Pattern and Process in the Comparative Study of Convergent Evolution*

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abstract: Understanding processes that have shaped broad-scale biodiversity patterns is a fundamental goal in evolutionary biology. The development of phylogenetic comparative methods has yielded a tool kit for analyzing contemporary patterns by explicitly modeling processes of change in the past, providing neontologists tools for asking questions previously accessible only for select taxa via the fossil record or laboratory experimentation. The comparative approach, however, differs operationally from alternative approaches to studying convergence in that, for studies of only extant species, convergence must be inferred using evolutionary process models rather than being directly measured. As a result, investigation of evolutionary pattern and process cannot be decoupled in comparative studies of convergence, even though such a decoupling could in theory guard against adaptationist bias. Assumptions about evolutionary process underlying comparative tools can shape the inference of convergent pattern in sometimes profound ways and can color interpretation of such patterns. We discuss these issues and other limitations common to most phylogenetic comparative approaches and suggest ways that they can be avoided in practice. We conclude by promoting a multipronged approach to studying convergence that integrates comparative methods with complementary tests of evolutionary mechanisms and includes ecological and biogeographical perspectives. Carefully employed, the comparative method remains a powerful tool for enriching our understanding of convergence in macroevolution, especially for investigation of why convergence occurs in some settings but not others.

Keywords: convergence, phylogenetic comparative methods, adaptive radiation, evolutionary process, adaptation.

Introduction

The phenomenon of phenotypic convergence plays a fundamental role in the study of organic evolution. Although convergence itself is not necessarily indicative of any particular evolutionary process (Losos 2011a; Speed and Arbuckle 2016), the repeated appearance of similar forms in disparate lineages stands in apparent contrast to the expected pattern of divergence over time during evolution and thus demands an explanation (Wake et al. 2011). Convergent evolution has been attributed to a great diversity of causes, at times being invoked as evidence for the importance of multiple and sometimes opposing evolutionary processes. As such, confusion persists around the connection between patterns of convergence, mechanisms of evolution, and modeled processes in comparative methods (see box 1 for definitions of these terms).

Our aim is to clarify these concepts and show how they relate to common assumptions in the comparative study of convergence, recommending best practices and advocating integrative ways to link convergent patterns with mechanistic hypotheses. We begin by reviewing the comparative study of phenotypic convergence in continuously valued traits and the factors that make it uniquely challenging to study deductively. We then discuss the relationship between pattern and process in the comparative study of convergence, giving special attention to the facts that (1) all comparative tools for studying convergence make inductive inferences about convergence and thus assume an underlying model of evolution and (2) despite the assumption of a modeled process, there can often be a many-to-one mapping of real evolutionary processes to modeled processes. Finally, we argue that because these limitations can hinder interpretation, integration of comparative phylogenetic models of convergence with other forms of inference is needed to increase confidence in links between pattern and process. We suggest several research directions to improve future prospects for gaining meaningful insights about evolutionary pro-

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Box 1: Definitions

Convergence

We define convergent phenotypic evolution (or "convergence") as the pattern of evolution in which species in two independently evolving lineages become phenotypically similar. Importantly, such a pattern is defined as convergence regardless of the evolutionary process that gave rise to it (Stayton 2015*a*). In this article, we will discuss convergent patterns in which lineages evolve greater phenotypic similarity than was exhibited by their ancestors. We do not discount convergence definitions that include patterns in which two or more lineages independently evolve similar traits even when their ancestors were also similar (i.e., parallelism; Arendt and Reznick 2008*a*, 2008*b*; Leander 2008; Scotland 2011; Wake et al. 2011; Rosenblum et al. 2014); nonetheless, for clarity and because most comparative convergence tools are specialized for the study of the evolution of greater similarity among descendants than ancestors, we do not discuss parallelism in this article. As any statement about convergence requires information about ancestral phenotypes, our discussion of the role of evolutionary process models in inferring ancestral phenotypes using phylogenetic comparative methods (see the main text) should be relevant regardless of the specific definition of convergence assumed.

Evolutionary Process/Evolutionary Mechanism

Evolutionary processes, which we use interchangeably with the term "evolutionary mechanisms," refer to specific underlying agents of evolutionary change, such as genetic drift or natural selection, that give rise to observed patterns of organismal diversity (Eldredge and Cracraft 1980; Chapleau et al. 1988). A fundamental goal in evolutionary biology is to test hypotheses about the evolutionary mechanisms that shape patterns of biological diversity through time.

Evolutionary Process Model

In this article, the term "evolutionary process model" refers to a model of the evolutionary process assumed by a phylogenetic comparative method. Most such methods assume phenomenological evolutionary models, which means that they are thought to represent macroevolutionary expectations arising from a given evolutionary process but do not explicitly model the mechanism of evolutionary change itself. For this reason, some evolutionary process models may be consistent with more than one mechanism of evolutionary change (see the main text).

Ecological Mechanism

We refer to "ecological mechanism" as an ecological interaction that is an agent of natural selection on an organism. Ecological mechanisms describe how an organism interacts with its environment or with other species, and include competition, mutualism, and abiotic tolerances, among others. There has been relatively little investigation of how different ecological mechanisms are expected to shape patterns of convergent evolution.

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cesses from the comparative study of convergent patterns, including extended model development, pairing comparative study with other approaches for studying the evolutionary process, and better incorporating fossil information.

The Potential Causes of Macroevolutionary Convergence

The investigation of convergence plays an important role in evolutionary study. To many, instances of convergence are interesting as evidence for adaptation or for the importance of ecology in the evolution of phenotypic diversity. For example, the evolution of pale dorsal coloration in numerous vertebrates and invertebrates inhabiting White Sands National Monument indisputably reflects adaptation for increased crypsis (Rosenblum et al. 2010), and the repeated evolution of cold tolerance in distantly related conifers is clearly attributable to adaptation to similar environmental conditions (Yeaman et al. 2016). Large-scale convergence between whole faunas occurring in similar ecological communities

and environments suggests that evolution can in some circumstances exhibit a surprising degree of predictability and that ecological factors can repeatedly and predictably shape macroevolutionary diversification (Nevo 1979; Conway Morris 2010; Mahler et al. 2013; Esquerré and Keogh 2016; Moen et al. 2016).

