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Repeated loss of variation in insect ovary morphology highlights the role of development in life-history evolution

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Abstract

The number of offspring an organism can produce is a key component of its evolutionary fitness and life-history. Here we perform a test of the hypothesized trade-off between the number and size of offspring using thousands of descriptions of the number of egg-producing compartments in the insect ovary (ovarioles), a common proxy for potential offspring number in insects. We find evidence of a negative relationship between egg size and ovariole number when accounting for adult body size. However in contrast to prior claims, we note that this relationship is not generalizable across all insect clades, and we highlight several factors that may have contributed to this size-number trade-off being stated as a general rule in previous studies. We reconstruct the evolution of the arrangement of cells that contribute nutrients and patterning information during oogenesis (nurse cells), and show that the diversification of ovariole number and egg size have both been largely independent of their presence or position within the ovariole. Instead we show that ovariole number evolution has been shaped by a series of transitions between variable and invariant states, with multiple independent lineages evolving to have almost no variation in ovariole number. We highlight the implications of these invariant lineages on our understanding of the specification of ovariole number during development, as well as the importance of considering developmental processes in theories of life-history evolution.

Introduction

Offspring number is a fundamental parameter in the study of life-history[1]. This number differs widely between organisms[1], and its variation is the foundation for several hypotheses about life-history evolution, including the prediction that there is an evolutionary trade-off between the number of offspring and their size (e.g. egg size)[1–3]. In insects, the number of egg-producing compartments in the ovary, called ovarioles, has been used as a proxy for potential offspring number in the study of life-history[4–6]. However, without an understanding of the phylogenetic distribution of ovariole number, this hypothesized relationship cannot be assessed across insects. Here we tested for the presence of a general trade-off between ovariole number and egg size by collecting thousands of records of ovariole number from the published literature, placing them in a phylogenetic context, and comparing them to other datasets of insect reproductive morphology.

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The insect female reproductive system includes a pair of ovaries, each of which contains a number of ovarioles[7] (Fig 1a). Each ovariole consists of an anterior germarium containing the stem cell niche or resting oogonia, developing oocytes arranged in an ontogenic series from anterior to posterior, and a posterior connection to a common oviduct. The number of ovarioles varies across species[6], and can vary across individuals in a population[4], as well as between the left and right ovary within a single individual[8]. Therefore total ovariole number may be an even or odd integer for an individual female insect. In addition to variation in the number of ovarioles, the tissue morphology within ovarioles varies across insects, and has been classified into several modes of oogenesis based on the presence and position of special oocyte-associated cells called nurse cells[7].

Here we compiled 3355 records of ovariole number from across 28 orders, 301 families, and 2103 species of insects. We combined these data with published datasets of egg size[9], fecundity[10,11], and body size[12], to test hypotheses about the evolutionary trade-off between offspring size and number. In these analyses we used an existing phylogeny of insects[13] to analyze evolutionary patterns in ovariole number, and found that hypotheses about life-history evolution do not hold generally true across insects. We then combined these data with published observations of the mode of oogenesis[7] and reconstructed the evolutionary history of the presence and position of nurse cells that contribute to the oocyte during oogenesis. We tested whether patterns in the distribution of ovariole number, egg size, or egg shape were driven by the evolution of nurse cells, and found no significant results. Instead we observe that the phylogenetic distribution of ovariole number suggests a model where the developmental mechanisms that govern ovariole number have shifted between variable and invariant states several times over the course of insect evolution. Based on this finding, we propose that the developmental mechanisms used to establish ovariole number in well-studied insects such as *Drosophila melanogaster* are unlikely to regulate ovariole number in all insects.

Methods

Gathering trait data

We searched the published literature for references to insect ovariole number using a predetermined set of 131 search terms, entered into Google Scholar (scholar.google.com) between June and October of 2019. Each search term was comprised of an insect taxonomic group and the words “ovariole number”. The taxonomic groups used in the search process included all insect orders, many large insect families, and taxonomic groups that are well-represented in the insect egg dataset[9]. For each Google Scholar search, we evaluated the first ten pages in the search results. For 61 search terms that had a large number of informative hits, significant representation in the egg dataset, or that corresponded to very speciose groups, we evaluated an additional 20 publications. The list of search terms is available in the supplementary file ‘ovariole_number_search_terms.tsv’.

Using this approach, we gathered 3355 records for ovariole number for 28 insect orders, 301 families, and 2103 species, using 448 publications that are listed in the supplementary file ‘ovariole_number_bibliography.pdf’. We matched these records to additional taxonomic information using the software TaxReformer[14]. For all subsequent analyses, we excluded observations made in non-reproductive individuals from eusocial species (e.g. workers), as well as two observations that represented significant outliers and could not be validated using additional sources[15,16]. See supplementary methods section 1 for details.

For records of ovariole number that reported intraspecific variation in ovariole number, we calculated the percent difference as follows: if ovariole number was reported as a range, percent difference was calculated as the $100 * ((max - min)/median)$; if ovariole number was reported as an average with deviations, percent difference was calculated as $100 * ((2 * deviation)/mean)$. When independent observations of ovariole number for a given species were available across multiple published records, we calculated the percent difference as the $100 * ((max - min)/median)$.

We combined the data we collected on total ovariole number with existing datasets of egg size and shape[9], insect lifetime fecundity and dry adult body mass[10,11,17], average adult body length per insect family[12], several lineage-specific measures of adult body size[18–22], and the mode of oogenesis[7]. See supplementary methods section 3.1 for details.

All continuous traits (ovariole number, egg volume, lifetime fecundity, and all measures of body size) were $\log_{10}$ transformed for subsequent analyses.

Phylogenetic analyses

The analyses in this manuscript were performed using the insect phylogeny published in Church et al., 2019[13], unless otherwise specified. For regressions involving body size data that were reported as insect family-level averages, we used the insect phylogeny published in Rainford et. al, 2014[23]. Analyses of Drosophilidae ovariole number, egg size, and body size were performed using a phylogeny newly assembled for this study. See supplementary methods section 2 for details.

To evaluate the robustness of our results to uncertainty in the phylogenetic relationships, all Phylogenetic Generalized Least Squares (PGLS) analyses were performed 1000 times over a posterior distribution of trees, using a Brownian Motion based covariance matrix in the R package ape (version 5.4.1)[24] and nlme (version 3.1.151)[25]. For regressions at the species and genus level, we reshuffled and matched records for each iteration to account for variation across records for the same taxon. For regressions at the family level we recalculated the average ovariole number per insect family, randomly downsampling the representation for each family by half. To weight traits by body size, we calculated the phylogenetic residuals[26] of each trait to body size, and then compared the evolution of these residuals using a PGLS regression. See supplementary methods section 3.2 for details.

For two regressions comparing egg size to ovariole number while accounting for adult body size, we tested alternative hypotheses of evolution by simulating new data. We considered two such hypotheses: no evolutionary correlation with ovariole number, and a strong correlation with ovariole number (slope of -1). For each trait we simulated 1,000 datasets using evolutionary parameters fit under a Brownian Motion model in the R packages geiger (version 2.0.7)[27], and phylolm (version 2.6.2)[28].

Ancestral state reconstruction of oogenesis mode was performed with the R package corHMM (version 1.22)[29], and models of trait evolution were compared using the R package Ouwie (version 1.57)[30]. Ancestral state reconstruction and model comparison were repeated 100 times over a posterior distribution of trees and resampling data to account for variation across records for the same taxon. See supplementary methods section 4.3.

Other comparisons of model fit were performed using the R package geiger(version 2.0.7)[27] and validated using a parametric bootstrap with the R package arbutus (version 0.1)[31]. See supplementary methods section 5.1.

Analyses of evolutionary rate were performed using BAMM (version 2.5.0)[32]. For this analysis, we calculated the average ovariole number ($\log_{10}$ transformed) for each genus present in the phylogeny (507 taxa). We used the R package BAMMtools (version 2.1.7)[33] to select appropriate priors, and ran BAMM for the maximum number of generations ($2 * 10^{-9}$), sampling every 10^6 generations. Convergence was evaluated both visually (Fig. S12) and numerically. Running BAMM for the maximum possible number of generations and selecting the optimum burn-in (Fig. S13) resulted in an effective size for the number of shifts of 482.51, and for the log-likelihood of 149.15. Repeated BAMM analyses showed similar distributions of high and low rate regimes, indicating the implications for ovariole number evolution are robust to uncertainty in rate estimates. See supplementary methods section 5.2 for details.

We visualized the results from the BAMM analysis to establish a threshold (10^{-4}) for assigning a binary rate regime to each node in the phylogeny, categorizing them as above (variable) or below (invariant) a threshold that separates these two peaks.

Data availability

The dataset of insect ovariole number is available at Dryad, doi:10.5061/dryad.59zw3r253.

Code availability

The code and phylogenetic trees required to reproduce all the analyses, figures, and generate the manuscript files are provided at 'https://github.com/shchurch/insect_ovariole_number_evolution_2020', commit 6cf446a. All analyses performed in R (version 4.0.3) were done so in a clean environment, built with conda (version 4.9.2), and instructions for rebuilding this environment are provided in the same repository.

Statistical significance

All phylogenetic regressions were performed using the maximum clade credibility (MCC) tree (the tree with highest credibility score from the posterior distribution of the Bayesian analysis). We considered a relationship significant when the p-value was below the threshold 0.01. To assess the robustness of results to uncertainty in phylogenetic relationships, we also repeated these analyses over the posterior distribution of phylogenetic trees and report the number of regressions that gave a significant result (see Table S1).

For two comparisons, we validated that our tests had sufficient statistical power using the selected threshold by comparing the distribution of p-values from regressions of observed data to regressions of data simulated under alternative hypotheses. We compared the results of analyses of our observed to those based on simulated data to evaluate the likelihood of false positives (comparing to data simulated under no correlation) and false negatives (comparing to data simulated with strong correlation).

Model comparisons of trait evolution were also performed over a posterior distribution and accounting for phenotypic uncertainty. For these analyses, we considered a model to have significantly better fit the data than other models when the difference in the corrected Akaike Information Criterion (AICc) was greater than two in every analysis iteration.

Results

Ovariole number diversity

Ovariole number varies by at least four orders of magnitude across insect species (Fig. 1b). We identify seven insect families with species that have been reported to have more than 1,000 total ovarioles, including several eusocial insects (e.g. queens of the termite species *Hypotermes obscuriceps*, Blattodea: Termitidae[34], and several ant species, Hymenoptera: Formicidae)[35,36] and non-eusocial insects (e.g. the blister beetle *Meloe proscarabaeus*, Coleoptera: Meloidae)[37]. We also find two independent lineages that have evolved to have only one functional ovariole: dung beetles in the tribe Scarabaeinae (Coleoptera: Scarabaeidae)[38], and grass flies in the genus *Pachylophus* (Diptera: Chloropidae)[39,40]. In these insects one of the two ovaries presumably established during embryogenesis is reported to atrophy during development[40,41], resulting in an asymmetric adult reproductive system. We also evaluated intraspecific variation in ovariole number, and found that, for species for which it has been reported, the average percent difference number within species is between 10% and 100% of the median value (Fig. S1).

