

# Insect egg size and shape evolve with ecology but not developmental rate

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Over the course of evolution, organism size has diversified markedly. Changes in size are thought to have occurred because of developmental, morphological and/or ecological pressures. To perform phylogenetic tests of the potential effects of these pressures, here we generated a dataset of more than ten thousand descriptions of insect eggs, and combined these with genetic and life-history datasets. We show that, across eight orders of magnitude of variation in egg volume, the relationship between size and shape itself evolves, such that previously predicted global patterns of scaling do not adequately explain the diversity in egg shapes. We show that egg size is not correlated with developmental rate and that, for many insects, egg size is not correlated with adult body size. Instead, we find that the evolution of parasitoidism and aquatic oviposition help to explain the diversification in the size and shape of insect eggs. Our study suggests that where eggs are laid, rather than universal allometric constants, underlies the evolution of insect egg size and shape.

Size is a fundamental factor in many biological processes. The size of an organism may affect interactions both with other organisms and with the environment<sup>1,2</sup>, it scales with features of morphology and physiology<sup>3</sup>, and larger animals often have higher fitness<sup>4</sup>. Previous studies have aimed to identify the macroevolutionary forces that explain the observed distributions in animal size<sup>1,5,6</sup>. However, the limited availability of data on the phylogenetic distribution of size has precluded robust tests of the predicted forces<sup>4,7</sup>. Here we address this problem by assembling a dataset of insect egg phenotypes with sufficient taxon sampling to rigorously test hypotheses about the causes and consequences of size evolution in a phylogenetic framework.

Insect eggs are a compelling system with which to test macroevolutionary hypotheses. Egg morphologies are extraordinarily diverse<sup>8</sup>, yet they can be readily compared across distant lineages using quantitative traits. Changes in egg size have been studied in relation to changes in other aspects of organismal biology<sup>9</sup>, including adult body size<sup>10–12</sup>, features of adult anatomy<sup>13</sup> and offspring fitness through maternal investment<sup>14</sup>. Eggs must also withstand the physiological challenges of being laid in diverse microenvironments, including in water, air, or inside plants or animals<sup>15</sup>. Furthermore, because the fertilized egg is the homologous, single-cell stage in the lifecycle of multicellular organisms, egg size diversity is relevant to the evolution of both cell size and organism size<sup>8,14</sup>.

Three classes of hypotheses have been proposed to explain the evolution of egg size and shape. The first suggests that geometric constraints due to the physical scaling of size and shape explain the diversity of egg morphology<sup>13,16–19</sup>. The second suggests that there is an interaction between egg size and the rate of development<sup>20–22</sup>. Finally, the third suggests that the diversification of size and shape is a response to ecological or life-history changes<sup>10,13,15,23</sup>. We use a phylogenetic approach to test all three of these hypotheses, and show that many presumed universal patterns in the size, shape and embryonic development of eggs are not supported across insects. Instead, we find that models that account for ecological changes best explain the morphological diversity in eggs of extant insects..

Using custom bioinformatics tools, we assembled a dataset of 10,449 published descriptions of eggs, comprising 6,706 species,

526 families and every currently described extant hexapod order<sup>24</sup> (Fig. 1a and Supplementary Fig. 1). We combined this dataset with backbone hexapod phylogenies<sup>25,26</sup> that we enriched to include taxa within the egg morphology dataset (Supplementary Fig. 2) and used it to describe the distribution of egg shape and size (Fig. 1b). Our results showed that insect eggs span more than eight orders of magnitude in volume (Fig. 1a, c and Supplementary Fig. 3) and revealed new candidates for the smallest and largest described insect eggs: respectively, these are the parasitoid wasp *Platygaster vernalis*<sup>27</sup> (volume =  $7 \times 10^{-7}$  mm<sup>3</sup>; Fig. 1c) and the earth-boring beetle *Bolboleaus hiaticollis*<sup>28</sup> (volume =  $5 \times 10^2$  mm<sup>3</sup>; Fig. 1c).

Plotting eggs by morphology revealed that some shapes evolved only in certain clades (Fig. 1a and Supplementary Figs. 4–7). For example, oblate ellipsoid eggs (aspect ratio < 1) are found only in stoneflies, moths and butterflies (Plecoptera and Lepidoptera; Fig. 1c, Supplementary Figs. 4, 5). Egg cases (oothecae) have evolved in multiple insect lineages<sup>29</sup>. To test whether oothecae constrain shape or size, we measured individual eggs within cases, and found that these eggs are morphologically similar to those of freely laid relatives (Supplementary Fig. 8). The most prominent pattern was that distantly related insects have converged on similar morphologies many times independently (Fig. 1a and Supplementary Fig. 7). This high degree of morphological convergence allowed us to robustly test trait associations across independent evolutionary events.

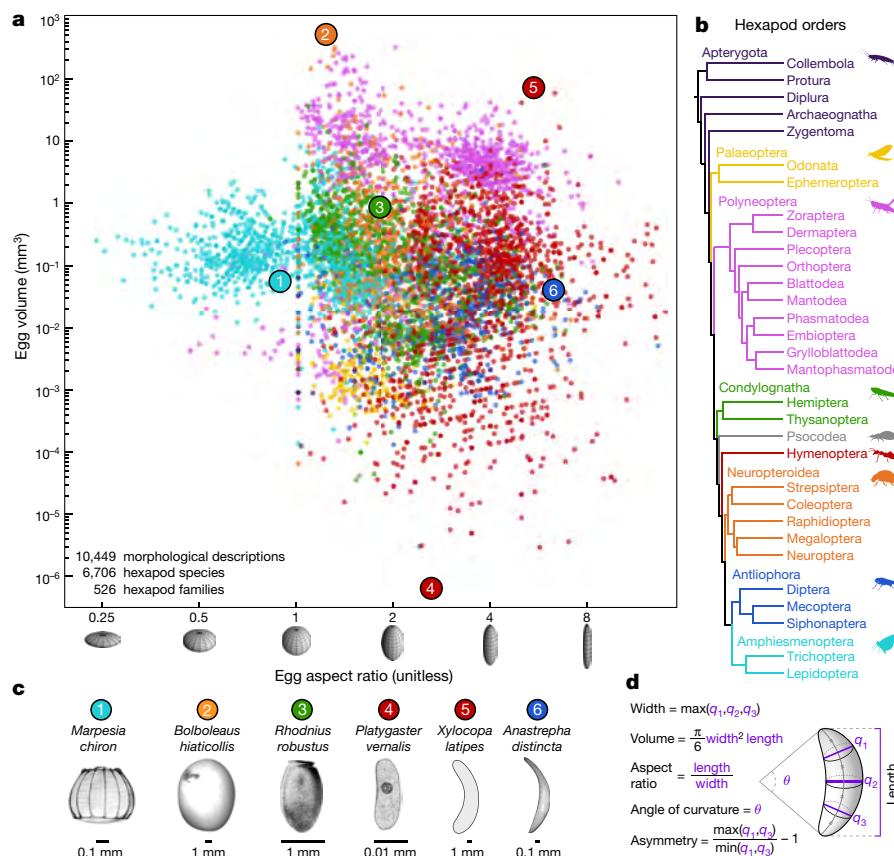
## Evolutionary allometry of insect eggs

Two opposing hypotheses based on predicted geometric constraints have been proposed to explain the evolutionary relationship between egg shape and size. One hypothesis posits that when eggs evolve to be larger, they become wider (increases in egg size are associated with decreases in aspect ratio)<sup>17,18</sup>. This hypothesis predicts a reduction in relative surface area as size increases, which has been proposed as a solution to the presumed cost of making eggshell material<sup>18</sup>. The alternative hypothesis proposes that when eggs evolve to be larger, they become longer (increases in egg size are associated with increases in aspect ratio)<sup>13,18,19</sup>. This hypothesis predicts a reduction in relative cross-sectional area as eggs become larger, which has been proposed

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**Fig. 1 | The shapes and sizes of hexapod eggs.** **a**, Eggs are plotted in a morphospace defined by volume ( $\text{mm}^3$ ) and aspect ratio (unitless) on a log scale. Points are coloured by clades as shown in **b**. **b**, Relationships are shown according to a previous study<sup>25</sup>, one of the backbone phylogenies

as a solution to the need for eggs to pass through a narrow opening during oviposition<sup>13,19</sup>.

To test these hypotheses about the physical scaling of size and shape, we began by modelling the evolutionary history of each morphological trait. This allowed us to determine whether distributions of extant shape and size have been shaped by phylogenetic relationships. For egg volume, aspect ratio, asymmetry and angle of curvature (Fig. 1d), we compared four models of evolution: Brownian motion, Brownian motion with evolutionary friction (Ornstein–Uhlenbeck), Brownian motion with a decreasing rate of evolution (early burst) and a non-phylogenetic model of stochastic motion (white noise). We found that models that accounted for phylogenetic covariance fit our data better than a non-phylogenetic model (white noise); in other words, the morphology of insect eggs tends to be similar in closely related insects (Supplementary Table 5). For egg size and aspect ratio, an early burst model in which evolutionary rate decreases over time, best describes the data (Supplementary Figs. 9–11). In previous studies, early burst models were rarely detected<sup>30</sup>. However, our findings are consistent with recent studies evaluating datasets that—similar to our data—comprise many taxa and orders of magnitude in morphological variation<sup>31,32</sup>. Having established appropriate phylogenetic models, we used these results to test hypotheses about the relationship between egg shape and size.

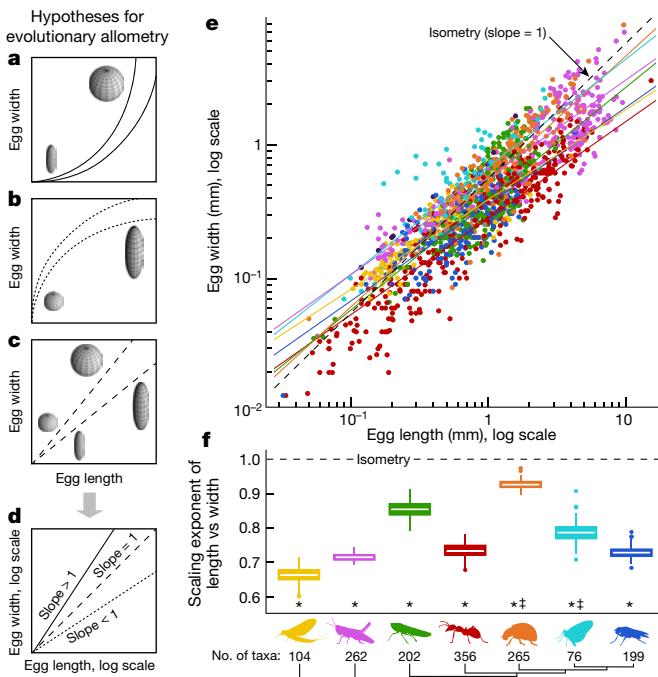
To test which aforementioned scaling relationship best describes insect egg evolution, we compared support for each of the two opposing hypotheses described above using a phylogenetic generalized least-squares approach to determine the scaling exponent of length and width (the slope of the regression of log-transformed length and log-transformed width). A slope less than one would support the first hypothesis (Fig. 2a), whereas a slope greater than one would support the second hypothesis<sup>33</sup> (Fig. 2b). An alternative third hypothesis is that

used in this study. Numbered points correspond to six eggs shown in **c**. **c**, Eggs selected to show a range of sizes and shapes, arranged by aspect ratio<sup>27,28,48–51</sup>. **d**, Size and shape are described using six features, calculated as shown.

egg shape remains the same as size changes; this would result in a slope near one (an isometric relationship; Fig. 2c). The relationships describing these hypotheses are shown in Fig. 2a–d. We found that across all insects, the second hypothesis is best supported: larger eggs have higher aspect ratios than smaller eggs ( $0 < P < 0.005$ , slope = 0.78; Fig. 2e and Supplementary Table 6), even when controlling for adult body size (Supplementary Fig. 14 and Supplementary Table 8). We found no support for the first hypothesis, which suggests that future hypotheses of egg shell evolution may need to account for additional factors such as chorion composition and thickness when considering potential fitness cost. However, the allometric relationship between size and shape evolves dynamically across the phylogeny, which has also been shown for metabolic scaling in mammals<sup>34</sup>. The third hypothesis, isometry, could not be rejected for beetles and their relatives, nor for butterflies, moths and caddisflies (respectively, Neuropteroidea  $P = 0.04$  and Amphiesmenoptera  $P = 0.01$ ; Fig. 2f, Supplementary Fig. 12 and Supplementary Table 7). Calculating the scaling relationship on lineage subgroups revealed that additional clades, including mayflies, crickets and shield bugs, also show an isometric relationship (Supplementary Fig. 13). The marked differences in scaling exponents are evidence that egg evolution was not governed by a universal allometric constant. Instead, evolutionary forces beyond the constraints of physical scaling (for example, development or ecology) are required to explain the morphological diversification of insect eggs.

## Developmental traits and egg evolution

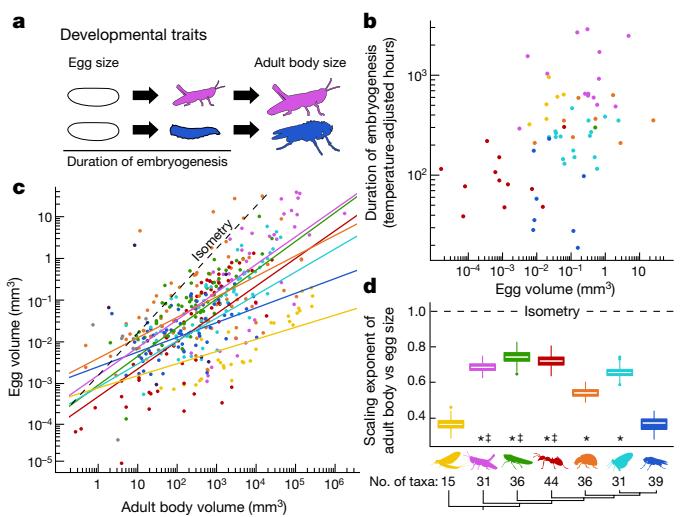
The egg is the starting material for embryogenesis, and the size of the hatchling is directly related to the size of the egg at fertilization<sup>35</sup>. It has been reported that embryogenesis takes longer in species with larger eggs<sup>22</sup> and that this relationship could influence size evolution<sup>20,21</sup>. This would be consistent with the observation that larger adult species



**Fig. 2 | The allometric relationship of egg shape and size evolves across insects.** **a–c**, Hypothesized relationships between size and shape: larger eggs are proportionally wider (**a**, solid line); larger eggs are proportionally longer (**b**, dotted line); shape and size scale isometrically (**c**, dashed line). **d**, Each hypothesis predicts a different scaling exponent—the slope of the regression between the log-transformed length and log-transformed width. Lines are as in **a–c**. **e**, Egg length and width plotted in log–log space. The dashed line represents a hypothetical 1:1 relationship (**c**). Solid lines are clade-specific phylogenetic generalized least-squares regressions; points are randomly selected representatives per genus. *n* numbers (genera): Palaeoptera, *n* = 104; Polyneoptera, *n* = 262; Condylgnathida, *n* = 202; Hymenoptera, *n* = 356; Neuropteroidea, *n* = 265; Amphiesmenoptera, *n* = 76; Antliophora, *n* = 199. **f**, The distribution of scaling exponents from phylogenetic generalized least-squares regressions, calculated over the posterior distribution. White lines, boxes, bars and dots represent median, 25–75th percentiles, 5–95th percentiles and outliers, respectively. Asterisks indicate a significant relationship ( $P < 0.01$ , exact values are shown in Supplementary Table 6) and double daggers indicate that the relationship is not distinguishable from isometry ( $P > 0.01$ , exact values are shown in Supplementary Table 7). *n* = 100 phylogenetic generalized least-squares regressions. Colours correspond to Fig. 1b.

have lower metabolic rates than smaller species<sup>36</sup>. To test this prediction across our egg dataset, we assembled published embryological records, and found that simply comparing egg volume and duration of embryogenesis yields the previously reported positive relationship<sup>22</sup> (Supplementary Fig. 17). However, a linear regression that does not account for phylogenetic relationships is inappropriate for this analysis owing to the covariance of traits on an evolutionary tree<sup>37</sup>. When we accounted for phylogenetic covariance, we found that there was no significant relationship between egg size and duration of embryogenesis across insects, such that eggs of very different sizes develop at a similar rate and vice versa ( $0.02 < P < 0.10$ ; Fig. 3b and Supplementary Table 11). These results suggest that the often-invoked trade-off between size and development<sup>20–22</sup> does not hold across insects.

We also tested the hypothesis that the size of the egg has a positive relationship with adult body size. Previous studies have reported this relationship in subsets of insects and have suggested that smaller insects lay proportionally larger eggs for their bodies<sup>11,35,38</sup>. Such a relationship between egg size and body size would result in an allometric scaling exponent that is less than one. We combined our dataset of egg size with published adult body length data for insect families<sup>39</sup>, and found that this relationship was not generalizable across all insect lineages. For example, in flies and their relatives (Antliophora), as well



**Fig. 3 | Developmental features do not co-vary with egg size.** **a**, Mature eggs undergo embryonic development, hatch and grow into adults. **b**, Egg volume ( $\text{mm}^3$ ) compared to duration of embryogenesis, defined as time from egg laying to hatching (hours), adjusted for incubation temperature. When phylogeny is accounted for, there is no significant relationship. **c**, Egg volume ( $\text{mm}^3$ ) compared to adult body volume, calculated as body length cubed ( $\text{mm}^3$ ). Dashed line represents a hypothetical 1:1 relationship (isometry). Solid lines are clade-specific phylogenetic generalized least-squares regressions; points are family- or order-level average egg size and median adult size. *n* numbers (family- or order-level averages): Palaeoptera, *n* = 15; Polyneoptera, *n* = 31; Condylgnathida, *n* = 36; Hymenoptera, *n* = 44; Neuropteroidea, *n* = 36; Amphiesmenoptera, *n* = 31; Antliophora, *n* = 39. **d**, The distribution of scaling exponents from phylogenetic generalized least-squares regressions. White lines, boxes, bars and dots represent median, 25–75th percentiles, 5–95th percentiles and outliers, respectively. Asterisks indicate a significant relationship ( $P < 0.01$ , exact values are shown in Supplementary Table 12) and double daggers indicate that the relationship is not distinguishable from isometry ( $P > 0.01$ , exact values are shown in Supplementary Table 13). *n* = 100 phylogenetic generalized least-squares regressions. Colours correspond to Fig. 1b.

as in mayflies and odonates (Palaeoptera), egg size is not predicted by body size, meaning that insects of similar body size lay eggs of different sizes (Antliophora  $P = 0.02$ , Palaeoptera  $P = 0.19$ ; Fig. 3c, d and Supplementary Table 13). In Polyneoptera, thrips and true bugs (Condylgnathida), and bees, ants and wasps (Hymenoptera), an isometric relationship between egg size and body size cannot be rejected (Polyneoptera  $P = 0.02$ , Hymenoptera  $P = 0.01$ , Condylgnathida  $P = 0.01$ ; Supplementary Fig. 18 and Supplementary Table 13). In general, the predictive power of the relationship between body size and egg size is low: average egg volume can vary by up to four orders of magnitude among species with a similar body size (Fig. 3c).

At the time of fertilization an egg is a single cell. We therefore tested whether the size of this cell evolved with the size of the genome, as has been observed for other cell types<sup>40</sup>, using a database of genome size for hexapods<sup>41</sup>. Although the data appeared to show a positive relationship between egg size and genome size (Supplementary Table 14), we found that this relationship was driven entirely by the lineage Polyneoptera (specifically grasshoppers, Acrididae). This lineage has evolved genome sizes that are an order of magnitude larger than other insects and has relatively large eggs (Supplementary Fig. 19). Across other insect lineages, egg volume and genome size are not significantly related ( $0 < P < 0.08$ ; Supplementary Table 14), and egg volume can range over six orders of magnitude for species with a similar genome size (Supplementary Fig. 19c). This indicates that genome size is not a general driver of egg size. The decoupling of genome size, body size and developmental rate from the evolution of egg sizes suggests that the diversification of insect eggs has not been universally constrained by development.

## Oviposition ecology explains egg morphology

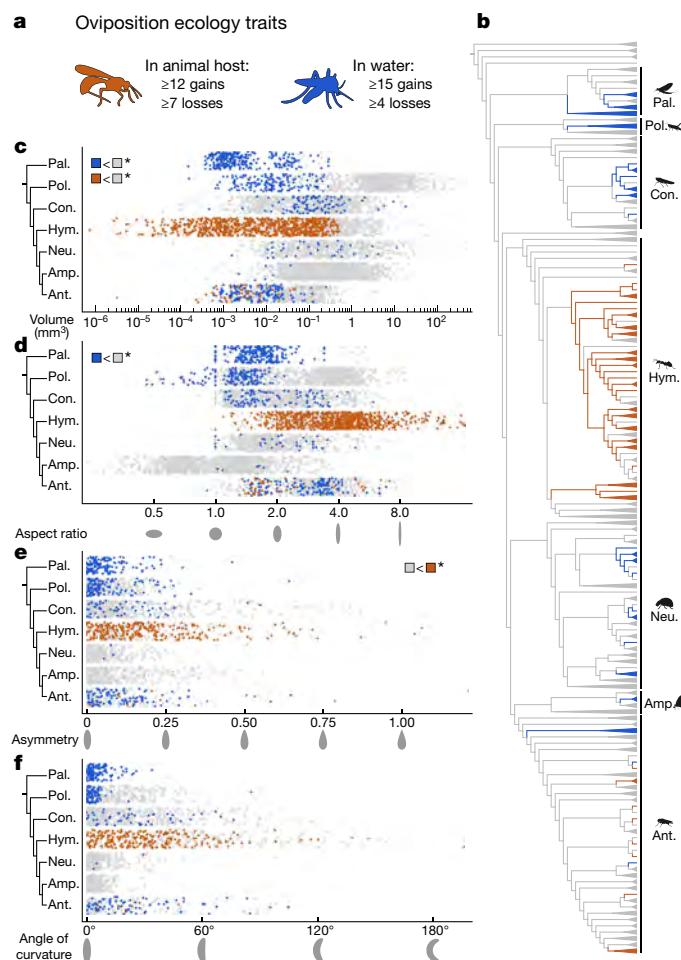
Egg size and shape have been predicted to evolve in response to changes in life history and ecology. Recent studies in birds have highlighted one such relationship, suggesting that birds with increased flight capability have more elliptical and asymmetrical eggs<sup>13</sup>. We investigated whether an analogous relationship exists between insect flight capability and egg shape. Unlike birds, insects have undergone hundreds of evolutionary shifts to flightless and even wingless forms<sup>42</sup>. We focused on two clades in which flight evolution has been extensively studied. Stick insects (Phasmatodea) have flightless and wingless species<sup>43,44</sup> (Supplementary Fig. 22), and many butterflies (Lepidoptera) show migratory behaviour<sup>45</sup>, which we used as a proxy for increased flight capability relative to non-migratory taxa (Supplementary Fig. 22). We found that, in contrast to birds, evolutionary changes in flight ability in these two insect clades were not associated with changes in egg shape (Ornstein–Uhlenbeck model with multiple optima per regime;  $\Delta\text{AICc}$  (Akaike information criterion)  $< 2$ , exact values are included in Supplementary Tables 18, 19).

Similar to flight capacity, the microenvironment that insect eggs experience varies widely, including being exposed to air, submerged or floating in water, or contained within a host animal<sup>8</sup>. Each microenvironment places different demands on the egg, such as access to oxygen and water during development<sup>15</sup>. Preliminary studies in small groups of insects have suggested that evolutionary changes in oviposition ecology and life history may drive the evolution of egg size and shape<sup>10,23</sup>. To test this prediction across all insects, we compiled records on two modes of oviposition ecology that have been extensively studied: oviposition within an animal host (internal parasitic oviposition) and oviposition in or on water. For each mode, we reconstructed ancestral changes along the insect phylogeny, and found that both aquatic and internal parasitic oviposition modes have been gained and lost multiple times independently (Fig. 4a, b and Supplementary Figs. 20, 21). This extensive convergent evolution allowed us to perform a strong test of whether egg size and shape evolution are explained by the evolution of oviposition ecology.

We found that the evolution of new oviposition environments is linked to changes in egg size and shape. Models that accounted for shifts to either aquatic or internal parasitic oviposition better explained size and shape distributions than models that did not (Ornstein–Uhlenbeck model,  $\Delta\text{AICc} > 2$ , exact values are shown in Supplementary Tables 15–17). In this analysis, we compared model fit for each ecology–trait pair separately, and found that these two ecological states were correlated with different egg morphologies. Specifically, shifts to aquatic oviposition were significantly associated with the evolution of smaller eggs with a lower aspect ratio (Fig. 4c, d and Supplementary Table 17), whereas shifts to internal parasitic oviposition were significantly associated with smaller, more asymmetric eggs (Fig. 4c, e and Supplementary Table 15). Moreover, we note that the smallest eggs are from parasitoid wasps that develop polyembryonically (that is, multiple embryos form from a single egg<sup>46</sup>; Supplementary Fig. 23). Neither oviposition mode is associated with consistent changes in the allometric relationship between size and shape (Supplementary Fig. 24).