Alternatively, convergence has been taken as evidence for constraints on the production of variation (Haldane 1932; Maynard Smith et al. 1985; Schluter 1996), manifested at one or more hierarchical levels of biological organization (Wake and Larson 1987; Wake et al. 2011). Such constraints can arise from biased mutation, pleiotropic gene networks, structural limitations, or limits on phenotypic variation imposed by ontogenetically nested developmental sequences (Gould 1980; Alberch 1982; Oster and Alberch 1982; Arnold 1992; McCune and Carlson 2004; Brakefield 2011; Streisfeld and Rausher 2011; Stern 2013). For example, Bright et al. (2016) concluded that the vast majority of craniofacial variation in predatory birds was attributable to conserved patterns of allometry and covariation between traits (phenotypic integration), with only a small amount of residual variation explained by feeding ecology. Convergence resulting from such factors suggests that genetic or developmental constraints play an important and perhaps dominant role in shaping the evolution of phenotypic diversity (Gould 1980, 2002; Alberch 1982; Wake and Larson 1987).

Finally, some degree of evolutionary convergence may be an expected outcome of chance, especially for traits with low dimensionality (Wagner 2000; Stayton 2008). These possibilities are not mutually exclusive, of course, and convergence due to chance may be most likely in scenarios in which constraints on the generation of variation restrict evolutionary outcomes to a small set of phenotypes with comparable fitness (Losos 2011a; Spor et al. 2014). Likewise, some authors have uncovered phylogenetic patterns suggesting that certain convergent adaptations are hierarchically constrained by the presence or absence of preadaptations (Marazzi et al. 2012; Beaulieu et al. 2013). For example, the convergent evolution of arboreal adaptations in oribatid mites appears contingent on the prior evolution of sexual reproduction and strong sclerotization (Maraun et al. 2009).

Challenges to Measuring and Studying Convergent Evolution

Despite its importance in evolutionary inquiry, convergence is difficult to directly identify, and once identified, it is difficult to ascribe to underlying mechanisms with certainty (Maynard Smith et al. 1985). A principal challenge in studying convergence is that it is rarely possible to study using deductive inference due to the difficulty of observing both ancestor and descendant phenotypes. Empirically, this is generally possible only in exceptional circumstances, such

as when the fossil record preserves unambiguous ancestor-descendant sequences (e.g., Bell 1987; McCune 1987), when source populations that gave rise to convergent daughter populations are still extant (e.g., Hoekstra et al. 2006; Rosenblum et al. 2010), and when convergence is particularly rapid (e.g., Pascoal et al. 2014), including in laboratory experiments on organisms with very short generation times (e.g., Meyer et al. 2012; Spor et al. 2014). Studies documenting convergence in this way represent some of the best and most cherished evidence for convergent evolution, but they are uncommon and are limited in what they can tell us about the evolution of convergent patterns across the tree of life.

Convergence has a long history of study despite the limited opportunity for deductive inference, but aside from exceptional cases such as those described above, much historical study of convergence has been qualitative in nature. Most of the canonical examples of convergence described in introductory biology textbooks, such as the streamlined profiles of fast-moving pelagic vertebrates or the winter pelage of Arctic foxes and snowshoe hares, are so visually striking and occur in such distant relatives that there can be little question about their convergent origins. What was historically lacking was a cohesive quantitative framework for inferring the trajectories of convergence; the lack of such a structure imposed formidable limits on the study of the ultimate drivers of convergent evolution. This framework emerged with the union of the comparative method with an explicitly phylogenetic perspective in the 1980s and 1990s (Felsenstein 1985; Harvey and Pagel 1991).

Phylogenetic Approaches to Studying Convergence

The advent of phylogenetic comparative approaches to studying trait evolution expanded the scope of convergence studies, making it possible to test quantitative hypotheses about convergent evolution in any group with sufficient phylogenetic and phenotypic information. This development effectively opened the quantitative study of convergence, previously limited to exceptional cases, to the entire tree of life. When viewed within a phylogenetic comparative framework, repeated convergence of any kind provides researchers with a degree of statistical replication rarely afforded to students of the explicitly historical science of evolution. Regardless of the question of interest, the repeated evolution of similar phenotypes in disparate lineages provides independent replicates in a grand, unplanned evolutionary experiment. The ability to repeatedly query putative cause and evolutionary effect allows investigators to overcome the risks of "just so" storytelling (Gould and Lewontin 1979) in the study of adaptation, structural constraint, and even chance (Maynard Smith et al. 1985; Harvey and Pagel 1991; Losos 2011a).

The development of tools for investigating convergence accelerated especially rapidly during the last decade (Speed

and Arbuckle 2016). New inductive tools provide a wide variety of methods for quantifying convergence—including its occurrence, frequency, extent, and historical trajectory. Such tools come in a variety of forms, the details of which are described in depth elsewhere (see Mahler and Ingram 2014; Stayton 2015a; Arbuckle and Speed 2016; Speed and Arbuckle 2016 for more in-depth descriptions). Most, however, can be classed into one of three categories: (1) statistical indices, which measure an expected emergent feature of convergent phenotypic evolution on a phylogeny; (2) ancestor reconstruction methods, in which ancestral phenotypes are estimated under some assumed evolutionary model and then used to identify and quantify convergence patterns; and (3) model-fitting approaches, in which evolutionary models explicitly incorporating processes expected to cause convergence are parameterized and compared to models in which any convergence occurs by chance.

All existing comparative methods for studying convergence have particular limitations and weaknesses, as we will discuss below. More importantly, however, is that all of these tools make inductive inferences about convergence, an approach that has practical consequences for the design and interpretation of comparative studies. Regardless of the method used, the results must be interpreted in light of an assumed model of the evolutionary process; as a result, it is not possible to decouple the quantification of convergent pattern from the study of evolutionary process using comparative data, as has been recently recommended (Stayton 2015a). This issue is compounded by the fact that many widely used evolutionary process models may plausibly represent multiple underlying evolutionary mechanisms—a potential many-to-one mapping of mechanism to model. At the heart of these issues is the complex relationship between pattern and process in comparative biology.