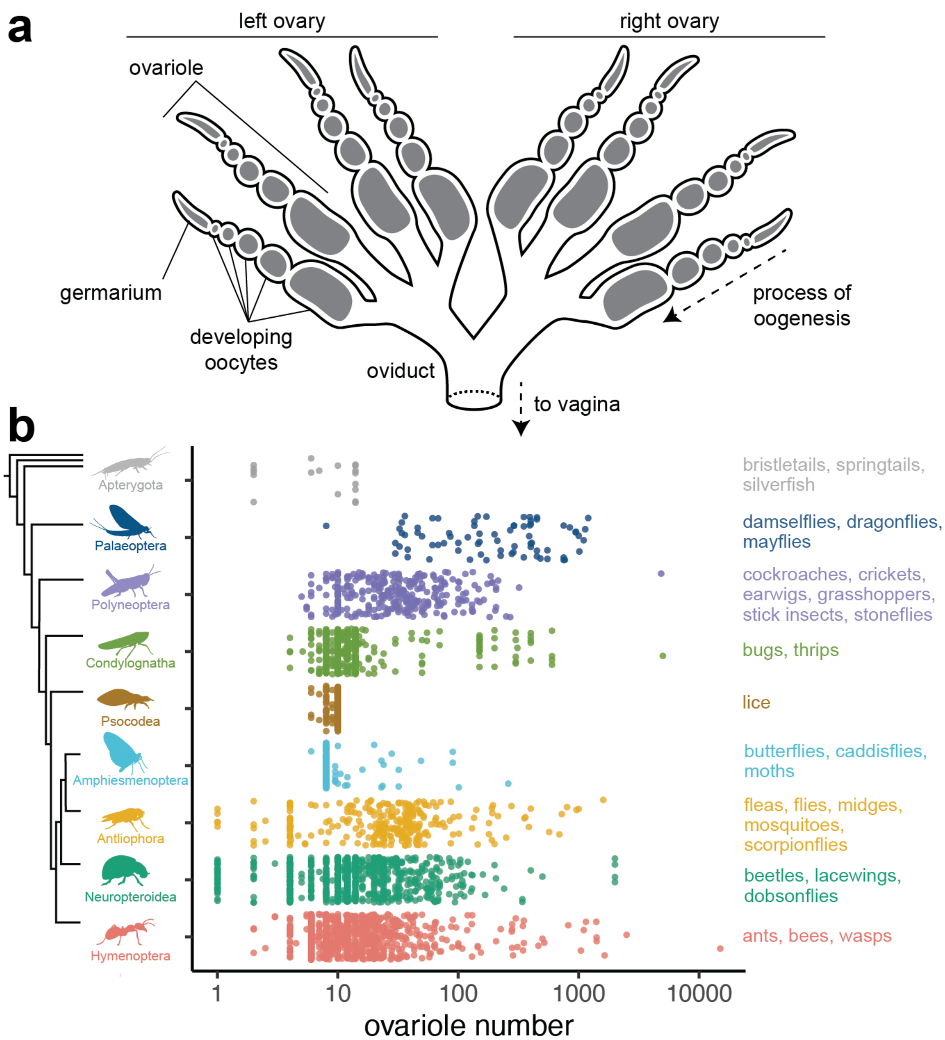

Figure 1: **The diversity of ovariole number across insects.** a, Schematic of a generalized insect female reproductive system, showing a pair of ovaries, each with four ovarioles. b, The range of total adult ovariole number, $\log_{10}$ scale, across nine groups of insects, arranged with random jitter on the y-axis within each group. Groups are, from top to bottom: Apterygota, Palaeoptera, Polyneoptera, Condylognatha, Psocodea, Amphiesmenoptera, Antliophora, Neuropteroidea, and Hymenoptera.

Ovariole number, egg size, and body size

Ovariole number has been hypothesized to be negatively correlated with egg size[5,21,42]. This hypothesis is based on the predictions that (1) female reproduction is resource-limited, therefore egg size should trade off with egg number, and (2) ovariole number can serve as a proxy for egg number[2,42]. We did not observe a significant negative relationship when comparing egg size and ovariole number across insect species (Fig. 2a, Table S1, p-value 0.195, n=306). We also compared egg size and ovariole number, combining data from species within the same genus to increase sample size, and again did not observe a significant relationship (Fig. S2, p-value 0.066, n=482). To verify this finding was not driven by the high ovariole numbers seen in the queens of some eusocial insects, we repeated this comparison excluding insects from families with eusocial representatives, with the same result (Fig. S3, p-value 0.209, n=415).

Given that this predicted relationship is often conditioned on body size, which is predicted to limit total potential reproductive investment[21,43], we combined data on ovariole number and egg size with data on insect adult body mass[10,11,17] and length[12]. When accounting for adult body mass, we observed a significant negative relationship between egg size and ovariole number across genera (Fig. 2b, S4, p-value 0.003, slope -0.399, n=61). To evaluate the robustness of this result, we repeated the analysis 1000 times, taking into account uncertainty in both the phylogeny and trait measurements. Out of 1000 regressions, 995 indicated a significant negative relationship (Table S1). We performed the same comparison accounting for adult body length, and likewise observed a significant negative relationship (Fig. S5, p-value <0.001, slope -0.52, n=126), supported by 966 of 1000 repeated analyses (Table S1).

We further explored these results using two methods: First, to evaluate our findings against alternative evolutionary hypotheses, we compared these results to regressions based on simulated data. Our results showed that when considering body size, the slope of the regression of egg size and ovariole number is more negative than we would expect to observe by chance, as assessed by comparing to data simulated with no evolutionary correlation (Fig. S6). However, for both adult body length and dry mass, the slope of the regressions on observed data are not within the range that would be expected under a strong negative correlation (slope of -1 in log-log space, Fig. S6). This suggests the presence of a weak evolutionary relationship between ovariole number and egg size, when accounting for body size.

Second, we assessed the relationship between egg size and ovariole number, accounting for body size, within four subclades of insects. We found that across Drosophilidae fly species, egg size is indeed strongly negatively correlated with ovariole number when accounting for body size (Fig. 2c, Table S2, p-value <0.001, slope -0.809, n=30). For grasshoppers and crickets (Orthoptera), beetles (Coleoptera), and wasps (Hymenoptera), we observed no significant relationship between ovariole number and egg size, even when accounting for body size (Fig. 2d, S7, Table S2, Orthoptera: p-value 0.485, n=40, Coleoptera: p-value 0.384, n=30, Hymenoptera: p-value 0.139, n=21). This indicates that, while a strong negative correlation between egg size and ovariole number exists for some insects, it does not represent a universal pattern across insect clades.

Finally, we tested whether ovariole number is positively correlated with adult body size, and in contrast to previous studies[4], we found no correlation between ovariole number and adult body mass or length across insects (Fig. S8, Table S3, body mass: p-value 0.618, n=61, body length: p-value 0.031, n=98). Of the four subclades considered, only insects in the order Orthoptera had a positive relationship between body size and ovariole number (Table S3, p-value 0.001, slope 0.35, n=40).

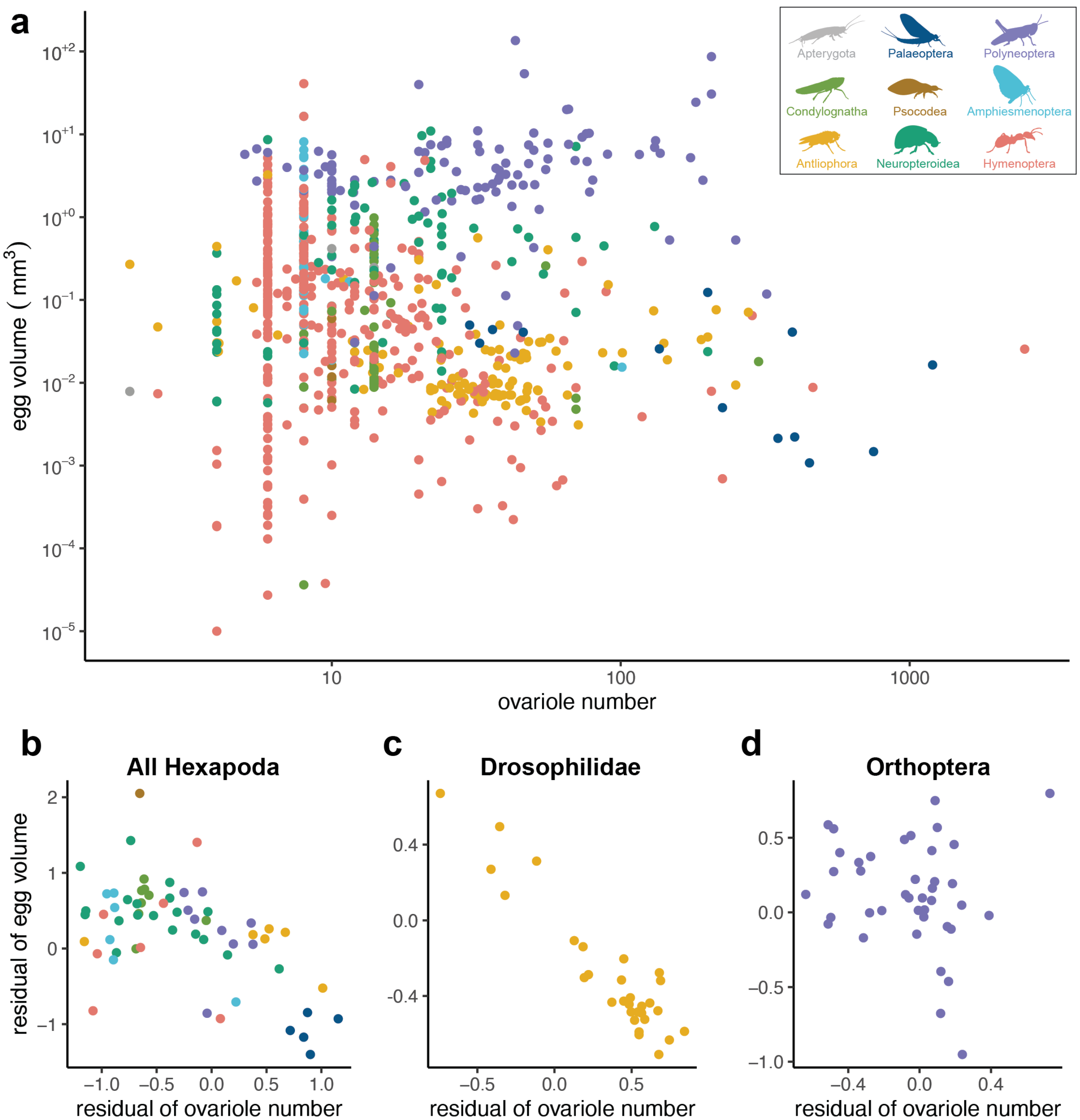

Figure 2: **Tests of the hypothesized trade-off between egg size and ovariole number.** a, Egg volume (mm^3) and ovariole number, both $\log_{10}$ scale; points represent insect species. See section *Modeling ovariole number evolution* for discussion of the enrichment of certain low values of ovariole number (points appearing vertically arranged) b, Egg volume and ovariole number, residuals to dry adult body mass, points represent genera. c, Drosophilidae egg volume and ovariole number, residuals to thorax length, points represent species. d, Orthoptera egg volume and ovariole number, residuals to body length, points represent genera.

Ovariole number and fecundity

If the hypothesized trade-off between the number and size of offspring is true for insects, then one explanation for the lack of a consistent negative relationship between ovariole number and egg size is that ovariole number may not be a reasonable proxy for offspring number. Previous research has shown that, across individuals within the same species, ovariole number is correlated with certain measurements of fecundity, such as maximum daily rate of egg production for *Drosophila*,[44,45] but not others, such as lifetime fecundity[46] or fitness in competition assays[47]. Few studies have compared fecundity and ovariole number across species[43], likely due to the difficulties of measuring fecundity consistently across insects, many of which lay eggs singly and continuously rather than in distinct clutches.

Using a previously reported dataset of lifetime fecundity measurements across insects[10,11], we assessed the relationship between lifetime fecundity and ovariole number. We observed a significant positive relationship (Fig. 3, p-value 0.002, slope 1.233, n=65), however, a substantial fraction of repeat analyses show these results are not robust to uncertainty (733 of 1000 regressions are not significant, Table S4). We note that this relationship is largely defined by the absence of insects with high ovariole number and low fecundity (Fig. 3, empty bottom right corner), while for insects with low ovariole number, fecundity varied over more than three orders of magnitude. We interpret our results, in conjunction with those previously reported, to suggest that ovariole number, when variable across insects in a lineage, may be one factor among many influencing the number of eggs produced. However, we caution against using ovariole number as a direct mathematical proxy for offspring number.

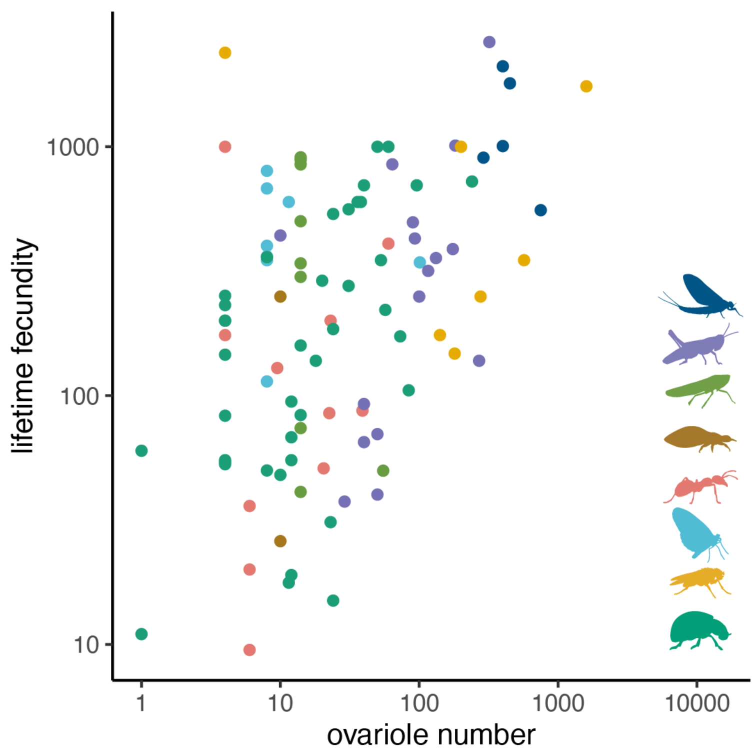

Figure 3: **The relationship between lifetime fecundity and ovariole number.** Both values are shown on a $\log_{10}$ scale. Points represent insect genera and are colored according to the groups shown in Fig. 1b.

