SUPPORTING INFORMATION

- 4 A cautionary note on using quantitative measures of phenotypic convergence
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SUPPLEMENTAL METHODS

12 Univariate model-fitting analyses

- One limitation of the *mvMORPH* multivariate models, which are used for our primary
- model-fitting analyses, is that they do not permit the evolutionary rate (σ) or strength of attraction to optima (α) to vary between the two selective regimes ('gliders' and 'non-
- gliders'). This likely results in poor model performance because the datasets were simulated such that 'gliders' and 'non-gliders' should have different rates and attraction
- strengths. For example, the 'non-gliders' are evolved by BM, and thus they are not expected to exhibit attraction to a trait optimum, whereas the convergent 'glider'
- lineages are expected to exhibit strong attraction due to being simulated by an OU process. Further, the phylogenetic half-life $(\ln(2)/\alpha)$ of the 'glider' regime cannot be
- calculated independent of the 'non-glider' regime if the α parameter is uniform across both regimes, which is the case with the multivariate models.
- Thus, we also fit seven univariate evolutionary models to the subset of simulated datasets, including several multiple-regime OU models that permit σ and α to vary
- between regimes. Using functions in the *OUwie R* package (Beaulieu et al. 2012), we fit these models to the first principal component (PC1) scores of a principal components
- analysis of the six simulated traits. The univariate models include uniform (or single-regime) BM and OU models, as well as a suite of multiple-regime OU models (i.e.,
- 'OUM' models of Beaulieu et al. 2012). The OU2 model keeps α and σ constant for both regimes, the OU2A model allows α (but not σ) to vary between regimes, the OU2V

model allows σ² (but not α) to vary between regimes, and the OU2VA model allows both σ and α to vary between regimes. As with the multivariate analyses, all models were
 fitted across 10 'simmaps' for each of the 30 datasets and relative support for models was measured using AICcW.

We recognize that fitting models to PC scores can lead to biased results (Uyeda et al. 2015), and thus our univariate results should be considered with caution. However, we feel that using PC1 scores here is justified for two reasons. First, the alternative option is to fit models to each of the six simulated traits individually, but four of the traits are evolved via a strong OU process and two traits are evolved via BM (in our subset of datasets used in model-fitting analyses; see Methods), and thus the model-fitting results are expected to vary considerably between those two types of traits. PC1 provides a single value for which results can be more easily interpreted compared to results for the six traits. Second, our conclusions concerning the use of model-fitting analyses for testing for convergence are based entirely on the multivariate model-fitting analyses (see Results & Discussion), and thus the results of the univariate model-fitting analyses (which are congruent with the multivariate results; Tables 2 and S1) do not influence the broad conclusions of this study. The univariate model-fitting analyses are simply a supplemental analysis that provide a fitted α value and phylogenetic half-life for the 'glider' regime.

Ct-measures

We used the *R* script from Zelditch et al. (2017) as a foundation for the updated functions for calculating *Ct*1–*Ct*4 and simulation-based *p*-values because they are computationally faster than the original *R* functions in the *convevol R* package (Stayton 2015, Stayton 2018). Note that the relevant *R* functions are titled *calcConv* (*C* calculations) and *convSig* (significance testing) in the *R* code of Zelditch et al. (2017), *convrat* and *convratsig* in the original *convevol R* package, and *convrat.t* and *convratsig.t* for our updated measures.

 $D_{max.t}$ measurement. The primary change made by the Ct-measures in comparison to Stayton's (2015) original C-measures is the way in which D_{max} is defined. Ct-measures were designed to ensure D_{max} (now referred to as $D_{max.t}$) was obtained