Pattern and Process

An important property of any evolutionary phenomenon is the extent to which it represents a pattern versus a process (box 1). For example, the term "adaptation" is meaningfully defined as both a process (e.g., adaptation occurs when a population evolves greater fitness via natural selection) and a pattern (e.g., an adaptation is a trait that increases an individual's fitness compared to individuals without that trait; Gould and Vrba 1982; Futuyma 2005). In the case of evolutionary convergence, we feel that in almost all scenarios convergence is best defined as a pattern (Stayton 2015a). Convergence is less meaningful as a process, because convergent evolution is nearly always an emergent outcome of evolutionary processes operating independently in multiple lineages rather than any intrinsically convergent processes. For example, short-limbed twig specialist anoles on different Antillean islands are similar be-

cause they have adapted to similar arboreal substrates (Williams 1983; Losos 2009), not because they have been selected to resemble one another. There are a few exceptions where species are directly selected to converge with one another, such as mimicry complexes (Endler 1981) or character convergence driven by competition for nonsubstitutable resources (MacArthur and Levins 1967; Abrams 1987; Fox and Vasseur 2008), but otherwise the evolutionary processes responsible for increasing similarity in a converging lineage are blind to the phenotype of the lineage to which it is converging. As standard evolutionary theory can explain the processes by which independent lineages evolve to be more similar, there is no need for a special theory of convergence (Speed and Arbuckle 2016), and convergence is thus best defined as a pattern.

Although we agree with several recent reviews that convergence should be defined as a pattern, we argue that when using the comparative approach, convergence must be studied with the evolutionary process in mind. We therefore reject arguments that comparative analyses of convergence should proceed in a two-step manner—first testing for convergent pattern, and then investigating potential evolutionary processes responsible for this pattern (Stayton 2015a, 2015b; Speed and Arbuckle 2016). In a recent review, Stayton (2015a) made a case for this two-step approach, specifically criticizing the use of process-based comparative tools for identifying convergence. Stayton's concern is defensible—in applying an evolutionary model to comparative data (e.g., multiple-optimum Ornstein-Uhlenbeck [OU]; Butler and King 2004), the investigator assumes that the process being modeled is an appropriate representation of trait evolution in lineages of interest. In the absence of appropriate model comparison, this could bias an investigation toward a particular evolutionary explanation for convergence. The risk of bias is arguably greatest for adaptive explanations (sensu Gould and Lewontin 1979), and Stayton marshaled evidence for adaptationist bias in convergence definitions provided in many prominent biology texts (Stayton 2015a). To safeguard against adaptationist biases, Stayton recommended that comparative studies first employ process-neutral statistical tools to identify and measure macroevolutionary convergence and then, patterns in hand, test alternative hypotheses about the evolutionary processes that may have given rise to these patterns.

While the goal to investigate convergence without making assumptions about process is a worthy one, in phylogenetic comparative biology it is impossible to study evolutionary pattern and process independently (Pagel and Harvey 1989; Harvey and Pagel 1991; Freckleton et al. 2011; Hunt 2012). The purpose of phylogenetic comparative methods is to study patterns that inherently arise as a consequence of evolutionary processes, both to understand how history has shaped these patterns and to infer

the processes associated with this history. As referenced above, phylogenetic comparative biology is largely an inductive science, due to the usual lack of direct observational evidence of historical processes and patterns. The comparative method provides a framework for testing hypotheses about these phenomena, but an essential component of this framework is the assumption of evolutionary process models.

Evolutionary Process Models Underlying Tests of Convergent Pattern

In the case of convergence, the assumption of an evolutionary process model is required at some step (often implicitly) by all available comparative tools. The most widely assumed model is Brownian motion, which is used to model trait evolution in a variety of contexts. Brownian motion is a very simple model that represents the expectations of continuous phenotypic evolution under neutral genetic drift (Lande 1976; Felsenstein 1988). Like most models used in phylogenetic comparative methods, Brownian motion is a phenomenological model of the evolution of mean species-level characters, reflecting macroevolutionary expectations but not incorporating microevolutionary mechanisms. It is often used to represent a hypothesis of neutral evolution (especially as a null model), but some have argued for its utility in representing other evolutionary mechanisms such as fluctuating directional selection or adaptive radiation on a dynamic adaptive landscape (although with important caveats; Felsenstein 1988; O'Meara et al. 2006). In studies of adaptation, a popular generalization of Brownian motion is the Ornstein-Uhlenbeck model (Hansen 1997; Butler and King 2004; O'Meara and Beaulieu 2014). The OU model includes a Brownian drift term as well as a parameter describing the strength of attraction to some optimum value. Extensions allow different lineages to be attracted to different optima, which may be interpreted as peaks on an adaptive landscape. Unlike Brownian motion, specific OU models can model processes consistent with deterministic evolutionary convergence, though it is important to note that both are evolutionary process models (box 1). Recently developed Lévy process models represent an alternative generalization of Brownian motion in which a Brownian drift process is punctuated by large, instantaneous shifts in trait value (i.e., evolutionary jumps; Eastman et al. 2013; Landis et al. 2013). Lévy process models lack parameters specifically expected to produce convergence but can be used to test hypotheses about the frequency of convergent jumps in groups for which the phenotypic similarity of certain species has already been established (Eastman et al. 2013).

Although all comparative methods for studying convergence employ evolutionary models in one fashion or another, the role and potential impact of the model vary across

approaches. Index methods implicitly use process models to generate a frame of reference with which to compare putatively convergent evolutionary patterns. For example, the Wheatsheaf index (Arbuckle et al. 2014) uses pairwise phylogenetic distances as a yardstick for evaluating and then weighting observed pairwise trait differences, to be contrasted with the correspondence between pairwise phylogenetic and trait differences expected under Brownian motion. Index tools have been described as "process-neutral" or "process-free" (Stayton 2015a; Speed and Arbuckle 2016), which is accurate in the sense that convergent patterns are not assumed to have evolved under any given evolutionary mechanism. However, these measures are useful only in reference to expectations under a particular evolutionary process model, which is sometimes unspecified but most often Brownian motion. Furthermore, because no underlying historical process model is applied to the data themselves, these tools can be limited by an inability to distinguish convergence from other causes of evolutionary similarity between distant relatives, such as a simple lack of divergence (Stayton 2015a; Speed and Arbuckle 2016). We suggest that additional insights may be gained by comparing statistical indices to distributions simulated under alternative models of the underlying process (sensu Slater and Pennell 2014).