Evolution of nurse cells

In addition to the number of ovarioles, insect ovary morphology has been classified into several modes of oogenesis based on the presence and position of cells that provide nutritive and patterning molecules to the oocyte, which are called nurse cells[7] (Fig. 4a). Egg formation in the well-studied species *D. melanogaster* is an example of a meroistic oogenesis mode, meaning that its ovarioles contain nurse cells of germ line origin that are connected to developing oocytes via cytoplasmic bridges[48]. In insects with a polytrophic meroistic arrangement, these nurse cells are clonally related and immediately adjacent to each oocyte. An alternative arrangement is seen in telotrophic meroistic ovaries, where oocytes in each ovariole are connected to a common pool of nurse cells located in the germarium[7]. Meroistic ovaries are thought to have evolved from an ancestral panoistic mode, meaning they lack nurse cells[7]. Using a previously published set of descriptions of these oogenesis modes across insects[7], we reconstructed the evolutionary transitions between these states. Consistent with previous analyses[7], we found that the ancestral insect likely had panoistic ovaries (lacking nurse cells), with several independent shifts to both telotrophic and polytrophic meroistic modes, and at least two reversals from meroistic back to panoistic (Figs. 4b, S10).

Using this ancestral state reconstruction, we then compared models of trait evolution to test whether evolutionary transitions in oogenesis mode helped explain the diversification of ovariole number and egg morphology. We found that, for the traits studied here, models that take into account evolutionary changes in mode of oogenesis do not consistently demonstrate a significant improvement over models that do not take these changes into account (ΔAIC < 2, Table S5). In other words, the evolution of nurse cells and their position within the ovary do not explain the diversification of egg size, egg shape, or ovariole number.

To analyze the robustness of these results to uncertainty in the tree topology and in the inference of ancestral states, we repeated each analysis over a posterior distribution of trees. For egg asymmetry and curvature, but not for volume or aspect ratio, we observed a few iterations where a model that takes into account oogenesis mode evolution was significantly favored over models that did not (ΔAIC > 2, Table S5). However, this result was infrequent over 100 repetitions of the analysis. We therefore interpret these results as suggestive of a possible relationship between mode of oogenesis and egg asymmetry and curvature, but one which cannot be confirmed given the current data available.

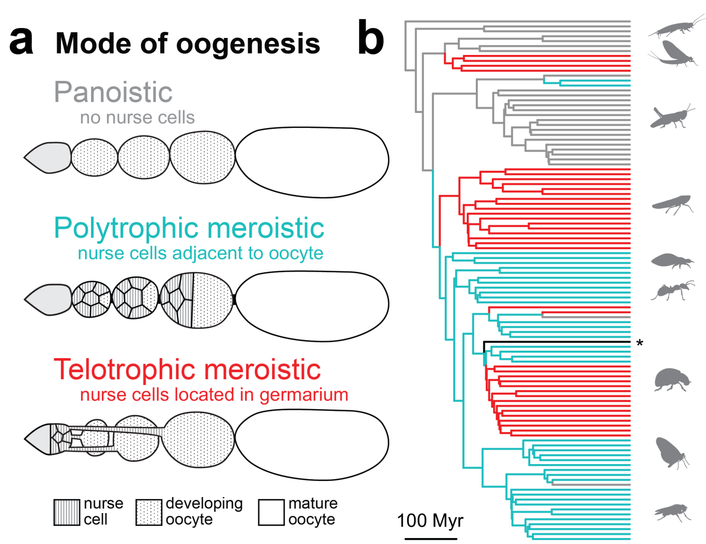

Figure 4: **The evolution of the presence and position of nurse cells.** a, Insect oogenesis was categorized into several modes by Büning[7] based on the presence and position of nurse cells. b, Phylogenetic reconstruction of mode of oogenesis. Scale bar indicates 100 million years (Myr). Gray = panoistic ovaries, without nurse cells, cyan = polytrophic meroistic ovaries, with nurse cells adjacent to maturing oocytes, red = telotrophic meroistic ovaries, with nurse cells located in germaria, black = unique meroistic ovary type observed in Strepsiptera. Insect taxonomic groups are, from top to bottom: Apterygota, Palaeoptera, Polyneoptera, Condylognatha, Psocodea, Hymenoptera, Neuropteroidea, Amphiesmenoptera, and Antliophora.

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Modeling ovariole number evolution

Using the dataset compiled here and a previously published phylogeny of insects (Fig. 5a)[13], we modeled the rate of evolutionary change in ovariole number (Figs. S11, S12, S13, S14). We observed substantial rate heterogeneity in the evolution of ovariole number (Fig. S14), meaning that for some lineages ovariole number has evolved rapidly where in others, ovariole number has evolved very slowly or not at all. The most striking example of this are the multiple lineages which have independently evolved invariant or near-invariant ovariole number across taxa (e.g. nearly all Lepidoptera have exactly eight ovarioles, Fig. 5b, Lepidoptera are part of Amphiesmenoptera, in cyan), from an ancestral variable state. These invariant lineages were identified by finding regions of the phylogeny that experience extremely low rates of ovariole number diversification (Figs. S14, S15). Using this approach, we found that invariant ovariole numbers have evolved at least nine times independently across insects, with several subsequent reversals from invariant to variable states (Fig. 5a).

We find that the rate of evolutionary change in ovariole number is correlated with the number of ovarioles: lineages with relatively low ovariole number also experience relatively low degrees of ovariole number change (Fig. S11). This is evidenced by the fact that, of the nine invariant lineages, none have greater than seven ovarioles per ovary (Fig. 5c). However we note that not all insects with low ovariole counts are in invariant lineages; many insects with fewer than 14 total ovarioles are in lineages with relatively high rates of intra- and interspecific ovariole number variation (Fig. 5)

The distribution of ovariole numbers across insects is enriched for even numbers of total ovarioles (Fig. 5c). While many insects show asymmetries in the number of ovarioles between the left and right ovaries, all of the invariant lineages are symmetric (at 4, 6, 8, 10, 12, and 14 total ovarioles). Additionally, for the insects identified as part of invariant lineages, none have any reported intraspecific variation in ovariole number. Therefore, invariant lineages have near-zero variation when comparing between species, between individuals within a species, and between the left and right ovary within an individual.

Using these results, we propose a multi-rate model, where the rate of ovariole number evolution differs based on the evolution of a discrete trait representing invariant or variable status. We propose that the evolution of this discrete trait is governed by a model where the likelihood of transitions from a variable to an invariant state is negatively correlated with the current number of ovarioles. Here we demonstrate that a multi-rate Brownian motion model far outperforms a single rate model in fitting the data (Δ AICc 1770.93). In addition, using a parametric bootstrap to evaluate model fit, we find evidence that processes beyond Brownian Motion processes are likely at play (Fig. S11)[31]. We suggest that as researchers continue to develop non-Gaussian models for continuous trait evolution[49], those models will be useful for describing the evolution of ovariole number.

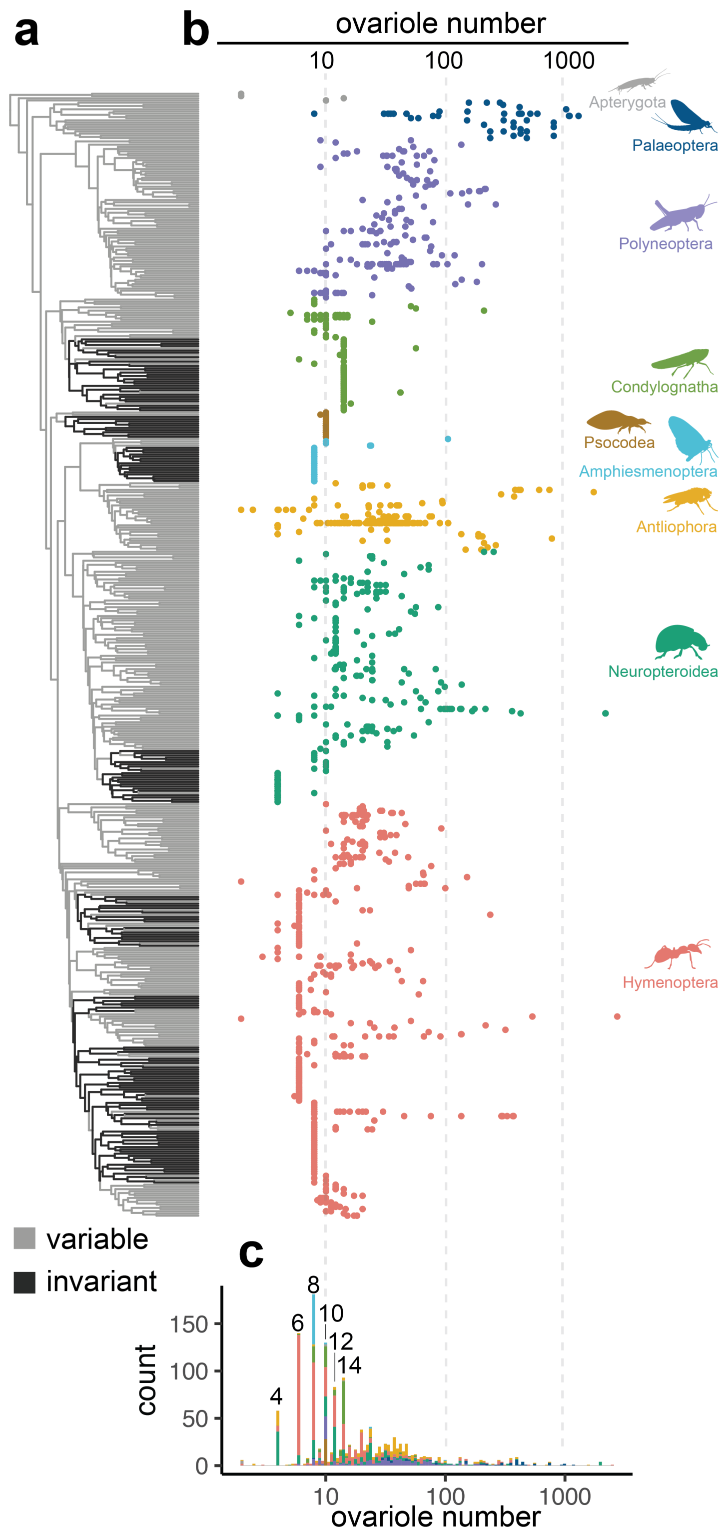

Figure 5: **The evolutionary distribution of ovariole number across insects.** a, Phylogeny of insect genera, colored according to the inferred rate regime of ovariole number evolution, variable in gray and invariant in black (see Supplementary Methods). b, Total ovariole numbers, shown on a $\log_{10}$ scale and arranged by insect genus according to the phylogeny. Tips with more than one point represent genera with multiple records for total ovariole number in the dataset. c, The distribution of values shown in (b), showing enrichment for even values in the left tail of the distribution.

Discussion

A frequently invoked life-history prediction is that, given a finite set of metabolic resources, organisms can either produce few offspring, each with high fitness, or many low-fitness offspring[1–3]. In insects, egg size and ovariole number are often used as proxies for offspring fitness[50] and number[44,45], respectively, and therefore it has been predicted that insects with more ovarioles lay smaller eggs than insects with fewer ovarioles[5,6,21,42]. Our results, using a dataset that spans 3355 observations across 2103 species, and that takes into account phylogenetic relationships, indicate that a generalized trade-off between insect egg size and ovariole number does not exist (Fig. 2).

Lineages of insects with invariant ovariole number illustrate this point. Despite having the same ovariole number, these lineages contain a range of egg sizes that is comparable to the four orders of magnitude observed across all insects (Fig. 2a). Furthermore, we observed no relationship between the evolutionary rates of change for ovariole number and egg size (Fig. S17). Therefore, if a trade-off between egg size and fecundity exists, factors beyond variation in ovariole number must contribute to fecundity. These factors might include variation in the rate of egg production per ovariole[51–54], among others[55,56].

We suggest that considering the evolution of developmental processes that govern ovariole number specification may be more useful in explaining patterns of diversity than predictions based on metabolic trade-offs. As evidence of this, we point to the fact that invariant lineages appear to have near-zero variation not only across species, but also within species, and between the left and right ovary within individuals. This suggests that the mechanism that determines ovariole number has become canalized in these groups. In contrast, our previous understanding of how ovariole number is regulated comes from research on *Drosophila melanogaster*, where the number of ovarioles can vary between the left and right ovaries within an individual, as well as across individuals within a population[57,58]. In this species, adult ovariole number is determined by cell proliferation and rearrangement during larval development[59,60]. Variation in adult number is derived primarily from variation in the number of "terminal filament precursor cells"[61,62], as well as from variation in the number of those precursor cells that group together to form the structure that initiates ovariole formation, known as a "terminal filament"[63]. Across species of *Drosophila*, variation in average adult ovariole number results primarily from variation in the average number of terminal filament precursor cells[62].