Given that Ornstein–Uhlenbeck models can be favoured when dataset size and measurement error are large<sup>47</sup>, we repeated these analyses 100 times using simulated ecological states independent of egg morphological traits. The results of this bootstrap analysis showed that our observed result, which favoured ecological models of morphological evolution, is unlikely to be caused by dataset size alone ( $P = 0.01$ ; Supplementary Table 20). Moreover, these results were robust to uncertainty in phylogenetic relationships, and to uncertainty in how taxa were classified for oviposition ecology (Supplementary Table 16). These findings provide evidence that the microenvironment that is experienced by the egg has had an important role in morphological evolution.

Insect eggs present an ideal case for testing the predictability of macroevolutionary patterns in size and shape. By comparing insect egg size and shape, we found that previous hypotheses about evolutionary trade-offs with developmental time, body size or the presumed cost of



**Fig. 4 | Shifts in oviposition ecology are associated with changes in egg morphology.** **a**, Two modes of oviposition ecology: laying eggs within an animal host (orange; for example, parasitoid wasps), and in water (blue; for example, mosquitoes). Other oviposition substrates (for example, terrestrial or within plants) are shown in grey. **b**, Ancestral state reconstruction of oviposition mode reveals both evolved multiple times (see Supplementary Figs. 17, 18). **c–f**, The distribution of egg features, coloured by ecology. **c**, Volume ( $\text{mm}^3$ ; shown on a log scale). **d**, Aspect ratio (unitless; shown on a log scale). **e**, Asymmetry (unitless). **f**, Angle of curvature (degrees). Asterisks indicate that the model that accounts for ecology fits the data better than a non-ecological model (Ornstein–Uhlenbeck model with multiple optima,  $\Delta\text{AICc} > 2$ , exact values are shown in Supplementary Tables 14–19).

egg shells do not hold. Although we showed that developmental time is not linked to egg size, we suggest that other features of development (for example, cell number and distribution) may scale in predictable ways across eight orders of magnitude in egg size. Finally, we provide evidence that the ecology of oviposition drives the evolution of egg size and shape.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1302-4>.

Received: 28 November 2018; Accepted: 14 May 2019;  
Published online 3 July 2019.

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**Acknowledgements** This work was supported by the National Science Foundation (NSF) under grant no. IOS-1257217 to C.G.E., NSF GRFP DGE1745303 to S.H.C. and by a Jorge Paulo Lemann Fellowship to B.A.S.d.M. from Harvard University. We thank members of the Extavour laboratory and B. Farrell, C. Dunn, D. McCoy, D. Rice, A. Kao, E. Kramer, J. Boyle, L. Bittleston, M. Srivastava, M. Johnson, P. Wilton, R. Childers and S. Prado-Irwin for discussion, and the Ernst Mayr Library at the Museum of Comparative Zoology at Harvard, and specifically M. Sears, for assistance in gathering references.

**Reviewer information** *Nature* thanks Clay Cressler and the other anonymous reviewer(s) for their contribution to the peer review of this work.

**Author contributions** S.H.C. and S.D. conceived the project and generated the dataset. S.H.C. performed statistical analyses. B.A.S.d.M. performed phylogenetic analyses. All authors contributed to experimental design, interpretation and writing.

**Competing interests** The authors declare no competing interests.

#### Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41586-019-1302-4>.

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## METHODS

**Creating the insect egg dataset.** A list of the 1,756 literature sources used to generate the egg dataset is provided in the Supplementary Information. A full description of the methods used to assemble the insect egg dataset has been published elsewhere<sup>24</sup>. Egg descriptions were collected from published accounts of insect eggs using custom software to parse text from PDFs and measure published images (Fig. 1d), followed by manual verification. Each entry in the egg dataset includes a reference to an insect genus and, when reported, species name. Scientific names were validated using TaxReformer<sup>24</sup>, which relies on online taxonomic databases<sup>52–56</sup>. The final sample size of the dataset (over 10,000 egg descriptions) was determined to be sufficient because it included thousands of instances of repeated evolution of similar egg size and shape.

**Measuring egg features.** Full trait definitions are described in the Supplementary Information and summarized in brief below. To resolve ambiguous cases and to measure published images, we used the definitions below.

**Egg length.** We defined egg length as the distance in millimetres (mm) from one end to the other of the axis of rotational symmetry.

**Egg width.** We defined egg width as the widest diameter (mm), measured perpendicular to the axis of rotational symmetry of the egg. For eggs described in published records as having both a width and breadth or depth (that is, the egg is a flattened ellipsoid<sup>57</sup>), we defined width as the wider of the two diameters, and breadth as the diameter perpendicular to both the width and length.

**Egg volume.** Volume (mm<sup>3</sup>) was calculated using the equation for the volume of an ellipsoid:  $(1/6)\pi lw^2$ , following previous studies<sup>12,58</sup>.

**Egg aspect ratio.** Aspect ratio was calculated as the ratio of length to width.

**Egg asymmetry.** Asymmetry was calculated as the ratio between the two egg diameters at the first and third quartile of the length axis, minus one. The first quartile was always defined as the larger of the two diameters.

**Angle of egg curvature.** The angle of curvature was measured as the angle (degrees) of the arc created by the end points and mid-point of the length axis.

**Phylogenetic methods.** A genus-level phylogeny was built by combining mitochondrial 18S and 28S sequencing data from the SILVA database<sup>59–62</sup> with phylogenetic constraints from published higher-level insect phylogenies<sup>25,26</sup>. To account for phylogenetic uncertainty in comparative analyses, trees were estimated using a hierarchical approach<sup>63,64</sup>. Separate phylogenies for each insect order were inferred in a Bayesian framework using MrBayes v.3.2.6<sup>65</sup> and 100 post-burn-in trees were randomly chosen for each order using the order-level backbone trees of two previous studies<sup>25,26</sup>. See Supplementary Information for further details.

**Annotating the egg dataset with developmental trait data.** For developmental traits, a set of references was assembled from the embryological and ecological literature, and then used to compile data on interval between syncytial mitoses, time to cellularization and duration of embryogenesis. Developmental rate observations were rescaled to approximate rates at a standardized temperature of 20 °C following previous studies<sup>66</sup>. For a full list of sources, methods used in this calculation, and further discussion of developmental trait definitions, see Supplementary Information.

**Annotating the egg dataset with life-history trait data.** For each of the ecological features of interest (internal parasitic oviposition, aquatic oviposition, flightlessness and migratory behaviour), taxonomic descriptions from the literature were matched to taxa in the insect egg dataset. For some taxonomic groups, it was not possible to classify all members unambiguously. In these cases, the ecological state was coded ‘uncertain’ and the potential effect of this uncertainty on results was tested. For each trait the ancestral state reconstruction was estimated using an equal-rates model (R package corHMM<sup>67</sup>, function rayDISC, node.states = marginal). For a full list of sources and methods used see Supplementary Information.

**Data analysis and evolutionary model comparison.** Egg length, width, volume and aspect ratio were log<sub>10</sub>-transformed. Angle of curvature and asymmetry were square-root-transformed.

Models of evolution were compared using the R package geiger<sup>68</sup>. For each trait (egg length, width, volume, aspect ratio, asymmetry and angle of curvature), the model fits of Brownian motion, Ornstein–Uhlenbeck and early-burst models were compared against a null hypothesis of a white noise model that assumes no evolutionary correlation (see Supplementary Information for details). The performance of the best-fitting model was further analysed by comparing expected values of parameters from simulations under the model to observed parameters using the R package arbutus<sup>69</sup>.

The ancestral state of volume, aspect ratio and angle of curvature were mapped on the summary phylogeny using the R package phytools<sup>70</sup> (v.0.6-44, function contMap). Evolutionary rate regimes of volume, aspect ratio and the angle of curvature were fitted on the summary phylogeny using the program BAMM<sup>71,72</sup> (v.2.5.0, R package BAMMtools v.2.1.6, setBAMMpriors, prior for expected number of shifts set to 10, for 10,000,000 generations).

All evolutionary regression analyses were performed using a phylogenetic generalized least-squares approach in the R packages ape<sup>73</sup> (v.5.0, correlation

structure = corBrownian) and nlme<sup>74</sup> (v.3.1-131.1). Given that the early-burst models best fit the data, we also tested a corBlomberg correlation structure, which invokes an accelerating–decelerating model of evolution, with the decelerating rate of trait change fixed at 1.3.

For comparisons performed at the genus level, each regression was repeated over 100 trees randomly drawn from the posterior distribution randomly selecting a representative entry per genus from the egg dataset. For comparisons performed at the family level, each regression was repeated 100 times calculating the family level average egg data from 50% of entries per family.

For phylogenetic regressions controlling for a third variable, we calculated the phylogenetic residuals of each variable against the dependent variable, and then calculated the phylogenetic regression of the residuals<sup>75</sup>. To test alternative hypotheses, new data were simulated using a fixed scaling exponent and the parameters of the best-fitting model with the R package phylom<sup>76</sup> (v.2.5, function ‘rTrait’).

Allometric regressions were performed over all insect taxa as well as for seven monophyletic groups of insects individually (Palaeoptera, Polyneoptera, Condylognatha, Hymenoptera, Neuropteroidea, Amphiesmenoptera and Antliophora). In addition, the scaling exponent between egg length and width was calculated for each monophyletic group of taxa that had more than 20 tips but fewer than 50 tips.

Following ancestral state reconstruction of ecological regimes, for each ecology–trait pair (internal parasitic or aquatic oviposition combined with volume, aspect ratio, asymmetry or curvature) the fit of a Brownian motion model, an Ornstein–Uhlenbeck model with a single optimum and an Ornstein–Uhlenbeck model with an independent optimum for each ecological state were compared using the R package OUwie<sup>77</sup> (version 1.50). These analyses were repeated over 100 trees randomly drawn from the posterior distribution, and randomly selecting a representative egg for each genus.

Plots were generated in R. Figures were assembled with Adobe Illustrator. Egg images that were reproduced from other publications were converted to greyscale, contrast adjusted, rotated, and then masked from their backgrounds using Adobe Photoshop.

**Statistical information.** For evolutionary regressions and parametric bootstraps, a significance threshold of 0.01 was used. All P values were rounded to the nearest hundredth. Exact values for all statistical comparisons are available in the figure legends and Supplementary Information. For evolutionary model comparisons, weighted AICc values were compared at a significance threshold of 2. Evolutionary regressions were performed 100 times each, taking into account phylogenetic and phenotypic uncertainty. For more details see Supplementary Information.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

## Data availability

The dataset of insect eggs is publicly available at Dryad (<https://datadryad.org>) with doi:10.5061/dryad.pv40d2r and has been described elsewhere<sup>24</sup>. The phylogenetic posterior distributions are provided as Supplementary Information (phylogeny\_posterior\_distribution\_misof\_backbone.nxs and phylogeny\_posterior\_distribution\_rainford\_backbone.nxs).

## Code availability

All code required to reproduce the analyses and figures shown here is available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution).

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#### Data collection

Data in this study were collected from descriptions of insect eggs in the primary literature. We used custom software to extract text descriptions and measure published images. All code used to generate the insect egg dataset is made freely available. Python code used to compile the dataset and extract text information from sources, as well as the R code used to convert the raw dataset to the final dataset is available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution). Python code used to measure published images of eggs is available at [https://github.com/sdonougue/Insect\\_Egg\\_Image\\_Parser](https://github.com/sdonougue/Insect_Egg_Image_Parser). Python code to cross-reference the egg dataset with taxonomic tools is available at <https://github.com/brunoasm/TaxReformer>.

#### Data analysis

All code required to reproduce the analyses in this study is made freely and publicly available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution), directory 'analyze\_data'. The software R, version 3.4.2, was used for all statistical analyses. Additional versions for R packages are listed in the methods and on the github repository.

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## Ecological, evolutionary & environmental sciences study design

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### Study description

The study describes the evolutionary analyses of egg size and shape from thousands of insect species. The dataset was assembled from the primary literature following an explicit and reproducible workflow. Phylogenies were assembled that were enriched for taxa in the egg dataset, and incorporated published relationships between insects. Using the dataset and phylogenies, regression analyses and ecological model comparisons were performed to test trait relationships across taxonomic groups. Regression analyses were performed 100 times to assess the sensitivity of results to both phylogenetic and phenotypic variation. Ecological model comparisons were performed over a series of classification methods to assess sensitivity to bias in ecological definitions. Significance thresholds were set for p-values < 0.01, and for model comparisons,  $\Delta AIC_c > 2$ . In all comparisons, the maximum number of descriptions that had both phylogenetic and phenotypic data were used. All results were robust to measures of sensitivity - no results were excluded from the publication based on conflicting or negative outcomes.

### Research sample

The research sample used to generate these results is a dataset of hexapod egg measurements collected from the primary literature. Hexapods were chosen as the appropriate scale because existing hypotheses about egg size and shape were made based on preliminary hexapod data. The dataset was collected from the literature following the methods described in Church et al. "A dataset of egg size and shape from more than 6,700 insect species", *Scientific Data*, (2019). The sample was collected using methods to maximize the number of descriptions as well as the representation across the phylogeny. The sample includes representatives from every major lineage, and our results assessing sampling bias indicated that our sampling scales with the diversity of described insects per lineage, such that most lineages have 1 representative per 100 species (see Church et al. 2018). The final sample size of the dataset (>10,000 egg descriptions) was determined to be sufficient because it included thousands of instances of repeated evolution of similar egg size and shape. This allowed for robust tests of evolutionary patterns and hypotheses.

### Sampling strategy

Evolutionary analyses were performed in such a way as to maximize the number of samples that could be compared using an evolutionary tree. Regression analyses were repeated 100 times to include both the effects of phylogenetic uncertainty, as well as the sampling uncertainty within an insect clade. This was accomplished by choosing a random tree from the posterior distribution, and by choosing a random representative description for each taxon, for each of the 100 repeated analyses. The sample size of each lineage specific regression was determined by the maximum number of egg descriptions which were available and could be placed on an enriched phylogenetic tree. Clades with too few taxa that met these criteria (threshold < 20 taxa, e.g. Psocodea) were excluded from the analyses.

### Data collection

The data was originally recorded by many thousands of entomologists, in separate publications, over 250 years. The data was aggregated following an explicit and reproducible workflow, which included using a number of predetermined search terms to query online databases and gather relevant publications. We used custom software (made freely available) to then extract egg descriptions from the literature, maximizing both the number of descriptions and the consistency across publications.

### Timing and spatial scale

Online literature databases were queried for relevant publications between October 2015 to August 2017, after which all predetermined terms had been searched and data collection was stopped. Publications were not excluded based on geography or language.

### Data exclusions

No text descriptions of eggs were excluded from the study, but a select number of re-measurements of published images of eggs were excluded based on sensitivity tests of the image measuring software using simulated egg shapes. Our analysis of this software indicated that in particular extreme combinations of traits, the software was less accurate in measuring features of egg shape (see Church et al. 2018). Therefore, using a pre-determined exclusion criterion based these results, the top 0.01% of entries for aspect ratio and asymmetry were excluded (~10 entries each), and curvature data was excluded for eggs with an aspect ratio <1. No further

	<p>data was excluded from any evolutionary analysis (e.g. regressions, model comparisons).</p>
Reproducibility	All experiments performed here are fully reproducible using the R code available at <a href="https://github.com/shchurch/Insect_Egg_Evolution">https://github.com/shchurch/Insect_Egg_Evolution</a> . All the data required to generate the figures is included in that repository, and a description of each code file is provided. In no case was an analysis repeated which provided a different result or a failed result, compared to what is reported here.
Randomization	For evolutionary analyses, a random tree from the posterior distribution and a representative egg description for each taxon was randomly chosen for each iteration of the regression experiments. Randomness was determined by shuffling the datasets in R.
Blinding	The data collection was not fully blinded, as the custom software cannot currently fully automate the process of data extraction from the literature. Therefore all data collection was assisted automatically based on explicit rules, and then manually verified. Evolutionary analyses were blinded, given that analyses for each lineage, model, or trait comparison were performed exactly equivalently using objective criteria (e.g. predetermined significance thresholds) and results were reported exactly as generated by R.

Did the study involve field work?  Yes  No

## Reporting for specific materials, systems and methods

### Materials & experimental systems

- |     |                       |
|-----|-----------------------|
| n/a | Involved in the study |
|-----|-----------------------|
- Unique biological materials
  - Antibodies
  - Eukaryotic cell lines
  - Palaeontology
  - Animals and other organisms
  - Human research participants

### Methods

- |     |                       |
|-----|-----------------------|
| n/a | Involved in the study |
|-----|-----------------------|
- ChIP-seq
  - Flow cytometry
  - MRI-based neuroimaging

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# Insect egg size and shape evolve with ecology but not developmental rate

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# Insect egg size and shape evolve with ecology but not developmental rate

## *Supplementary Information*

Samuel H. Church<sup>\*,1,†</sup>, Seth Donoughe<sup>\*,1,2</sup>, Bruno A. S. de Medeiros<sup>1</sup>, Cassandra G. Extavour<sup>1,3,†</sup>

This document contains Supplementary Methods, Supplementary Figures S1-S24, and Supplementary Tables S1-S22. These provide additional methodological details, a more complete description of the diversity of insect eggs, ancestral state reconstructions, and evolutionary model fitting results.

## Contents

<b>1</b>	<b>The insect egg dataset</b>	<b>2</b>
1.1	Defining egg traits . . . . .	2
<b>2</b>	<b>Estimating phylogenetic relationships</b>	<b>4</b>
2.1	Obtaining genetic data for genera in the egg dataset . . . . .	4
2.2	Verifying sequence identity . . . . .	4
2.3	Estimating phylogenies for insect orders . . . . .	6
2.4	Building the backbone phylogenies . . . . .	7
<b>3</b>	<b>Morphological diversity of insect eggs</b>	<b>12</b>
3.1	Distribution of egg traits within insect clades . . . . .	12
3.2	Insect egg morphospace . . . . .	12
3.3	Morphological distribution of eggs laid in egg cases . . . . .	16
<b>4</b>	<b>Evolutionary history of egg traits</b>	<b>20</b>
4.1	Evolutionary model fitting . . . . .	20
4.2	Ancestral state reconstructions and evolutionary rate . . . . .	21
<b>5</b>	<b>Allometric slopes of egg shape vary across insects</b>	<b>24</b>
5.1	Calculating allometric exponents using phylogenetic generalized least squares (PGLS) . . . . .	24
5.2	Dynamic evolution of the allometry of egg shape and size . . . . .	24
5.3	Accounting for body size in egg shape and size allometries . . . . .	28
5.4	Testing additional shape allometries . . . . .	28
<b>6</b>	<b>Egg size and development</b>	<b>30</b>
6.1	Collecting developmental time data . . . . .	30
6.2	Comparing egg size and developmental time . . . . .	31

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6.3	Egg size and body size . . . . .	31
6.4	Egg size and genome size . . . . .	33
7	<b>Evolutionary history of ecological traits</b>	<b>35</b>
7.1	Parasitoid and internal oviposition . . . . .	35
7.2	Aquatic insects and oviposition . . . . .	36
7.3	Migration, flight, and wingless insects . . . . .	36
7.4	Testing eco-evolutionary models of egg evolution . . . . .	40
7.5	Distribution of polyembryonic insects in egg morphospace . . . . .	42
7.6	Allometry and ecology . . . . .	42
8	<b>Summary of Phylogenetic Generalized Least Squares (PGLS) results</b>	<b>45</b>
	<b>References</b>	<b>47</b>

## 1 The insect egg dataset

A complete description of the methods used to compile the insect egg dataset is published in an accompanying article<sup>1</sup>. Here, we briefly summarize those methods. Descriptions of insect eggs were assembled from the published entomological literature using custom bioinformatic software. A list of the 1,756 literature sources used to generate the egg dataset is provided as a supplemental file, ‘bibliography\_egg\_dataset.pdf’. Each entry in the dataset includes an insect’s genus name and, if it was available from the source publication, the species name. Every entry also includes text measurements of egg dimensions and/or a published image of an insect egg. Published images were subsequently measured using custom software to extract additional egg size and shape information. Taxonomic names were checked against databases for synonyms and matched to online sequence databases for building phylogenies, using the software TaxReformer<sup>1</sup>. The dataset has been statistically assessed for accuracy of measurement tools as well as potential sources of variation (e.g. intraspecific variation and variation across publications), and the results of those assessments are also included in the publication describing the dataset<sup>1</sup>.

### 1.1 Defining egg traits

The trait descriptions in this section are reproduced from the accompanying article that describes the insect egg dataset<sup>1</sup>. For each trait listed below we used the descriptions of egg length and width as presented in the original publications. Given that conventions vary across entomologists and insect taxonomic groups, we present the following definitions to resolve ambiguous cases and to serve as a suggestion for future egg descriptions.

*Egg:* The term *egg* is used to describe several successive developmental stages, including the mature oocyte, the zygote at the one-cell stage, and the developing embryo in its eggshell. When multiple descriptions were available

within a single publication, for consistency we selected measurements that were recorded closest to the time of fertilization, given that in some insects it has been documented that the dimensions of the egg change over time (typically <20% change in length due to water exchange during embryonic development)<sup>2–6</sup>. In most insects the egg is oviposited outside the adult body, However, in viviparous insects, eggs proceed through some or all of embryonic development within the body of the mother. The egg is often enveloped in a secreted eggshell called the chorion<sup>6</sup>, which may have elaborations (e.g. dorsal appendages or opercula)<sup>7</sup>. We selected egg measurements that excluded chorionic elaborations over those that included them, as our goal was to measure the comparable cellular material across species.

*Length:* To resolve ambiguous cases, and when measuring egg features from images, we defined egg length as the distance in millimeters (mm) of the axis of rotational symmetry. This definition maximizes consistency with published descriptions of egg length. Under this definition, length is not always longer than width (as defined below). For some insect groups (e.g. Lepidoptera) the axis of rotational symmetry is sometimes referred to in the literature as *height*<sup>8–10</sup>. For published images with a scale bar, we measured both the straight and curved length of the egg (for those eggs that are curved), but for all analyses and figures, we used the straight length of the egg in order to maximize consistency with published records. Further details on how egg traits were measured from egg images are available<sup>1</sup>.

*Width and breadth:* To resolve ambiguous cases, and when measuring egg features from images, we defined width as the widest diameter (mm), measured perpendicular to the axis of rotational symmetry of the egg. For some insect groups this axis is referred to in the literature as diameter<sup>8</sup> or breadth<sup>11</sup>. For eggs described in published records as having a length, width, and breadth or depth (i.e., the egg is a flattened ellipsoid<sup>12</sup>), we considered *width* as the wider of the two diameters, and *breadth* as the diameter perpendicular to both width and length. For published images with a scale bar, we measured width as the widest of the three egg diameters at the first quartile, midpoint, and third quartile of the length axis. We did not measure breadth from published images.

*Volume:* Volume (mm<sup>3</sup>) was calculated using the equation for the volume of an ellipsoid, following previous studies<sup>13,14</sup>. The formula is  $\frac{1}{6}\pi lwb$ , with *l*, *w*, and *b* as length, width, and breadth, respectively. This simplifies to  $\frac{1}{6}\pi lw^2$  when the egg is rotationally symmetric. For records in which the volume was reported but egg length and width were not, we used the reported volume. For all other entries, we recalculated volume from the measurements in the text and from measurements of images published with a scale bar.

*Aspect ratio:* We calculated aspect ratio as the ratio of length to width. An aspect ratio of one corresponds to a spherical egg. An aspect ratio less than one corresponds to an egg that is wider than long (oblate ellipsoid). An aspect ratio greater than one corresponds to an egg that is longer than it is wide (prolate ellipsoid). We note that egg *ellipticity* has been used to describe egg shape in birds<sup>15,16</sup> and that it can be calculated as the aspect ratio minus one. Analyses testing the sensitivity of our measurement software for egg images indicated that the variance in measured aspect ratio is highest for eggs with extremely high aspect ratios<sup>1</sup>. Therefore we excluded the eggs in the top 0.1 percentile of aspect ratio from subsequent analyses. We recorded the aspect ratio from images published with or without a scale bar, as aspect ratio is a scale-free attribute.

*Asymmetry:* We defined asymmetry as  $\frac{\max(q_1, q_3)}{\min(q_1, q_3)} - 1$ , where *q*<sub>1</sub> and *q*<sub>3</sub> are the egg diameters at the first and third

quartile of the curved length axis. Therefore an egg with an asymmetry of zero has quartile diameters with equal length. Baker's  $\lambda$  value, used to measure asymmetry in bird eggs<sup>16</sup>, can be converted to the asymmetry parameter used in the present study (as shown in Fig. S6). Analyses testing the sensitivity of our image measuring software indicated that the variance is highest for eggs with extremely high values of asymmetry<sup>1</sup>. We therefore excluded the eggs in the top 0.1 percentile of asymmetry from subsequent analyses. Asymmetry was only recorded from published egg images.