Ancestral state reconstruction (ASR) methods critically rely on an assumed model for quantification of both the frequency and the strength of convergence. Although several kinds of ASR methods have been used to assess convergence, they all model a historical trajectory of evolution under an assumed model (almost always Brownian motion) and then analyze estimated ancestral phenotypes to detect or quantify convergence (reviewed in Stayton 2015a, 2015b; Arbuckle and Speed 2016; Speed and Arbuckle 2016). ASR methods have been used to study convergence since the dawn of the comparative methods era (e.g., Donoghue 1989; Brooks and McLennan 1991; Losos 1992) but have gained renewed popularity with the recent development of phylomorphospace tools for visualizing evolutionary trajectories and quantifying the frequency and strength of convergence (Sidlauskas 2008; Stayton 2011, 2015b). Stayton (2015b) and Speed and Arbuckle (2016) classified available ASR methods as process-free on the grounds that they do not assume that convergent evolutionary patterns were the result of adaptive mechanisms. These approaches are not truly process-free, however—they rely on parameter estimates from a model that assumes the observed patterns evolved under a process consistent with Brownian motion, such as genetic drift (as well as some, but certainly not all, alternative evolutionary mechanisms; Felsenstein 1988; Hansen and Martins 1996; O'Meara et al. 2006). ASR methods can employ alternative macroevolutionary process models, including models with explicitly adaptive processes, so long as it is possible to reconstruct ancestral states under such

models (e.g., Elliot and Mooers 2014; Uyeda and Harmon 2014). However, this is rarely done, perhaps because tools for carrying out ASR have not kept pace with the rapid development of methods for fitting alternative models of trait evolution.

Naturally, evolutionary process models play a prominent role in methods for studying convergence that are explicitly based on model fitting. Such tools take one of two approaches. In the first, an investigator parameterizes an evolutionary process model in a way that explicitly incorporates hypothesized convergence events, fits the model to data, and then compares the fit to that of an alternative model lacking convergence. This is most commonly done using multiple-optimum OU models to represent the evolution of a clade on an adaptive landscape, with occasional peak shifts in which a lineage escapes the influence of its historical adaptive peak and is attracted to another (Hansen 1997; Butler and King 2004; Bartoszek et al. 2012; Beaulieu et al. 2012; O'Meara and Beaulieu 2014). Because it is straightforward to design OU models that permit independent lineages to evolve toward a shared adaptive peak, they provide a natural framework for the investigation of adaptive convergence. Generalized OU models permit a great deal of flexibility in parameterization, including multiple attraction strengths or rates of Brownian drift in addition to multiple optima (Beaulieu et al. 2012) and multivariate OU (Bartoszek et al. 2012), although highly complex OU models can suffer from parameter identifiability issues (Ho and Ané 2014; O'Meara and Beaulieu 2014; Cressler et al. 2015; Cooper et al. 2016b; Khabbazian et al. 2016). Most methods using OU models require a prior hypothesis for the phylogenetic placement of adaptive peak shifts, which limits their utility in estimating the frequency of convergence and precludes tests for convergence in clades where putatively convergent taxa have not been identified. These limitations can be avoided by using a second type of modeling approach in which the number or rate of evolutionary peak shifts is estimated as a model parameter. To achieve this, some such tools simply extend the multiple-peak OU modeling framework by automating the evaluation of candidate peak shift configurations (Ingram and Mahler 2013; Uyeda and Harmon 2014; Khabbazian et al. 2016), while alternative methods assume a Lévy process model of punctuated evolution (Eastman et al. 2013; Landis et al. 2013). Both techniques allow assessment of the frequency of evolutionary shifts, including convergence events (Eastman et al. 2013; Ingram and Mahler 2013).

Why Treating Comparative Approaches as Process-Free Can Lead to Problems in the Study of Convergence

For each of the comparative approaches to studying convergence outlined above, the resulting inferences about convergent evolution critically depend on the assumed model of the underlying evolutionary process. Quantitative measures of convergent pattern from a given method may differ markedly if an alternative model of the evolutionary process is assumed. This can be particularly problematic for Brownian motion–based ASR methods described as process-free which may overestimate or underestimate the frequency of convergence in groups evolving on rugged adaptive landscapes and yield inaccurate estimates of the strength or extent of convergence in any circumstance in which Brownian motion is a poor model of the true evolutionary process. To illustrate, we consider a clade diversifying on an adaptive landscape in which several subclades have undergone peak shifts to much larger phenotype values but without convergence to the same optima (fig. 1). The reconstruction of ancestral states assuming Brownian motion imposes an averaging effect on ancestral phenotype estimates that is most pronounced at the root of the tree. This reconstruction substitutes the true pattern of iterated divergence from small to large phenotype values with a pattern in which at least four major lineages converge from intermediate to small values. Several ASR-based convergence metrics suggest substantial convergence in this clade (fig. 1A). In contrast, if the true (i.e., generating) Ornstein-Uhlenbeck model is instead assumed when carrying out ASR, the same pattern-based metrics accurately capture the lack of true convergence (fig. 1B). This is a particularly striking example but we suspect not an unrepresentative one, due to the well-documented tendency of Brownian motion–based ASR methods to infer increasingly intermediate ancestral states for deeper nodes (Schluter et al. 1997; Oakley and Cunningham 2000). Similar problems can be anticipated any time ASR methods are used to investigate a group for which Brownian motion is not a reasonably good representation of the evolutionary process, and model misspecification can likewise lead to failure to identify convergence events or grossly inaccurate estimates of the strength or extent of convergence.