from comparisons of synchronous time points along the evolutionary paths leading to the putatively convergent taxa of interest. In this way it prevents the inflation of $D_{\text{max t}}$ that resulted from comparison of asynchronous nodes (e.g., tips and internal nodes) which often occurred when using the original metrics on lineages with outlying morphologies (Figs. 3C and 4). Several modifications to the source R code were made to facilitate this change. Candidate $D_{\text{max.t}}$ measurements for putatively convergent lineages are now measured at each internal node along the branch paths from the most recent common ancestor (MRCA) of the lineages (e.g., see Figures 4 and 5B). At each of these points we extracted the phenotypic distance between lineages as the euclidean distance between the ancestral reconstruction at the focal node and the coincident reconstruction along the branch path of the other lineage. Where this corresponds to a point along a branch (which is most cases) the ancestral state is estimated using formula [2] from Felsenstein (1985), which allows ancestral states to be interpolated at any point along a given branch from reconstructions at the branch's ancestral and descendant nodes. The code for this was largely repurposed from the contMap function of the phytools R package (Revell 2012). If no contemporaneous point exists on the opposite path for a given internal node (e.g., when comparing extinct and extant taxa), then a measurement is not taken at that node. All distances measured between paths are stored for each pair of user defined tips. $D_{\text{max},t}$ is the maximum of these distance values, but it is restricted to predate either focal tip (i.e., $D_{\text{max,t}}$ cannot equal D_{tip}).

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Restriction of $D_{\text{max.t}}$ to predate the focal tips means the minimum Ct1 value is no longer set to zero as in the original C1-measure. This allows for some degree of divergence to be captured (i.e., relatively more negative Ct1 values may represent greater divergence). However, users are cautioned from using this to test the magnitude of divergence between clades. This is because in divergent clades $D_{\text{max.t}}$ will almost always be the last time point before the oldest focal tip. The method will thus reflect only a small portion of the period when lineages were undergoing divergent evolution. Degree of divergence will then be a function of both phenotypic rates of evolution and of subtending branch length. The latter will in many practical situations be a function of sampling, with long subtending branches due to poor sampling likely to inflate divergence measures substantially since they will provide the best scenario for a large

time difference between D_{max} and D_{tip} (and thus capture the greatest proportion of divergent evolution).

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The changes to D_{max} were the most consequential of those made to modify the original C-measures. However, a number of other new options were also included. These are briefly described below. Full documentation of these options will be available as part of the next update to the *convevol R* package (Stayton, 2018).

User-defined groups. The first new option is for users to provide grouping assignments to the tips being tested, thus allowing comparisons of clades with multiple lineages, whereas the original C-measures are limited to comparisons of individual lineages. This option removes pairwise comparison between tips within the same group (e.g., two flying squirrels would not be compared if all flying squirrels are defined as one group) and returns results for each unique comparison between groups in addition to overall results. This option is useful if it is hypothesized that two (or more) clades converged, and relieves the user from needing to average tip values of a clade or manually define all of the desired comparisons. When using this option, the overall (for all pairwise comparisons) and comparison-specific Ct and p values are returned. Overall results are provided as both raw values (means of all pairwise comparisons, excluding within-group comparisons) and weighted values. The latter allows each inter-group comparison to impact the overall average equally, so that larger within group sample sizes don't skew overall results. For instance, if there are three putatively convergent groups (Group A, Group B, and Group C), and Groups A and B both include a single lineage and Group C includes 10 lineages, then there would be 21 total pairwise comparisons among groups (one for A-B, 10 for A-C, and 10 for B-C). Although constituting one third of the unique inter-group comparisons, Ct measurements taken from comparison of Groups A and B constitute less than 5% of those used to compute overall (average) Ct values. Thus, Groups A and B have a relatively smaller impact than Group C on the overall Ct scores and p-values. The weighted output scales the Ct results (and associated *p*-values) so that each unique inter-group comparison contributes equally to the overall results, whereas the raw overall result simply reports the mean value for all 21 pairwise comparisons. Both weighted and unweighted values are reported in the default output printed by the updated convSig function, but we

recommend the weighted result be used by default when comparing groups.

Nevertheless, the raw result may be preferable in cases in which researchers believe that the more heavily sampled group(s) should have a larger impact on overall results.

Note that it is possible to define groups even when those consist of a single tip. While doing so will not change which pairwise comparisons the model considers, it will provide the user with unique *Ct* scores and *p*-values for each comparison. This can be especially useful when the degree of convergence varies across the lineages of interest (e.g., see the pairwise results for anole species in Figure S5 and Table S2).