*Angle of curvature:* We defined the angle of egg curvature as the angle of the arc created by the endpoints of the length axis and the midpoint of  $q_2$  (the width of the egg at the point perpendicular to the straight length axis). Analyses testing the sensitivity of our image measuring software indicated that the variance in curvature increases when the curvature and aspect ratio are low<sup>1</sup>. We therefore did not calculate curvature for eggs with an aspect ratio of one or less. Angle of curvature was only recorded from published egg images.

## 2 Estimating phylogenetic relationships

### 2.1 Obtaining genetic data for genera in the egg dataset

While there are published order-level<sup>17</sup> and family-level<sup>18</sup> phylogenies for insects, to our knowledge there is no tree that includes all genera for which we assembled egg data. To address this, we produced a new tree by combining publicly available sequence data for the genera in the egg dataset with phylogenetic results from published insect evolutionary studies<sup>17,18</sup>. Sequence data for 18S and 28S ribosomal RNA were obtained from the SILVA database<sup>19–22</sup>, a curated set of sequences for both the small and large ribosomal units. Sequences classified as Hexapoda in the SILVA database (release 128) were downloaded and associated with the corresponding National Center for Biotechnology Information (NCBI) ID using NCBI Entrez tools implemented in Biopython<sup>23</sup>. Each NCBI ID was then searched on the Open Tree of Life Taxonomy (OTT) to obtain the corresponding OTT ID, the identifier used to link sequence data to the egg dataset. Finally, the dataset was curated by keeping only the longest sequence available for each species and genus in the egg dataset.

### 2.2 Verifying sequence identity

To avoid inclusion of mislabeled or uninformative sequences, the data downloaded from the SILVA database were filtered using a phylogenetic criterion. First we created a reference dataset of ribosomal RNA sequences from the Misof et al. (2014)<sup>17</sup> order-level dataset, as downloaded from the NCBI Sequence Read Archive (SRA). Raw reads from the SRA were filtered with Trimmomatic (version 0.32)<sup>24</sup> and mapped to the SILVA sequences to identify ribosomal RNA, using bowtie2 (version 2.2.9)<sup>25</sup>. Ribosomal RNA reads were assembled using Trinity, and the identity of the longest assembled contig was checked using BLAST in NCBI. For some taxa in the Misof et al. (2014) read archive we could not assemble rRNA sequences *de novo*, and in these cases we used reference sequences from the SILVA database which corresponded to the same genus in the Misof et al. (2014) tree.

Next, the reference sequences were aligned using MAFFT (version 7.245)<sup>24</sup> with the E-INS-I algorithm in Geneious

(Biomatters) and trimmed manually. Reference alignments used for 18S and 28S are available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution), directory ‘phylogeny’. Candidate SILVA sequences that matched an insect genus in the egg dataset by name were added to this reference alignment with MAFFT (option --keeplength, --addlong, and the default alignment algorithm). Aligned candidate SILVA sequences were placed on the Misof et al. (2014)<sup>17</sup> phylogeny using the evolutionary placement algorithm implemented in RAxML (version 8.2.9<sup>24,26</sup>). Candidate sequences that were placed in a different insect order on the phylogeny than the order reported in OTT were removed from the dataset.

Evolutionary placement	Misof et al. (2014) <sup>17</sup>	Open tree taxonomy	SILVA
Archaeognatha	Archaeognatha	Archaeognatha	Archaeognatha
Coleoptera	Coleoptera	Coleoptera	Coleoptera
Collembola	Collembola	Collembola	Collembola
Dermoptera	Dermoptera	Dermoptera	Dermoptera
<b>Blattodea</b>	<b>Blattodea, Isoptera</b>	<b>Blattodea</b>	<b>Blattodea, Isoptera</b>
Diplura	Diplura	Diplura	Diplura
Diptera	Diptera	Diptera	Diptera
Embioptera	Embioptera	Embioptera	Embioptera
Ephemeroptera	Ephemeroptera	Ephemeroptera	Ephemeroptera
Grylloblattodea	Grylloblattodea	Grylloblattodea	Grylloblattodea
Hemiptera	Hemiptera	Hemiptera	Hemiptera
Hymenoptera	Hymenoptera	Hymenoptera	Hymenoptera
Lepidoptera	Lepidoptera	Lepidoptera	Lepidoptera
Mantodea	Mantodea	Mantodea	Mantodea
Mantophasmatodea	Mantophasmatodea	Mantophasmatodea	Mantophasmatodea
Mecoptera	Mecoptera	Mecoptera	Mecoptera
Megaloptera	Megaloptera	Megaloptera	Megaloptera
Neuroptera	Neuroptera	Neuroptera	Neuroptera
Odonata	Odonata	Odonata	Odonata
Orthoptera	Orthoptera	Orthoptera	Orthoptera
Phasmatodea	Phasmatodea	Phasmatodea	Phasmatodea
Plecoptera	Plecoptera	Plecoptera	Plecoptera
Protura	Protura	Protura	Protura
<b>Psocodea</b>	<b>Psocodea</b>	<b>Phthiraptera, Psocoptera</b>	<b>Phthiraptera, Psocoptera</b>
Raphidioptera	Raphidioptera	Raphidioptera	Raphidioptera
Siphonaptera	Siphonaptera	Siphonaptera	Siphonaptera
Strepsiptera	Strepsiptera	Strepsiptera	Strepsiptera
Thysanoptera	Thysanoptera	Thysanoptera	Thysanoptera
Trichoptera	Trichoptera	Trichoptera	Trichoptera
Zoraptera	Zoraptera	Zoraptera	Zoraptera
<b>Zygentoma</b>	<b>Zygentoma</b>		<b>Lepismatidae, Thysanura</b>

Table S1: **Equivalence of order-level taxonomic concepts of main sources of data.** Differences in taxonomic names between data sources are shown in bold.

Order	Genera with OTT IDs in the egg dataset	Genera with 18S data	Genera with 28S data	Genera with any rRNA data
Archaeognatha	2	2	2	2
Coleoptera	381	255	171	279
Collembola	8	7	6	7
Dermoptera	7	5	1	5
Blattodea	74	52	45	57
Diplura	3	3	3	3
Diptera	271	114	186	207
Embioptera	2	1	1	1
Ephemeroptera	76	62	42	62
Grylloblattodea	2	2	2	2
Hemiptera	431	185	139	215
Hymenoptera	635	341	338	394
Lepidoptera	1025	69	89	136
Mantodea	6	6	6	6
Mantophasmatodea	3	2	3	3
Mecoptera	7	3	3	3
Megaloptera	6	2	1	2
Neuroptera	32	20	2	20
Odonata	53	42	48	49
Orthoptera	184	89	66	93
Phasmatodea	113	45	58	61
Plecoptera	71	61	40	63
Protura	2	2	2	2
Psocodea	29	17	2	17
Raphidioptera	1	1	0	1
Siphonaptera	14	11	11	12
Strepsiptera	5	2	0	2
Thysanoptera	7	4	2	4
Trichoptera	23	13	3	14
Zoraptera	1	1	1	1
Zygentoma	2	2	2	2

Table S2: Number of genera from egg dataset included in DNA sequence alignments.

### 2.3 Estimating phylogenies for insect orders

Ribosomal RNA sequences that passed the filtering criteria were aligned using UPP (version 4.3.1)<sup>27,28</sup>, which allowed us to align thousands of full and partial rRNA sequences. Bayesian clock models require an impractical computation time when applied to hundreds or thousands of sequences. Therefore, instead of performing a single phylogenetic analysis for all insects in our study, we divided the alignment into taxonomic orders and inferred a distribution of trees for each order individually (all orders included here have been recovered as monophyletic in previous studies<sup>17</sup>). For each order-level alignment, one outgroup sequence was included from every other order. The representative outgroup sequences were randomly selected from those taxa with both 18S and 28S sequences,

or from taxa with 18S when both sequences were not available for a given order.

Order-level alignments were trimmed by removing regions at the alignment margins with less than 20% of the species included. Internal sites of the alignment that were represented by fewer than ten sequences were also removed, as were sequences with fewer than 100 total unambiguous sites. It has been shown that trimming of sites with excessive amounts of missing data speeds up computation and does not interfere with phylogenetic inference, while more aggressive criteria for trimming usually results in lower-quality trees<sup>29</sup>. After trimming, ribosomal genes were concatenated into a single dataset (see Table S2 for statistics on genera with sequence data included in this study).

For each alignment we generated a distribution of phylogenetic trees under a Bayesian framework with MrBayes (version 3.2.6<sup>30</sup>). Alignments were partitioned by gene, using a general time-reversal (GTR) model<sup>31</sup> with invariant sites and gamma rate variation applied to each partition. Molecular clock rates were allowed to vary according to the Independent Gamma rates model. The birth-death model was used for the tree topology prior, with speciation and extinction priors derived from previous inferences of diversification rate for insects based on the Rainford et al. (2014) tree<sup>32</sup>.

Insect families that are present in the Rainford et al. (2014) study and are considered monophyletic on the Open Tree of Life (OTL) were constrained to be monophyletic in our phylogenetic analysis. We used “soft constraints” for these relationships, meaning that taxa were allowed to be placed freely within an order if they belonged to families that were not considered monophyletic on the OTL or were not present in the Rainford et al. (2014) study. Insect orders, excluding the outgroup sequences, were also constrained to be monophyletic. We used the estimated divergence times from the Misof et al. study (2014) as the calibration time between orders, while nodes within each order were not time calibrated.

For each alignment we ran six metropolis-coupled Markov chains, with four chains per run, for at least 25 million generations, saving every 10,000 generations and removing the first 10% of trees as burn-in. Convergence was assessed by the standard deviation of split frequencies between the six runs and by checking traces for each parameter in Tracer<sup>33</sup>. Convergence was achieved (<0.05 split frequencies) for all orders except Diptera (Table S3 and S4). In this case, inspection of trace files revealed that three of the six markov chains converged to a local maximum with lower likelihood, and we removed these from further analyses. In subsequent analyses we used a random sample drawn from the posterior distribution to account for uncertainty in relationships.

## 2.4 Building the backbone phylogenies

We incorporated the results from published phylogenetic studies of insects<sup>17,18</sup> into our analysis using phylogenetic backbones. For each order, a random sample of 100 trees from the posterior distribution was grafted onto one of two alternative backbone phylogenies, one from Misof et al. (2014)<sup>17</sup> and one from Rainford et al. (2014)<sup>18</sup>, which differ in both the inferred relationships between orders (shown in Fig. S1) and the estimated divergence times. This grafting approach is similar to that used to infer other large-scale phylogenies, such as those for seed plants<sup>34</sup> and birds<sup>35</sup>. Maximum clade credibility trees (MCC) were also generated by grafting the MCC tree of each order to the corresponding backbone (Fig. S2). The final 100 trees drawn from the posterior distributions are available as the

supplementary files ‘phylogeny\_posterior\_distribution\_misof\_backbone.nxs’ and ‘phylogeny\_posterior\_distribution\_rainford\_backbone.nxs’.

Hereafter we refer to the resulting genus-level trees as the “Misof backbone tree” and the “Rainford backbone tree”. All primary figures and tables shown in this study are based on the Misof backbone tree, with a comparison of the results between the backbones given in Table S21.

Rainford et al. (2014)<sup>18</sup> topology and divergence times were readily available from their supplementary data, but Misof et al. (2014)<sup>17</sup> provided divergence times only as a table, with a time tree included as a figure. We added the Misof backbone<sup>17</sup> divergence times as annotations to their respective nodes in a new cladogram. A tree file containing these annotations is included in the present study at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution) file ‘fully\_annotated\_misof.nexml’.

Tree and alignment manipulations throughout the pipeline were done by custom bash and python scripts using Biopython<sup>23</sup> and Dendropy<sup>36</sup>. Some steps of this pipeline made use of GNU parallel<sup>37</sup>.

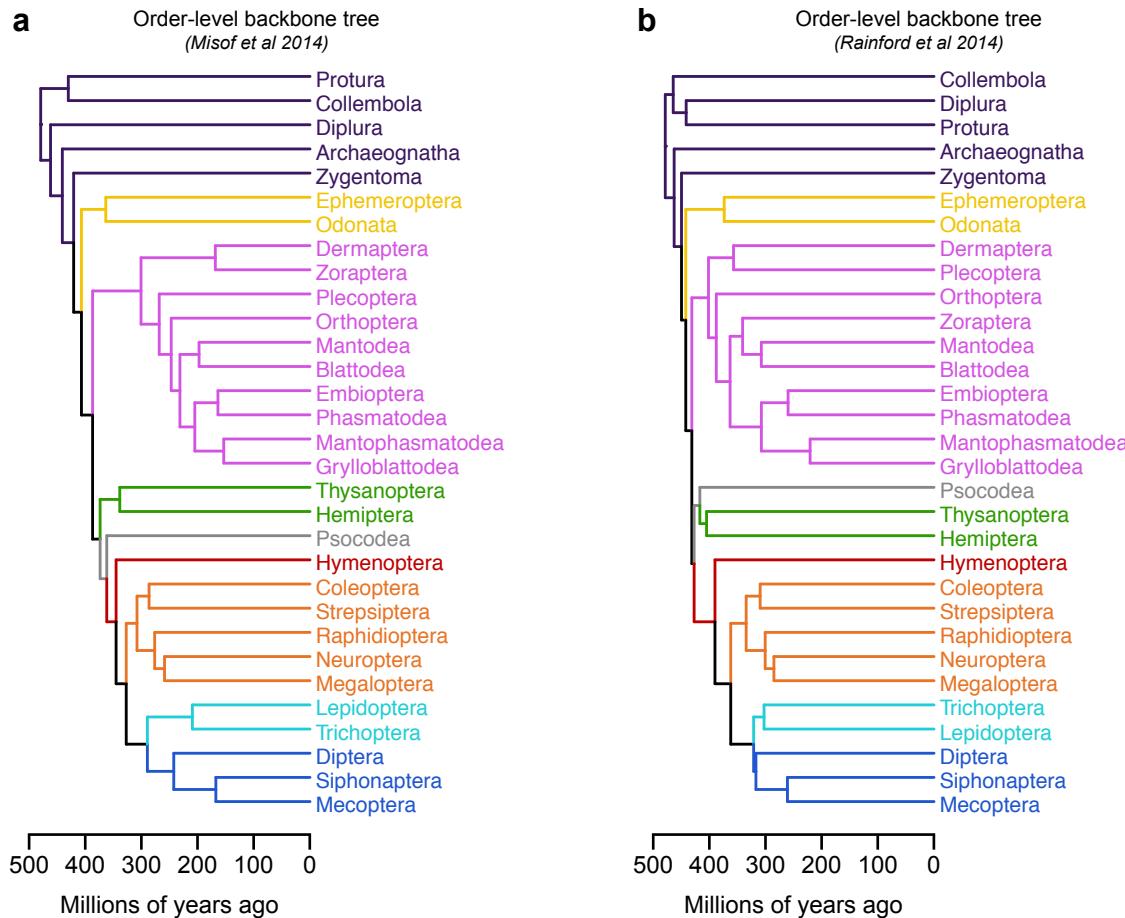


Figure S1: Relationships between insect orders in two backbone phylogenies. **a**, Order-level backbone tree from Misof et al. (2014)<sup>17</sup>. **b**, Order-level backbone tree from Rainford et al. (2014)<sup>18</sup>.

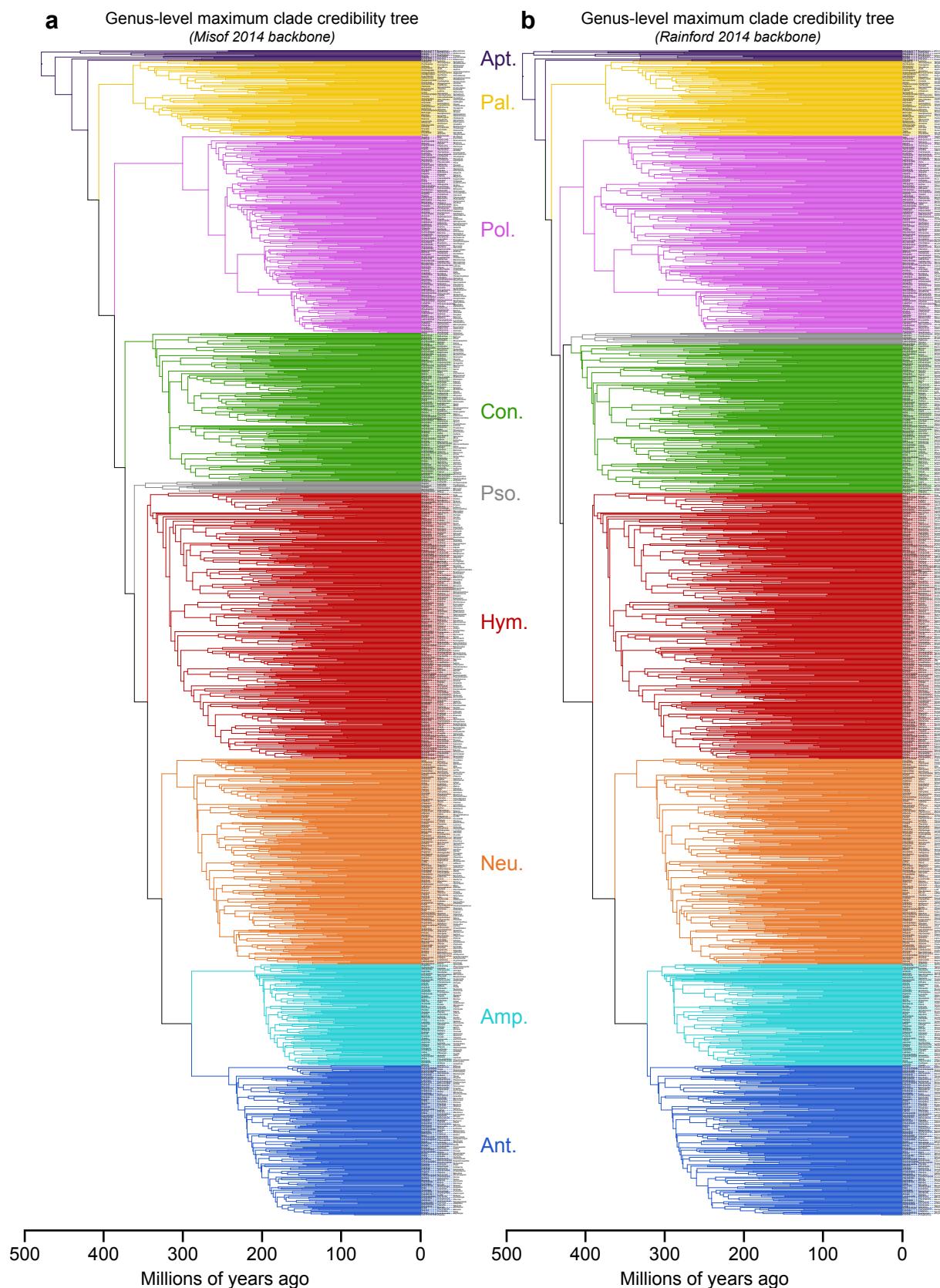


Figure S2: **Maximum clade credibility hexapod phylogenies.** a, Genus-level maximum clade credibility tree with the backbone tree from Misof et al. (2014) fixed as a constraint<sup>17</sup>. b, Genus-level maximum clade credibility tree with the backbone tree from Rainford et al. (2014) fixed as a constraint<sup>18</sup>. Colors correspond to the clades shown in Fig. S1

Taxon	Post-burn-in samples	ESS (likelihood)	ESS (prior)	Standard deviation of split frequencies	Number of tips in ingroup
Archaeognatha	191582	158416	29774	0.00000	2
Coleoptera	168768	2568	1505	0.00219	279
Collembola	196430	159517	17209	0.00000	7
Dermoptera	192982	161111	19329	0.00028	5
Blattodea	184724	55326	5125	0.00161	57
Diplura	191738	161361	29803	0.00000	3
Diptera	69964	1167	685	0.01511	207
Ephemeroptera	200286	79544	4986	0.00256	62
Grylloblattodea	192970	200957	27967	0.00000	2
Hemiptera	196350	10049	1949	0.00254	216
Hymenoptera	116106	1061	1037	0.00374	394
Lepidoptera	359072	11835	3366	0.00097	136
Mantodea	189820	139162	15509	0.00057	6
Mantophasmatodea	190132	159398	20418	0.00009	3
Mecoptera	190162	184041	30823	0.00000	3
Megaloptera	188398	169329	30842	0.00000	2
Neuroptera	187666	115866	13574	0.00151	20
Odonata	185388	37135	3956	0.00165	49
Orthoptera	183450	40848	1722	0.00008	93
Phasmatodea	185258	46340	4450	0.00282	61
Plecoptera	188678	61924	3706	0.00095	63
Protura	192862	180886	31648	0.00000	2
Psocodea	191848	139724	13090	0.00003	17
Siphonaptera	135260	92697	8488	0.00075	12
Strepsiptera	151750	134099	28530	0.00000	2
Thysanoptera	153506	152350	22569	0.00000	4
Trichoptera	136880	114901	8835	0.00018	14
Zygentoma	192566	168588	31878	0.00000	2

Table S3: Convergence statistics for phylogenetic analyses using Misof tree<sup>17</sup> as backbone. Out of six runs, Diptera only includes the three that converged to similar likelihood values.

Taxon	Post-burn-in samples	ESS (likelihood)	ESS (prior)	Standard deviation of split frequencies	Number of tips in ingroup
Archaeognatha	191582	158416	29774	0.00000	2
Coleoptera	168768	2568	1505	0.00219	279
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Trichoptera	136880	114901	8835	0.00018	14
Zygentoma	192566	168588	31878	0.00000	2

Table S4: Convergence statistics for phylogenetic analyses using Rainford tree<sup>18</sup> as backbone. Out of six runs, Diptera only includes the three that converged to similar likelihood values.

### 3 Morphological diversity of insect eggs

#### 3.1 Distribution of egg traits within insect clades

To place the diversity of insect propagule sizes in context, we compared their distribution to a recently published study of eggs in birds<sup>16</sup>, as well as to an estimated range of extant plant seed sizes (Fig. S3, panel a). We found that insect eggs range across eight orders of magnitude in volume, from  $10^{-6}$  to  $10^2$  mm<sup>3</sup>. In comparison, bird eggs range across three orders of magnitude in volume, based on the largest (*Aepyornis sp.*, length 238 mm, width 164 mm) and smallest egg (*Hylocharis xanthusii*, length 12.1 mm, width 8.0 mm) included in the Stoddard et al. (2017)<sup>16</sup> dataset. Angiosperm seed volumes range over more than 11 orders of magnitude, from the dust-seeds of orchids (*Paphiopedilum barbatum*, volume  $5.69 * 10^{-5}$  mm<sup>3</sup>)<sup>38</sup> to the giants seeds in palms (*Lodoicea maldivica*, length ~300 mm, width ~280 mm)<sup>39</sup>. Both birds and angiosperms are younger and less speciose than insects<sup>17,40–42</sup>.