The issue we discuss here is shared across phylogenetic comparative biology. Hunt (2012) made similar points about the measurement of evolutionary rate, showing that measures based on process models were more meaningful across evolutionary timescales than traditional interval-based (and process-free) rate measures. However, these rate estimates were accurate only if the investigator assumed the correct model of evolution, due to the complex and model-specific relationship between evolution's tempo (i.e., change over time) and mode (the process underlying this change). Due to the inseparability of tempo and mode, Hunt argued that the two must be considered in concert in studies of the evolutionary rate. A similar consideration applies to comparative studies of lineage diversification rates among clades, which are more accurately estimated using methods that assume an underlying diversification
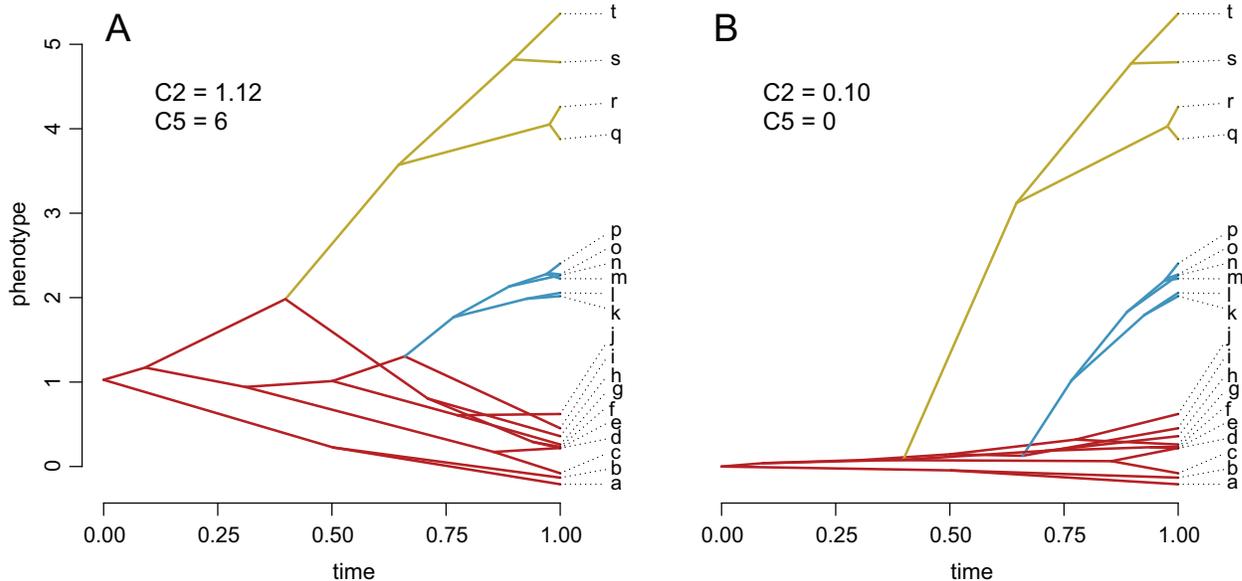
Figure 1: Models assumed when reconstructing ancestral states can dramatically affect inferences about the frequency and strength of convergent evolution. Here, data for 20 species were simulated using a known phylogeny under a three-optimum Ornstein-Uhlenbeck (OU) process with strong selection and no convergent evolution ($\alpha = 4$; $\sigma^2 = 1$; $\theta = 0, 3, 5$; total tree length $= 1$; colors represent correspondence to phenotypic optima). We reconstructed ancestral states assuming a standard Brownian motion model (*A*) and a three-optimum OU model (*B*) that closely represents the true evolutionary process under which the data were generated (the number of optima and phylogenetic locations of shifts between optima were known a priori; all other parameters were estimated). We then used ancestral state reconstruction–based comparative methods from Stayton (2015*a*) to estimate the frequency (C5) and magnitude (C2) of convergent evolution for the set of species with small phenotypes (species a–j; several related measures of the magnitude of convergence yield similar results but are not shown). C5 tallies the number of independent lineages that cross into the phenotype space occupied by the focal set of species (here this space is simply defined as the range of extant phenotype values for this set). C2 indicates the phenotypic distance closed by evolution for this set of species and is calculated as the average value of ($D_{max} - D_{tips}$) for all pairs of species in the focal set, where D_{max} is the maximum phenotypic difference between a pair of species since their divergence and D_{tips} is the phenotypic difference between the same pair of species in the present. Note that assuming Brownian motion in this example (*A*) leads to an overestimate of the frequency and strength of convergence events in this subset of species (from intermediate to small phenotype values). If we assume the true OU model (*B*), we correctly infer no convergences (C5 = 0) and two divergences from small to large phenotype. Because assuming a different evolutionary model can fundamentally alter comparative inference about convergent evolution, we contend that there is no such thing as a process-free comparative measure of convergence.

model than with process-free methods that simply control for elapsed time (Rabosky 2012). These examples reflect a general truth—pattern and process are inseparable in the study of phylogenetic comparative data, and it is not possible to make inferences about evolutionary patterns without assuming something about the evolutionary process (Pagel and Harvey 1989; Freckleton et al. 2011; Hunt 2012). Not all comparative inferences are equal, of course, and some may be more robust than others to violations of model assumptions. However, convergence metrics that explicitly incorporate model-based reconstruction of ancestral phenotypes are likely to be particularly sensitive to violations of assumptions about the underlying evolutionary model (Oakley and Cunningham 2000).

Given the need to assume an evolutionary process to study convergence, how can one avoid the potential for adaptationist bias? The potential for such bias is irrefutable (Hansen 2014; Stayton 2015*a*, 2015*b*), but this is a

risk that can be managed in part through conscientious consideration of alternative evolutionary models during analysis and careful interpretation of results (see box 2 for discussion of best practices). The fit of adaptive models should always be compared to nonadaptive alternatives, and interpretation should favor results obtained under the best-performing model or, in the absence of a single best model, results obtained under all plausible candidate models. However, applying these best practices can only take one so far in avoiding adaptationist pitfalls, due to the issue that evolutionary process models may effectively model more than one evolutionary mechanism.

Many-to-One Mapping of Real Evolutionary Processes to Modeled Processes

Most available phylogenetic comparative methods employ phenomenological models of the evolutionary process that

Box 2: Best Practices

The comparative method has important limitations that must be taken into account in any study (Losos 2011*b*; Maddison and FitzJohn 2015; Rabosky and Goldberg 2015; Cooper et al. 2016*a*), including studies that focus on convergence. Here we recommend several considerations that we think are essential to making strong inferences about historical patterns and processes of convergence.

Study Design

The comparative approach investigates patterns that result from uncontrolled natural processes rather than experimental manipulation (Freckleton et al. 2011). Nonetheless, the considerations that guide experimental design equally apply to comparative analyses.

Statistical replication is necessary for addressing most questions about convergence, although the relevant form and degree of replication can depend on the question being asked. For example, if one simply wishes to test whether two taxa have in fact converged, this can be tested with a simple model comparison or ancestral state reconstruction (ASR)–based test, although the scope of inference will be limited. Other study objectives will require relatively diverse clades to have any statistical power. For example, testing whether a shift to a new habitat is consistently associated with convergence will require a system containing numerous habitat shifts. It will almost never be possible to determine the cause of single convergence events using comparative methods alone because of the inability to rule out the possibility that an observed correlation is spurious (Gould and Lewontin 1979; Maddison and FitzJohn 2015).

Study design should also involve consideration of phylogenetic scale. Many evolutionary models can be useful at some scales but inadequate at others (Estes and Arnold 2007; Hunt 2012). For example, larger clades are more likely to have been shaped by a more heterogeneous mixture of evolutionary processes (Beaulieu et al. 2013). At the very smallest phylogenetic scales, it may not be possible to distinguish complex evolutionary models from simpler alternatives (Boettiger et al. 2012), even if the former better reflect reality.