When considering the developmental processes that could give rise to invariant ovariole number, we propose that the major determinants of ovariole number known from *Drosophila* may not apply. To achieve an invariant ovariole number, these processes might instead include mechanisms for strict counting of individual cells or discrete cell subpopulations. In the former, if the cells that ultimately comprised a terminal filament were derived by mitotic division from a single progenitor, rather than by cellular rearrangements as is the case in *Drosophila*[59], then an invariant ovariole number could be achieved via strict control of the number of precursor cells. Alternatively, an invariant ovariole number could be achieved by partitioning the starting population of precursor cells into a tightly regulated number of subpopulations. This would again be a departure from known mechanisms in *Drosophila*, in which a variable number of precursor cells are gathered into terminal filaments until the population is depleted[59,63]. The determining factor for partitioning the precursor pool could be, for example, a spatially variable morphogen emanating from adjacent tissues[64] or a reaction-diffusion patterning process[65] within the developing ovary, as these have been shown to generate fixed numbers of multicellular structures in other developmental contexts[66–68]. These predictions could be tested by characterizing the dynamics of cell number and position across invariant lineages, and making comparisons to corresponding data from their variable relatives.

The evolutionary transitions between variable and invariant ovariole number are reminiscent of other quantitative traits across multicellular life, including patterns of variability and invariance in arthropod segment number[69,70], vertebrate digit number[71,72], or the number of angiosperm floral organs[73,74]. Across these systems, the evolutionary history of morphogenetic counting mechanisms is poorly understood. We suggest that insect ovariole number presents an ideal case to study this phenomenon. In particular, we note the evidence that invariance has evolved convergently at least nine times, as well as the evidence of several reversals back to variability from an invariant ancestral state (Fig. 5). These convergent lineages provide an opportunity to test the predictability of evolutionary changes to counting mechanisms, by asking whether convergent evolution of invariance involves convergent canalization of shared molecular mechanisms.

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Author Contributions

SHC led the data collection, analysis, and writing of the manuscript. NM performed the initial literature search, data collection, and analysis. BASdM assembled all phylogenies for analysis. SD, BASdM, and CGE contributed to data analysis, visualization, discussion, and writing.

Competing Interests

The authors declare no competing interests.

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Supplemental files for

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Supplemental files for this manuscript consist of the following:

- Supplementary Methods (this document)
- Ovariole Number Bibliography (this document)
- Ovariole number search terms (download here)

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Repeated loss of variation in insect ovary morphology highlights the role of development in life-history evolution - Supplementary Methods

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Contents

1 Gathering ovariole number records

We searched the published literature for references to insect ovariole number using a predetermined set of 131 search terms, entered into Google Scholar (scholar.google.com) between June and October of 2019. Each search term consisted of an insect taxonomic group and the words "ovariole number". This list was created to include all insect orders, many large insect families, and groups well-represented in the insect egg dataset. The list of search terms is available in the supplementary file 'ovariole_number_search_terms.tsv'.

For each search term, we evaluated all publications in the first page of results (ten publications). For 61 search terms that had a large number of informative hits, significant representation in the egg dataset, or that corresponded to very speciose groups, we evaluated an additional 20 publications. If a publication reported ovariole number for one or more insect species, we recorded the following information: (1) genus, (2) species name, when available, (3) taxonomic order, (4) sample size, when available, (5) ovariole number, and (6) additional notes (e.g. for eusocial insects, whether the observation was made in a reproductive or non-reproductive individual). This dataset is made publically available at Dryad (doi:10.5061/dryad.59zw3r253).

Ovariole number was recorded as either an average with deviations, a range, or a single total value. When multiple types of data were available from a single publication, we recorded only a single type, with priority given to averages over ranges, and to both over single total values. Ovariole number was recorded as the total number of ovarioles per female, summing over both the left and right adult ovaries. When authors reported ovariole number from a single ovary, the total value was calculated by doubling the reported value. When authors described differences between the two ovaries, this information was recorded in an additional notes column.

For records of ovariole number that reported intraspecific variation in ovariole number, we calculated the percent difference as follows: if ovariole number was reported as a range, percent difference was calculated as the $100 * ((max - min)/median)$; if ovariole number was reported as an average with deviations, percent difference was calculated as $100*((2*deviation)/mean)$. When independent observations of ovariole number for a given species were available across multiple published records, we calculated the percent difference as the $100 * ((max - min)/median)$ (Fig. S1).

Using this approach, we gathered 3355 records for ovariole number from 460 publications. A full list of publications is provided in the supplementary file 'ovariole_number_bibliography.pdf'. We matched the scientific names to additional taxonomic information using the software TaxReformer[1] and found additional taxonomic data for 3252 of the 3355 records. We verified that TaxReformer had found a valid match by comparing the originally recorded taxonomic order to the order populated by online databases, and removed 22 taxonomic records for which these values did not match. For all subsequent analyses, we also excluded observations made in non-reproductive individuals from eusocial species (workers), as well as two observations which represented significant outliers and could not be validated using additional sources or figures[2,3].

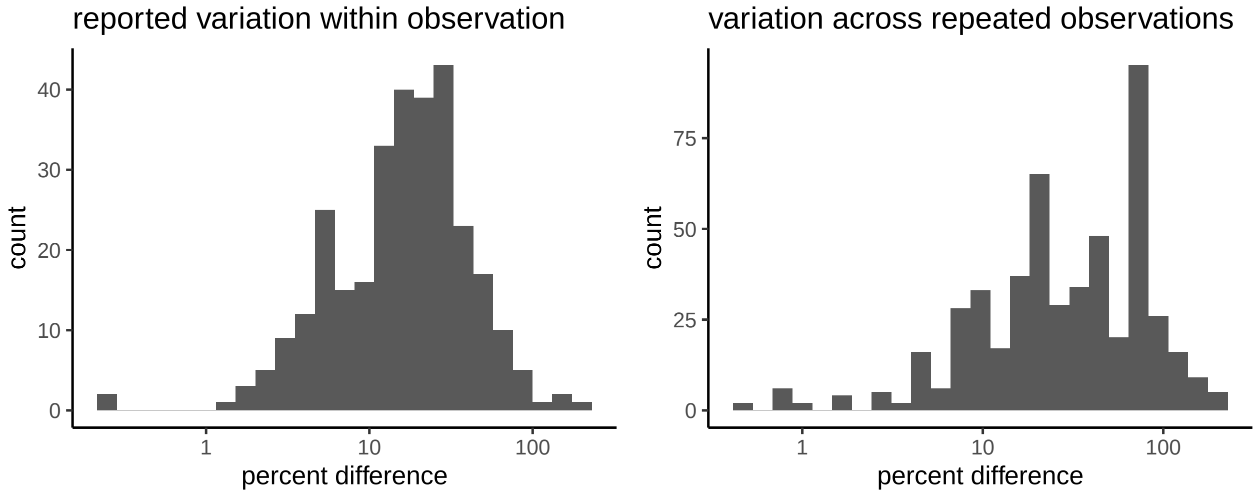

Figure S1: **Intraspecific variation in ovariole number.**

2 Phylogenetic trees

The analyses herein were performed using the insect phylogeny published in Church et al, 2019[4], unless otherwise specified. This phylogeny was constructed by combining ribosomal genetic data from 1726 insect genera, published originally in the SILVA database[5], with constrained, time-calibrated nodes for each insect order, published originally in Misof et al, 2014[6]. This phylogeny is enriched for insect genera with records in the egg trait dataset, and also has considerable overlap with the genera included in this ovariole number dataset (508 genera). For generalized least squares analyses and trait model comparisons, analyses were performed over a posterior distribution of trees associated with this published phylogeny[4].

For regressions involving body size data that were reported as insect family-level averages, we used the insect phylogeny published in Rainford et. al, 2014[7].

Analyses of Drosophilidae ovariole number, egg size, and body size were performed using a phylogeny newly assembled for this study. Published genetic data for 317 Drosophilidae species were retrieved from NCBI in June of 2019[8–16]. These data encompassed 41 gene regions including mitochondrial, nuclear, and ribosomal genes. When multiple sequences for a gene region were available from the same species, the one with the least amount of missing data was selected. Each gene region was aligned using the program MAFFT[17], model auto selected). Alignments were concatenated and trimmed to 3% occupancy across species using the program phyutlity[18]. Documentation including accession numbers, sequence files, and alignments are available in the supplementary directory 'https://github.com/shchurch/insect_ovariole_number_evolution_2020/phylogeny/Drosophilidae_sequences/'.

To the extent possible, sequence data were not curated beyond what was downloaded from NCBI, with the following exceptions: [1] two sequences labeled as 16S that did not align to other 16S sequences were removed manually. [2] COI sequences were trimmed to remove regions with large quantities of missing sites prior to alignment. [3] One species name (*D. albovittata*) was corrected for typographical error. [4] Sequences identified as *Drosophila crassifemur* were taxonomically corrected to *Scaptomyza crassifemur*[19].

Phylogenetic estimation of the Drosophilidae data were performed using RAxML (model GTRGAMMA), setting the split between Hawaiian *Drosophila* and *Scaptomyza* as the root of the tree[8,11]. The final tree was pruned to remove undescribed species (e.g. *Drosophila* nr *dorsigera*), and was time-calibrated using the R package ape, function chronos (default parameters, version 5.4.1)[20]. This tree is available in the supplementary file 'https://github.com/shchurch/insect_ovariole_number_evolution_2020/phylogeny/Drosophilidae_time_calibrated.tre'.

3 Phylogenetic regressions

3.1 Combining datasets

We combined the data we collected on total ovariole number with existing datasets of egg size and shape[21], insect lifetime fecundity and dry adult body mass[22–24], average adult body length per insect family[25], and several lineage-specific measures of adult body size[26–30].

Ovariole number and egg size[4] data were combined by matching records across datasets for the same insect species (Fig 2a). When multiple records existed for a given species, the dataset was randomly shuffled and a single matching record was selected. This variation across records for the same species was accounted for in regressions by reshuffling and matching records at each iteration of the analysis. We also matched records for insects in the same genus following the same reshuffling method, which allowed us to test whether results were robust with a larger sample size when an exact species match was not available (Fig. S2).

Average adult body length per insect family[25] was matched to the average ovariole number for the corresponding families (Fig. S5). The Rainford et al, 2016[25] dataset contains a small number of average adult body lengths at the order level (e.g. Strepsiptera), which were matched to their equivalent group in the ovariole number dataset. To test the effect of uncertainty in the estimated average ovariole number on our results, the dataset for each family was downsampled by half at each iteration of the regression analysis.

Ovariole number, egg volume, lifetime fecundity, and adult body mass[22–24] were combined by matching records at the species level and genus level, using the same method as described above (Figs. 2b, 3, and S4). We excluded one value from this dataset which appeared to include a typographical error for lifetime fecundity (Hymenoptera: Trichogrammatidae, lifetime fecundity recorded as 0.1[22]).

Several lineage-specific measurements for body size were matched to the ovariole number and egg size datasets, as follows: Drosophilidae thorax length[29] was matched at the species level (Fig. 2c), Orthoptera body length[28] was matched at the genus level (Fig. 2d), Hymenoptera mesosoma width[27] was matched at the genus level, and Curculonoidea elytra length[26] was matched at the genus level (Fig. S7).