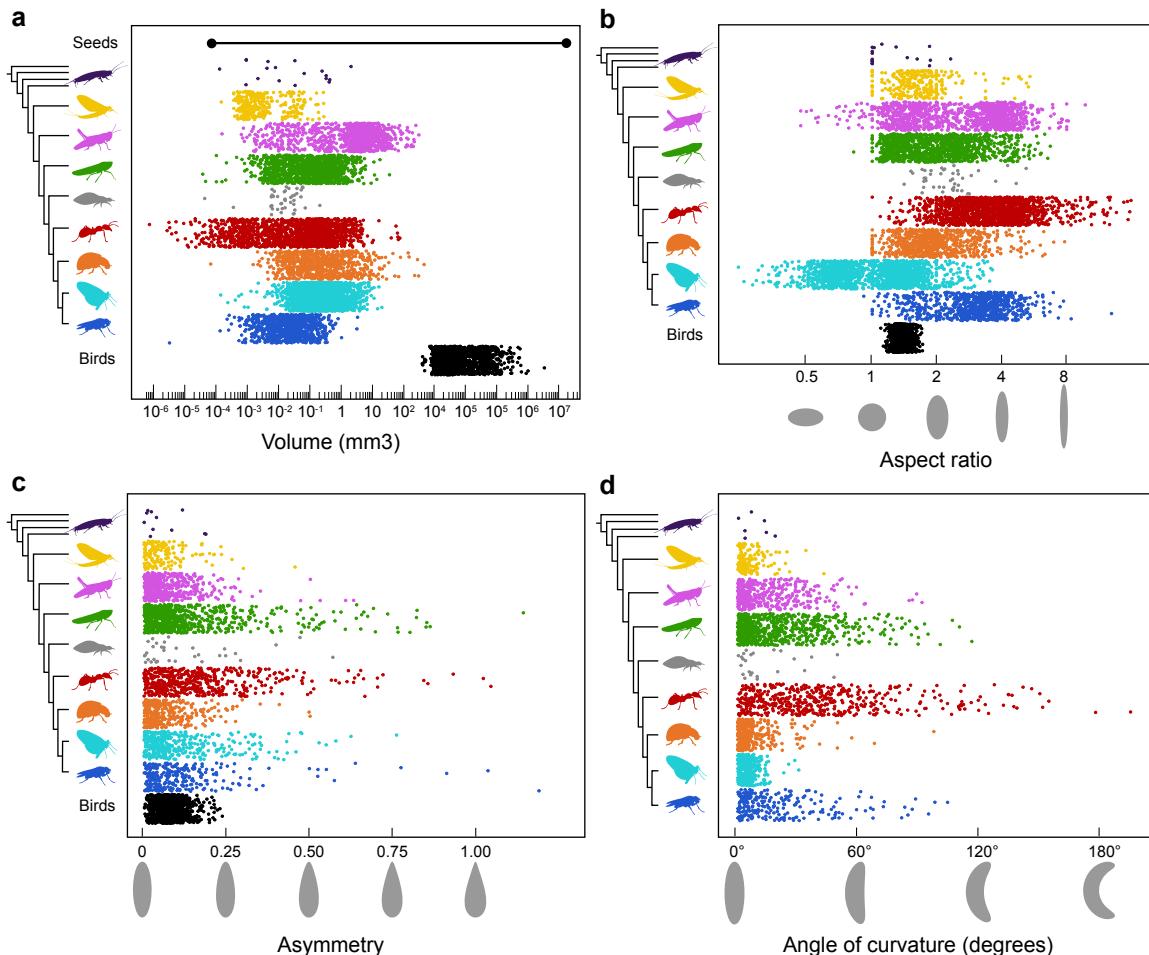
We also compared the distribution of shape parameters across insect groups. Egg aspect ratio is distributed heterogeneously across insect groups (Fig. S3 panel b). Insect eggs with an aspect ratio less than one (the egg is an oblate ellipsoid, that is, width is greater than length) have evolved and diversified in at least two main groups, Amphiesmenoptera (within Lepidoptera) and Polyneoptera (within Plecoptera). Across diverse groups of insects, some eggs were reported as exactly spherical (aspect ratio of one). In the morphospace shown in main text Fig. 1a, for example, these eggs form a conspicuous vertical alignment of datapoints for which aspect ratio equals exactly one. We attribute this pattern in the data to a tendency among researchers to describe near-spherical eggs as exactly spherical in cases when they did not measure length and width separately. Insect eggs vary with respect to aspect ratio to a much greater extent than bird eggs, affording an opportunity to test hypotheses about shape evolution across a greater diversity of possible shapes (Fig. S6).

Insect egg shapes vary considerably in the degree of asymmetry and the angle of curvature (Fig. S3, panels c and d). Like bird eggs, insect eggs range from completely symmetrical to highly asymmetrical, with extreme asymmetry found mainly in Hymenoptera and Condylognatha. Unlike in birds, insect eggs are often curved along the longitudinal axis of the egg. A high degree of curvature has evolved in Hymenoptera, Condylognatha, Antliophora, and Polyneoptera (specifically in the orders Hymenoptera, Hemiptera, Diptera, and Orthoptera).

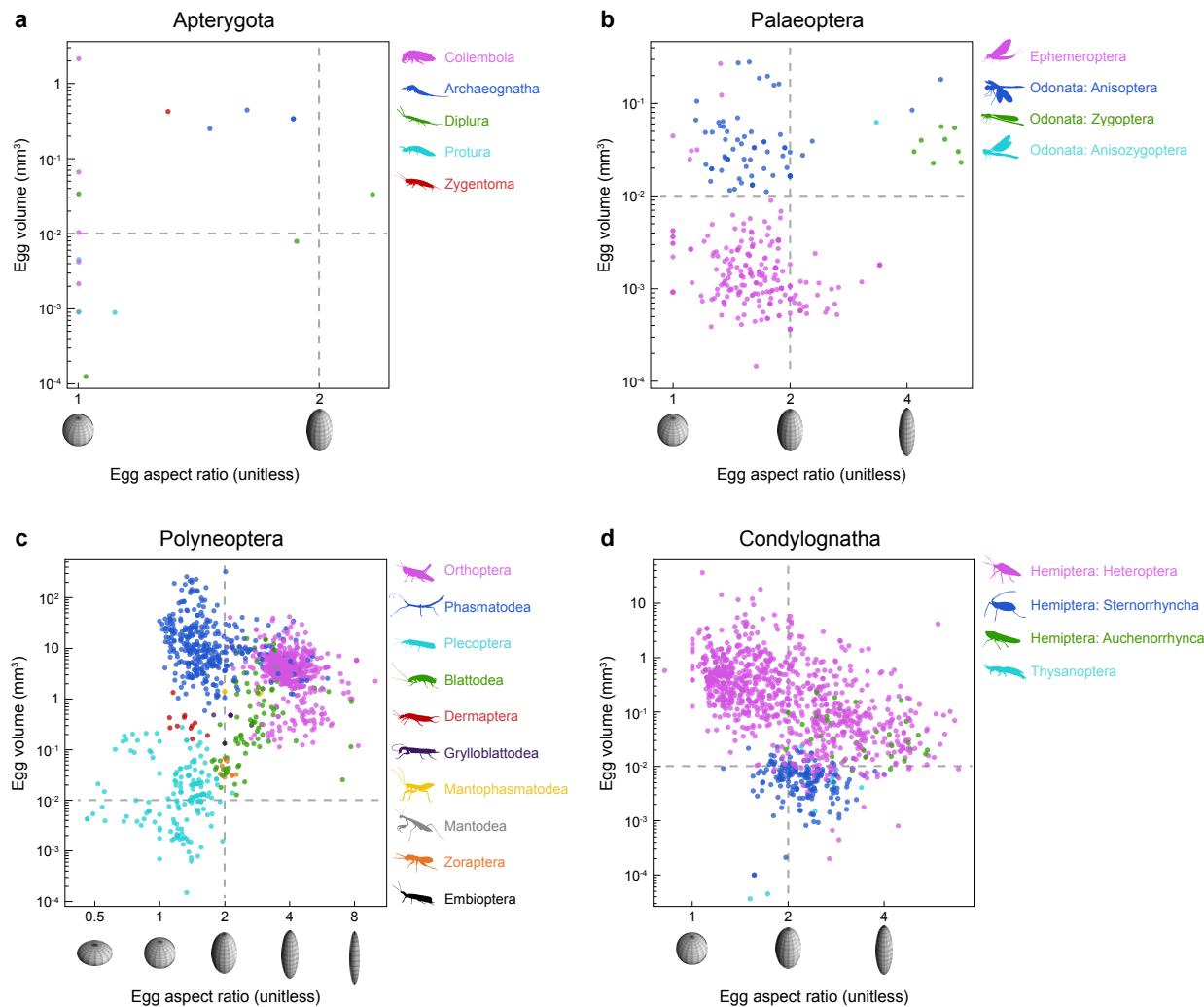
To further explore the patterns of egg morphological evolution at a finer scale, we separately plotted each of the eight groups shown in Figure 1, coloring points according to several constituent subgroups (Figs. S4 and S5). This revealed that the broad patterns apparent at the scale of the whole insect phylogeny are recapitulated at the scale of more recently diverged clades. Clades occupy distinct, yet overlapping regions of the morphospace.

#### 3.2 Insect egg morphospace

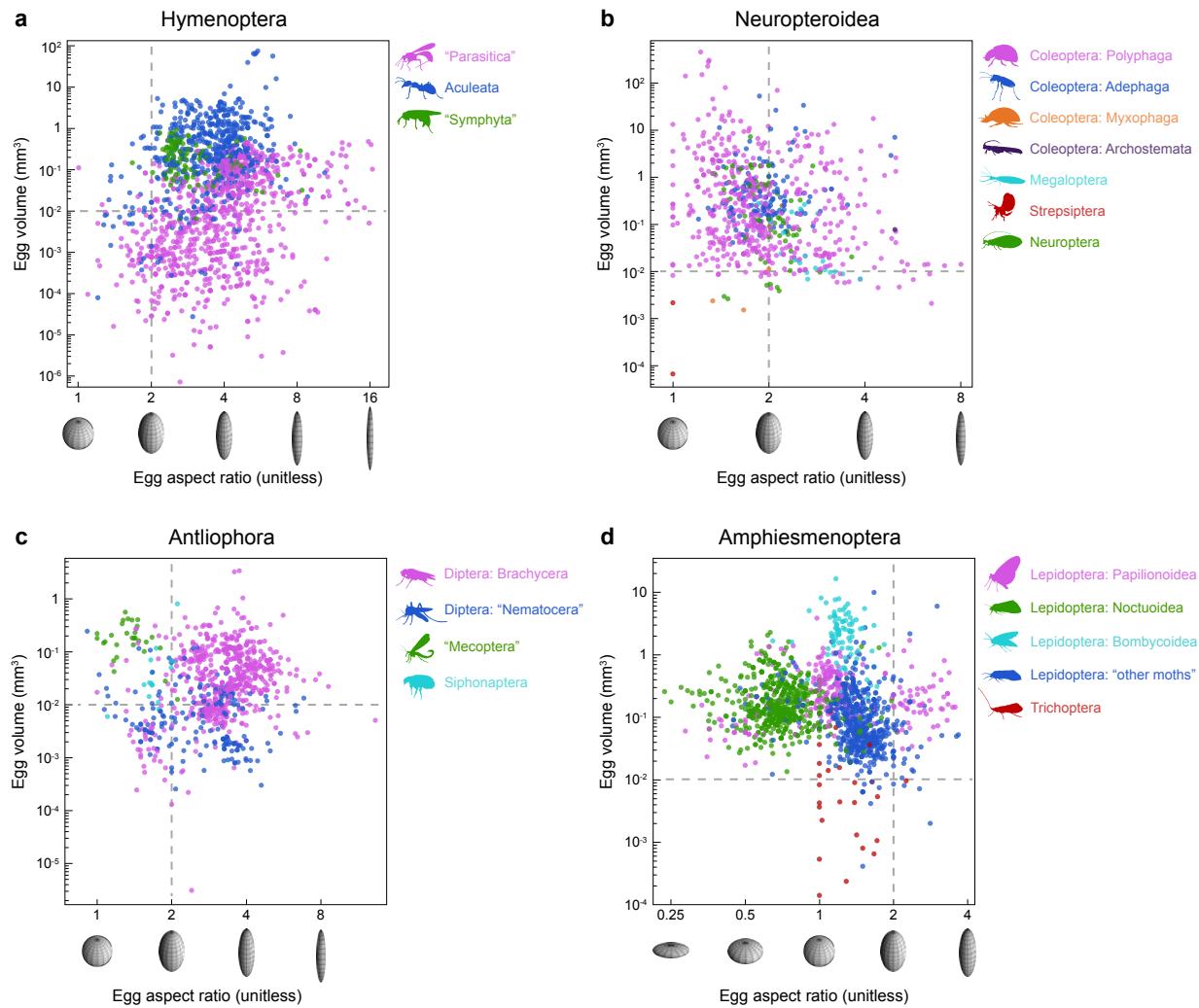
Recent work by Stoddard and colleagues showed that bird morphospace, defined by aspect ratio and asymmetry, was bounded such that no bird eggs are both asymmetrical and have an aspect ratio close to one<sup>16</sup>. This is not true for insects (Fig. S6 and S7).



**Figure S3: Distributions of egg shape and size in insect groups.** In each panel egg traits are plotted by phylogenetic group on the y-axis (within a group, points are randomly spread vertically). All groups are monophyletic clades with the exception of Apterygota, which is paraphyletic with respect to all other insects. Colors correspond to the clades shown in Fig. S1. **a.** Egg volume ( $\text{mm}^3$ , log transformed) across insect clades and compared to the distribution of extant bird egg sizes<sup>16</sup> (bottom row) and the range of angiosperm seed sizes (top row). The lower bound of seed size is represented by the orchid *Acanthephippium sylhetense*<sup>38</sup>; the upper bound is represented by the palm *Lodoicea maldivica*<sup>39</sup>. **b.** Aspect ratio (unitless, log transformed) across insect clades and compared to the distribution of extant bird eggs<sup>16</sup>. **c.** Asymmetry (unitless) across insect clades and compared to the distribution of extant bird eggs<sup>16</sup>. **d.** Angle of curvature (degrees) across insect clades.



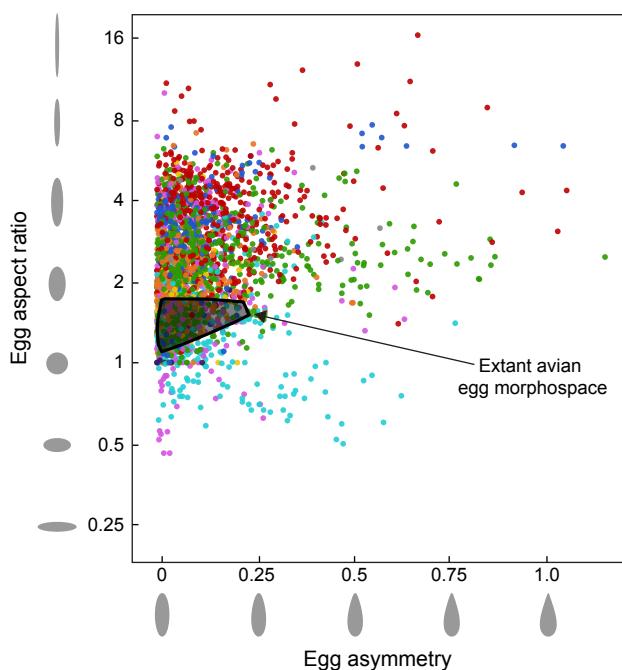
**Figure S4: Distributions of non-Holometabola egg shape and size, labeled by taxonomic orders and other subgroupings.** Each panel depicts the morphospace defined by egg aspect ratio (unitless; x-axis) and egg volume ( $\text{mm}^3$ ; y-axis), plotted on a log scale. Points are colored according to the subgroups listed at the right of each plot. All labeled subgroups are monophyletic. **a**, Apterygota; **b**, Palaeoptera; **c**, Polyneoptera; **d**, Condylgnatha.



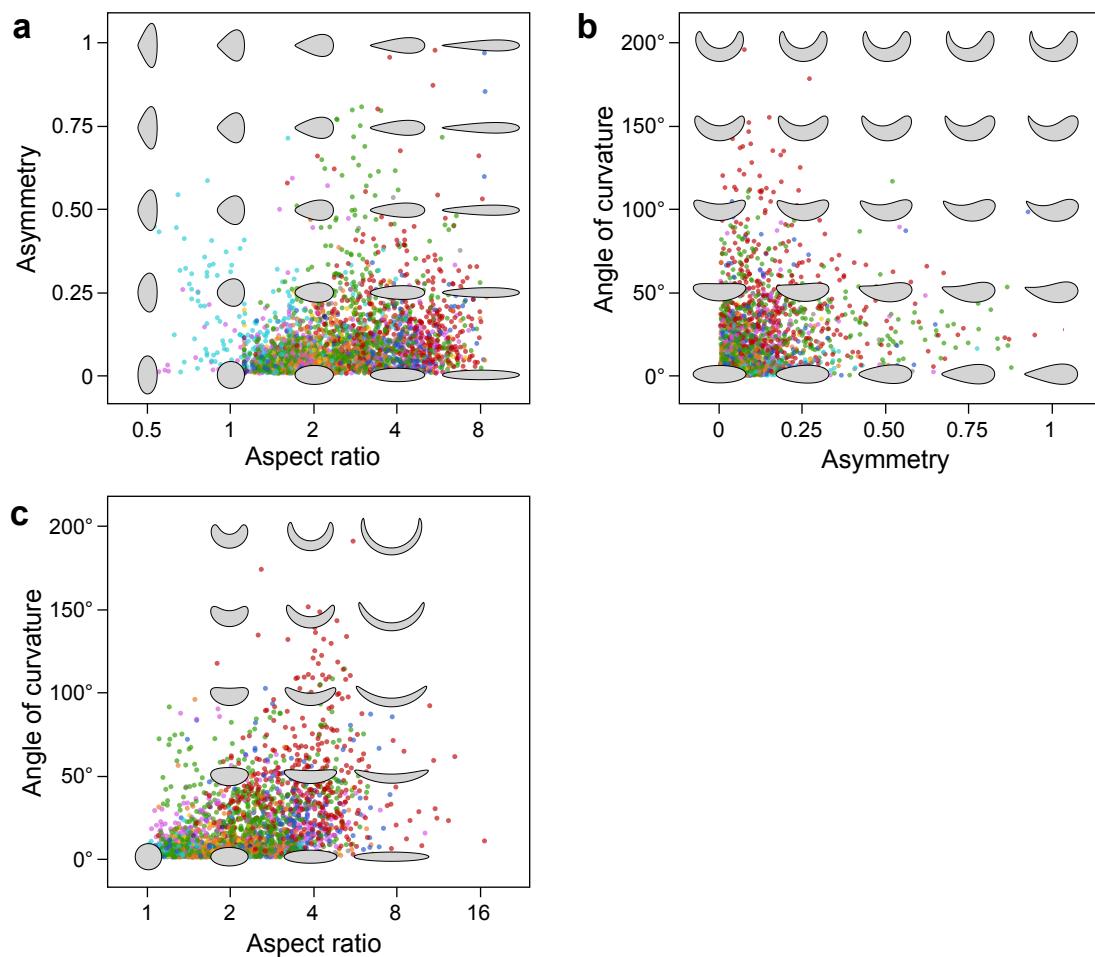
**Figure S5: Distributions of Holometabola egg shape and size, labeled by taxonomic orders and other subgroupings.** Each panel depicts the morphospace defined by egg aspect ratio (unitless; x-axis) and egg volume ( $\text{mm}^3$ ; y-axis), plotted on a log scale. Points are colored according to the subgroups listed at the right of each plot. All labeled subgroups are monophyletic with the exception of groups labeled in quotation marks. **a**, Hymenoptera; **b**, Neuropteroidea; **c**, Antliophora; **d**, Amphiesmenoptera.

### 3.3 Morphological distribution of eggs laid in egg cases

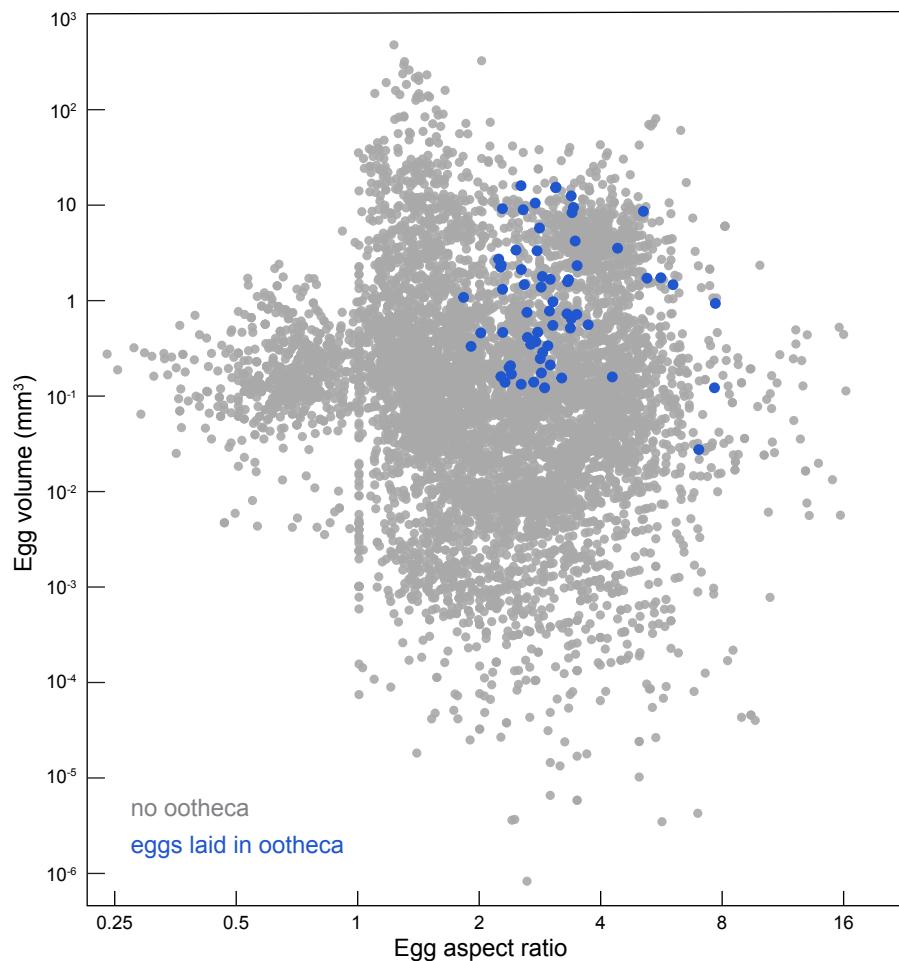
Egg cases appear to have evolved convergently across insect lineages, including in cockroaches (Blattodea, partial), mantises (Mantodea), some stick insects (Phasmatodea: Korinninae), some beetles (Coleoptera: Cassidinae), and one termite species (Blattodea: *Macrotermes darwiniensis*)<sup>43–45</sup>. In these groups, descriptions of the shape and size of the egg cell within the case are relatively less frequent in the literature. Instead, most observations are of the morphology of the case itself. However, among the ootheca-bearing insects for which egg morphological data could be collected, we observed no marked difference in egg size or aspect ratio relative to the distribution of other insect eggs (Fig. S8).



**Figure S6: Comparison of insect and bird egg morphospace occupancy.** The distribution of insect and avian eggs in the shape space defined by asymmetry and aspect ratio (plotted on a log scale). Both traits are unitless ratios. Points represent entries from the egg dataset, colored according to the clades defined in Fig. S1. The range of morphospace occupied by birds<sup>16</sup> is shown in gray.



**Figure S7: Distributions of insects in egg morphospace.** The distribution of insect eggs in the shape space defined by **a** asymmetry and aspect ratio (log scale), **b** angle of curvature and asymmetry, and **c** angle of curvature and aspect ratio (log scale). Theoretical eggs are drawn as laterally oriented silhouettes in gray. The morphospace described by angle of curvature and aspect ratio is bounded at an aspect ratio of one, according to the definition of angle of curvature. See Section 1.1 for details.



**Figure S8: Morphological distribution of eggs laid in an ootheca.** The distribution of eggs laid in an ootheca (blue) in the space defined by volume ( $\text{mm}^3$ ) and aspect ratio (unitless). Both traits are plotted on a log scale. Gray points represent eggs of insects that are not laid in an egg case.

## 4 Evolutionary history of egg traits

### 4.1 Evolutionary model fitting

We compared models of evolution with respect to six parameters of egg size and shape using the R package geiger<sup>46</sup>. For each parameter we tested the fit of a Brownian motion model (BM), Ornstein-Uhlenbeck model (OU), Early-Burst model (EB), and stochastic white-noise process (WN) using the Misof backbone<sup>17</sup> maximum clade credibility (MCC) phylogeny.

An Early-Burst model of evolution with a decreasing rate of evolution best explains ( $\Delta\text{AICc} > 2$ ) the observed distributions of length, width, volume and aspect ratio (Table S5;  $\alpha$  values for parameters as follows—log transformed, length: -0.005, width: -0.003, volume: -0.003, aspect ratio: 0.002). In contrast, for egg asymmetry and angle of curvature, OU and BM models are the best fit, respectively.

	$\Delta\text{AICc}$ , BM	$\Delta\text{AICc}$ , OU	$\Delta\text{AICc}$ , EB	$\Delta\text{AICc}$ , WN
Volume	52.31	54.32	0.00	1718.56
Aspect Ratio	5.11	7.12	0.00	1109.93
Asymmetry	31.58	0.00	33.61	94.82
Curvature	0.00	2.02	0.33	321.51
Length	59.76	61.77	0.00	1707.63
Width	34.42	36.43	0.00	1549.46
Cubic body length - family	0.00	1.73	2.03	247.61
Egg volume - family	0.00	1.83	2.03	258.28

Table S5: **Evolutionary model fitting results.** Comparing the fit ( $\Delta\text{AICc}$ ) of evolutionary models, including Brownian Motion (BM), Ornstein-Uhlenbeck (OU), Early-Burst (EB), and stochastic white-noise process (WN).