Conservative $D_{max.t}$ option. When providing user-defined groups, a conservative $D_{max.t}$ option is available that limits candidate $D_{max.t}$ measurements to a time point predating the origination of both focal groups (i.e., the nodes of the MRCAs of each group). This is to prevent $D_{max.t}$ being skewed by an early transition of one lineage toward a shared adaptive optimum that is outlying in morphospace, which can result in inflated Ct scores, especially when the origins of the clades are very different in age. This issue is discussed in the Supplemental Results and illustrated in Figure S3. Note that this option is only meaningful when user defined groups are provided. When one of those groups consist of a single lineage the node immediately ancestral to the tip is used. Using this method, long branches can substantially alter inferred $D_{max.t}$ values. We have provided the option to print relevant information about the restrictions put on $D_{max.t}$ when using this method (by setting VERBOSE = TRUE in convrat.t). We strongly suggest that users investigate the impact of using the conservative $D_{max.t}$ option before committing to significance tests.

Updated Ct4 computation. In addition to changes to $D_{\text{max.t}}$, we also altered the way in which the C4-measure is computed. The new version (called Ct4) redefines $L_{\text{tot.clade}}$, which is the value used to standardize the C2 value (D_{max} subtracted by D_{tip}) to obtain C4. $L_{\text{tot.clade}}$ is described by Stayton (2015) as reflecting the total amount of morphological evolution which occurs in the clade originating with the MRCA of two putatively convergent tips. In the original C-measures, $L_{\text{tot.clade}}$ values were obtained as a sum of the phenotypic distances from all pairwise comparisons between nodes in the clade, but this does not fully account for phylogenetic structure and is heavily influenced by sampling intensity. We have updated this to now be the sum of the phenotypic

distances accumulated along each branch in the clade of interest. This change brings C4 closer to the original description of the metric.

Measuring convergence of single traits. By default, the original C-measures do not support investigation of convergence in a single trait (although see Spear and Williams, 2020; Law, 2022). To circumvent this limitation we have added code to the convrat.t function which appends an invariant trait (with value zero) to datasets consisting of a single trait. This approach was taken due to ease of integration with existing code, and although crude will provide the same phenotypic distances as would be obtained from the single trait.

Model output. Additional changes were made to increase the amount of information returned to the user and facilitate plotting of results. This includes the addition of the novel *plot.C* function, which is described in the 'Measuring convergence through time via Ct-measures' section of the main text (with example output in Figure 5B).

SUPPLEMENTAL RESULTS

Univariate model-fitting analyses

For univariate models fit to PC1 scores the OU2VA model, which allows varying rates and attraction strengths between regimes, is the best fitting model at all trait optimum values for both convergence and divergences datasets (Table S1). However for convergence datasets, the null model (BM1) is the second best-fitting model when the trait optimum is zero and 20, and the total AICcW values for all OU2 models increases with greater optima values, indicating increased evidence of convergence in morphological outliers. These results are consistent with the results of the multivariate evolutionary models (Table 2).

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Table S1. Tests of convergence among lineages of the simulated datasets using evolutionary models fit to univariate data (PC1 scores). Model-fitting results for each trait optimum are the mean AICcWs of 50 phylogenetic trees (five datasets with 10 'simmaps' each). Model support for the two-regime models (any variation of the OU2 model) could be interpreted as support for convergence because this model reflects evolution of the putatively convergent lineages toward a shared adaptive peak (but see the Results & Discussion). Abbreviations: AICcW, small-sample corrected Akaike weights; BM, Brownian motion; OU, Ornstein-Uhlenbeck.

	Model	Trait optimum					
		0	20	50	100		
Convergence simulations	BM1	0.157	0.043	0.000	0.000		
	OU1	0.058	0.015	0.000	0.000		
	OU2	0.041	0.020	0.001	0.000		
	OU2A	0.016	0.014	0.103	0.338		
	OU2V	0.058	0.022	0.023	0.000		
	OU2VA	0.670	0.885	0.873	0.661		
Divergence simulations	BM1	_	-	0.000	0.000		
	OU1	_	-	0.000	0.000		
	OU2	_	-	0.000	0.000		
	OU2A	_	-	0.116	0.331		
	OU2V	_	-	0.001	0.020		
	OU2VA	_	_	0.882	0.649		

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In the main text, we discuss a few factors that likely explain why the two-regime OU models are unexpectedly the best-fitting models to divergent data. Namely, the tworegime OU may be the best-fitting of bad-fitting models, with the BM1 and OU1 models even worse fits to the data. An additional factor that may contribute to the relatively strong fits of two-regime OU models to divergence datasets is that we treated the datasets as we would with empirical datasets and used 'simmaps' for ancestral state reconstructions of regime states (gliding or non-gliding), rather than use the known node information (via the simulation data). For instance, the two marsupial glider groups in our dataset are closely related (but believed to have evolved gliding independently), and thus the 'simmaps' might commonly (and mistakenly) reconstruct the MRCA of those lineages as having gliding behavior.