3.2 Phylogenetic Generalized Least Squares (PGLS) analyses

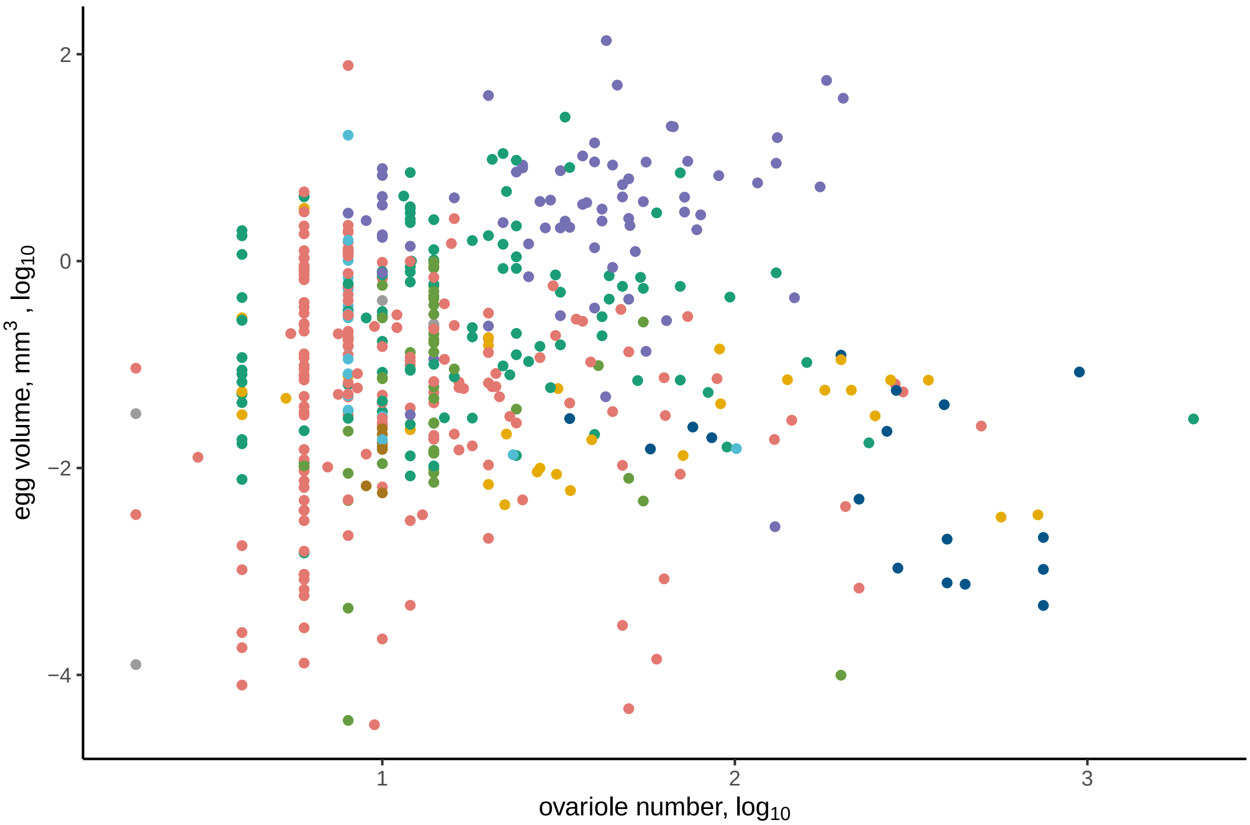

Figure S2: **Egg volume vs ovariole number, matching records at the genus level.**

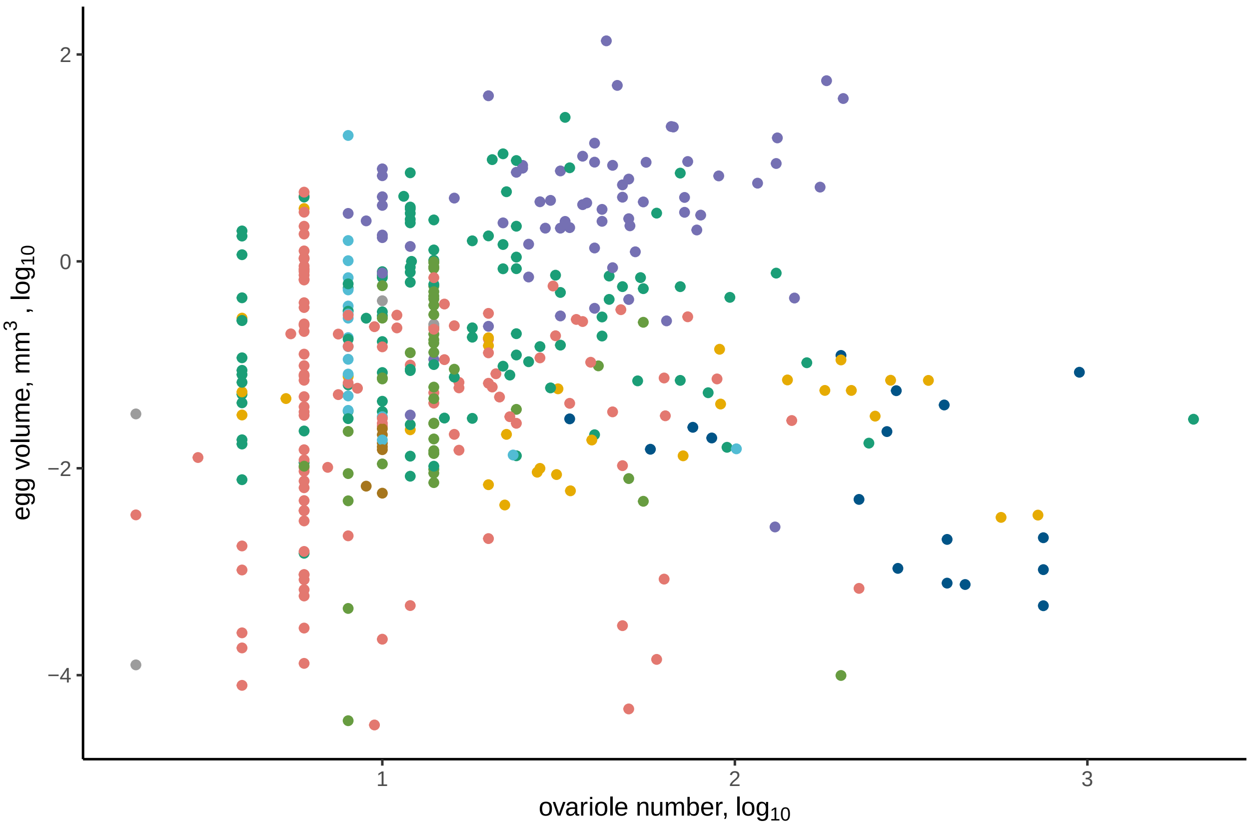

Figure S3: **Egg volume vs ovariole number, matching records at the genus level, excluding records from families with eusocial insects.**

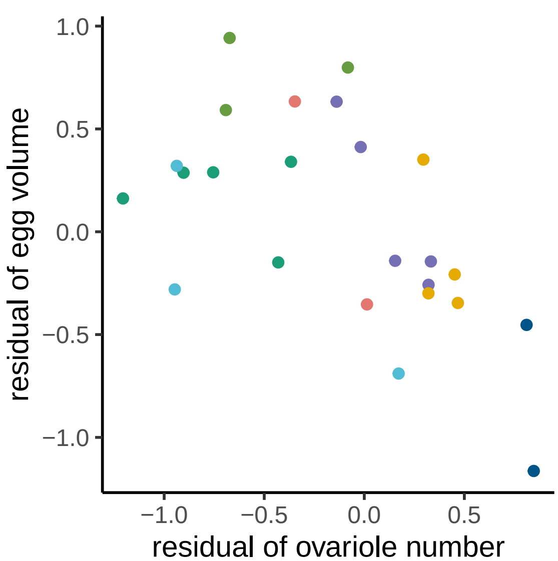

Figure S4: **Egg volume vs ovariole number, phylogenetic residuals to dry adult body mass, matching records at the species level.**

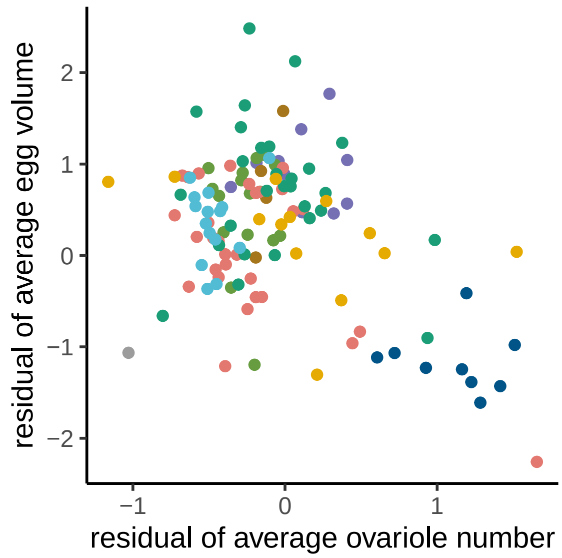

Figure S5: **Family average egg volume vs ovariole number, phylogenetic residuals to adult body length.**

We ran each Phylogenetic Generalized Least Squares (PGLS) regression over the Maximum Clade Credibilty (MCC) tree. For each regression, we also repeated each PGLS analysis 1000 times, accounting for phylogenetic and phenotypic uncertainty, using the R packages ape (version 5.4.1)[20] and nlme (version 3.1.151)[31]. In these analyses we used a Brownian Motion based covariance matrix for traits.

For regressions using data matched across species or genera, we reshuffled and matched records at each iteration to account for variation across records for the same taxon. For regressions on family-level average data, we recalculated the average ovariole number per insect family, downsampling the representation for each family by half. No posterior distribution was available with the previously published family level phylogeny[7].

To account for body size, we calculated the phylogenetic residuals[32] of each trait to body size, and then compared the evolution of these residuals using a PGLS regression.

For regressions of egg size and ovariole number when accounting for adult body size, we compared the results of our regression analyses to distributions estimated using simulated data under alternative hypotheses. We fit a Brownian motion model to the phylogenetic residuals of egg size and body size (R package geiger, version 2.0.7)[33], and then used the parameters of this fitted model to simulate new datasets (R package phylolm, version 2.6.2)[34]. We performed this resimulation using the datasets of egg size and body length at the family level, and egg size and body mass at the genus level. We simulated 1000 datasets each under two hypotheses: no correlation (slope=0) and a strong negative correlation (slope=-1). We performed the regressions as described above and compared the distribution of p-values and slopes to values from regressions on observed data.

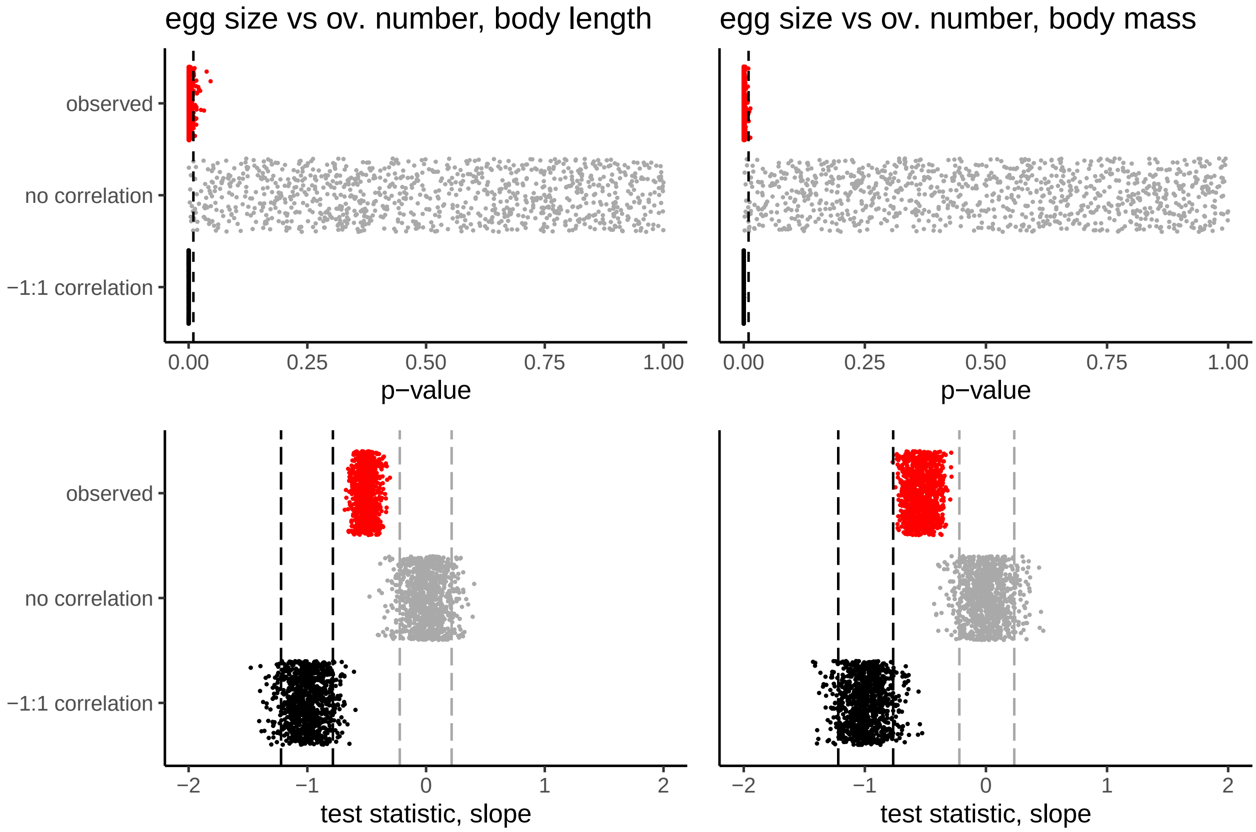

Figure S6: **Using simulated data to test alternative hypotheses of evolutionary relationships.** Top row, distributions of p-values over 1000 replicate regressions, dashed black line indicates threshold of 0.01. Bottom row, distribution of estimated slopes between egg size and ovariole number, dashed lines indicate 95% interval of simulated distributions. Left, comparing egg size and ovariole number, accounting for body length at the family level. Right, comparing egg size and ovariole number, accounting for body mass at the genus level. Red=observed values, gray=simulated with no correlation, black=simulated with a -1:1 correlation. n=1000 regressions.