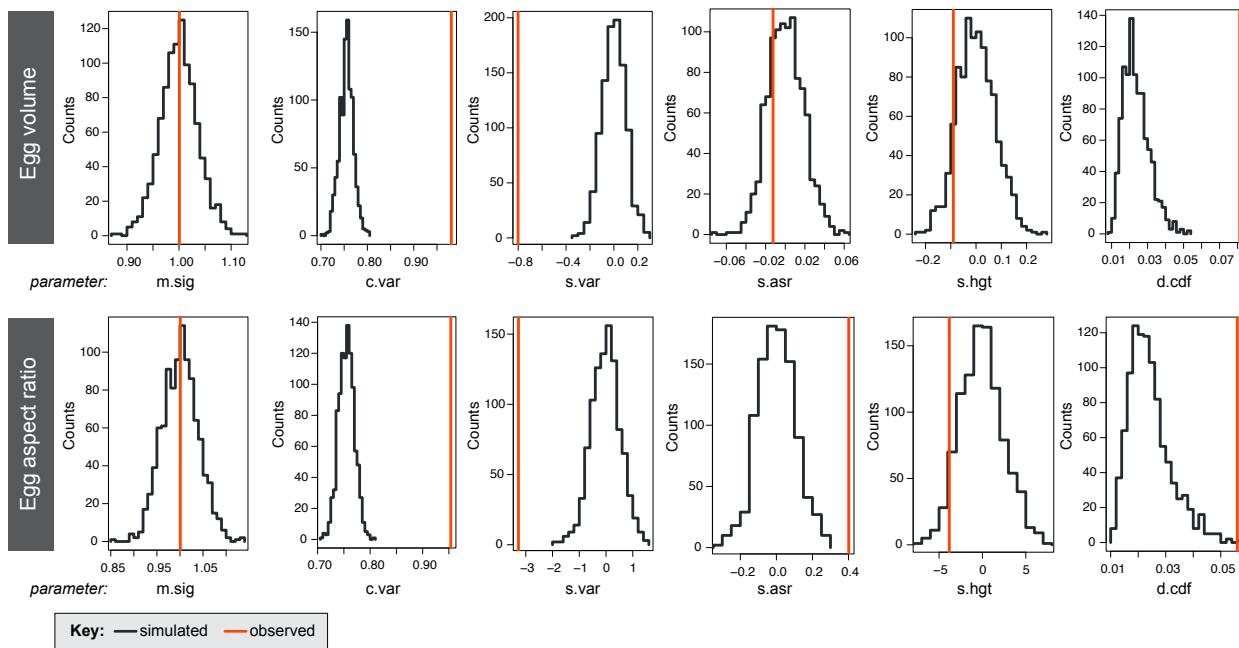
In order to better test the fit of the Early-Burst model to our data, we performed a parametric bootstrap of the model using the R package arbutus<sup>47</sup> (Fig. S9). This package simulates 100 additional datasets using the optimized parameters of the model and compares six descriptive parameters from the observed dataset to the null distribution generated with simulation. The results of the six parameter comparisons are as follows:

1. **m.sig:** *mean of the squared contrasts.* The rate of evolution of both egg volume and aspect ratio is well estimated by the Early-Burst model (the observed value falls within the null distribution).
2. **c.var:** *coefficient of variation of the absolute value of the contrasts.* For both egg volume and aspect ratio there is additional rate heterogeneity, beyond the decreasing rate of evolution fit with the Early-Burst model, which is not well accounted for (the observed value falls well outside the null distribution).
3. **s.var:** *slope of a linear model fitted to the absolute value of the contrasts against their expected variances.* For both egg volume and aspect ratio, contrasts are smaller than expected based on their branch lengths, suggesting possible branch length error.
4. **s.asr:** *slope of a linear model fitted to the absolute value of the contrasts against the ancestral state at the corresponding node.* For egg volume there is no correlation between the rate of evolution and the state (larger

eggs do not evolve faster). However, for aspect ratio, more elliptical eggs evolve faster, suggesting rate-state interactions.

5. **s.hgt**: *slope of a linear model fitted to the absolute value of the contrasts against node depth*. The Early-Burst model accounts well for the decreasing rate of evolution in the data.
6. **d.cdf**: *the D statistic from a Kolmogorov-Smirnov test comparing the distribution of contrasts to an expected normal distribution*. For both egg volume and aspect ratio the data do not fit a normal distribution of contrasts well, suggesting there are likely non-Brownian motion based processes at play (e.g. jump-diffusion processes).

These results suggest that the Early-Burst model fits some aspects of the data well, specifically the overall rate of evolution and its deceleration over time. However, it also suggests a more complex evolutionary history than can be captured in this model alone, including additional rate heterogeneity, rate-state interactions, and possible jump-diffusion-like processes.

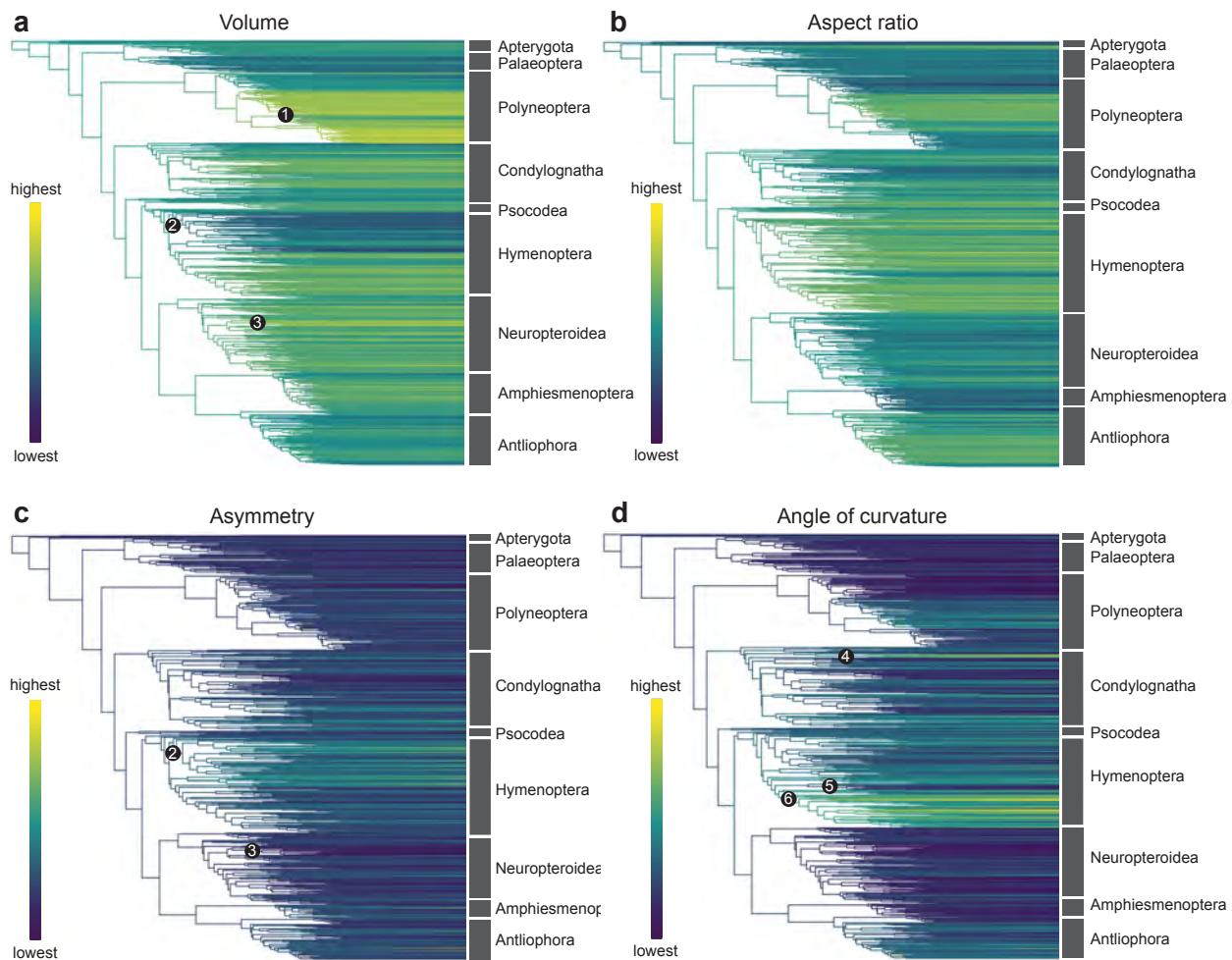


**Figure S9: Parametric bootstrap of the Early-Burst model for insect egg size and aspect ratio.** The results of a parametric bootstrap of the best fitting evolutionary model, the Early-Burst model, for egg volume ( $\text{mm}^3$ ) and aspect ratio, calculated by the R package *arbutus*<sup>47</sup>. In each of the 6 panels, the observed statistic (red line) is compared using a two-tailed test to a null distribution generated from re-simulation (black distribution). See Section 4.1 for details on the interpretation of each parameter.  $n = 1000$  simulated datasets for all panels.

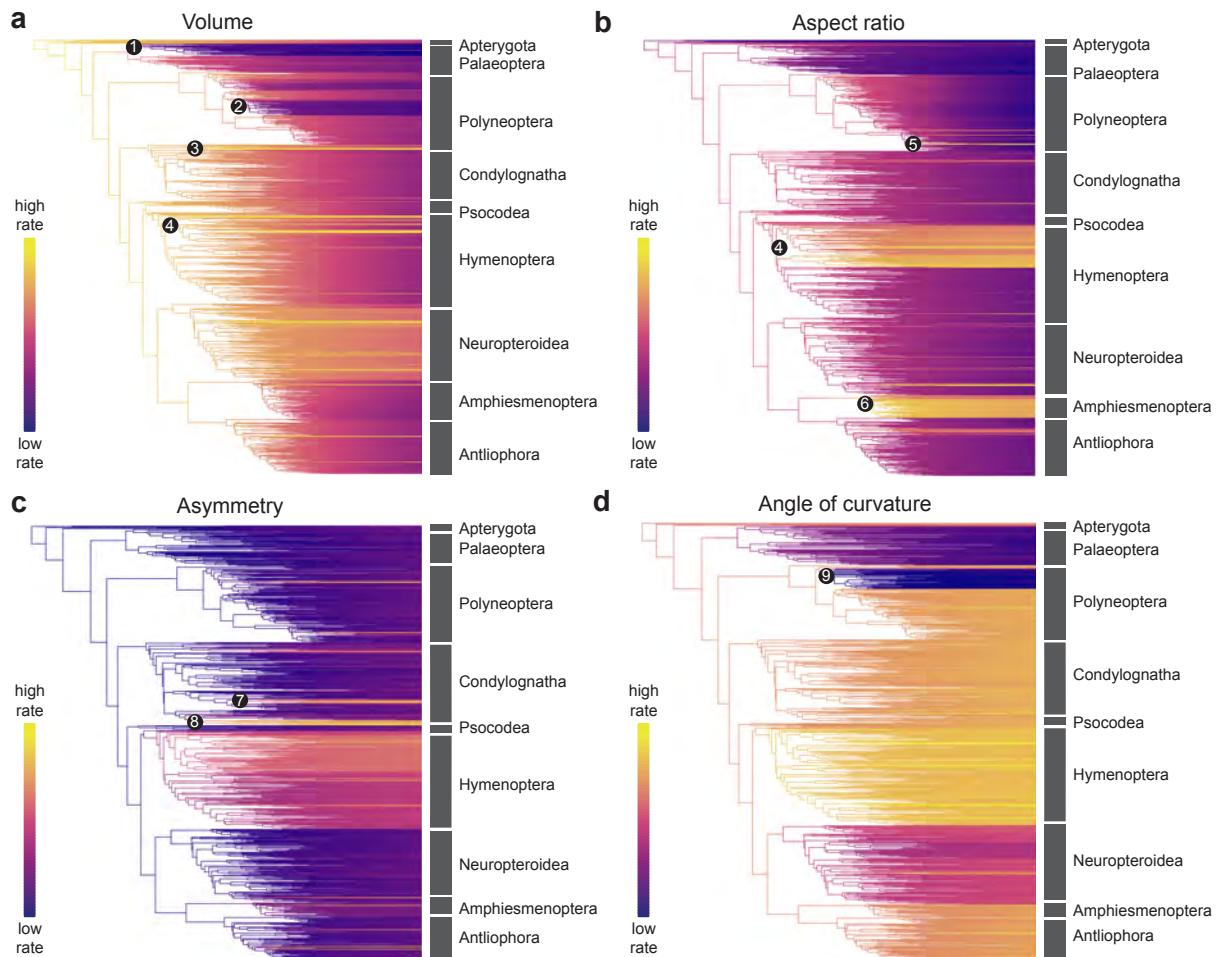
## 4.2 Ancestral state reconstructions and evolutionary rate

Given the additional complexity in trait evolution suggested by the evolutionary model analyses, we explored the evolutionary history of egg size and shape further by reconstructing the ancestral state for the continuous traits egg volume, aspect ratio, asymmetry and the angle of curvature using the R package *phytools*<sup>48</sup> (version 0.6-44,

function contMap). We also fit a rate regime map for each of these traits using the program BAMM in the R package BAMMtools (version 2.5.0) and setBAMMpriors (version 2.1.6). The prior for expected number of shifts was 10, with 10,000,000 generations. Consistent with the results of the model comparison, we observe that the rate of evolution for volume and aspect ratio generally decreases across insects, but that large shifts in rate have occurred multiple times. For example, there are dramatic increases in the rate of volume evolution in parasitoid Hymenoptera, and in the rate of aspect ratio evolution in Noctuoidea (Amphiesmenoptera: Lepidoptera).



**Figure S10: Ancestral state reconstructions of egg morphological parameters.** Ancestral state reconstructions of **a** egg volume ( $\text{mm}^3$ ; log scale), **b** aspect ratio (unitless; log scale), **c** asymmetry (unitless; square root scale), and **d** angle of curvature (degrees; square root scale). Low parameter values are shown in purple and high parameter values are shown in yellow. Circled numbers indicate selected large shifts in individual lineages: 1. Termitidae, 2. “Parasitica” (partial), 3. Scarabaeoidea, 4. Delphacidae, 5. Formicidae, 6. Apoidea.



**Figure S11: Evolutionary rate regimes** Evolutionary rate regimes calculated with the software BAMM<sup>49</sup> of **a** egg volume (mm<sup>3</sup>; log scale), **b** aspect ratio (unitless; log scale), **c** asymmetry (unitless; square root scale), and **d** angle of curvature (degrees; square root scale). Low rates are shown in purple and high rates are shown in yellow. Circled numbers indicate selected large shifts in individual lineages: 1. Odonata, 2. Acrididae, 3. Aphidoidea, 4. “Parasitica” (partial), 5. Phasmatidae, 6. Lepidoptera, 7. Reduviidae (partial), 8. Miridae (partial), 9. Plecoptera.

## 5 Allometric slopes of egg shape vary across insects

### 5.1 Calculating allometric exponents using phylogenetic generalized least squares (PGLS)

Allometric relationships can be described using a power law, in which two traits  $x$  and  $y$  are related according to  $y = bx^a$ <sup>50</sup>. The scaling exponent  $a$  can be estimated for a group of taxa as the slope of a regression between two continuous traits in log-log space, accounting for the non-independence of phylogenetically correlated data with a phylogenetic generalized least squares approach (PGLS)<sup>51</sup>.

All PGLS comparisons were performed in R using the packages ape<sup>52</sup> (version 5.0) and nlme<sup>53</sup> (3.1-131.1). The principle findings of this paper were calculated using a Brownian-Motion based correlation structure (corBrownian). We also tested the robustness of results when using an Accelerating-Decelerating based correlation structure with a fixed decelerating rate of evolution (corBlomberg,  $g = 1.3$ ) to approximate the Early-Burst model, which best describes egg size and aspect ratio evolution. For a comparison of PGLS results under these covariance matrices, see the summary in Section 8.

PGLS comparisons of egg size, shape, and developmental time were performed at the genus level over a posterior distribution of trees. The principle findings reported in this paper use the posterior distribution based on the Misof backbone phylogeny<sup>17</sup>. We also test the robustness of results to uncertainty in the backbone by using the posterior distribution based on the Rainford backbone<sup>18</sup>. For a comparison of PGLS results using these backbone phylogenies, see the summary in Section 8. For each iteration over the posterior distribution we selected a random representative entry per genus from the insect egg dataset. We therefore report the range of observed p-values, intercepts, and slopes (allometric exponents) accounting for both the phylogenetic and sampling uncertainty.

PGLS comparisons involving body size were performed at the family/order level using the published Rainford phylogeny<sup>18</sup>. To test the sensitivity of our results to sampling discrepancies between the egg dataset and published body size data, we downsampled the egg dataset by 50% and repeated each PGLS involving body size 100 times.

### 5.2 Dynamic evolution of the allometry of egg shape and size

The results of a PGLS comparison between log-egg length and log-egg width show a significant allometric relationship with a slope less than one across insects. However, the scaling exponent of length vs. width varies considerably across insect lineages (Table S6, main text Fig. 2 and Fig. S13).

We compared our results to alternative hypotheses of size and shape evolution by simulating new egg length and width datasets under known models and analyzing them using the same methods. We tested two hypotheses: (1) that egg length and width have a 1:1 relationship (isometry), and (2) that egg length and width evolve independently. For each hypothesis we simulated data with the same parameters as the observed data (number and phylogenetic position of taxa, fitted evolutionary model parameters, EB model for both length and width) using the R package phylolm<sup>54</sup> (version 2.5; function ‘rTrait’). The p-value of each hypothesis was calculated as the count of scaling exponents (the slope of the PGLS regression) that are more extreme than our test statistic, which is the median observed scaling exponent of each of the seven major insect groups analysed.

	p-value	slope	intercept	sample size
Hexapoda	0 - <0.005	0.76 - 0.81	-0.28 - -0.26	1488
Hymenoptera	0 - <0.005	0.68 - 0.78	-0.58 - -0.54	355
Condylognatha	0 - <0.005	0.80 - 0.91	-0.42 - -0.38	202
Antliophora	0 - <0.005	0.69 - 0.79	-0.48 - -0.42	199
Neuropteroidea	0 - <0.005	0.90 - 0.97	-0.31 - -0.28	265
Amphiesmenoptera	0 - <0.005	0.71 - 0.91	-0.21 - -0.14	76
Polyneoptera	0 - <0.005	0.70 - 0.75	-0.28 - -0.25	262
Palaeoptera	0 - <0.005	0.60 - 0.72	-0.45 - -0.38	104

Table S6: Results of PGLS regression of egg length and width.

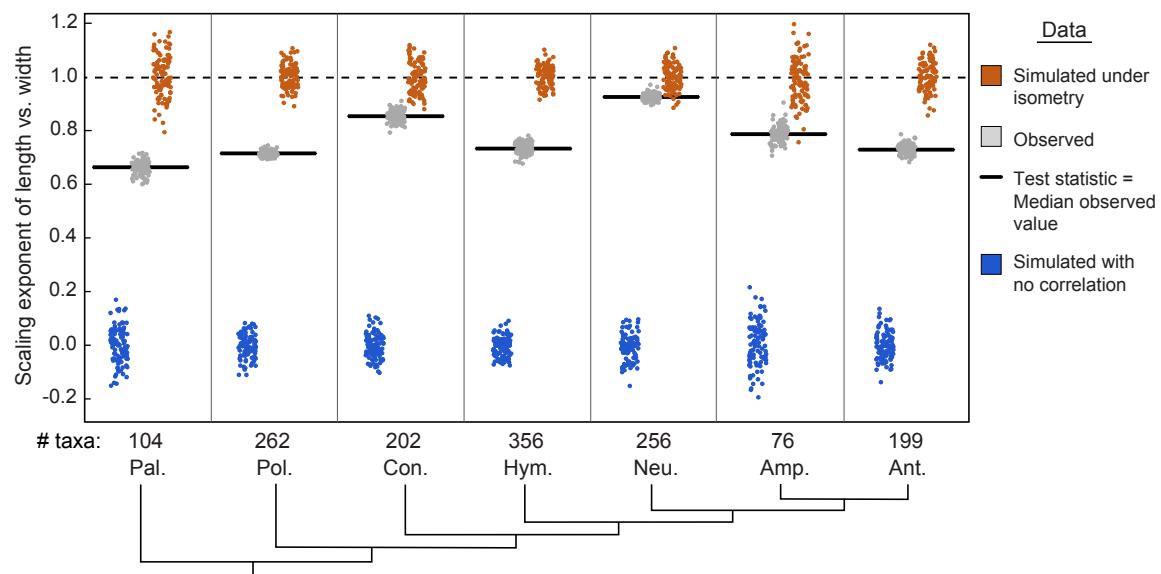
Our results show that the first hypothesis, isometry, cannot be rejected for the lineage Neuropteroidea (beetles and relatives, p-value, isometry = 0.04) and Amphiesmenoptera (moths, butterflies, and caddisflies, p-value, isometry = 0.01, Fig. S12 and Table S7). The second hypothesis, that egg length and width evolve independently, can be rejected for all lineages (p-value, no relationship <0.01, out of 100 bootstraps, no values were greater than the test statistic)

	test statistic	p-value, isometry	p-value, no relationship
Palaeoptera	0.67	<0.01	<0.01
Polyneoptera	0.72	<0.01	<0.01
Condylognatha	0.86	<0.01	<0.01
Hymenoptera	0.74	<0.01	<0.01
Neuropteroidea	0.93	0.04	<0.01
Amphiesmenoptera	0.79	0.01	<0.01
Antliophora	0.73	<0.01	<0.01

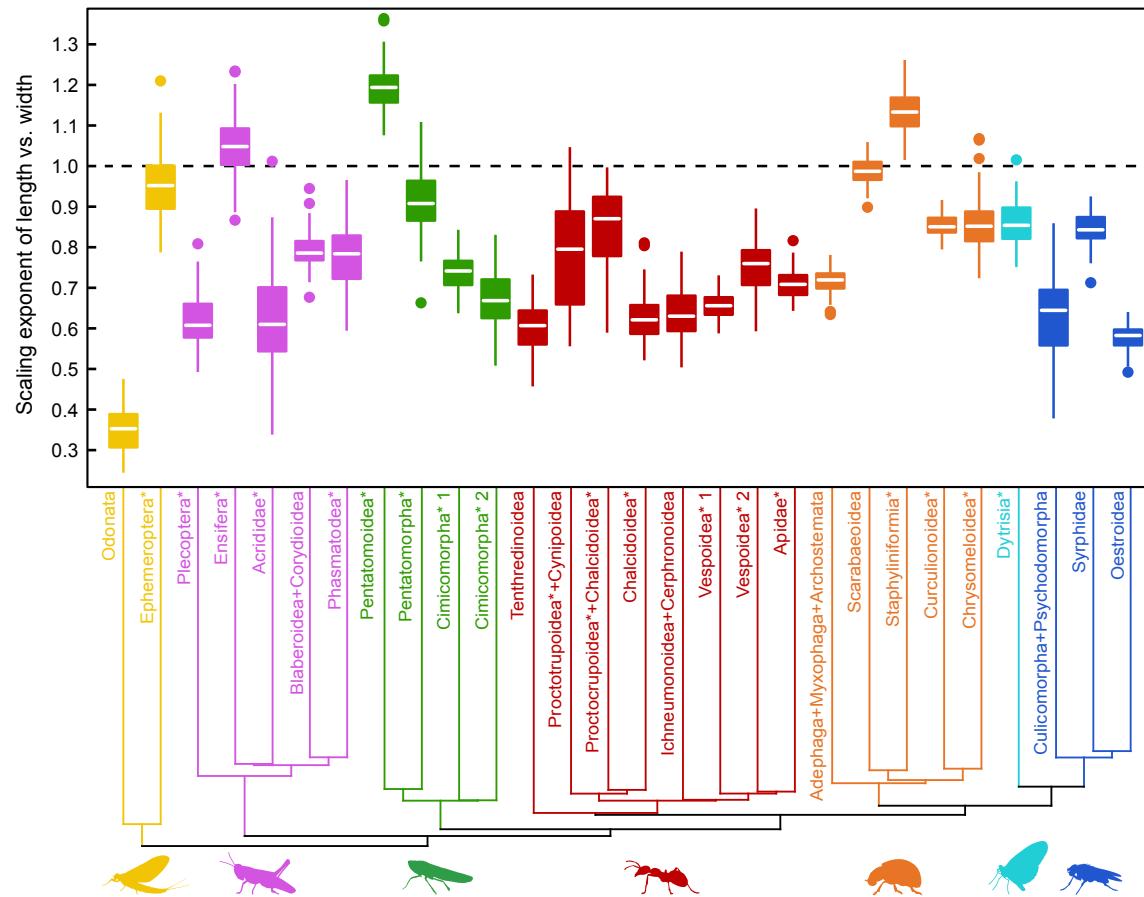
Table S7: Results of a parametric bootstrap of alternate hypotheses of egg shape and size evolution. For a two-tailed parametric bootstrap, a p-value of &lt;0.01 indicates that out of 100 bootstraps, no values were greater / less than the test statistic. n = 100 simulated datasets.

The seven lineages selected for comparison are large monophyletic lineages of insects, but it is also informative to estimate allometries for other clade divisions. To better represent the dynamic evolution of the scaling exponent, we broke down the insect phylogeny further. First, we identified the nodes in the phylogeny that had a sufficient number of descendant tips with morphological data to calculate the allometric exponent. We then identified the minimum number of unique nodes such that no node had more than 50 descendant tips. We repeated the PGLS comparison of log-egg length and log-egg width for each of these groups, and plotted the distributions of scaling exponents on the phylogeny (Fig. S13).

Our results show that additional subgroups of insects have a near-isometric relationship between egg size and shape, including lineages within Palaeoptera, Polyneoptera, and Hemiptera. Most lineages have a scaling exponent less than 1, supporting the prediction that larger eggs will tend to be proportionally longer than smaller eggs<sup>16,55,56</sup>.