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C1-C4 and Ct1-Ct4 applied to simulated data

216 In the main text we only present results for C1 (Fig. 3C, Table 1) and Ct1 (Fig. 5A, Table 1), which were applied to both the simulated convergence datasets and the 218 simulated divergence datasets. However, Stayton (2015) developed four distancebased convergence measures (C1-C4) and one frequency-based measure (C5), with 220 C1 being the primary measure, and we altered C1-C4 to produce the Ct1-Ct4 measures. Here, we provide full results for C1–C4 (Fig. S1) and Ct1–Ct4 (Fig. S2), 222 which are also applied to both the convergence and divergence datasets. See the Methods and Stayton (2015) for descriptions of the four convergence measures, and 224 see the Methods for information on the simulated datasets. Note that the Ct4 measure is calculated differently than the C4 measure (see Supplemental Methods). For C1–C4, 226 all results for divergence simulations are greater than zero (Fig. S1), incorrectly indicating convergence, whereas the Ct1-Ct4 scores for divergence datasets are 228 generally at or below zero (Fig. S2).

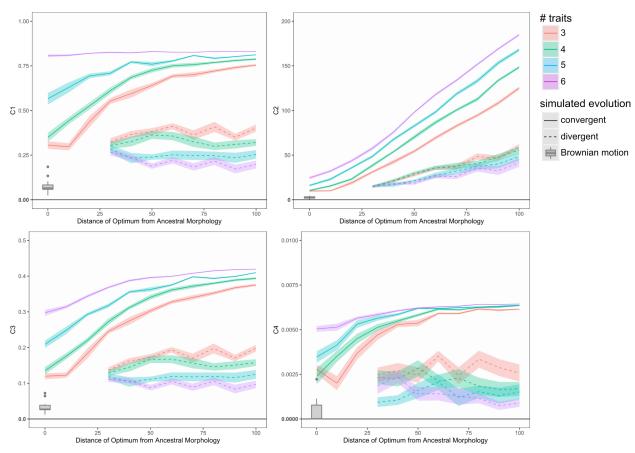


Figure S1. Plots of means and standard errors of C1–C4 scores for simulated convergent lineages (solid lines) and divergent lineages (dashed lines). Datasets varied in the number of convergent/divergent traits (represented by the different colored lines) and in the distance of trait optima from the ancestral morphology (approximated as the center of morphospace). Means and standard errors are computed from 15 simulated datasets. Greater C1–C4 values indicate greater convergence. We did not simulate divergence for trait optima of 0, 10, and 20 because at these optima our simulation methods may have inadvertently generated convergence patterns (see Methods and Figure 3). As a second means of simulating divergence, we allowed the lineages of interest ('gliders') to evolve via BM. These are provided as box-and-whisker plots, summarizing 15 simulated datasets of six traits (see Methods). Note that the divergence results are all greater than zero, incorrectly indicating convergence.