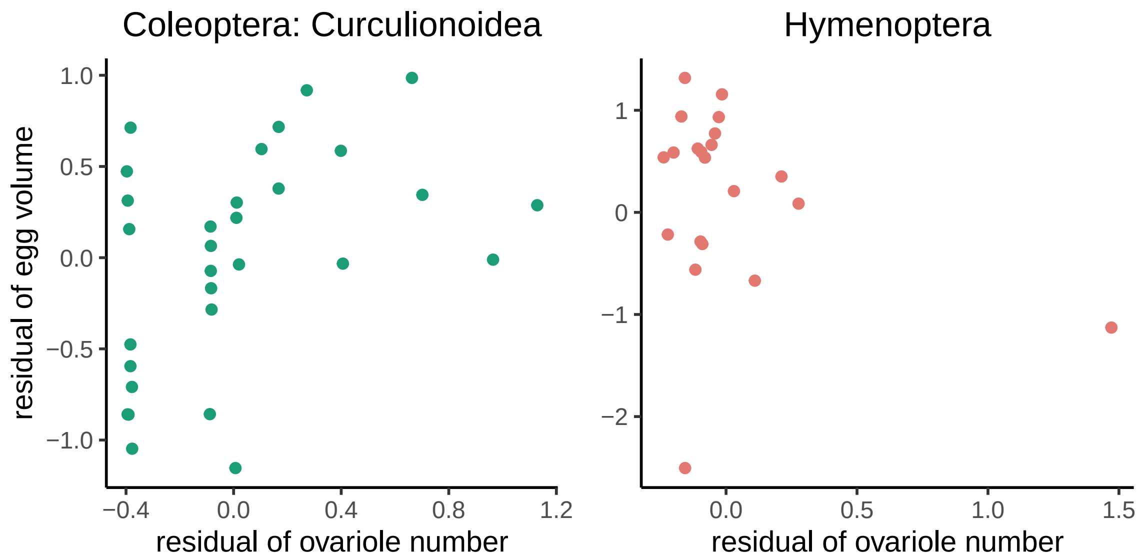

Figure S7: **Additional lineage-specific comparisons of egg volume vs ovariole number, phylogenetic residuals to body size, matching records at the genus level.** Weevils (Curculionoidea, left) were measured using elytra length and wasps (Hymenoptera, right) were measured using mesosoma width.

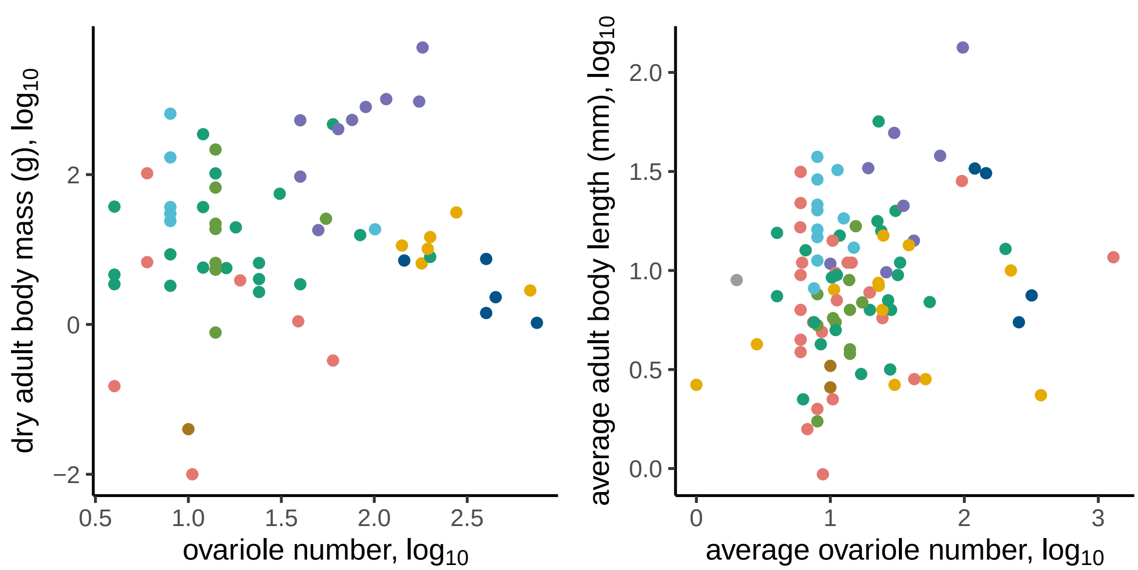

Figure S8: **Adult body size vs ovariole number.** Adult body mass, matching records at the genus level (left), and family-level average adult body length (right).

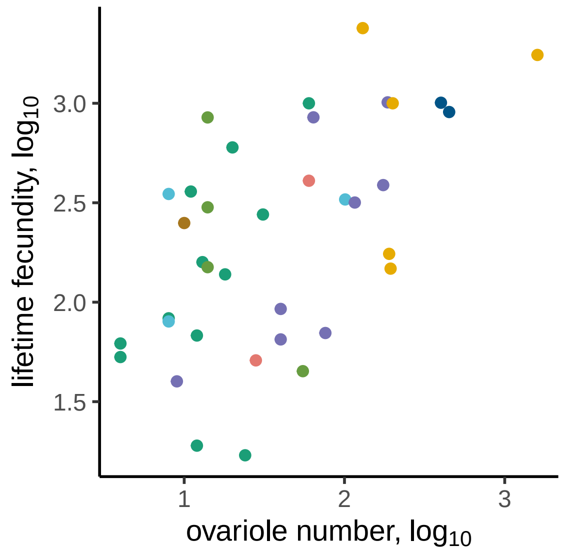

Figure S9: **Lifetime fecundity vs ovariole number, matching records at the species level.**

Table S1: Results of PGLS analysis of ovariole number and egg size across a posterior distribution. The 'data match' columns describes how observations were matched across datasets, e.g. matching records for the same species, genera, or using family-level averages.

analysis	data match	slope	MCC p-value	num. sig. / 1000	taxa
ovariole number vs egg volume	species	-0.426 – -0.082	0.195	43	306
ovariole number vs egg volume	genus	-0.356 – -0.128	0.066	470	482
ovariole number vs egg volume, residuals to body mass	species	-0.646 – -0.333	0.003	833	24
ovariole number vs egg volume, residuals to body mass	genus	-0.769 – -0.284	0.003	995	61
ovariole number vs egg volume, residuals to body length	family average	-0.685 – -0.304	<0.001	966	98

Table S2: Results of PGLS analysis of ovariole number and egg size across a posterior distribution.

analysis	data match	slope	MCC p-value	num. sig. / 1000	taxa
Drosophilidae ovariole number vs egg volume, residuals to thorax length	species	-0.814 – -0.799	<0.001	1000	30
Orthoptera ovariole number vs egg volume, residuals to body length	genus	-0.315 – 0.379	0.485	0	40
Curculionoidea ovariole number vs egg volume, residual to elytra length	genus	-0.293 – 0.633	0.384	0	30
Hymenoptera ovariole number vs egg volume, residuals to mesosoma width	genus	-2.131 – -0.288	0.139	13	21

Table S3: Results of PGLS analysis of ovariole number and body size across a posterior distribution.

analysis	data match	slope	MCC p-value	num. sig. / 1000	taxa
ovariole number vs body length	species	0.025 – 0.208	0.618	0	24
ovariole number vs body mass	genus	0.095 – 0.299	0.546	0	61
ovariole number vs body mass	family average	0.123 – 0.177	0.031	29	98
Drosophilidae ovariole number vs thorax length	species	0.223 – 0.223	0.031	0	30
Orthoptera ovariole number vs body length	genus	0.132 – 0.450	0.001	993	40
Curculionoidea ovariole number vs elytra length	genus	-0.211 – 0.257	0.917	0	30
Hymenoptera ovariole number vs mesosoma width	genus	-0.112 – 0.355	0.482	0	21

Table S4: Results of PGLS analysis of ovariole number and fecundity across a posterior distribution.

analysis	data match	slope	MCC p-value	num. sig. / 1000	taxa
ovariole number vs lifetime fecundity	species	0.324 – 0.542	0.011	311	37
ovariole number vs lifetime fecundity	genus	-0.275 – 0.601	0.002	267	65

4 Evolution of nurse cells

4.1 Combining datasets

We used the descriptions of the mode of oogenesis recorded by Büning[35]. This author catalogued the ovary morphology for 136 insect genera, categorizing them into four modes: those without nurse cells (panoistic), with nurse cells adjacent to each clonally related, developing oocyte (polytrophic meroistic), with all nurse cells located in the germarium (telotrophic meroistic), and a unique mode of oogenesis reported only in Strepsiptera (reduced polytrophic meroistic ovaries).

Of the 136 genera observed by Büning, 70 are represented in the phylogeny used here[4]. Another 36 come from families or orders that have representative genera in the phylogeny, and within which all observations have the same recorded mode of oogenesis, when more than one was recorded. Therefore, we used a substitute genus as the phylogenetic tip for these 36 groups, bringing the total overlap between dataset and phylogeny to 106 taxa.

4.2 Reconstructing evolutionary shifts in oogenesis mode

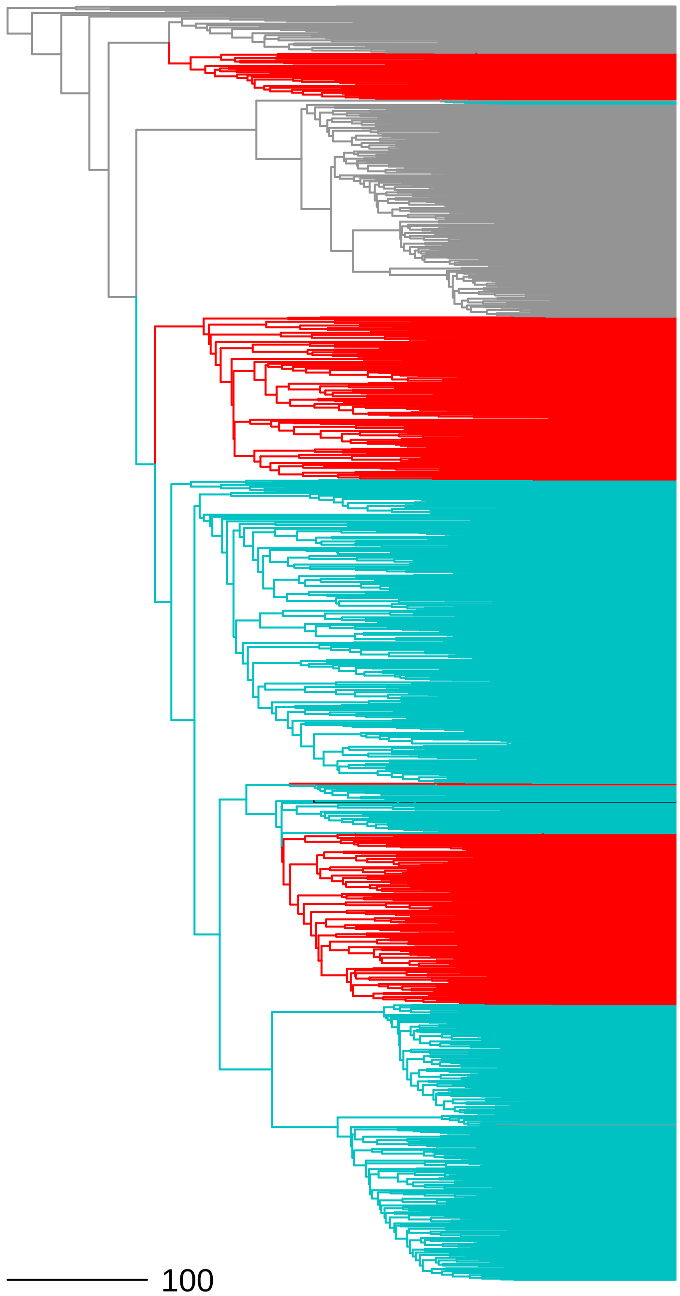

Figure S10: **Ancestral state reconstruction of oogenesis mode, full phylogeny.** Scale bar indicates 100 million years. Gray = panoistic, red = telotrophic meroistic, cyan = polytrophic meroistic, black = unique meroistic mode found in Strepsiptera.