**Figure S12: Testing alternate hypotheses of egg size and aspect ratio evolution using a parametric bootstrap.** The distribution of the scaling exponent of length vs. width calculated from data simulated under alternate hypotheses compared using a two-tailed test to the observed distribution of scaling exponents (gray, test statistic = median value, black bar) for seven insect lineages. Alternate hypotheses include that egg shape and size are unrelated (slope = 0, blue), and that egg shape and size have an isometric relationship (slope = 1, orange). n = 100 simulated datasets for each comparison.

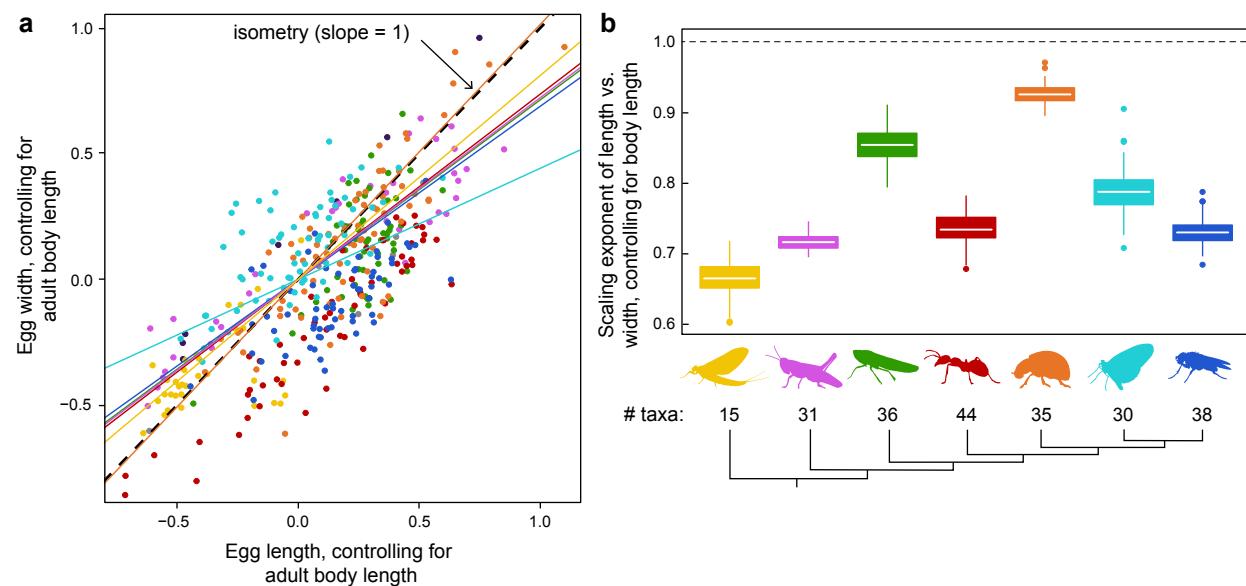


**Figure S13: Evolution of the relationship between egg size and aspect ratio across insect lineages.** The distribution of scaling exponents of length vs. width across all monophyletic clades in our dataset with more than 20 and fewer than 50 tips. All other taxa in the dataset not falling into a clade with these qualities have been excluded. Asterisks indicate that the clade is an unnamed subgroup of the named taxonomic group listed. White lines, boxes, bars, and dots represent median, 25-to-75th percentiles, 5-to-95th percentiles, and outliers.  $n = 100$  PGLS regressions. The dashed black line represents a hypothetical 1:1 relationship (isometry). Colors correspond to the clades shown in Fig. S1.

### 5.3 Accounting for body size in egg shape and size allometries

Given that hypotheses about the relationship between egg shape and size invoke egg scaling constraints within the insect body<sup>16,55–57</sup>, we tested the effect of accounting for body size on our results. We matched the previously published<sup>58</sup> median body length (see Section 6.4 for details) to the average egg length and width for 417 insect families and 9 insect orders. We controlled for adult body size in the egg allometry comparison by calculating the phylogenetic residuals<sup>59</sup> of log-egg length and log-egg width against the log-adult body length.

Consistent with analyses that did not account for body size, in Neuropteroidea, egg length scales near-isometrically with width when accounting for body size, while in other insect clades larger eggs for a given body size are proportionally longer (Fig. S14 and Table S8). In the groups Palaeoptera, Amphiesmenoptera, and Condylognatha, the relationship between egg width and length is not significant. However these clades have some of the lowest sample sizes at the family-level, therefore our ability to detect relationships is weakest (Fig. S14).



**Figure S14: Allometry of egg size and aspect ratio, controlling for adult body size.** **a**, PGLS regression of egg width (mm, log transformed) and length (mm, log transformed), comparing the phylogenetic residuals of both traits against adult body length (mm, log transformed). The colored lines are the phylogenetic regression for each clade on the summary tree, colors correspond to the clades shown S1. Colored points are family- or order-level averages. n = family- or order-level clades: Palaeoptera = 15, Polyneoptera = 31, Condylognatha = 36, Hymenoptera = 44, Neuropteroidea = 35, Amphiesmenoptera = 30, Antliophora = 38. **b**, The distributions of scaling exponents of length vs. width, controlling for adult body length, for seven monophyletic insect clades. Scaling exponents were calculated by resampling 50% of taxa for each clade, and recalculating the average egg size, see section 5.1. White lines, boxes, bars, and dots represent median, 25-to-75th percentiles, 5-95th percentiles, and outliers. n = 100 PGLS regressions,. In both panels the dashed black line represents a hypothetical 1:1 relationship (isometry).

### 5.4 Testing additional shape allometries

In addition to comparing the relationship between egg aspect ratio and egg size, we also tested the relationship between aspect ratio and two other features of egg shape: asymmetry and angle of curvature. We compared each

	p-value	slope	intercept	sample size
Hexapoda	0 – <0.005	0.64 – 0.74	0	235
Hymenoptera	0 – <0.005	0.67 – 0.90	0	44
Condylognatha	0 – 0.12	0.30 – 0.85	0	36
Antliophora	0 – <0.005	0.54 – 0.69	0	38
Neuropteroidea	0 – <0.005	0.91 – 1.06	0	35
Amphiesmenoptera	0 – 0.15	0.19 – 0.48	0	30
Polyneoptera	0 – <0.005	0.65 – 0.76	0	31
Palaeoptera	0.05 – 0.75	0.06 – 0.46	0	15

Table S8: Results of PGLS regression of egg length and width, controlling for body size.

shape parameter (square root transformed) to log of egg length, controlling for egg width using phylogenetic residuals. This allows us to ask whether eggs which are longer given their width (higher aspect ratio) are also more asymmetrical or more curved.

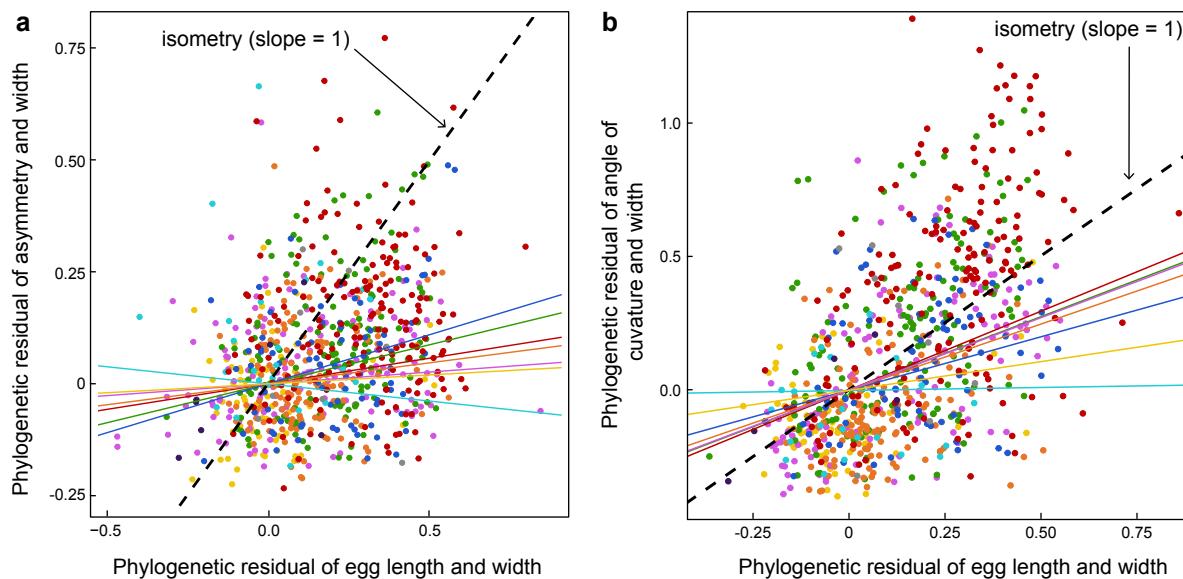
Our results show that eggs with a higher aspect ratio (proportionally longer for their width) are not more asymmetrical than low aspect ratio counterparts (Fig. S15 and Table S9). Across insects, eggs with a higher aspect ratio tend to be more curved, though this relationship is likely driven by the lineages with very curved eggs (Hymenoptera, Condylognatha, and Antliophora; Fig. S15 and Table S10).

	p-value	slope	intercept	sample size
Hexapoda	0 – 0.06	0.07 – 0.17	0	796
Hymenoptera	0.02 – 0.96	0 – 0.20	0	174
Condylognatha	0 – 0.70	0.04 – 0.49	0	149
Antliophora	0 – 0.74	0.04 – 0.45	0	80
Neuropteroidea	0.05 – 0.86	0.02 – 0.17	0	141
Amphiesmenoptera	0.27 – 0.99	-0.26 – 0	0	24
Polyneoptera	0.04 – 1.00	-0.12 – 0.18	0	142
Palaeoptera	0 – 0.98	-0.03 – 0.30	0	71

Table S9: Results of PGLS regression of egg length and asymmetry, controlling for egg width.

	p-value	slope	intercept	sample size
Hexapoda	0 – <0.005	0.44 – 0.60	0	781
Hymenoptera	0 – <0.005	0.50 – 0.85	0	174
Condylognatha	0 – 0.02	0.40 – 0.74	0	149
Antliophora	0 – 0.54	0.13 – 0.58	0	79
Neuropteroidea	0 – 0.18	0.19 – 0.55	0	141
Amphiesmenoptera	0.26 – 1.00	-0.33 – 0.18	0	22
Polyneoptera	0 – 0.24	0.18 – 0.69	0	133
Palaeoptera	0.06 – 0.99	0 – 0.30	0	70

Table S10: Results of PGLS regression of egg length and curvature, controlling for egg width



**Figure S15: Allometry of egg asymmetry, angle of curvature, and aspect ratio.** **a**, PGLS regression of egg asymmetry (unitless; square root transformed) and length (mm; log transformed), comparing the phylogenetic residuals of both traits against egg width (mm; log transformed). n = genera: Palaeoptera = 71, Polyneoptera = 142, Condylognatha = 149, Hymenoptera = 174, Neuropteroidea = 141, Amphiesmenoptera = 24, Antliophora = 80. **b**, PGLS regression of egg curvature (degrees; square root transformed) and length (mm; log transformed), comparing the phylogenetic residuals of both traits against egg width (mm; log transformed). n = genera: Palaeoptera = 70, Polyneoptera = 133, Condylognatha = 149, Hymenoptera = 174, Neuropteroidea = 141, Amphiesmenoptera = 22, Antliophora = 79. In both panels the dashed black line represents a hypothetical 1:1 relationship (isometry), colored lines are the phylogenetic regression for each clade, and colored points are representative eggs from each genus in the phylogeny. Colors correspond to the clades shown in Fig. S1.

## 6 Egg size and development

We tested the relationship between the evolution of egg morphology, embryonic development, and adult size. To compare traits across species, we collected descriptions of developmental times and adult size from the insect literature.

### 6.1 Collecting developmental time data

We collected literature sources that described the development of insects and used them to assemble a dataset of three developmental traits. The developmental time data and corresponding original sources are available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution), file ‘development.tsv’. The developmental traits considered were as follows:

*Interval between syncytial mitoses:* Insects in most lineages that have been studied begin embryogenesis with a series of syncytial nucleus divisions (mitotic divisions with absent or incomplete cytokinesis)<sup>60,61</sup>. For sources that reported a single estimate of the time interval between mitotic divisions, we used that value (converted to hours). When a source reported multiple intervals, we used the mean duration of the reported mitotic intervals that occur before nuclei initially reach the periphery of the egg. We did not collect mitotic interval data from the species of polyembryonic

insects that develop holoblastically.

*Time to cellularization:* This trait was included only for species with syncytial development. When sources reported a single time point, we used it (converted to hours). If a range was reported, we used the midpoint of that range.

*Duration of embryogenesis:* We define embryogenesis as the development that takes place prior to *hatching*, which is the point at which a mobile first instar insect (larva or nymph) exits the egg.

We only included data from sources that reported the temperature at which the embryo developed, as developmental rate typically varies with incubation temperature<sup>62,63</sup>. Moreover, data from many animals, including insects, are consistent with the hypothesis that the temperature-dependence of developmental rate is due the general temperature-dependence of reaction kinetics<sup>64</sup>. Thus, we followed the method of recent work<sup>64,65</sup> to re-scale all developmental times to a standardized temperature of 20 °C using the Boltzmann-Arrhenius equation with the  $E_i/k_B$  factor set to 8000K, where  $E_i$  is the activation energy and  $k_B$  is Boltzmann's constant. All temperature-adjusted developmental times were  $\log_{10}$  transformed.

## 6.2 Comparing egg size and developmental time

The three measures of developmental time described above were compared to egg volume using a PGLS regression over 100 trees randomly drawn from the posterior distribution. Only species present in both the development and the egg dataset were compared. For species with developmental records that had more than one egg description in the dataset, a random matching egg entry was chosen for each iteration over the posterior distribution of trees.

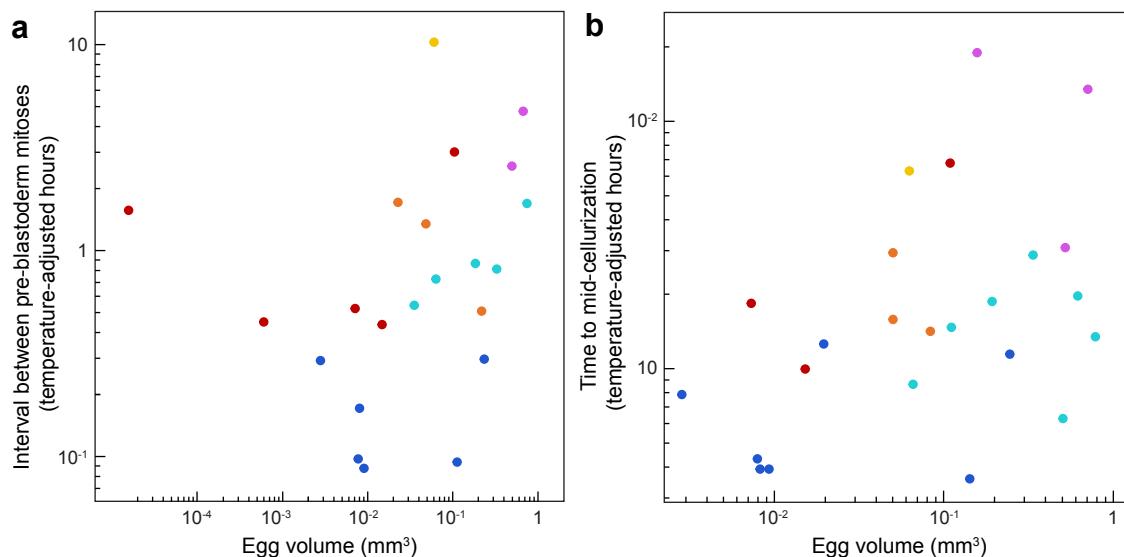
None of the three developmental parameters had a significant relationship to egg volume across the insect phylogeny (Fig. S16, Table S11). Furthermore, we observed that if phylogeny was not taken into account, we could recover a spurious relationship between egg volume and duration of embryogenesis ( $p$ -value = 0.001, adjusted  $R^2$  = 0.195, Fig. S17; using a linear model on the same data included in the phylogenetic regression). Given that a previous study had reported a significant relationship between developmental time and egg size<sup>65</sup>, we suggest that the results of that study were likely due to the artifact caused by failing to account for the phylogenetic non-independence of phenotypes.

	p-value	slope	intercept	sample size
egg volume vs duration of embryogenesis	0.02 – 0.10	0.08 – 0.12	2.66 – 2.73	46
egg volume vs interval between pre-blastoderm mitoses	0.18 – 0.71	0.03 – 0.12	0.20 – 0.34	16
egg volume vs time to cellularization	0.14 – 0.96	-0.02 – 0.24	1.48 – 1.75	18

Table S11: Results of PGLS regression of developmental time and egg size

## 6.3 Egg size and body size

We compared the predicted evolutionary relationship of egg size and body size<sup>66,67</sup> by matching the egg dataset to published records of insect body length. Rainford et al. (2016)<sup>58</sup> described the maximum and minimum adult body length for 764 insect families and 10 insect orders, of which 426 are represented in the insect egg dataset. From these

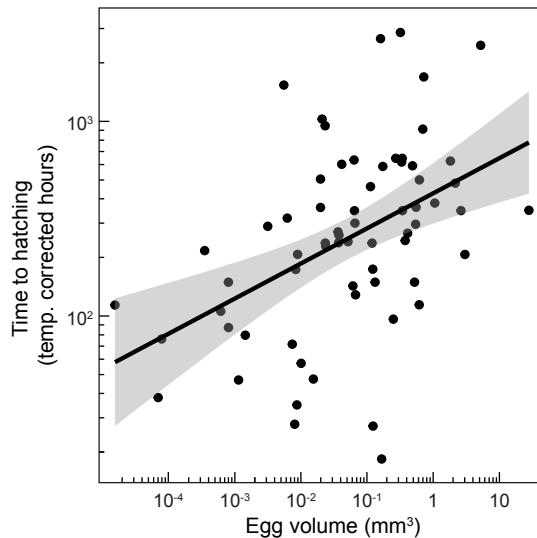


**Figure S16: Comparisons of egg size with additional measures of embryonic development time.** **a**, Embryonic time measured as the mean reported hours between mitoses in the pre-blastoderm stage (temperature adjusted<sup>64</sup>; log scale), compared to egg volume (mm<sup>3</sup>; log scale). **b**, Embryonic time measured as the reported hours to the midpoint of cellularization (temperature adjusted<sup>64</sup>; log scale), compared to egg volume (mm<sup>3</sup>; log scale). In both panels, each point represents an insect species for which both developmental and egg morphological data were available. Colors correspond to the clades shown in Fig. S1.

we calculated the median body length for each family, and matched this to the average egg volume from the insect egg dataset for the same family. Given that the median body lengths reported in Rainford et al. (2016)<sup>58</sup> may have been drawn from a different subset of species per family than the average egg size from our egg dataset, we tested the impact of sampling by randomly reducing the number of entries in each family in the egg dataset by 50% and reanalyzing the data 100 times.

We compared the allometric relationship between egg size and body size with PGLS regression across the family-level phylogeny published by Rainford et al. (2014)<sup>18</sup>. Our results showed that across the insect phylogeny, smaller insects lay proportionally larger eggs (that is, there is a significant allometric relationship with a slope less than one; main text Fig. 3 and Table S12). Within the insect lineages Palaeoptera and Antliophora, however, body size does not predict egg size (that is, there is no statistically significant relationship between egg size and body size). These results are robust to downsampling the egg dataset for each family/order, indicating that they are not due to an artifact of sampling differences between the egg size and body size datasets.

To test our results against alternative hypotheses, we simulated egg size and body size datasets under known evolutionary models and analyzed them using the same methods. We followed the same parametric bootstrap method as described in 5.2, using here the best fitting models (Table S5) for body size and egg size to simulate family-level egg volume data. Our results show that the first hypothesis, an isometric relationship between egg size and body size, cannot be rejected for the lineages Polyneoptera, Condylognatha and Hymenoptera (p-value, isometry = 0.02, 0.01, and 0.02 respectively). The second hypothesis, that egg size and body size evolve independently, cannot be rejected for the lineages Palaeoptera (p-value, no relationship = 0.02).



**Figure S17: Non-phylogenetic linear regression of developmental time and egg size.** For illustration, we show that a regression that failed to account for phylogeny would find a spurious significant relationship ( $p$ -value 0.001, adjusted  $R^2 = 0.195$ ) between duration-of-embryogenesis (temperature adjusted<sup>64</sup>; log scale) and egg volume ( $\text{mm}^3$ ; log scale). The black line is the fitted regression, with 95% confidence intervals shown in gray. Each point represents an insect species for which developmental and egg morphological data were available for a member of a genus that could be included in the insect phylogeny described in Section 2.  $n = 66$  genera.

	p-value	slope	intercept	sample size
Hexapoda	$0 - <0.005$	0.53 – 0.60	-3.29 – -2.98	238
Hymenoptera	$0 - <0.005$	0.63 – 0.81	-3.81 – -3.28	44
Condylognatha	$0 - <0.005$	0.64 – 0.83	-3.53 – -2.98	36
Antliophora	$0 - 0.03$	0.28 – 0.44	-2.84 – -2.33	39
Neuropteroidea	$0 - <0.005$	0.49 – 0.60	-2.77 – -2.32	36
Amphiesmenoptera	$0 - <0.005$	0.58 – 0.74	-3.84 – -3.34	31
Polyneoptera	$0 - <0.005$	0.62 – 0.75	-3.26 – -2.77	31
Palaeoptera	$0 - 0.01$	0.28 – 0.46	-3.98 – -3.36	15

Table S12: Results of PGLS regression of egg volume and adult body length cubed

#### 6.4 Egg size and genome size

We compared the volume of the egg cell to the size of the genome contained within it. To obtain genome size data, we queried the Animal Genome Size Database<sup>68</sup> in February of 2019. Of the 1,154 unique hexapod species with recorded genome sizes in the database, 177 had a corresponding egg volume in our dataset, representing 89 unique genera in our phylogeny. For these taxa, we compared egg volume to genome size, measured as C-value (haploid nuclear content) using the same approach as described for other PGLS analyses (see Section 5.1). We repeated this analysis on a larger dataset by matching egg size to genome size records by genus ( $n$ , unique genera = 173), selecting a random representative when more than one description was available for a given genus.

When considering all insects, our results showed a positive relationship between egg volume and genome size, though the slope of this relationship was low (slope 0.11 – 0.17; Fig. S19, panels a and b). Visualizing the genome-egg

	test statistic	p-value, isometry	p-value, no relationship
Palaeoptera	0.36	<0.01	0.02
Polyneoptera	0.68	0.02	<0.01
Condylognatha	0.74	0.01	<0.01
Hymenoptera	0.72	0.02	<0.01
Neuropteroidea	0.54	<0.01	<0.01
Amphiesmenoptera	0.66	<0.01	<0.01
Antliophora	0.37	<0.01	<0.01

Table S13: Results of a parametric bootstrap of egg size and body size. For a two-tailed parametric bootstrap, a p-value of <0.01 indicates that out of 100 bootstraps, no values were greater / less than the test statistic. n = 100 simulated datasets.

