gorb, H. Rajabi, Triple Stiffness: A Bioinspired Strategy to Combine
541 Load-Bearing, Durability, and Impact-Resistance. *Adv. Sci.* **8**, 2004338 (2021c).
- 542 [46] K. Saito, H. Nagai, K. Suto, N. Ogawa, T. Tachi, R. Niiyama, Y. Kawahara, Insect wing
543 3D printing. *Sci. Rep.* **11**, 1-8 (2021).
- 544 [47] J. H. Dirks, D. Taylor, Veins improve fracture toughness of insect wings. *PLoS ONE* **7**,
545 e43411 (2012).
- 546 [48] H. Rajabi, A. Darvizeh, A. Shafiei, D. Taylor, J. H. Dirks, Numerical investigation of insect
547 wing fracture behaviour. *J. Biomech.* **48**, 89-94 (2015).
- 548

549 **Figure legends**

550 **Fig. 1. Double-layer membrane; microscopy and basic physical testing.** (A) Transmission electron
551 micrograph of the double-layer membrane from the hind wing of the beetle *Pachnoda marginata*.
552 (B) Physical testing of a 3D printed double-layer membrane. The structure is compliant in
553 downward bending but stiff in upward bending. Scale bars: 5 μm (A), 2 cm (B).

554
555 **Fig. 2. Results of the computational study.** (A,B) Quantitative (A) and qualitative (B) comparisons
556 of the asymmetric response of the double-layer and single-layer membrane models (down/up
557 asymmetry: displacement in downward bending to displacement in upward bending;
558 compression/tension: displacement in compression to displacement in tension). The results are
559 presented for both down/up and compression/tension asymmetric responses. (C) Influence of the
560 design parameters on the asymmetric response of the double-layer membrane model. The right-
561 side panels show the design parameters and how they were varied among the models. The
562 intensity of the colours in the lowermost row of the right-hand side panel indicates the relative
563 elastic modulus of the layers, with darker colour (black) representing the highest elastic moduli
564 and the brighter colour (white) representing the lowest elastic modulus. For the sake of
565 presentation, two outlier data points (from upper layer width model 2 and lower layer thickness
566 model -2) have been removed from the plot in panel C.

567
568 **Fig. 3. Double-layer hinge in application.** (A) Double-layer membrane as a compliant hinge in
569 modular designs. The structure used in these examples exhibited a desirable bending asymmetry
570 (Ai). Taking advantage of the asymmetric behaviour of the double-layer membrane hinge, we used
571 that to connect a series of square plates and fold them in various ways (Aii-v) and also form a
572 variety of geometric shapes (Avi-ix). (B) Assembly of the modular design shown in panel Aix. (C)
573 Disassembly of the modular design shown in panel Aix. (D, E) Using the double-layer hinge in an
574 adaptive airless tire. The tire was tested in compression between two rigid plates (D). The loading
575 was applied in two orientations: between the hinges (upper row) and along the hinges (lower
576 row). (F) Using the double-layer hinge in a metamaterial with a zero Poisson's ratio. The
577 metamaterial was tested in compression and the results were used to characterise its mechanical
578 behaviour in loading (upper row) and unloading (lower row).

579

580