Using these 106 records for ovary type, we reconstructed the ancestral state at each node of the published phylogeny of 1705 insect genera using an equal-rates model that allows for missing data (Fig. S10, R package corHMM, version 1.22[36] function rayDISC, node.states = 'marginal').

4.3 Oogenesis mode model comparison

Table S5: Average corrected AIC (AICc) value from model comparison

analysis name	BM1	BMS	OU1	OUM
ovariole number	477.20195	473.03372	479.22592	482.42889
egg volume	3295.74949	3281.71001	3297.75729	3299.52446
egg aspect ratio	-1486.86444	-1506.89208	-1484.85630	-1483.01934
egg asymmetry	-763.10658	-785.44797	-808.70150	-810.07385
egg curvature	62.36224	35.70801	63.46489	64.20869

Table S6: Results of model comparison analysis over posterior distribution, showing the number of iterations out of 100 where the difference in model fit (ΔAICc) was greater than 2.

analysis name	BMS vs. BM1	OU1 vs. BM1	OUM vs. BM1	OUM vs. OU1	taxa
ovariole number	90	0	0	0	506
egg volume	100	0	0	0	1567
egg aspect ratio	100	0	0	0	1488
egg asymmetry	100	100	100	20	844
egg curvature	100	1	1	1	781

Using the ancestral state reconstruction of evolutionary shifts in the mode of oogenesis, we inferred the most likely mode of oogenesis for all nodes and unobserved extant tips in the phylogeny (Fig. S10). We then compared the fit of models of trait evolution that take into account these shifts in oogenesis mode against those that do not. These comparisons were performed with the R package OUwie (version 1.57)[37].

Each analysis compared four models of evolution: single-rate Brownian Motion (BM1), multi-rate Brownian Motion (BMS), single-optimum Ornstein-Uhlenbeck (OU1), and an Ornstein-Uhlenbeck model with different optima for each mode of oogenesis (OUM).

These comparisons were repeated 100 times over a posterior distribution of trees. At each iteration we selected a random representative trait record for each genus in the phylogeny, when multiple records were available.

5 Modeling rate of ovariole number change

5.1 Parametric bootstrap of Brownian Motion model

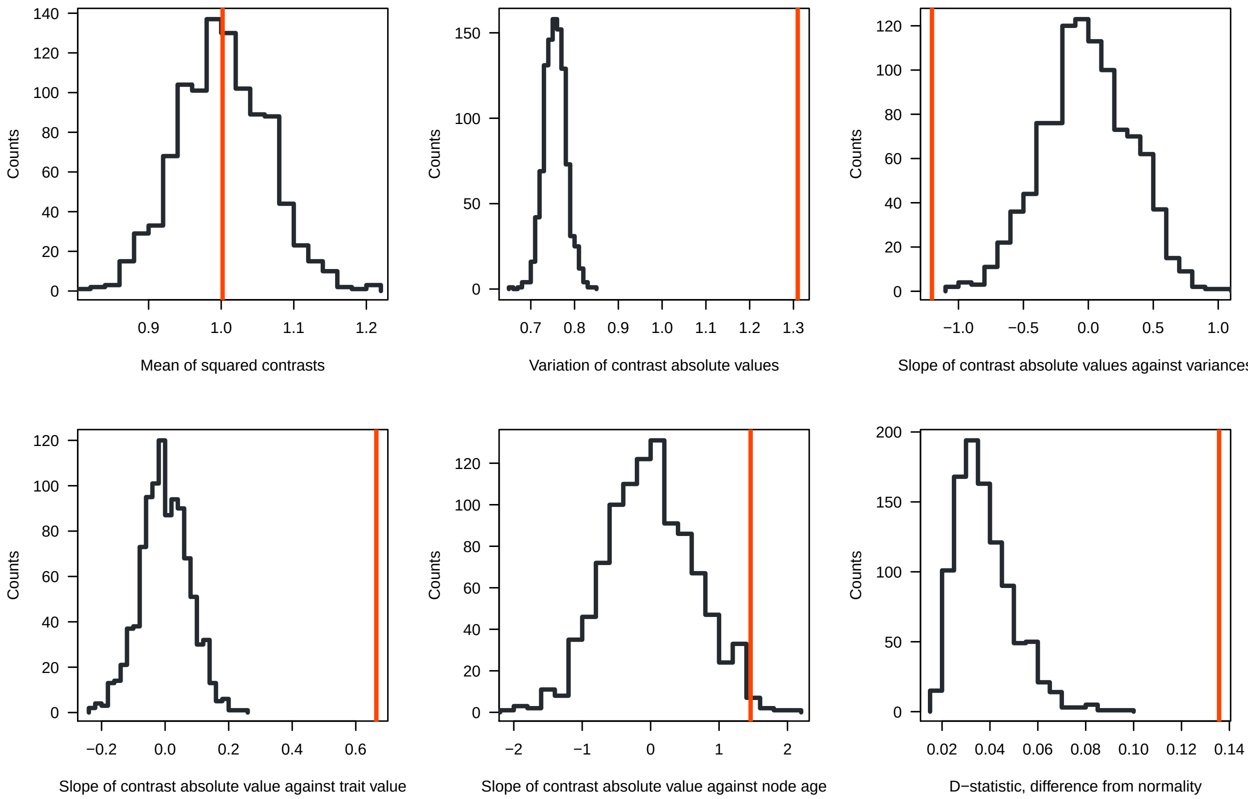

Figure S11: **Bootstrap analysis of Brownian Motion model for ovariole number evolution, using the R package arbutus.** In each panel the red line represents the observed value and the black distribution represents the bootstrap simulation. See Section 5 for details on each parameter.

We evaluated the fit of a Brownian Motion (BM) model for ovariole number evolution using the R package arbutus (version 0.1[38], Fig. S11). In this approach, a BM model is fit to the data (R package geiger, version 2.0.7)[33], and the resulting parameters of the model are used to simulate 1000 new datasets. Six statistical parameters are used to compare the phylogenetic contrasts of the observed data to the simulated data, and their interpretations are as follows[38]:

1. *Mean of squared contrasts.* The rate of evolution of ovariole number can be well estimated by the Brownian Motion model (the observed value falls within the null distribution).
2. *Coefficient of variation of the absolute value of the contrasts.* There is substantially more variation in contrasts than expected by chance, indicating heterogeneity in the rate of evolution beyond what a single-rate Brownian Motion model predicts (the observed value falls well outside the null distribution).
3. *Slope of a linear model fitted to the absolute value of the contrasts against their expected variances.* Contrasts are larger than expected on short branches in the phylogenetic tree, resulting in a negative slope. This could be explained by error in estimation of branch lengths.
4. *Slope of a linear model fitted to the absolute value of the contrasts against the ancestral state at the corresponding node.* The number of ovarioles is more correlated with contrast values than would be expected by chance. Phylogenetic nodes with a low ovariole number experience lower rates of evolution.

5. *Slope of a linear model fitted to the absolute value of the contrasts against node depth.* Contrast values are not correlated with time, falling within the null distribution. Therefore the rate of ovariole number change is not increasing or decreasing over time.
6. *The D statistic from a Kolmogorov-Smirnov test comparing the distribution of contrasts to an expected normal distribution.* 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).

5.2 Assessing rate heterogeneity

Given the result that our dataset contains substantial rate heterogeneity, we identified regions of the tree with high and low rates of ovariole number evolution using the software BAMM (version 2.5.0)[39]. For this analysis, we calculated the average ovariole number for each genus in the insect phylogeny[4]. Average ovariole number was $\log_{10}$ transformed, and the tree was filtered to include only tips for which there were corresponding ovariole number data (sample size = 508). We used the R package BAMMtools (version 2.1.7)[40] to select priors, and ran BAMM for the maximum number of generations ($2 * 10^9$), sampling every 10^6 generations.

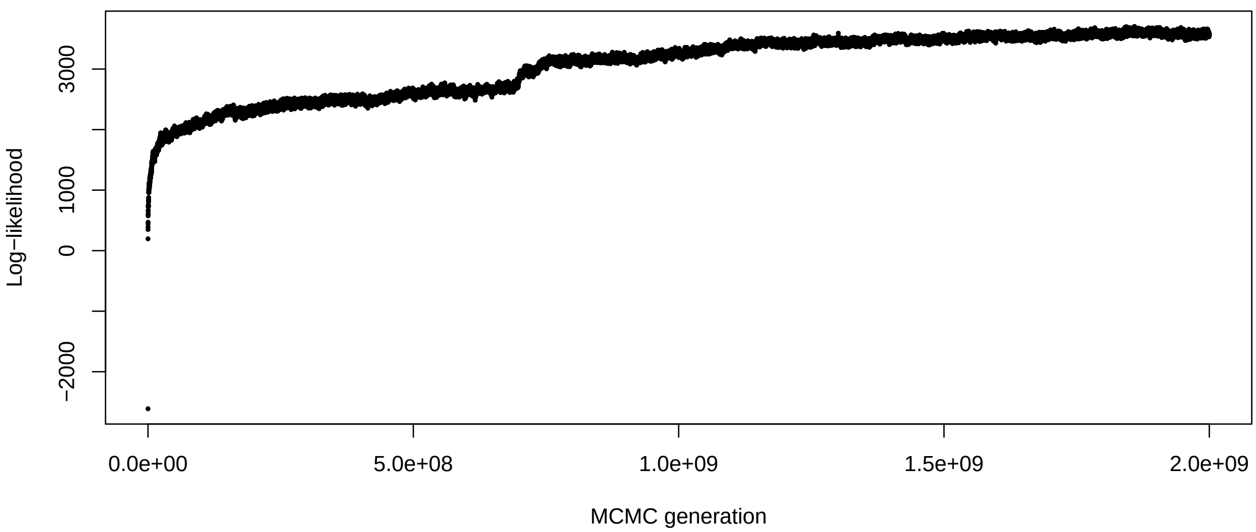

Figure S12: Convergence of trait diversification rate analysis

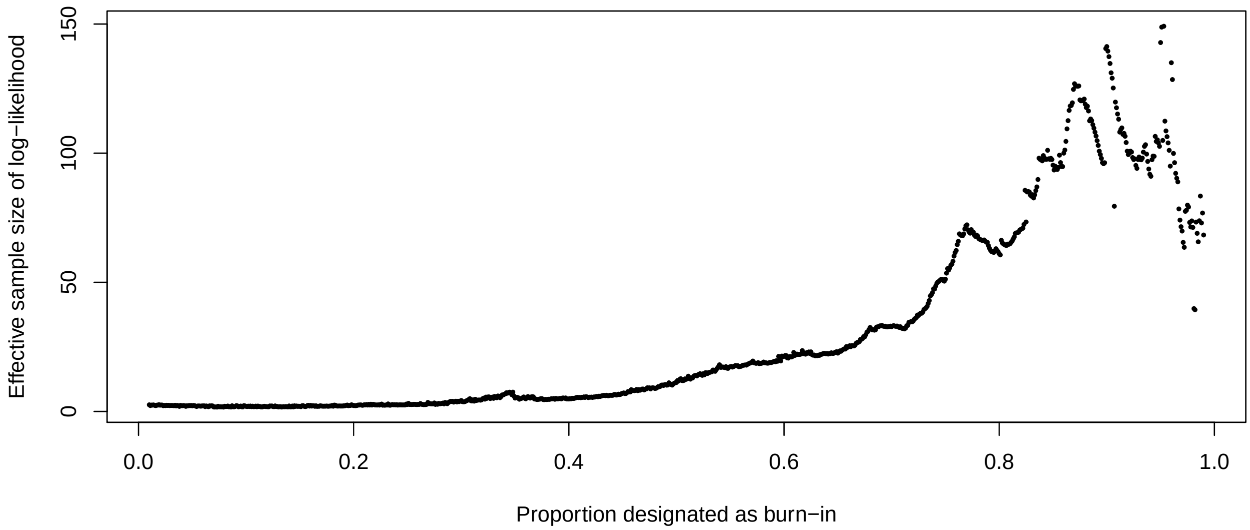

Figure S13: **Comparison of burn-in proportions.** The burn-in proportion that maximized the effective size was used in subsequent analyses.

Convergence was evaluated both visually (Fig. S12) and numerically by comparing the effective sample size for number of shifts and log-likelihood to the standard recommended by the software (>200). We determined the most appropriate burn-in proportion to use by finding the maximum effective sample size of the log-likelihood across an array of possible burn-in proportions (Fig. S13). Running BAMM for the maximum possible number of generations and selecting the optimum burn-in (Fig. S13) resulted in an effective size for the number of shifts of 482.51, and for log-likelihood of 149.15. Repeated BAMM analyses showed similar distributions of high and low rate regimes, indicating the implications for ovariole number evolution are robust to uncertainty in rate estimates. See Supplemental Methods Section 5.2 for details.