Model Comparison

Alternative evolutionary process models can differ profoundly in how they reconstruct historical patterns (fig. 1), making it essential to compare models in any phylogenetic study of convergence. While model comparison has become routine in many areas of comparative biology (Posada and Crandall 1998; Harmon et al. 2010; Morlon 2014; Pennell et al. 2015), it is often neglected in phylogenetic studies of trait convergence. This may be because common tools for measuring convergence assume Brownian motion evolution; investigators interested in assuming alternative models must customize existing tools to do so. This is especially true for ASR methods (but see Elliot and Mooers 2014; Uyeda and Harmon 2014). Because ancestral state estimates can differ so profoundly under alternative evolutionary models, we suspect that a greater appreciation for the importance of model comparison might result from the development of more flexible ASR tools.

Although model comparison is essential for studying convergence, we caution against discussing results from alternative models on equal footing when some models clearly outperform others. Comparative studies commonly report and interpret the results of several alternative methods, with results from different methods regarded as complementary. This is to be encouraged when methods are internally consistent with one another but can be misleading when they assume different models of evolution, especially if these differences lead to meaningful differences in the quantification of convergent evolution. For example, if Brownian motion is found to yield a much worse fit to data than a multiple-peak Ornstein-Uhlenbeck (OU) model (such as in the toy example in fig. 1), the use of comparative methods that assume Brownian motion, such as most ASR and index methods, does not meaningfully contribute to our understanding of convergence and may even undermine it. Care should be taken that results that rely on alternative evolutionary process models are themselves regarded as fundamentally distinct (and potentially incompatible) rather than complementary per se.

Model Parameters and Model Adequacy

The parameters of fitted evolutionary models can be richly informative with respect to convergence, and many of the interesting features of evolutionary convergence that have inspired pattern-based tools may be effectively captured by the parameters of evolutionary models. For example, the strength of attraction in an OU model can be interpreted as a rate of adaptation in lineages that converge on a shared adaptive peak and may represent the balance between historical constraint and adaptation (Hansen 1997, 2012; Beaulieu et al. 2012; Collar et al. 2014).

Inspection of model parameters can also be used to identify when models provide a poor fit to data. For example, multi-optimum OU models frequently return estimates for some optima that fall outside the observed range of species trait data. This may reflect ongoing adaptation toward an extreme phenotype (Hansen 1997) or a mismatch between model assumptions and reality (Mahler and Ingram 2014). Some data sets cannot be fit well by multi-optimum OU models, highlighting the importance of testing whether a model can adequately reproduce key patterns in the data rather than simply assessing which model from a set of candidates fits best (Pennell et al. 2015). Simulation-based approaches can help ensure robust inference in virtually any scenario, including empirical conditions for which model performance may yet be unknown (Boettiger et al. 2012; Mahler et al. 2013; Elliot and Mooers 2014; Slater and Pennell 2014; Pennell et al. 2015; Clarke et al. 2017).

may plausibly represent more than one kind of evolutionary mechanism—that is, a many-to-one mapping of true evolutionary mechanism to modeled macroevolutionary process (Hansen and Martins 1996; O'Meara et al. 2006; Revell et al. 2008; Hansen 2012; Pennell 2014). For example, a single-peak OU model may represent adaptive evolution in a clade that has already reached a phenotypic optimum (Hansen 1997), or it could represent evolutionary stasis due to a constraint on the production of variation (e.g., Harmon et al. 2010). Many-to-one mapping is possible for a diversity of evolutionary process models, from Brownian motion to early burst and saltational macroevolutionary models (Freckleton and Harvey 2006; O'Meara et al. 2006; Mahler et al. 2010; Venditti et al. 2011; Pennell et al. 2014). Although many such models were introduced with specific microevolutionary mechanisms in mind, they describe variation at a comparatively coarse macroevolutionary scale and contain no direct link to such fine-scale mechanisms. The lack of mechanistic detail in these models presents another formidable limitation to the interpretation of macroevolutionary convergence. The investigator must consider such possibilities in any analysis of convergence—as we will argue below, such considerations can be aided by investigation of the study group using complementary approaches that allow more direct tests of mechanism and by considering the natural history of the organisms and their environments.

Integrative Approaches to the Study of Macroevolutionary Convergence

A complete understanding of any evolutionary phenomenon requires knowledge of both the detailed mechanisms by which evolutionary change occurs (i.e., the how) and the circumstances that ultimately bring about such change or shape its course (i.e., the why). Replicated convergence provides a powerful framework for both avenues of inquiry. The power of this replication has been harnessed in combination with high-throughput sequencing technologies in the last decade to greatly increase our understanding of the molecular mechanisms behind convergent phenotypic change (Elmer and Meyer 2011; Stern 2013; Rosenblum et al. 2014). By comparison, somewhat less progress has been made in understanding the ecological and phylogenetic context in which convergence occurs.

The phylogenetic comparative method can be especially useful for addressing questions about causes of convergent evolution because it is well suited for investigation at the large spatial and temporal scales at which such factors shape the evolution of biodiversity. In many cases, though, comparative models on their own may fail to distinguish among alternative hypotheses about the causes of convergent evolution, even when carefully applied. This is an intrinsic feature of the comparative approach that results from the many-to-one mapping of process to pattern in macroevolution (Hansen and Martins 1996; Pennell 2014). Thus, the comparative approach will often be much more powerful when integrated with complementary avenues of investigation. Here we discuss ways in which comparative inferences about the processes underlying convergent evolution can be strengthened by the incorporation of (1) more diverse causal mechanisms, (2) biogeography, and (3) fossil data into comparative approaches to studying convergence.

Incorporating a Greater Diversity of Causal Mechanisms into Evolutionary Process Models

A key goal in the study of evolution is to understand how microevolutionary mechanisms shape macroevolution, but elucidating this link has proved challenging (Uyeda et al.

2011; Rosindell et al. 2015). The comparative study of convergence can help to evaluate this relationship to the extent that we can make meaningful connections between potential causative factors and convergent pattern. Candidate factors that may result in macroevolutionary convergence include developmental mode (e.g., Wake 1982), genome architecture (e.g., Stern 2013), changes in climate (e.g., Yeaman et al. 2016), mutualistic interactions that involve phenotype matching (e.g., Hoyal Cuthill and Charleston 2015), repeated antagonistic interactions (e.g., Siepielski and Benkman 2007), and competition for nonsubstitutable resources (e.g., Abrams 1987; Scheffer and van Nes 2006). However, despite ongoing research interest in these areas, we still lack answers to basic questions such as, Do evolutionary shifts in reproductive system change the likelihood that clades will exhibit convergence? Is convergence due to abiotic selection more or less common than convergence due to biotic selection? and How likely is convergence to occur, persist, or break down under antagonistic or mutualistic selection?