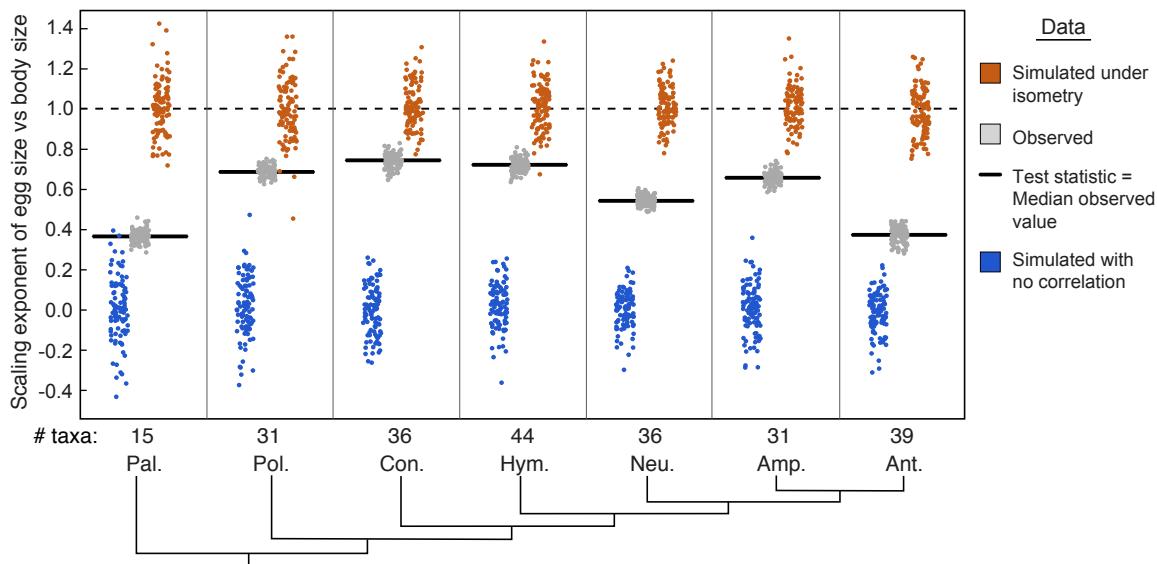
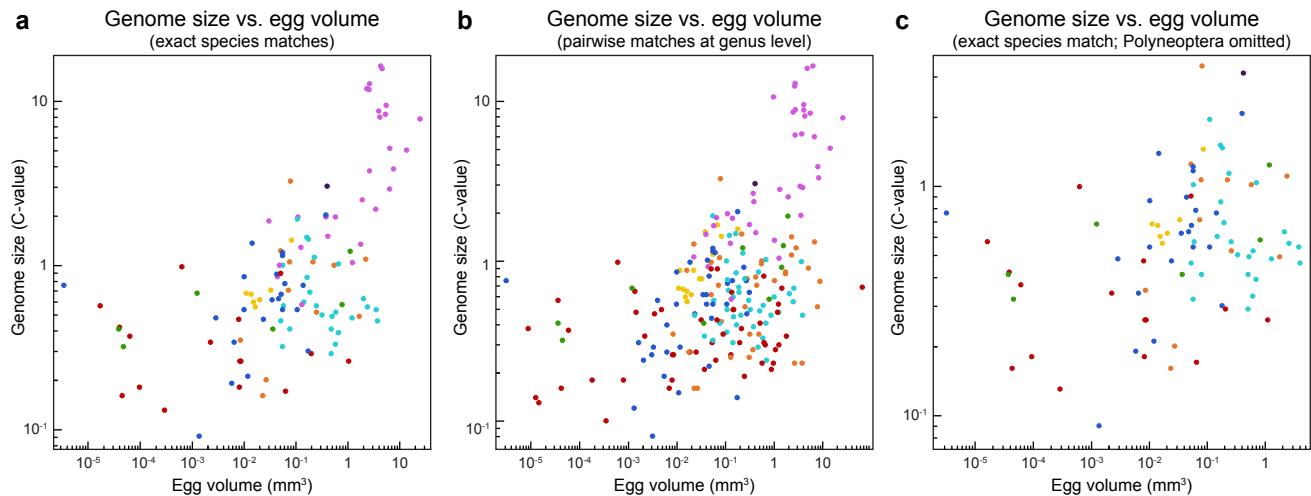


Figure S18: Testing alternative hypotheses of egg size and adult body size evolution using a parametric bootstrap. The distribution of scaling exponents of egg size vs. body size calculated from data simulated under alternate hypotheses compared to the observed distribution of the scaling exponent (gray, test statistic = median value, black bar), for seven insect lineages. Alternate hypotheses include that egg shape and adult body size are unrelated (slope = 0, blue), and that egg shape and adult body size have an isometric relationship (slope = 1, orange). n = 100 simulated datasets for each comparison.

size space revealed that a single lineage, Polyneoptera (and specifically, Acrididae) has evolved genomes nearly an order of magnitude larger than other recorded insects (Fig. S19). These insects also have relatively large eggs. Given that a single lineage that has several unique characters can bias phylogenetic studies, even when employing a PGLS approach<sup>69</sup>, we repeated the analysis excluding Polyneoptera. In this analysis, we found no relationship between genome size and egg size across non-Polyneopteran insects. Although none of the smallest insect eggs (volume < 0.01 mm<sup>3</sup>) have the largest genomes (C-value > 1), insects of nearly the same genome size range over six orders of magnitude in egg volume variation (Fig. S19). These data suggest that genome size is not a general factor driving egg size evolution across insects.



**Figure S19: Comparisons of egg size with genome size.** Each panel shows genome size (C-value; log scale) compared to egg volume (mm<sup>3</sup>; log scale). Colors correspond to the clades shown in Fig. S1. **a**, Comparison among insect species for which both egg volume and genome size data were available. **b**, Comparison of egg volume and genome size by pair-wise matches at the genus level. **c**, Comparison plotted as in **a**, but with Polyneoptera omitted.

p-value	slope	intercept	sample size	clade
0 – <0.005	0.11 – 0.14	0.11 – 0.17	89	Hexapoda
0.45 – 0.99	-0.01 – -0.05	-0.52 – -0.34	16	Hymenoptera
0.11 – 0.98	0 – 0.09	-0.37 – -0.05	6	Condylognatha
0.13 – 0.89	0.01 – 0.11	-0.27 – -0.06	20	Antliophora
0.14 – 0.44	0.08 – 0.16	-0.08 – -0.01	10	Neuropteroidea
0.07 – 0.86	0.03 – 0.21	-0.34 – -0.25	7	Amphiesmenoptera
0 – <0.005	0.31 – 0.36	0.52 – 0.57	22	Polyneoptera
0.01 – 0.03	0.36 – 0.39	0.47 – 0.52	7	Palaeoptera
0 – <0.005	0.09 – 0.12	0.09 – 0.15	173	Hexapoda, by genus
0 – 0.08	0.05 – 0.09	-0.08 – -0.01	67	Hexapoda, w/o Polyneoptera

Table S14: Results of PGLS regression of egg volume and genome size (C-value).

## 7 Evolutionary history of ecological traits

### 7.1 Parasitoid and internal oviposition

We compiled a list of parasitoid insects from multiple published reviews<sup>70–75</sup>. The table of parasitoid insect taxa and the code used to perform ecological analyses is available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution), file ‘ecology\_table\_parasitoid.tsv’. We used this list to classify taxa in the insect egg dataset as non-parasitoid or parasitoid, including ecto- and endoparasitoids, and excluding kleptoparasitic and gall-forming insects. We further classified parasitoid taxa as laying eggs externally or internally to their hosts. Insects that were listed as strictly endoparasitic with no reference to eggs laid externally, and for which no additional information was available, were considered to lay eggs internally. Reviews of parasitism across insects differed in the taxonomic level described. For each source, we used the lowest recorded taxonomic level to annotate taxa in the egg dataset. For some

clades it was not possible to classify all members unambiguously (e.g., the lowest description described the group as having “some parasitoids”). In order to test the impact of this uncertainty on our analyses we implemented both a “relaxed” classification system, in which taxa with ambiguous records were also coded as parasitoid / internal, and a “strict” classification system, in which only taxa that could be unambiguously defined as parasitoid / internal were coded as such.

We reconstructed the evolutionary history of both internal parasitic oviposition and ecto- or endoparasitoid habit (Fig. S20) on the Misof backbone MCC phylogeny<sup>17</sup> using an equal-rates model (R package corHMM<sup>76</sup>, version 1.22, function rayDISC, node.states=marginal). Using the relaxed classification method, we recovered 22 evolutionary shifts to ecto- or endoparasitoid habit across Hymenoptera, Antliophora, and Neuropteroidea, with 12 shifts to internal oviposition. We also found evidence for 8 reversals from parasitoid habit and 7 reversals from internal oviposition. These numbers likely reflect a minimum bound as more changes may have occurred in groups that are not represented in the insect egg dataset and phylogeny.

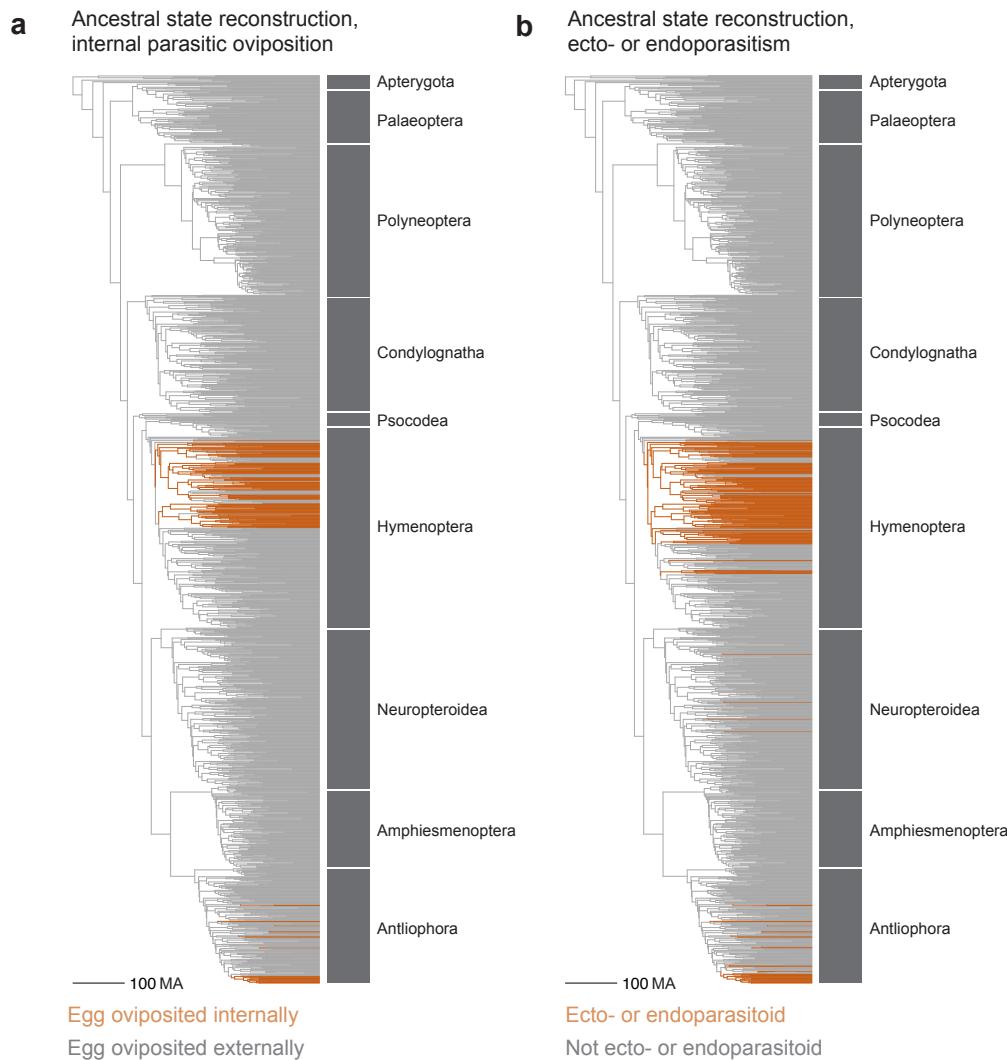
## 7.2 Aquatic insects and oviposition

We compiled a list of aquatic taxa in our dataset from multiple published reviews<sup>75,77–95</sup>. The table of aquatic insect taxa and the code used to perform ecological analyses is available at [https://github.com/shchurch/Insect\\_Egg\\_Evolution](https://github.com/shchurch/Insect_Egg_Evolution), file ‘ecology\_table\_aquatic.tsv’. Taxa were first classified as broadly aquatic, including semi-aquatic or riparian, and excluding insects that lay eggs within aquatic plants (phytophilous) or overhanging water. We further classified aquatic insects as laying eggs in water or out of water. We used the same relaxed and strict classification methods as described for parasitoid insects.

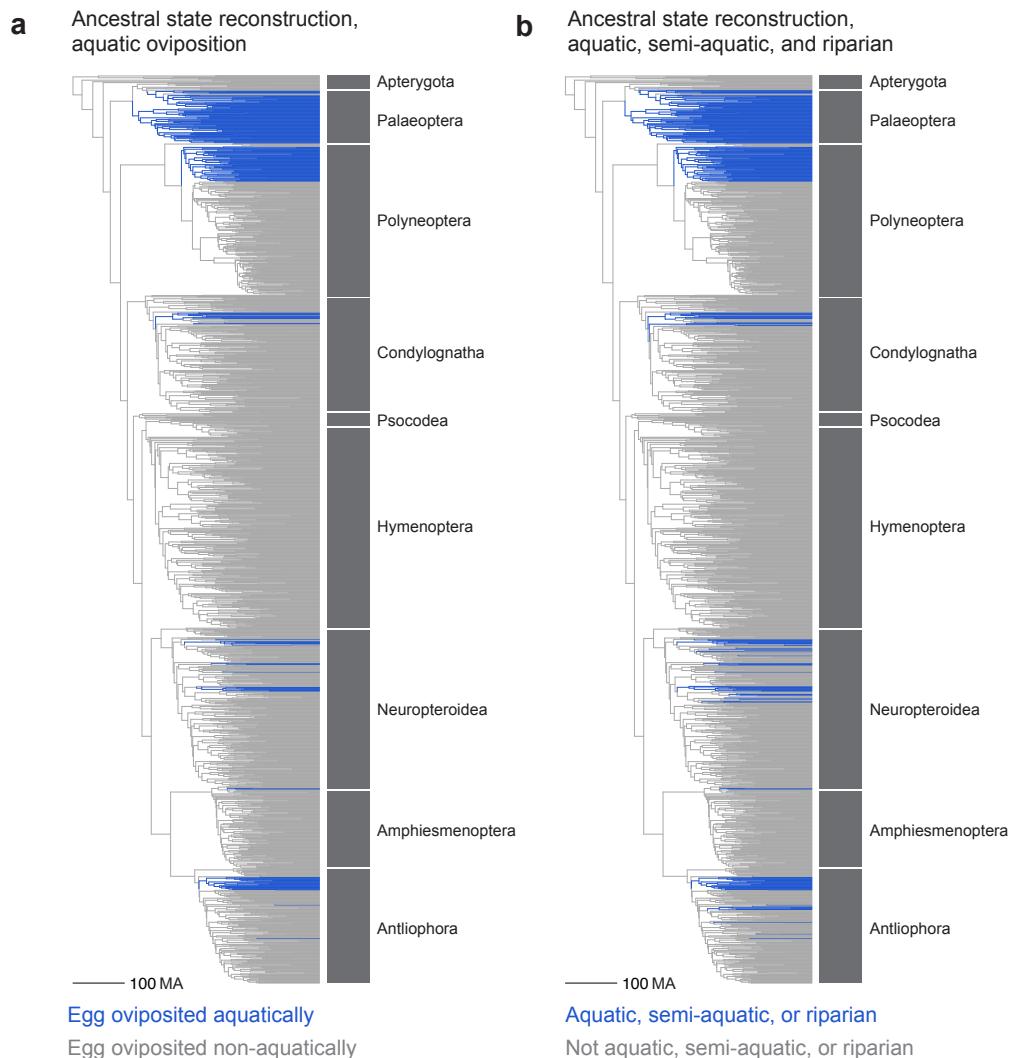
Using the same methods described above, we reconstructed the evolutionary history of aquatic and semiaquatic insects and oviposition in water (Fig. S21). Using the relaxed classification method, we recovered 32 separate transitions to aquatic or semiaquatic larval habit, and 15 transitions to aquatic oviposition. We also recovered 5 reversals to non-aquatic, semiaquatic, or riparian habit and 5 reversals to non-aquatic oviposition. As described above, these numbers are likely a minimum of the number of possible transitions.

## 7.3 Migration, flight, and wingless insects

There have likely been thousands of evolutionary shifts to flightless and wingless forms in insects<sup>96</sup>. We analyzed flight ability in Phasmatodea and Lepidoptera, using different metrics for flight ability in each. For Phasmatodea, we used published reviews to classify stick insects as either capable of flying or flightless (the latter category including both wingless and partially winged species that are not capable of flying)<sup>97,98</sup>. Phasmatodea taxa that could not be reliably classified in our dataset were excluded from subsequent analyses. For Lepidoptera, we analyzed migratory behavior as a proxy for the capability of flying longer distances than non-migratory Lepidoptera. We used published reviews of migratory insects to identify taxa in our dataset known to exhibit long-distance migration<sup>99–104</sup>. The ancestral state reconstructions of these traits are shown in Fig. S22.



**Figure S20: Ancestral state reconstruction of parasitoid oviposition ecology and life-history.** Ancestral state reconstructions using the “relaxed” classification method of **a** oviposition within an animal host, and **b** endoparasitoid and ectoparasitoid life history. Lineages that descend from a node reconstructed with a more than 50% likelihood of the derived state (internal or parasitoid, respectively) are shown in orange. Scale bar represents 100 million years.



**Figure S21: Ancestral state reconstruction of aquatic oviposition ecology and life-history.** Ancestral state reconstructions using the “relaxed” classification method of **a**, oviposition in water, and **b**, aquatic, semi-aquatic, or riparian life history (excluding ovipositing in aquatic plants or overhanging water). Lineages that descend from a node reconstructed with a more than 50% likelihood of the derived state (aquatic) are shown in blue. Scale bar represents 100 million years.

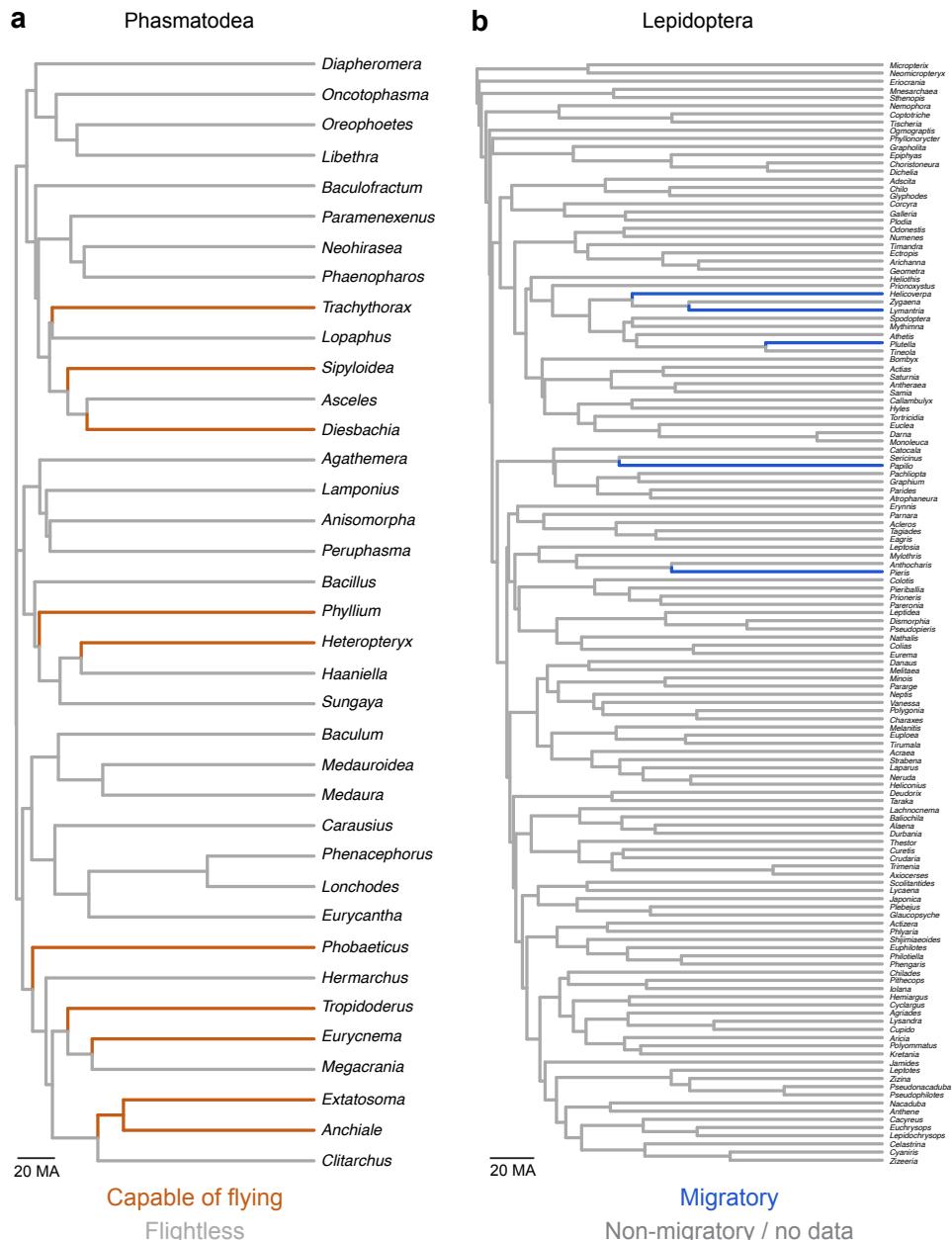


Figure S22: Ancestral state reconstructions of flight capability in selected clades. **a**, Ancestral state reconstruction of flightless (gray) vs capable of flying (orange) Phasmatodea. **b**, Ancestral state reconstruction of migratory behavior (blue) in Lepidoptera. Lineages that descend from a node reconstructed with more than 50% likelihood of the derived state (capable of flying or migratory) are shown in color. Scale bar in million years.

## 7.4 Testing eco-evolutionary models of egg evolution

We used the ecological records for parasitoid (Section 7.1) and aquatic (Section 7.2) oviposition modes in a comparison of evolutionary models. For a set of 100 trees randomly drawn from the posterior distribution, we reconstructed the ancestral state for each oviposition mode. Using these 100 reconstructions, for each egg morphological trait (volume, aspect ratio, asymmetry, and angle of curvature) we compared the fit of evolutionary models that account for ecological history (OU model with different optima for each ecological regime) to models which do not take ecology into account (BM, OU with a single optimum) using the R package OUwie<sup>105</sup> (version 1.50). We counted the number of comparisons in which the ecological OU model was significantly better fit ( $\Delta\text{AICc} > 2$ ), and considered a fraction  $> 0.9$  as unambiguous support.

Our results show that models that account for internal parasitic oviposition consistently fit the data best for both egg volume and asymmetry, but not for aspect ratio or curvature (Table S15). Insect lineages that oviposit in animal hosts typically have smaller eggs (OUM  $\theta$  values for egg volume, log transformed, non-internal: -1.82, internal: -3.66) and more asymmetrical eggs (OUM  $\theta$  values for egg asymmetry, sq. root transformed, non-internal: 0.24, internal: 0.42), than lineages that do not oviposit in animal hosts. These results are consistent when considering either the Misof or Rainford backbone phylogenies, when considering all endo- and ectoparasitoids, and when excluding any taxa that could not be unambiguously categorized as internal parasitoids (Table S16).

	freq. OUM best fit	ave. $\Delta\text{AICc}$ , OUM vs. BM1	ave. $\Delta\text{AICc}$ , OUM vs. OU1
volume	1.00	28.32	30.32
aspect ratio	0.00	-3.87	-1.88
asymmetry	1.00	64.18	14.58
angle of curvature	0.00	-2.52	-1.39

Table S15: Comparing evolutionary models (average  $\Delta\text{AICc}$  values) of egg morphology and internal parasitic oviposition using the “relaxed” classification method. Average  $\Delta\text{AICc} > 2$  for an ecological OU model (OUM) compared to both a Brownian Motion (BM1) and a single-optimum OU model (OU1) was considered significant support.

	Misof MCC	Rain. MCC	Strict method	Broader eco. definitions
internal oviposition, volume	OUM	OUM	OUM	OUM
aquatic oviposition, volume	OUM	OUM	OUM	OUM
internal oviposition, aspect ratio	BM1	BM1	BM1	BM1
aquatic oviposition, aspect ratio	OUM	OUM	OUM	OUM
internal oviposition, asymmetry	OUM	OUM	OUM	OUM
aquatic oviposition, asymmetry	OU1	OU1	OU1	OU1
internal oviposition, angle of curvature	BM1	BM1	BM1	BM1
aquatic oviposition, angle of curvature	BM1	BM1	BM1	BM1

Table S16: Testing the robustness of model comparison results. OUM indicates that an ecological OU model best fit the data ( $\Delta\text{AICc} > 2$ ). OU1 indicates an OU model with a single optimum, while BM1 indicates a model of Brownian Motion best fit the data or that neither OU model received significant support. “Misof MCC” and “Rain. MCC” refer to the backbone phylogeny used. “Strict method” indicates that taxa that could not be unambiguously identified as internal parasitic or aquatic ovipositors were excluded from those modes. “Broader eco. definitions” included all endo- and ecto-parasitoids or aquatic and riparian insects with internal parasitic or aquatic insects, respectively.

With respect to aquatic oviposition, models accounting for this characteristic consistently fit the data best for both

egg volume and aspect ratio, but not asymmetry or curvature (Table S17). Insect lineages that oviposit in water typically have smaller eggs (OUM  $\theta$  values for egg volume, log transformed, non-aquatic: -1.58, aquatic: -3.14) and more spherical eggs (OUM  $\theta$  values for egg aspect ratio, log transformed, non-aquatic: 0.21, aquatic: -0.07), than lineages that do not oviposit in water. These results are consistent when considering either the Misof or Rainford backbone phylogenies, when considering insects that oviposit either aquatically or in riparian habitats, and when excluding any taxa that could not be unambiguously categorized as aquatic (Table S16).

	freq. OUM best fit	$\Delta\text{AIC}_c$ , OUM vs. BM1	$\Delta\text{AIC}_c$ , OUM vs. OU1
volume	1.00	27.42	29.42
aspect ratio	1.00	13.87	15.87
asymmetry	0.02	49.79	0.19
angle of curvature	0.36	2.27	3.40

Table S17: Comparing evolutionary models (average  $\Delta\text{AIC}_c$  values) of egg morphology and and aquatic oviposition using the “relaxed” classification method.