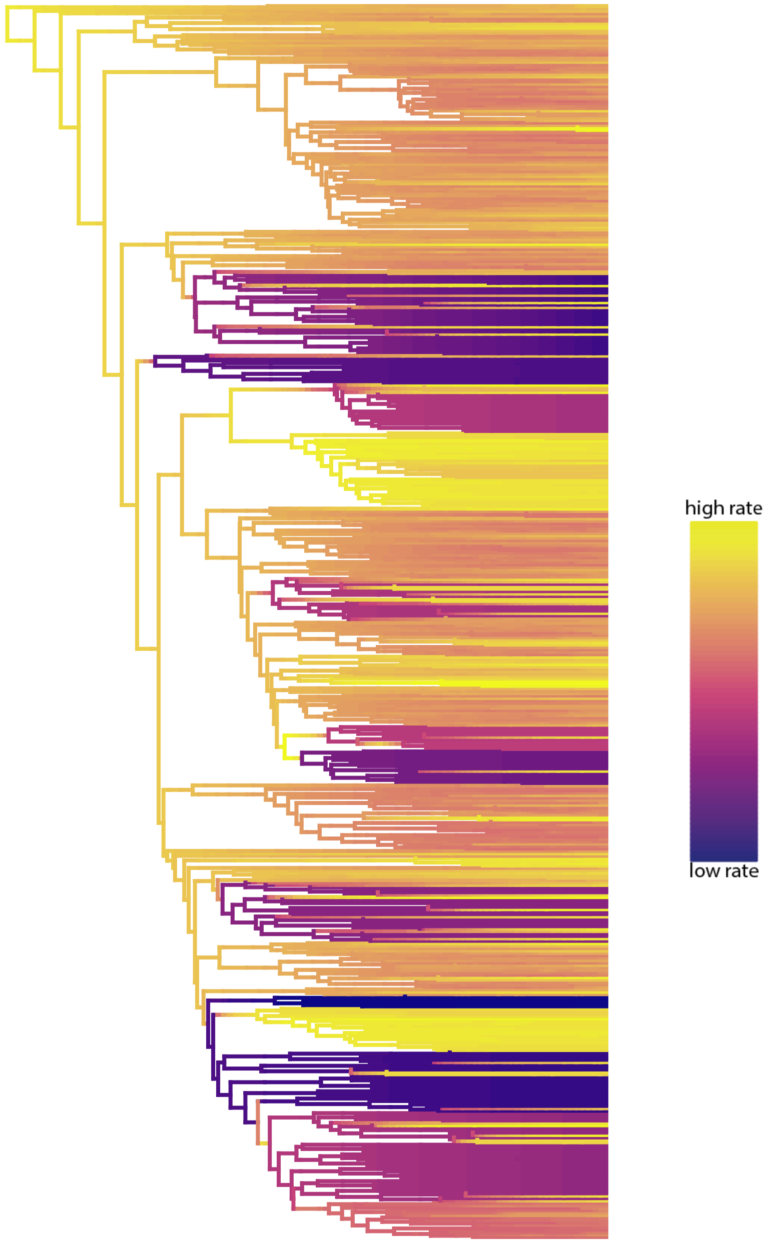

Figure S14: **Best rate shift configuration from BAMM trait diversification analysis on ovariole number.** Purple = low rate of evolution, yellow = high rate of evolution.

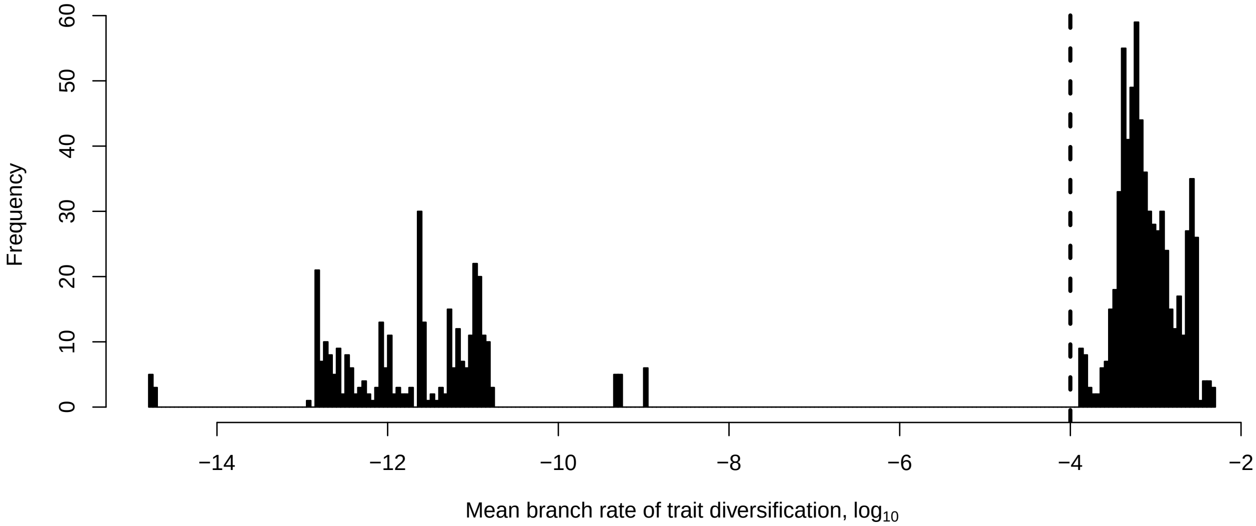

Figure S15: **Distribution of trait diversification rates.** Dotted line shows threshold used to assigned rate regimes.

The best configuration of rate shift regimes shows multiple independent clades with very low rates of evolution (Fig. S14). Visualizing the distribution of mean rates along branches revealed a discontinuous distribution, with one peak at a moderate rate of evolution and several clusters at extremely low rates, separated from the first peak by over six orders of magnitude (Fig. S15). We used this visualization to establish a threshold (10^{-4}) for assigning a binary rate regime to each node in the phylogeny, categorizing them as above (variable) or below (invariant) a threshold that separates these two peaks.

5.3 Rate model comparison

We tested whether a BM model of evolution that incorporates the binary state (variable or invariant) as independent rate regimes can better explain the distribution of ovariole numbers than a single rate BM model, by comparing model fit using the R package OUwie (version 2.5)[37]. We find that a multi-rate model is significantly favored over a single-rate model (Δ AICc 1770.93).

5.4 Comparing rates of trait diversification

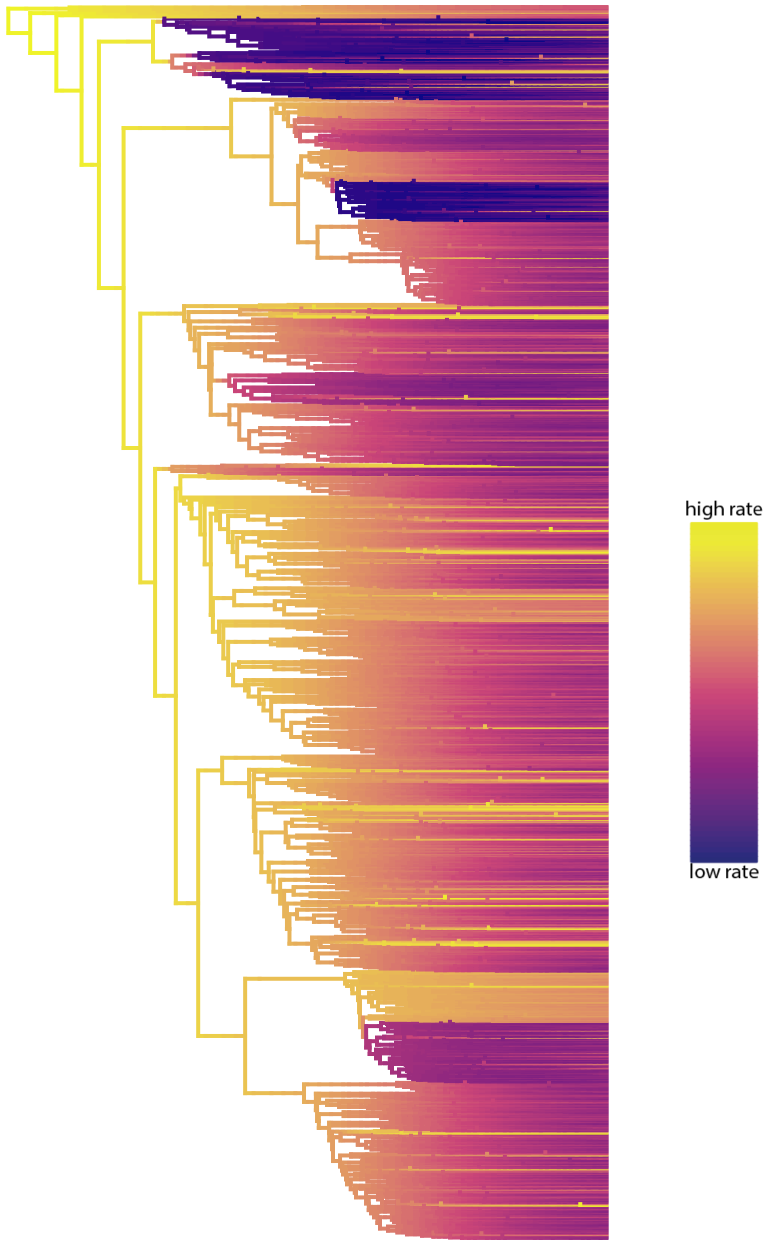

Figure S16: **Best rate shift configuration from BAMM trait diversification analysis on egg volume.** Purple = low rate of evolution, yellow = high rate of evolution.

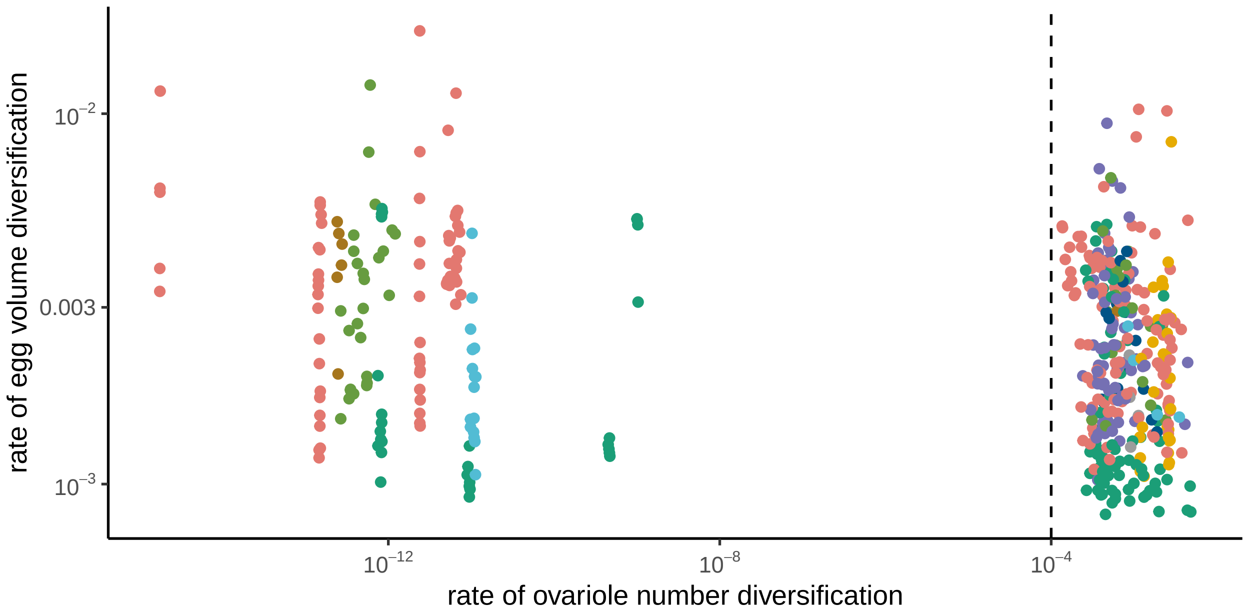

Figure S17: **Rates of trait diversification of egg volume and ovariole number.** Points are colored by phylogenetic groups shown in Fig 1a. Dotted line shows threshold used to assigned rate regimes.

We assessed the rate of egg volume diversification across insects using the same method of assessing rate heterogeneity as described in Section 5.2 (Fig. S16). This analysis converged in $7 * 10^9$ generations (the effective size for the number of shifts and log-likelihood were >200, 670.2 and 753.42 respectively). We compared the correlation between the rates of trait diversification for ovariole number and egg volume by matching the mean rate predicted for each insect genus (the tips of the phylogeny from the BAMM analyses, Fig. S17).

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Ovariole number bibliography

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