One source of improvement may come from renewed attention to model development. As the scope of phylogenetic comparative methods has grown in recent years, models that focus on constrained or bounded evolution have received somewhat less attention than those inspired by explicitly adaptive mechanisms. New work in this area could help to diversify the scope of comparative inquiry (e.g., Boucher and Démery 2016). Future developments in the field should also work to clarify what kinds of macroevolutionary patterns we expect to arise from different ecological processes. Recently developed comparative models based on simple species interactions provide a welcome first step in this direction (Yoder and Nuismer 2010; Pennell and Harmon 2013; Nuismer and Harmon 2015; Drury et al. 2016; Clarke et al. 2017). Although these methods do not explicitly model convergence, the ecological processes underlying them may result in convergent phenotypes. In addition, recent years have seen the rapid development of a more sophisticated theory of species coexistence and community ecology (Chesson 2000; Hubbell 2001; Pennell and Harmon 2013; Vellend 2016), and future modeling efforts would do well to identify a set of expected evolutionary outcomes that reflects current ecological thinking. Combining modern ecological theory with the phylogenetic replication made possible in comparative studies of convergence will make for a powerful approach to studying the macroevolutionary signature of ecological mechanisms. We speculate that a principal roadblock to the development of more diverse and detailed macroevolutionary models has been the difficulty (or impossibility) of representing such models as closed-form likelihood expressions. Simulation-based approaches (including approximate Bayesian computation methods) may be required to fully diversify the models available in our macroevolutionary tool kit (e.g., Elliot and Mooers 2014; Clarke et al. 2017).

Even the development of improved models may not overcome the issue of many-to-one mapping of mechanism to evolutionary process model. However, hypotheses and models are not the same thing, and the utility of the comparative method depends on the ability of the investigator to use natural history knowledge and comparative tools together to craft specific mechanism-inspired hypotheses that can be tested using comparative data. In addition to improvements associated with integrating more diverse causal mechanisms into comparative methods, the study of convergence will be aided by designing studies that creatively use ecological experiments to test for specific ecological mechanisms acting to produce patterns observed at the clade level (Weber and Agrawal 2012). Ecological hypotheses about the drivers of convergence generally contain predictions about the relationship between trait similarity, abundance, and the relative fitness of species in a given community (table 1). For example, in instances where convergence is hypothesized to result from selection for Müllerian mimicry (i.e., selection for greater phenotype matching among aposematic species), experiments manipulating trait similarity in contemporary communities can be paired with phylogenetic tests of convergence (in relation to timing of sympatry). The prediction in this case is that (1) the reduction of phenotypic similarity decreases species fitness by increasing predation and (2) convergence occurred when species were in sympatry, not before. This integrative framework can be applied to antagonistic hypotheses as well and represents a powerful approach to testing adaptive hypotheses about the ecological drivers of convergence.

Integrating Biogeographic Approaches into Comparative Studies of Convergence

Integrating an understanding of species and clade biogeography can greatly enhance attempts to link ecological process to macroevolutionary pattern. Evolving lineages can directly interact only when they co-occur, and accounting for co-occurrence patterns will be essential if we are to distinguish the influence of species interactions on convergence from alternative factors. Furthermore, biogeographic perspectives can disentangle the influence of species range overlap from abiotic factors such as climate or soil type. The biogeographic approach is ripe for application to convergence generally, and in table 1 we outline several ways in which phylogenetic comparative methods may be combined with such an approach to augment their resolving power when investigating the ecological and evolutionary processes underlying convergent patterns.

The incorporation of a biogeographic perspective has yielded new insights in recent studies of replicated adap-

Table 1: Examples of hypothesized mechanisms driving patterns of convergence and predictions from integrated analysis

Hypothesized underlying mechanism	Biogeographic predictions	Predictions for patterns of coexistence of convergent forms	Ecological predictions
Convergence due to chance	Convergence is independent of biogeography	Probability of convergence is independent of community context	Manipulating the density of a trait in a community does not change the selective value of the trait
Convergence due to selection driven by physical environment (e.g., climate, light)	Convergence is correlated with shared physical conditions	Probability of convergence is independent of range overlap with convergent species	Manipulating the density of a trait in a community does not change the selective value of the trait
Convergence due to competition resulting in niche partitioning and character displacement	Convergence may or may not be correlated with physical environment	Convergent forms evolve in allopatry but only where they are sympatric with a competitor	Negative density-fitness relationship: the abundance of a phenotype in the community decreases the selective value of that phenotype. Convergent communities should exhibit similar patterns of niche partitioning
Convergence due to competition for nonsubstitutable resources	Convergence may be correlated with particular abiotic conditions across phylogeny (e.g., an essential nutrient)	Convergent forms evolve in sympatry	Resource limitation leads to selection for greater similarity in the shared phenotype: supplementing resource decreases selection on this trait
Convergence due to facilitation/mutualism	Convergence may or may not be correlated with physical environment	Probability of convergence is independent of range overlap with convergent species	Average fitness is a positive function of the abundance of the mutualist and a negative function of the abundance of similar competitors
Convergence due to commensalism	Convergence may or may not be correlated with physical environment	Probability of convergence is independent of range overlap with convergent species	Average fitness is a positive function of the abundance of the commensal host
Convergence due to predation/parasitism	Convergence may or may not be correlated with physical environment	Convergent forms evolve in allopatry or sympatry but only where they are sympatric with an antagonist	Average fitness is a negative function of the abundance of the antagonist

Note: Linking pattern to process is a central challenge in comparative biology. However, in some cases, integrating multiple forms of inference can help researchers narrow possible pattern-to-process links. Here we provide several examples of how this framework could be applied to phylogenetic comparative studies of convergence. It is important to note that while inferring past causation with absolute certainty is impossible, explicitly considering the predictions of alternative hypotheses can help researchers identify mechanisms consistent with observed patterns. We provide several examples of mechanistic hypotheses, which are not necessarily mutually exclusive (a fact that should be accounted for in the design of a comparative study).