Within both Phasmatodea (Table S18) and Lepidoptera (Table S19), models that account for the evolutionary history of flight ability do not fit any egg morphological data significantly better than those that do not.

	freq. OUM best fit	$\Delta\text{AIC}_c$ , OUM vs. BM1	$\Delta\text{AIC}_c$ , OUM vs. OU1
volume	0.00	-3.98	-1.64
aspect ratio	0.00	-2.19	-1.53
asymmetry	0.02	-2.94	-1.33
angle of curvature	0.00	-4.08	-2.57

Table S18: Comparing evolutionary models (average  $\Delta\text{AIC}_c$  values) of egg morphology and flightlessness in Phasmatodea.

	freq. OUM best fit	$\Delta\text{AIC}_c$ , OUM vs. BM1	$\Delta\text{AIC}_c$ , OUM vs. OU1
volume	0.00	-3.58	-1.57
aspect ratio	0.00	-3.74	-1.54
asymmetry	0.00	-3.81	-1.47
angle of curvature	0.00	-1.92	-1.96

Table S19: Comparing evolutionary models (average  $\Delta\text{AIC}_c$  values) of egg morphology and migratory behavior in Lepidoptera.

Previous studies have suggested that OU models can be favored simply due to the size of large phylogenetic datasets, even when using corrected AIC values for comparison<sup>106</sup>. We tested whether the egg dataset would likewise show a tendency to favor ecological OU models (OUM) by simulating new ecological states with no relationship to observed egg traits, and then performing the same model comparison described above. If support for an OUM model was a consequence of dataset size, continuous, trait distribution, or the underlying tree structure, simulations with random ecological traits would be expected to consistently favor OUM against both non-ecological models (BM1 and OU1).

To simulate random ecological datasets with comparable phylogenetic distributions to our observed oviposition datasets, we estimated the transition matrices for internal parasitic and aquatic oviposition, and used these to simulate

100 new ecology datasets for each ecology-trait pair that had been best fit by an OUM model using the observed data (R package geiger<sup>46</sup>). The results of this bootstrap approach showed that OUM models are infrequently selected due simply to the size or phylogenetic distribution of our data (Table S20, frequency of OUM models ranging from 0.03-0.14). Furthermore, we evaluated the likelihood of the simulated ecological data favoring an OUM model to the same degree as in our observed data, by counting the number of model comparisons on simulated data that had an  $\Delta\text{AICc}$  favoring OUM greater than the minimum  $\Delta\text{AICc}$  of our observed data. For each bootstrap analysis the likelihood was low (joint p-value = 0.01 or 1/100 analyses), therefore the size and phylogenetic distribution of our dataset cannot account for the support we recovered for ecological hypotheses of egg morphological evolution.

ecology	trait	data	freq. OUM	p-value, BM1	p-value, OU1	joint p-value
internal	volume	observed	1.00			
internal	volume	simulated	0.14	0.01	0.01	0.01
internal	asymmetry	observed	1.00			
internal	asymmetry	simulated	0.03	0.89	0.01	0.01
in water	volume	observed	1.00			
in water	volume	simulated	0.04	0.01	0.01	0.01
in water	aspect ratio	observed	1.00			
in water	aspect ratio	simulated	0.03	0.01	0.01	0.01

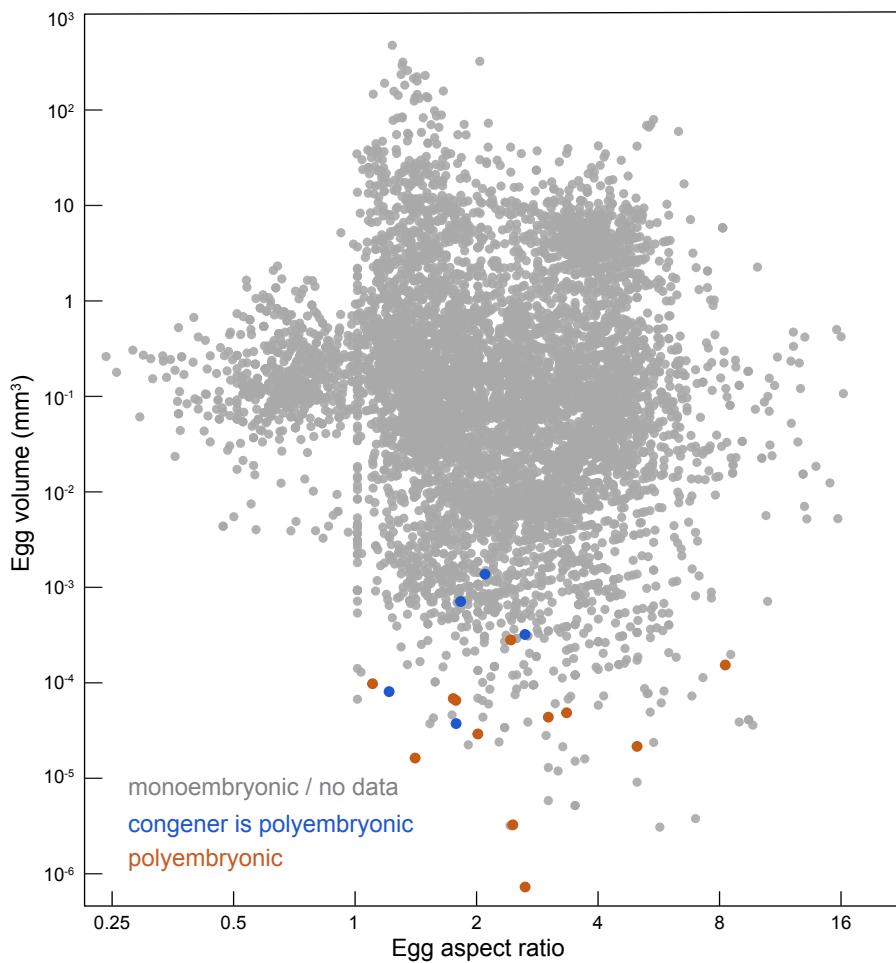
Table S20: **Bootstrap analysis of results supporting ecological OU models.** The p-values are calculated as the frequency of recovering  $\Delta\text{AICc}$  values between OUM and either BM1 or OU1 using simulated ecological data that are greater than the smallest  $\Delta\text{AICc}$  value for the same model comparison on observed data (a one-tailed test). The joint p-value is the frequency of analyses where both model comparisons were greater than the smallest observed values, and represents the likelihood of recovering support for an ecological OU model by chance that is equal to or above our observed support. n = 100 simulated datasets for each comparison.

## 7.5 Distribution of polyembryonic insects in egg morphospace

In polyembryonic insects, one egg develops into multiple embryos<sup>107</sup>. Observing that the smallest egg in the dataset is laid by a polyembryonic wasp, we collected records on polyembryony across insects and plotted their presence in insect egg morphospace<sup>107–113</sup>. Polyembryony has evolved at least five times in insects<sup>107</sup>, four times in Hymenoptera and once in Strepsiptera. In those polyembryonic lineages for which we have egg shape and size data, we observe that all polyembryonic insects are among the smallest eggs (below  $10^{-3} \text{ mm}^3$  in volume; Fig. S23). We hypothesize that additional instances of polyembryony will be observed when detailed embryological studies are conducted on insect species that lay particularly small eggs.

## 7.6 Allometry and ecology

To test for a possible interaction between ecology and the evolution of the allometric relationship between size and shape, we compared the scaling exponent of length vs. width (slope in log-log space) between groups that have converged upon the same ecological state. First, we identified the nodes where an ecological shift was most likely to have occurred (the probability of an ecological state being different than the parent node was above 50%), and then further identified those nodes that had a sufficient number (threshold > 20) of descendant tips with

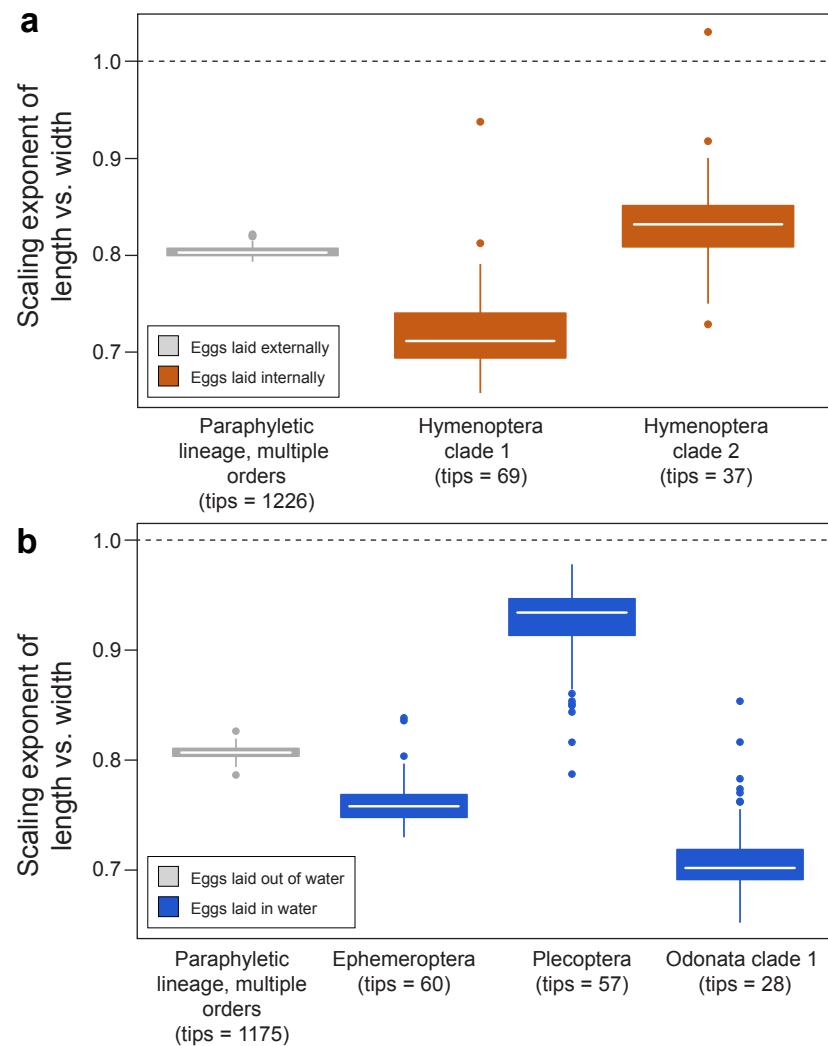


**Figure S23: Distribution of polyembryonic insects in egg morphospace.** The distribution of the eggs of polyembryonic insects (orange) and their congeners (blue) in the space defined by volume ( $\text{mm}^3$ ) and aspect ratio (unitless). Both traits are plotted on a log scale. Gray points represent eggs of insects that develop monoembryonically or taxa for which no information on monoembryony vs. polyembryony was found.

egg morphological data to robustly calculate the scaling exponent. For internal oviposition there were two clades (both in Hymenoptera) that met these requirements, and for aquatic oviposition there were three (Ephemeroptera, Plecoptera, and a subset of Odonata).

We calculated the allometric exponent as the slope of the phylogenetic regression between log-egg length and log-egg width, over 100 trees randomly drawn from the posterior distribution. We compared the slopes to the slope of the paraphyletic group of insects with the ancestral state (non-internal or non-aquatic oviposition). If transitions to new oviposition ecologies were predictive of a change in the allometric relationship, clades with the derived ecology would show consistent shifts up or down relative the ancestral ecological state.

Our results show dynamic evolution of the allometric exponent, but no consistent directional shift across ecologically convergent clades (Fig. S24). Because the number of shifts with sufficient sample size is low, further exploration by expanding the number of described egg morphologies in other internal and aquatic lineages would strengthen the power of this comparison.



**Figure S24: Comparing allometric slope by ecological regimes.** The scaling exponent of egg length vs. width, comparing clades with convergent ecological regimes to paraphyletic lineages with the ancestral state. **a**, Comparing the allometric exponent between two independent lineages of internal oviposition, and the paraphyletic non-internal lineage (gray). **b**, Comparing the allometric exponent between three independent lineages of aquatic oviposition (blue), and the paraphyletic non-aquatic lineage (gray). The scaling exponents are calculated over a posterior distribution of trees and accounting for intrageneric variation. Only lineages with more than 20 genera with egg descriptions are included. See Fig. S20 and S21 for details on lineage composition. In both panels, white lines, boxes, bars, dots represent median, 25-to-75th percentiles, 5-95th percentiles, and outliers. n = 100 PGLS regressions. The dashed black line represents a hypothetical 1:1 relationship.

## 8 Summary of Phylogenetic Generalized Least Squares (PGLS) results

To test the robustness of our results to the phylogenetic backbone, we repeated each PGLS comparison using the Rainford et al. (2018)<sup>18</sup> backbone phylogeny (see Section 5.1 for more details). We found that no results were significantly different than those calculated using the Misof et al. (2018)<sup>17</sup> backbone phylogeny (Table S21).

We also repeated each PGLS comparison using a covariance matrix based on a decelerating rate of evolution, using the corBlomberg function in the R package nlme<sup>53</sup> (see Section 5.1 for more details). We found that no results were significantly different than those calculated using a Brownian-Motion based covariance matrix (Table S22).

analysis	clade	Rain. p-value	Rain. slope	Misof p-value	Misof slope	sample size
egg volume vs duration of embryogenesis	Hexapoda	0 – 0.03	0.12 – 0.15	0.02 – 0.10	0.08 – 0.12	46
egg volume vs interval between pre-blastoderm mitoses	Hexapoda	0.14 – 0.76	0.03 – 0.14	0.18 – 0.71	0.03 – 0.12	16
egg volume vs time to cellularization	Hexapoda	0.09 – 0.58	0.10 – 0.26	0.14 – 0.96	-0.02 – 0.24	18
genome C-value vs egg volume	Hexapoda	0 – <0.005	0.08 – 0.15	0 – <0.005	0.11 – 0.14	89
egg length vs width	Hexapoda	0 – <0.005	0.77 – 0.82	0 – <0.005	0.76 – 0.81	1488
egg length vs width	Hymenoptera	0 – <0.005	0.69 – 0.78	0 – <0.005	0.68 – 0.78	355
egg length vs width	Condylognathia	0 – <0.005	0.78 – 0.90	0 – <0.005	0.80 – 0.91	202
egg length vs width	Antliophora	0 – <0.005	0.68 – 0.80	0 – <0.005	0.69 – 0.79	199
egg length vs width	Neuropteroidea	0 – <0.005	0.89 – 0.96	0 – <0.005	0.90 – 0.97	265
egg length vs width	Amphiesmenoptera	0 – <0.005	0.73 – 0.98	0 – <0.005	0.71 – 0.91	76
egg length vs width	Polyneoptera	0 – <0.005	0.70 – 0.78	0 – <0.005	0.70 – 0.75	262
egg length vs width	Palaeoaptera	0 – <0.005	0.61 – 0.71	0 – <0.005	0.60 – 0.72	104
egg length vs asymmetry, residuals to egg width	Hexapoda	0 – 0.08	0.07 – 0.18	0 – 0.06	0.07 – 0.17	796
egg length vs asymmetry, residuals to egg width	Hymenoptera	0.01 – 0.95	-0.01 – 0.22	0.02 – 0.96	0 – 0.20	174
egg length vs asymmetry, residuals to egg width	Condylognathia	0.01 – 0.40	0.08 – 0.29	0 – 0.70	0.04 – 0.49	149
egg length vs asymmetry, residuals to egg width	Antliophora	0 – 0.23	0.15 – 0.43	0 – 0.74	0.04 – 0.45	80
egg length vs asymmetry, residuals to egg width	Neuropteroidea	0.06 – 0.97	-0.01 – 0.16	0.05 – 0.86	0.02 – 0.17	141
egg length vs asymmetry, residuals to egg width	Amphiesmenoptera	0.28 – 0.99	-0.27 – 0.01	0.27 – 0.99	-0.26 – 0	24
egg length vs asymmetry, residuals to egg width	Polyneoptera	0.08 – 0.99	-0.11 – 0.18	0.04 – 1.00	-0.12 – 0.18	142
egg length vs asymmetry, residuals to egg width	Palaeoaptera	0.04 – 0.99	0 – 0.21	0 – 0.98	-0.03 – 0.30	71
egg length vs angle of curvature, residuals to egg width	Hexapoda	0 – <0.005	0.40 – 0.60	0 – <0.005	0.44 – 0.60	781
egg length vs angle of curvature, residuals to egg width	Hymenoptera	0 – <0.005	0.49 – 0.81	0 – <0.005	0.50 – 0.85	174
egg length vs angle of curvature, residuals to egg width	Condylognathia	0 – 0.04	0.32 – 0.92	0 – 0.02	0.40 – 0.74	149
egg length vs angle of curvature, residuals to egg width	Antliophora	0.01 – 0.61	0.10 – 0.50	0 – 0.54	0.13 – 0.58	79
egg length vs angle of curvature, residuals to egg width	Neuropteroidea	0 – 0.11	0.21 – 0.54	0 – 0.18	0.19 – 0.55	141
egg length vs angle of curvature, residuals to egg width	Amphiesmenoptera	0.30 – 1.00	-0.29 – 0.20	0.26 – 1.00	-0.33 – 0.18	22
egg length vs angle of curvature, residuals to egg width	Polyneoptera	0 – 0.04	0.34 – 0.67	0 – 0.24	0.18 – 0.69	133
egg length vs angle of curvature, residuals to egg width	Palaeoaptera	0.05 – 0.45	0.11 – 0.32	0.06 – 0.99	0 – 0.30	70

Table S21: Results of PGLS regression analysis using the Rainford backbone phylogeny<sup>18</sup>

analysis	clade	Blom. p-value	Blom. slope	Brown. p-value	Brown. slope	sample size
egg volume vs duration of embryogenesis	Hexapoda	0.07 – 0.28	0.07 – 0.11	0.06 – 0.28	0.07 – 0.11	46
egg volume vs interval between pre-blastoderm mitoses	Hexapoda	0.30 – 0.87	0.02 – 0.12	0.32 – 0.84	0.02 – 0.12	16
egg volume vs time to cellularization	Hexapoda	0.07 – 0.45	0.13 – 0.32	0.08 – 0.44	0.15 – 0.32	18
genome C-value vs egg volume	Hexapoda	0 – <0.005	0.10 – 0.15	0 – <0.005	0.11 – 0.14	89
egg length vs width	Hexapoda	0 – <0.005	0.76 – 0.82	0 – <0.005	0.76 – 0.81	1488
egg length vs width	Hymenoptera	0 – <0.005	0.68 – 0.78	0 – <0.005	0.68 – 0.78	355
egg length vs width	Condylognatha	0 – <0.005	0.77 – 0.90	0 – <0.005	0.80 – 0.91	202
egg length vs width	Antliophora	0 – <0.005	0.68 – 0.80	0 – <0.005	0.69 – 0.79	199
egg length vs width	Neuropteroidea	0 – <0.005	0.90 – 0.98	0 – <0.005	0.90 – 0.97	265
egg length vs width	Amphiesmenoptera	0 – <0.005	0.72 – 0.93	0 – <0.005	0.71 – 0.91	76
egg length vs width	Polyneoptera	0 – <0.005	0.70 – 0.78	0 – <0.005	0.70 – 0.75	262
egg length vs width	Palaeoptera	0 – <0.005	0.60 – 0.88	0 – <0.005	0.60 – 0.72	104
egg length vs asymmetry, residuals to egg width	Hexapoda	0 – 0.25	0.04 – 0.18	0 – 0.06	0.07 – 0.17	796
egg length vs asymmetry, residuals to egg width	Hymenoptera	0.03 – 1.00	-0.08 – 0.19	0.02 – 0.96	0 – 0.20	174
egg length vs asymmetry, residuals to egg width	Condylognatha	0 – 0.89	-0.10 – 0.42	0 – 0.70	0.04 – 0.49	149
egg length vs asymmetry, residuals to egg width	Antliophora	0 – 0.29	0.10 – 0.45	0 – 0.74	0.04 – 0.45	80
egg length vs asymmetry, residuals to egg width	Neuropteroidea	0.05 – 0.94	-0.08 – 0.17	0.05 – 0.86	0.02 – 0.17	141
egg length vs asymmetry, residuals to egg width	Amphiesmenoptera	0.18 – 0.96	-0.33 – -0.01	0.27 – 0.99	-0.26 – 0	24
egg length vs asymmetry, residuals to egg width	Polyneoptera	0.10 – 0.99	-0.16 – 0.12	0.04 – 1.00	-0.12 – 0.18	142
egg length vs asymmetry, residuals to egg width	Palaeoptera	0 – 0.97	-0.01 – 0.33	0 – 0.98	-0.03 – 0.30	71
egg length vs angle of curvature, residuals to egg width	Hexapoda	0 – <0.005	0.40 – 0.61	0 – <0.005	0.44 – 0.60	781
egg length vs angle of curvature, residuals to egg width	Hymenoptera	0 – <0.005	0.49 – 0.84	0 – <0.005	0.50 – 0.85	174
egg length vs angle of curvature, residuals to egg width	Condylognatha	0 – 0.02	0.40 – 0.73	0 – 0.02	0.40 – 0.74	149
egg length vs angle of curvature, residuals to egg width	Antliophora	0.01 – 0.95	-0.01 – 0.60	0 – 0.54	0.13 – 0.58	79
egg length vs angle of curvature, residuals to egg width	Neuropteroidea	0 – 0.41	0.12 – 0.57	0 – 0.18	0.19 – 0.55	141
egg length vs angle of curvature, residuals to egg width	Amphiesmenoptera	0.28 – 1.00	-0.27 – 0.23	0.26 – 1.00	-0.33 – 0.18	22
egg length vs angle of curvature, residuals to egg width	Polyneoptera	0 – 0.37	0.17 – 0.68	0 – 0.24	0.18 – 0.69	133
egg length vs angle of curvature, residuals to egg width	Palaeoptera	0.08 – 0.90	0.02 – 0.30	0.06 – 0.99	0 – 0.30	70
egg length vs width, residuals to body size	Hexapoda	0 – <0.005	0.64 – 0.71	0 – <0.005	0.64 – 0.74	235
egg length vs width, residuals to body size	Hymenoptera	0 – <0.005	0.67 – 0.89	0 – <0.005	0.67 – 0.90	44
egg length vs width, residuals to body size	Condylognatha	0 – 0.23	0.23 – 0.78	0 – 0.12	0.30 – 0.85	36
egg length vs width, residuals to body size	Antliophora	0 – <0.005	0.56 – 0.69	0 – <0.005	0.54 – 0.69	38
egg length vs width, residuals to body size	Neuropteroidea	0 – <0.005	0.87 – 1.04	0 – <0.005	0.91 – 1.06	35
egg length vs width, residuals to body size	Amphiesmenoptera	0 – 0.10	0.22 – 0.42	0 – 0.15	0.19 – 0.48	30
egg length vs width, residuals to body size	Polyneoptera	0 – <0.005	0.64 – 0.77	0 – <0.005	0.65 – 0.76	31
egg length vs width, residuals to body size	Palaeoptera	0.05 – 0.94	-0.04 – 0.48	0.05 – 0.75	0.06 – 0.46	15
egg volume vs cubic body length	Hexapoda	0 – <0.005	0.53 – 0.60	0 – <0.005	0.53 – 0.60	238
egg volume vs cubic body length	Hymenoptera	0 – <0.005	0.62 – 0.77	0 – <0.005	0.63 – 0.81	44
egg volume vs cubic body length	Condylognatha	0 – <0.005	0.62 – 0.84	0 – <0.005	0.64 – 0.83	36
egg volume vs cubic body length	Antliophora	0 – 0.04	0.28 – 0.44	0 – 0.03	0.28 – 0.44	39
egg volume vs cubic body length	Neuropteroidea	0 – <0.005	0.49 – 0.64	0 – <0.005	0.49 – 0.60	36
egg volume vs cubic body length	Amphiesmenoptera	0 – <0.005	0.59 – 0.72	0 – <0.005	0.58 – 0.74	31
egg volume vs cubic body length	Polyneoptera	0 – <0.005	0.59 – 0.73	0 – <0.005	0.62 – 0.75	31
egg volume vs cubic body length	Palaeoptera	0 – 0.03	0.26 – 0.42	0 – 0.01	0.28 – 0.46	15

Table S22: Results of PGLS regression using a Blomberg correlation structure with a fixed deceleration parameter at 1.3

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# Egg Dataset Bibliography

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*Note:* This document is a list of the 1,756 published sources that were used to generate the assembled dataset of insect egg traits. ‘Diss.’ indicates a PhD dissertation, whereas ‘MA thesis’ indicates a Master’s thesis. For more information on the dataset, please see Church et al. 2019: “A database of egg size and shape from more than 6,700 insect species” (*Scientific Data*). It describes the criteria that were used to include sources, definitions of each trait, and details on the procedure that was used to collect data from each source.

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