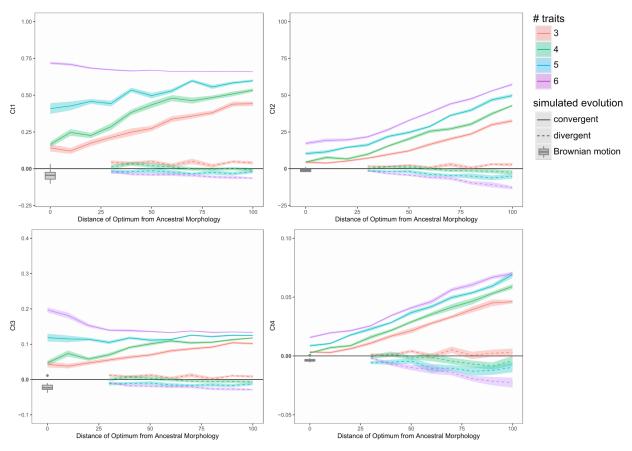


Figure S2. Plots of means and standard errors of Ct1-Ct4 scores for simulated convergent lineages (solid lines) and divergent lineages (dashed lines). Datasets varied in the number of convergent/divergent traits (represented by the different colored lines) and in the distance of trait optima from the ancestral morphology (approximated as the center of morphospace). Means and standard errors are each computed from 15 simulated datasets. Greater Ct1-Ct4 values indicate greater convergence. We did not simulate divergence for trait optima of 0, 10, and 20 because at these optima our simulation methods may have inadvertently generated convergence patterns (see Methods and Figure 3). As a second means of simulating divergence, we allowed the lineages of interest ('gliders') to evolve via BM. These are provided as box-and-whisker plots, summarizing 15 simulated datasets of six traits (see Methods). Note the differences in the scaling of the vertical axes of the Ct2 and Ct3 plots relative to the C2 and C3 plots (Fig. S1), respectively. (The scaling for C4 and Ct4 is different because these measures are calculated differently.) Also, note the different position of zero relative to results in the Ct1-Ct4 plots versus the position in C1-C4 plots (Fig. S1), as well as the overlap in the Ct1-Ct4 plots of divergence data simulated by both BM and OU processes.

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Ct-measures – the influence of origination times on results

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As discussed in the main text, the Ct-measures limit candidate $D_{max,t}$ measurements to specific time slices at internal nodes, and thus the timing of evolutionary change among putatively convergent lineages can influence the results of Ct-measures. For instance, if different lineages of interest evolve toward (or away from) a specific morphology at different points in time, then the $D_{\text{max.t}}$ measurement may not measure the morphologically farthest distances between the lineages. This issue may be magnified when convergence is expected to be linked to adaptive changes (e.g., adaptations for gliding behavior) that evolved at specific times. For instance, if colugos (i.e., Dermoptera or 'flying lemurs') evolved traits associated with gliding behavior approximately 60 Ma, and flying squirrels (Pteromyini) evolved traits associated with gliding approximately 25 Ma (e.g., Grossnickle et al. 2020), then most of the candidate $D_{\text{max.t}}$ measurements will be comparisons of dermopterans with gliding traits to stem flying squirrels without gliding traits (from 60 to 25 Ma). If the older lineage (colugos) has already undergone considerable evolutionary change by the time that the younger lineage (flying squirrels) originated, then much of the convergent evolutionary change of the older lineage is not captured by the morphological distances measured at 'time slices,' which are limited to the time period in which the lineages overlap. Ideally, most candidate $D_{\text{max,t}}$ measurements would be comparisons of non-gliding stem colugos and non-gliding stem flying squirrels that lack the adaptive traits associated with gliding. This issue might lead to candidate $D_{\text{max.t}}$ measurements being smaller than expected, or at least smaller than those calculated by measures that ignore time (e.g., C-measures).

Conversely, if the putatively convergent taxa evolve toward outlying regions of morphospace, then the asynchronous origins of the clades could inflate the *Ct*-measures. We illustrate this in Figure S3. In the conceptual illustrations, the *Ct*1 score is consistently 0.3 when convergent lineages originate at the same time and/or when lineages evolve toward the ancestral morphology. However, when lineages originate at different times and evolve toward an outlying region of morphospace, then the *Ct*1 score is 0.7. Thus, researchers should be cautious when applying Ct measures to datasets with outlying taxa of various origination ages, and we offer some suggestions in the main text for mitigating this issue. It is also worth noting that this latter scenario

assumes that the convergent lineages can reach adaptive zones; if the later-evolving convergent lineage is still evolving toward outlying morphospace (i.e., it has yet to reach an adaptive peak or zone) then the aforementioned issue may have less of an influence on *Ct* results.