tive radiations in which entire well-structured ecological guilds have evolved convergently (Schluter 2000; Mahler and Ingram 2014). The existence of numerous replicated adaptive radiations suggests an important and deterministic role for interspecific competition and subsequent character displacement as a cause of convergence into the same set of niches (e.g., Frédérich et al. 2013; Grundler and Rabosky 2014; Esquerré and Keogh 2016; Moen et al. 2016). An alternative possibility, however, is that such convergence results more from biomechanical trade-offs involved in specializing on particular resources than from competitive interactions per se and that such specialists may have emerged

via mechanisms other than interspecific competition. Here, information about range overlap can be informative. If interspecific competition played a role in the replicated evolution of ecological specialists, we would expect the convergent species to occur allopatrically and to have evolved only a single time in a given region, but we would have no such expectation if competition were not important in this divergence. This pattern is observed in replicated Greater Antillean *Anolis* radiations and in concert with experimental studies of both competition and character displacement (Pacala and Roughgarden 1982; Leal et al. 1998; Stuart et al. 2014), strongly suggests a role for competition in contributing

to the repeated evolution of similar ecomorphs on different islands (Mahler et al. 2013).

Other ecological mechanisms will leave distinct patterns in biogeographic patterns of convergent taxa. Cichlids in African lakes are well known for replicated radiations in different lakes (Wagner et al. 2012), but Muschick et al. (2012) showed that within Lake Tanganyika, numerous convergent species co-occur within the lake. The pattern of sympatric convergent taxa (see also Kozak et al. 2009; Ingram and Kai 2014) challenges the hypothesis of competition-driven character displacement and might instead suggest competitive character convergence (MacArthur and Levins 1967; Abrams 1987; Scheffer and van Nes 2006). While a great deal of work is needed to validate the hypothesis that competition can drive convergence between coexisting taxa across entire clades, the possibility highlights the need for an increased understanding of the expected biogeographic and macroevolutionary consequences of a broader range of ecological processes.

Revisiting the Fossil Record

The overwhelming majority of comparative phylogenetic studies are conducted using only extant species. Inferences from comparative analyses therefore suffer an unfortunate temporal asymmetry, whereby estimates of both historical pattern and process are associated with increasing levels of uncertainty as one looks further back in time (Schluter et al. 1997; Cunningham et al. 1998; Oakley and Cunningham 2000; Losos 2011*b*). For this reason alone, fossil data can make very large marginal improvements to the accuracy of comparative inference, and the incorporation of fossil information into comparative studies of convergence promises to help distinguish among alternative evolutionary models and refine parameter estimates of key evolutionary processes. Recent years have witnessed encouraging progress in the merging of paleontology and comparative phylogenetic methods, both with the development of integrative new models for phylogenetic inference and divergence dating (e.g., Ronquist et al. 2012; Heath et al. 2014; Drummond and Stadler 2016; Zhang et al. 2016) and for the fitting of comparative models of continuous trait evolution (Slater et al. 2012; Slater and Harmon 2013; Hunt and Slater 2016).

There has been enough progress to demonstrate that fossil data can dramatically improve comparative inference and in some cases shift the weight of evidence to alternative hypotheses (Slater et al. 2012; Mitchell 2015; Slater 2015; Hunt and Slater 2016). In studies of convergence, even one or a few fossil data points indicating trait values of ancestors may be critical in distinguishing between alternative scenarios (e.g., the histories depicted in fig. 1*A*, 1*B*). By anchoring ancestors in trait space, the incorporation of fossil data can potentially separate conver-

gent pattern from process and allow more powerful hypothesis tests than can be achieved using information solely about extant species. The integration of fossils into molecular phylogenetic frameworks remains far from routine, however, and a key hurdle is the often fragmentary nature of fossil data and the considerable uncertainty often associated with phylogenetic placement of such fossils. Future efforts to address these challenges should yield large dividends for the comparative study of convergence.

Conclusions

The phylogenetic comparative method provides a rich set of tools for answering questions about convergence, including many that are otherwise inaccessible to biologists. Models of the evolutionary process are at the core of all comparative methods, however, and these models can profoundly influence the outcomes of comparative studies of convergence. This intrinsic link between pattern and process in phylogenetic comparative methods can be a liability if ignored but can be a powerful asset when models are explicitly used to test hypotheses about the ecological and evolutionary processes that give rise to phenotypic patterns. Future progress in the comparative study of convergence should result from development of more realistic models of ecological and evolutionary processes, better integration of comparative study with complementary research on biogeography and ecology, and the growing incorporation of fossil information into phylogenetic investigations currently dominated by extant taxa.

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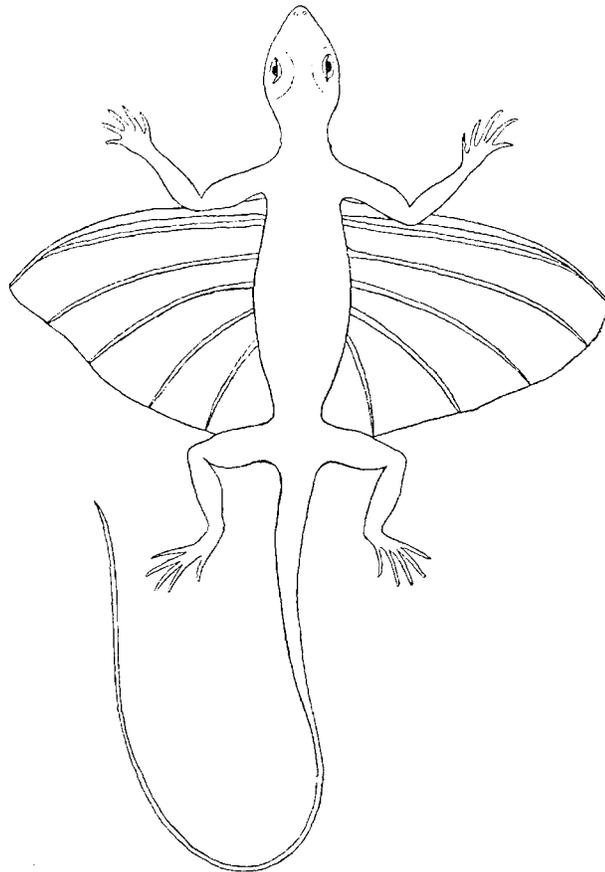
"There are in all about twenty species of Draco, inhabiting the East Indies. The power of flight is not very great, but probably exceeds that of Ptychozoön." Figured: *Draco volans*. From "Volant Adaptation in Vertebrates" by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).