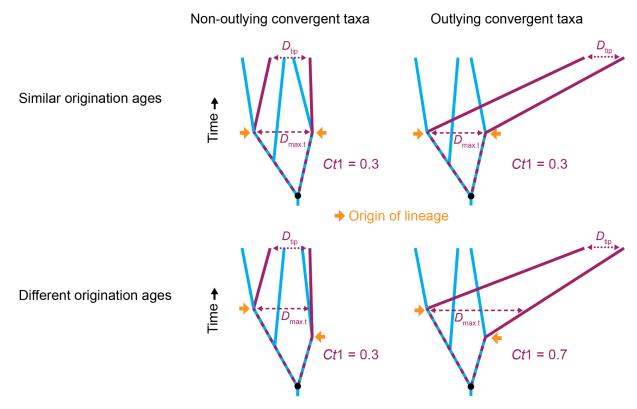


Figure S3. Conceptual illustrations demonstrating how Ct1 results can be influenced by a combination of outlying morphologies and varying origination times among convergent lineages. The Ct1 score is 0.3 in three of the scenarios but inflates to 0.7 when lineages both originate at different times and are outliers in morphospace (bottom right). To help mitigate this issue, we have included an option as part of the convrat.t function that allows users to limit candidate $D_{max.t}$ measurement to the time period prior to the origination of the focal lineages (see Supplemental Methods). See the main text for descriptions of Ct1, $D_{max.t}$, and D_{tip} .

Influence of the number of traits on Ct results

As discussed in the main text (see Results & Discussion), the number of traits used in analyses (with all else equal) can bias the Ct scores. Inference of ancestral states via BM tends to average variation at internal nodes; thus, D_{tip} typically increases at a higher rate than $D_{max.t}$ for each non-convergent trait that is added to a dataset. (Here, we use "non-convergent traits" to refer to BM-evolved traits that are not selected to evolve toward a trait optimum via an OU process. These are often divergent, although it should be noted that BM-evolved traits could still be convergent by chance.) This is illustrated in Figure S4. The effect of this pattern is that an increased number of traits in analyses (with all else equal) could result in a relative decrease in Ct scores, unless those added traits are strongly convergent.

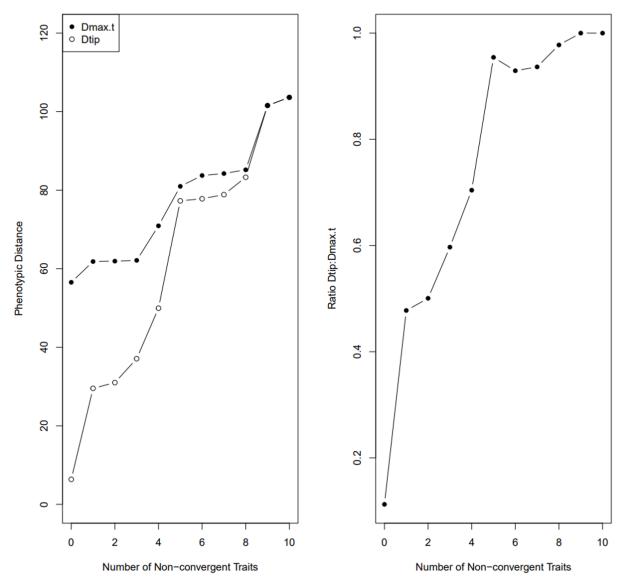


Figure S4. Illustration of how the number of traits used in analyses can influence Ct-measures, demonstrating the increased rate at which D_{tip} values increase relative to $D_{max.t}$ as additional non-convergent traits are included in analyses. (Here, 'non-convergent traits' refers to BM-evolved traits, which are expected to be divergent in most cases.) The left panel shows D_{tip} and $D_{max.t}$ measured between two 'glider' lineages with two simulated convergent traits (optimum = 100) and varying number of additional traits simulated via BM. The right panel shows the ratio between the D_{tip} and $D_{max.t}$ values.

Empirical example - Anolis 'twig' ecomorphotype

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348 To test the novel Ct-measures and compare Ct results to those of C-measures (see the Empirical examples subsection of the Results & Discussion), we re-analyzed a classic 350 example of convergence among Anolis lizards (Mahler et al. 2013), focusing specifically on five 'twig' ecomorphotype lineages. We chose this ecomorphotype because the taxa 352 are morphological outliers that occupy a unique region of Anolis morphospace (Huie et al. 2021), and they have especially strong C-measure scores (Stayton 2015, Huie et al. 354 2021), although we believe that this is due in part to the lineages being morphological outliers (see Results & Discussion). Following the methods of Mahler et al. (2013), we 356 size-corrected the traits via PGLS regression of each trait against the snout-to-vent length via PGLS. The Ct-measure results for this analysis are provided in Figure S5 and Table S2. Whereas the C1 score is 0.36 (Stayton 2015), but we find the overall Ct1 358 score to be near zero for both the raw and weighted results (Table S2). This helps to 360 highlight the inflated C-measure results due to the issues highlighted in the Results & Discussion. However, note that there is considerable diversity in the results among the 362 ten pairwise comparisons; four are strongly statistically significant, whereas some (e.g., Anolis occultus and the A. paternus clade) show considerable divergence (Ct1 = -0.763; 364 Table S2). To highlight the differences between convergent and non-convergent (or not significant convergence) pairwise comparisons, we separate those comparisons in 366 Figure S5. Thus, we recommend that researchers examine and report results for pairwise comparisons whenever examining more than two putatively convergent 368 lineages.

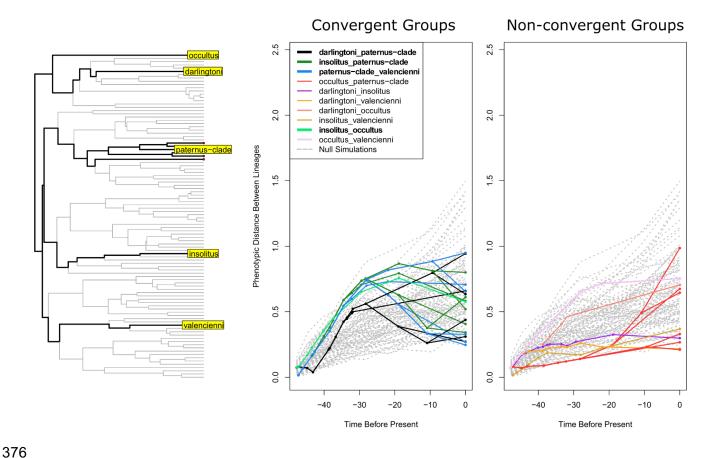


Figure S5. Summary of empirical tests of convergence in *Anolis* species belonging to the 'twig ecomorph' (Mahler et al. 2013). We size-corrected (via PGLS regression) and then analyzed the ten skeletal traits of the dataset of Mahler et al. (2013), with taxa assigned to groups based upon unique origins of the 'twig' ecomorphotype (see the *Ct-measures* section of the Supplemental Methods). The plots are the output of the *plot.C* function of the convevol R package, although the distance-through-time plot has been split to show statistically significant (left) and not significant (right) pairwise comparisons separately (see also Table S2). Significant pairwise comparisons are also indicated in bold in the key. Note that two of the 'non-convergent' comparisons in the right panel do have a positive *Ct*1 value, but they are statistically not significant (Table S2). There are 50 null simulations (light gray lines).

Table S2. Ct-measure values obtained for analyses run using the anole dataset of Mahler et 398 al. (2013; ten standardized skeletal traits). Values are reported for overall comparison of ten'twig ecomorph' species in five groups (corresponding to each independent origin of the 400 ecomorph; Fig. S5). Pairwise comparisons of groups are also illustrated in (Fig. S5). See the Supplemental Methods for an explanation of the difference between 'overall raw' and 402 'overall weighted' results. Note that 'pat' refers to a five-species clade that includes Anolis paternus and four closely related species, whereas all other 'twig' taxa include a single 404 lineage (Fig. S5); see the Methods for updates to the convevol R package that allow for comparisons among taxa with more than one lineage. Asterisks denote values returned as 406 significantly different from null simulations (. - p < 0.1, * - p < 0.05, ** - p < 0.01). Abbreviations: dar. Anolis darlingtoni; ins. Anolis insolitus; occ. Anolis occultus; pat. Anolis 408 paternus; val, Anolis valencienni.

	Ov	erall	Pairwise comparisons									
	Raw	Weighted	dar - pat	ins - pat	pat - val	occ - pat	dar - ins	dar - val	dar - occ	ins - val	ins - occ	occ - val
Ct 1	-0.01**	-0.057**	0.147**	0.323**	0.346**	-0.763	0.083 .	0.161.	-0.521	-0.527	0.237**	-0.055
Ct 2	0.072**	0.022**	0.086**	0.254**	0.261**	-0.216	0.027 .	0.042 .	-0.241	-0.127	0.179**	-0.039
Ct 3	0.039**	0.012**	0.047**	0.111**	0.140**	-0.090	0.013 .	0.023 .	-0.117 .	-0.063	0.071*	-0.018
41 Ct 4	0.002**	-0.006 .	0.003**	0.019**	0.011**	-0.007	0.001.	0.001.	-0.089	-0.005	0.006**	-0.001

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